# FISH HABITAT MAPPING

# **Preface: European Commission's 'Scientific Support** to Policies' Action EnviEFH: Environmental Approach to Essential Fish Habitat Designation

Vasilis D. Valavanis

© Springer Science+Business Media B.V. 2008

Under the Sixth Framework Programme (FP6) for research, the Commission of the European Communities (CEC) has launched its 'Scientific Support to Policies' (SSP) initiative promoting science to the decision-making process. To improve the quality of policy decisions and to promote the participation of researchers in the policy arena, CEC has funded a number of SSP actions in three priority areas: sustainable management of natural resources, health and security, and economic potential of an enlarging Europe. EnviEFH (Environmental Approach to Essential Fish Habitat Designation) was a 27-month SSP Action (December 2005-February 2008) in the priority area of sustainable management of natural resources under the theme of Fisheries and Aquaculture.

The overall aim of the EnviEFH Action was to integrate available scientific knowledge on species biology, ecology, and genetics in order to identify those water bodies and underlying surface critical to the long-term survival and health of fish populations in the Mediterranean Sea and adjacent areas. Those

Guest editor: '	V. D. Valavanis		
Essential Fish	Habitat Mapping in	n the	Mediterranean

V. D. Valavanis (🖂)

areas, known as Essential Fish Habitats (EFH), are necessary to fish for spawning, breeding, feeding, or growth to maturity. In the European Communities, the term EFH was only recently and indirectly introduced during the ongoing reforming of the common fisheries policy (CFP). The concerted approach to protect species habitats through the Habitat Directive and the declaring of fisheries protection zones through the Marine Strategy Directive are initial efforts to introduce the spatial component in fishery management under the CFP.

The participant organizations and involved scientific teams in the EnviEFH SSP Action are listed in Table 1, while a photograph from the kick-off meeting is shown in Fig. 1.

As many marine species distributions are affected by the state of the marine environment, the general approach of the EnviEFH action was to let environmental variation show us where EFH occurs. Thus, we have created an extensive geographic information system database of remotely sensed satellite imagery and extracted a number of habitat descriptors including (besides environmental descriptors) distances from mapped thermal fronts and marine productivity hotspots in an effort to include ocean processes in habitat mapping. We used a number of statistical approaches and new technologies depicted in the articles of this issue and we tried to identify EFH by assembling and analyzing surveyed fisheries datasets on small, large, and demersal commercial resources of the Mediterranean and adjacent areas.

Marine Geographic Information Systems Laboratory, Institute of Marine Biological Resources, Hellenic Centre for Marine Research, P.O. BOX 2214, 71003 Iraklion Crete, Greece e-mail: vasilis@her.hcmr.gr

Participants	Scientific teams	Subcontractors
Hellenic Centre for Marine Research (HCMR), Institute of Marine Biological Resources (IMBR) Crete/Athens, Greece	<ul> <li>V. D. Valavanis, CY. Politou, A. Machias, E. Lefkaditou, M. Giannoulaki, G. Tserpes, A. Palialexis, A. Kapantagakis, C. Gkani, A. Siapatis, S. Kavadas, J. Dokos, P. Cosmopoulou, C. Papakonstantinou</li> </ul>	
Consejo Superior de Investigaciones Cientificas (CSIC), Instituto de Ciencias del Mar (ICM) Barcelona, Spain	<ul><li>P. Martin, F. Maynou, L. Recasens, P. Sanchez, P. Olivar, I. Palomera, A. Sabates, J. Cartes, F. Sarda, M. Demestre</li></ul>	
Centre National de la Recherche Scientifique (CNRS), Ecosystemes Coralliens: Structure et Fonctionnement, Laboratoire d'Ecologie Aquatique Tropicale et Mediterraneenne (EPHE) Perpignan, France	S. Planes, R. Lecomte, P. Lenfant, R. Crec'hriou, G. Criquet, G. Cadiou, G. Bernard, E. Roussel, L. Le Direach	GIS Posidonie P. Bonhomme
University of Aberdeen (UNIABDN), School of Biological Sciences (Zoology) Aberdeen, United Kingdom	G. J. Pierce, J. Wang, B. Santos, I. Katara, J. Smith	Highland Statistics, Ltd. A. F. Zuur, E. Ieno

 Table 1
 The EnviEFH consortium



Fig. 1 EnviEFH consortium meeting. From right and round the table: P. Bonhomme (GIS Posidonie, France), C.-Y. Politou, J. Dokos, P. Cosmopoulou, C. Papaconstantinou, A. Palialexis, A. Kapantagakis (HCMR, Greece), G. Pierce and J. Wang (Univ. Aberdeen, UK), P. Martin and P. Sanchez (ICM, Spain), R. Crec'hriou (EPHE, France), and V. Valavanis (HCMR-Greece)

The contents of this issue include 21 articles that are organized as follows: an overview of approaches on species habitat modeling presents what methods and tools are currently available in the field followed by a comparison of four modeling approaches using marine species data. This is followed by a summary of teleconnection patterns between large-scale meteooceanic phenomena and local environmental variation in the Mediterranean. Next, the species-specific articles are included: three on cephalopods, two on shrimp, one on hake, seven on small pelagics, and one on swordfish. Finally, the issue concludes with studies on the interactions of cetaceans and longline fisheries, the remote sensing of major ocean processes, the recent invasion of a zooplanktivorous ctenophore in the Mediterranean, and the development of a tool for selection and visualization of 4-dimensional marine ocean data.

We wish to acknowledge the EnviEFH project officers in the Directorate-General Fisheries and Maritime Affairs (Brussels, Belgium), Jacques Fuchs, Snorri-Runar Palmason, Jose-Perez Mauriz, Petter Fossum, and Apostolos Peltekis, for their extensive help and support throughout the duration of the project. We thank the many scientists, acting as anonymous referees, who further advanced with constructive comments on earlier versions of the articles in this issue (reviewers' names are listed below). We are grateful to Martine van Bezooijen (Springer) and Koen Martens (Royal Belgian Institute of Natural Sciences) for providing the outlet for publication of EnviEFH output in *Hydrobiologia*.

Finally, we encourage visiting the EnviEFH website for further updated information (http://arch.her. hcmr.gr/enviefh/). The site remains online after the end of the EnviEFH action (February 2008) and it will be updated regularly with relevant information on marine species habitat modeling. We hope that readers of this special issue of *Hydrobiologia* will find it useful and inspiring for further developments in the field.

# List of reviewers

Christos Arvanitidis Jose M. Bellido Fabio Carocci Paul Eastwood Anastasios Eleftheriou Sarah Faulwetter Stratis Georgakarakos John Haralabous Consuelo Hermosilla Argyris Kapantagakis Xeni Kechagioglou Constantin Koutsikopoulos Drosos Koutsoumbas Catherine Longo Maite Arsuaga Louzao Corinne Martin Gema Martinez Geoff Meaden Jaime Mejuto John D. Neilson Andreas Palialexis Ignacio Sobrino Stylianos Somarakis Kate Stark Michael J. Tetley Konstantinos Tsagarakis George Tserpes Vasilis Valavanis George Vardanis Claire Waluda

## FISH HABITAT MAPPING

# Modelling of essential fish habitat based on remote sensing, spatial analysis and GIS

Vasilis D. Valavanis · Graham J. Pierce · Alain F. Zuur · Andreas Palialexis · Anatoly Saveliev · Isidora Katara · Jianjun Wang

© Springer Science+Business Media B.V. 2008

**Abstract** We review the variety of existing modelling approaches applied to species habitat mapping and we discuss issues arising from the availability and nature of sampled biological data and corresponding ecological and environmental habitat descriptors, as well as the different spatial analysis approaches that are selected according to specific hypotheses. We focus on marine species habitat mapping, presenting an overview of work on

Guest Editor: V. D. Valavanis Essential Fish Habitat Mapping in the Mediterranean

V. D. Valavanis (⊠) · A. Palialexis Marine GIS Laboratory, Institute of Marine Biological Resources, Hellenic Centre for Marine Research, Thalassocosmos 71003, Heraklion Crete, Greece e-mail: vasilis@her.hcmr.gr

G. J. Pierce

Centro Oceanográfico de Vigo, Instituto Español de Oceanografía, P.O. Box 1552, 36200 Vigo, Spain

#### A. F. Zuur

Highland Statistics Ltd, 6 Laverock road, AB41 6FN Newburgh, UK

# A. Saveliev

Faculty of Geography and Ecology, Kazan State University, 8 Kremlyovskaya St., 420008 Kazan, Republic of Tatarstan, Russian Federation

G. J. Pierce · I. Katara · J. Wang School of Biological Sciences (Zoology), University of Aberdeen, Tillydrone Avenue, AB24 2TX Aberdeen, UK modelling fish habitat carried out through a European Communities Policy-Support Action, EnviEFH 'Environmental Approach to Essential Fish Habitat (EFH) Designation' (2005–2008). The selection of the appropriate habitat model is dataset-specific and the resulting EFH maps are often similar in spite of using different models. Derived EFH maps are based on either environmental ranges (used as minimum and maximum environmental habitat descriptors) or probability of occurrence values. We apply model outputs to regions larger than sampled areas making use of the capacity of satellite data to cover wide areas.

**Keywords** Marine species · Statistical modelling · Fisheries · Environment · Ecology

# Introduction

The identification of Essential Fish Habitats (EFH), i.e. areas or volumes of water and bottom substrates that provide the most favourable habitats for fish populations to spawn, feed and mature throughout their full life cycle, is important for the conservation of biodiversity and sustainable fisheries management. The sustainability of fish populations and their associated fisheries could be conserved by limiting anthropogenic stressors in such habitats.

One of the foundational concepts underlying the ecosystem approach to fisheries management

(EAFM) is that different geographic areas have different biological production capacities and that it may be advantageous to focus applying science and management to protect overfished areas and areas of degraded habitats (Lutchman, 2003). EFH analysis should be able to identify those areas within the distribution of a species that contribute most to sustain the long-term viability of a population. Although it may be difficult to define the boundaries of EFH (for example, whether it should be the most important 10% or 15% or 20%, etc, of habitat), the definition of EFH areas, combined with management which recognizes the importance of such areas, represents a first step towards facilitating EAFM concepts and will thus contribute to the sustainability of marine ecosystems and their living marine resources as well as delivering the socioeconomic benefits with a healthy and sustainable fishery.

The extensive spatiotemporal variability, which characterizes dynamic marine ecosystems, presents inherent difficulties for the development of predictive species-habitat models. In order to identify relationships among ocean processes, environmental parameter distribution, biological responses and corresponding species distributions, scientific information and statistical analysis of habitat descriptors must accommodate the life cycle characteristics of the targeted species.

Satellite imagery provides an extensive (virtually worldwide) knowledge-base of sea-surface conditions, readily available in high or low resolution forms, allowing the mapping of important ocean processes that influence species distributions, albeit with the limitations that sub-surface phenomena cannot be described in this way and satellite data are available only since the early 1980s. In addition, extensive large-scale survey investigations often provide time-series of certain species distributions and sometimes also oceanographic data for the whole water column, allowing studies of relationships between environmental change and species environmental preferences. Finally, spatial statistical analysis and Geographic Information Systems (GIS) technology provide the tools to model species-habitat relationships and their variability and identify essential habitat areas (see, for example, Pierce et al., 2001, 2002; Valavanis et al., 2002, 2004).

Overviews of predictive species-habitat modelling approaches have been presented for various species groups in terrestrial (Guisan & Zimmermann, 2000; Elith & Burgman, 2002), freshwater (e.g. Olden & Jackson 2002; Behrouz et al., 2006) and marine ecosystems (e.g. Ferguson et al., 2006; Redfern et al., 2006). Related studies underline the fact that many marine species have wide distribution ranges and respond to environmental variation by changing their distribution patterns and habitat use (Perry et al., 2005; Laurel et al., 2007; Morrell & James, 2008). The marine environment is fundamentally dynamic: over a fixed background of bathymetry and seabed substrate, oceanographic conditions and prey availvary in time (diurnally, seasonally, ability interannually) and space (vertically and horizontally) at various scales.

In the present article, we summarize a range of modelling approaches available to model specieshabitat relations and map EFH for living marine resources, particularly fish, although some of these methods have been applied more often than others marine species datasets.

#### Objectives of essential fish habitat modelling

Fundamentally, EFH modelling is an applied science (in that it provides EFH maps based on analyzed scientific data), very often with the ultimate aim of providing tools to support the sustainable exploitation of living marine resources. Given the relatively low level of knowledge about external factors influencing the population dynamics of marine species, many published models are empirical, making few or no prior assumptions about underlying causal mechanisms, rather than mechanistic (process) or functional (e.g. optimization) models. Thus a relationship described by an empirical model may reflect a direct causal link, an indirect link or simply a coincidental (and most likely temporary) correlation. The whole process has been denigrated as "data mining" rather than hypothesisdriven science (Guisan et al., 2002). While various philosophers of science (e.g. Popper, 1963) (and indeed some national government funding bodies) have viewed falsification of hypotheses as the only legitimate form of scientific endeavor, in reality science is a much more complex process (e.g. Lakatos, 1970; Kuhn, 1996) and, indeed, European research funding under the Framework Programmes has mainly targeted at science that offers economic and societal benefits rather science that aims solely to advance theory. We would argue that, in the context of applied sciences, such as fisheries science, data mining is a perfectly legitimate approach, which can lead to predictions and/or forecasts of fish distribution and abundance that are both testable and can be used to inform rational marine resource management. It is important to recognize that empirical models remain a form of hypothesis (regardless of whether an underlying causal mechanism can be identified) until, after an appropriate estimation of goodness-of-fit, they are tested on independent datasets. The majority of existing publications arguably fail in this respect, although most advance testable hypotheses.

Aside from the 'data mining' argument, there are at least two additional reasons for skepticism about the power and validity of empirical models based on environmental predictors. First, inclusion of a large number of putative explanatory variables in a model may led to overfitting, reducing predictive capacity and generality (Clark, 2005), assuming, that is, that a high ratio of explanatory variables to data points and/ or collinearity between explanatory variables do not preclude fitting any model in the first place. A second issue is that the population dynamics of many (if not most) exploited species are driven by the amount, distribution and variability of fishing mortality, past and present. While this is true, the spatial distribution of EFH and abundance is still likely to be strongly dependent on the characteristics of the biotic and physical environment. As abundance increases, it may be expected that species expand from core 'preferred habitat' into increasingly marginal habitats. In this sense at least, knowledge of both the drivers of abundance and the habitat requirements (EFH) remains essential. In addition, environmental predictors may explain a high proportion of variance in recruitment strength and thus, in short-lived species (e.g. cephalopods, some small pelagic fish), a high proportion of variation in total abundance (Pierce et al. 2008, this volume).

The analysis of species distribution data has reached high statistical sophistication in recent years (Elith et al., 2006; Heikkinen et al., 2006). However, even the most complicated models cannot guarantee the improvement of our knowledge on the determinants of species distribution (Dormann et al., 2007).

# Data acquisition and preparation

Species distribution modelling is only as good as the data used. The right sampling strategy can improve model results considerably and reduce the risk of making an inaccurate, biased or imprecise prediction. For that purpose, Hirzel & Guisan (2002) suggested some factors that could increase sampling efficiency. These are the increase of sample size, the use of regular sampling, and the use of environmental information to stratify sampling. Uncertainty, on which model inference and prediction depends, declines asymptotically with increasing sample size. The four strategies most frequently discussed are regular sampling (i.e. grid sampling), random sampling, equal random-stratified sampling, and proportional random-stratified sampling. A fifth approach, called gradsect (Austin & Heyligers, 1989, 1991), is close to a random-stratified sampling (either equal or proportional depending on its design) but sampling is concentrated within a few geographic transects designed across the main landscape gradients, mainly to reduce study costs (timeand cost-effective surveys) (Hirzel & Guisan, 2002; Hirzel & Arlettaz, 2003).

Examples of environmental and fish survey/fisheries datasets that may be used for EFH modelling are listed in Table 1. Fishery-independent survey datasets include a variety of surveyed parameters from fisheries acoustic data, experimental trawl data, ichthyoplankton and egg data. Usually at a coarser spatial resolution, commercial catch and fishing effort data can also provide distribution and abundance information for post-recruit fish. Environmental (ecogeographic) parameters that are likely to be relevant include interpreted satellite images for sea surface temperature (SST), chlorophyll-a (Chl-a), photosynthetically active radiation (PAR), euphotic depth (EUD), sea level anomaly (SLA), wind speed and direction, and modeled data for sea surface salinity (SAL) and surface currents (SSC). Hydrographic survey data can provide additional information on subsurface and sea bottom conditions. Spatial location variables and spatial patterns analyzed with statistical and geostatistical tools may add predictive power by acting as surrogates for one or more unknown environmental variables, or variables that cannot be measured easily. They can also potentially capture genuine geographic effects, such as proximity to favourable habitat features (e.g. spawning sites), or

Parameter	Sensor/Model	Units	Resolutions	Source
Sea Surface Chlorophyll-a (CHLO)	SeaWiFS	mg/m <sup>3</sup>	0.0833333°	http://oceancolor.gsfc.nasa.gov
Sea Surface Chlorophyll-a (CHLO)	MODISA	mg/m <sup>3</sup>	0.0833333° and 0.0416667°	http://oceancolor.gsfc.nasa.gov
Sea Surface Temperature (SST)	AVHRR	°C	0.0128748°	http://eoweb.dlr.de:8080
Sea Surface Temperature (SST)	MODISA	°C	0.0833333° and 0.0416667°	http://oceancolor.gsfc.nasa.gov
Photosynthetically Active Radiation (PAR)	SeaWiFS	einstein/m <sup>2</sup> /day	0.0833333°	http://oceancolor.gsfc.nasa.gov
Sea Surface Wind Speed and Direction (WIND)	QSCAT	m/sec and ° from N	0.25°	www.ssmi.com
Sea Surface Current Speed and Direction (SSC)	Merged T/P, Jason–1, ERS-2, Envisat	cm/sec and ° from N	0.125°	www.jason.oceanobs.com
Mean Sea Level Anomaly (MSLA)	Merged Jason-1, Envisat, ERS-2, GFO, T/P	cm	0.2942888°	www.jason.oceanobs.com
Sea Surface Salinity (SAL)	CARTON-GIESE SODA, CMA BCC GODAS, and NOAA NCEP EMC CMB GODAS models	psu	0.3333309°	http://iridl.ldeo.columbia.edu
Euphotic Depth (ZEU)	SeaWiFS (Lee and/or Morel)	m	0.0833333° and 0.0416667°	http://oceancolor.gsfc.nasa.gov
Bathymetry (BATH)	GEBCO	m	0.0166666°	www.ngdc.noaa.gov
Bathymetry (BATH)	Geosat and ERS-1	m	0.0280322°	http://ibis.grdl.noaa.gov/SAT/

Table 1 A list of datasets, their description and source that they were used in marine species habitat modelling

The listed datasets are commonly georeferenced in a GIS database under the EnviEFH Project requirement (world-wide and/or Mediterranean coverage, weekly and/or monthly resolutions for the general period 1997-current, some earlier to 1997)

where juvenile dispersal is aided by particular habitat combinations (Francis et al., 2005). Similarly, inclusion of time of day, month/season and year in models may capture temporal patterns without explaining them.

For ocean processes, SST and Chl-a data can be used to locate thermal and productivity-enhancing fronts (Ullman & Cornillon, 2000; Valavanis et al., 2005), and marine productivity hotspots (Valavanis et al., 2004) and thus determine the distance of each sampling point from such features. Fixed physical features include bathymetry and derived variables, such as seabed slope, depth and slope variability, aspect, distances from coast and specific bathymetry zones, and sea bottom substrate types (where available). The final selection of candidate explanatory variables for EFH modelling is, as far as possible, based on knowledge of the biology and ecology of the species. Ideally, explanatory variables should describe characteristics of the ecology of the species and indicate the presence/strength of relevant ocean processes (e.g. upwelling or fronts) by using, for example, distances of surveyed points from such processes (Table 2). It may be important to include temporally and/or spatially displaced (e.g. timelagged and teleconnected) environmental conditions (e.g. because the distribution of adults reflects processes affecting earlier life stages).

 Table 2
 Typical GIS output table including surveyed fisheries data (spatiotemporal and biological measurements) as well as derived habitat environmental and other descriptors\*

		SF	PATIAL		FISH	ERIES	TEMPORAL					HAE	ITAT I	DESCRIP	TORS				
No	LAT	LON	X	Y	ANCH	SARD	month	SSTm	CHLm	PARm	ALTm	SALm	DEP	Dcoast	Chl-AN	SST-AN	Dist-MPH	SED	Dfronts
1	39.67	25.07	849326.6	4399545.5	0	1398	may04	17.25	0.124	53.557	-0.354	38.388	-162	5677	-0.011	1.25	0	4	147902
2	39.69	25.07	849219.8	4401389.5	0	137	may04	17.38	0.124	53.665	-0.345	38.384	-179	4104	-0.011	0.25	0	4	149861
3	39.71	25.07	849098.8	4403231.5	0	0	may04	17.38	0.124	53.776	-0.339	38.382	-193	2153	NA	NA	NA	4	120048
4	39.72	25.07	848951.6	4405074.0	0	0	may04	17.5	0.124	54.005	-0.333	38.38	-192	3675	NA	-0.13	NA	3	115489
5	39.74	25.07	848771.1	4406910.0	2526	0	may04	17.5	0.124	54.128	-0.326	38.377	-177	1917	-0.013	0.88	0	3	100341
6	39.75	25.07	848659.3	4407951.0	0	0	may04	17.5	0.124	54.253	-0.32	38.375	-159	7370	-0.014	0.63	0	3	90599
7	39.75	25.06	847451.7	4408240.0	0	0	may04	17.5	0.136	54.256	-0.246	38.374	-167	6231	0.01	0.13	0	3	63389
8	39.77	25.06	847696.4	4410078.0	0	0	may04	17.38	0.143	54.393	-0.269	38.37	-148	1205	-0.013	0.13	0	3	82044
9	39.79	25.06	847959.0	4411899.0	0	0	may04	17.13	0.15	54.493	-0.262	38.367	-115	1283	-0.014	0	0	2	89459
10	39.80	25.07	848075.3	4413745.0	0	0	may04	17	0.157	54.721	-0.256	38.366	-95	3687	-0.01	0.13	0	4	73837
11	39.82	25.07	848005.6	4415589.5	2736	0	may04	16.75	0.173	54.821	-0.25	38.364	-64	5520	0.011	-1	1	4	64944
12	39.83	25.06	847642.7	4416778.5	0	0	may04	-9999	0.171	54.852	-0.244	38.361	-16	2399	-0.011	0.25	0	4	46951
13	39.47	25.28	868503.5	4379981.5	0	0	jun04	22.5	0.104	59.806	-0.847	38.425	-166	3986	0.01	-0.5	1	4	48395
14	39.49	25.28	868477.4	4381825.0	0	0	jun04	22.5	0.104	59.723	-0.888	38.422	-149	3417	NA	NA	NA	3	57233
15	39.51	25.29	868475.4	4383674.5	0	0	jun04	22.38	0.103	59.661	-0.985	38.416	-139	3012	0.01	0.13	0	3	42807
16	39.52	25.29	868476.3	4385493.5	0	0	jun04	22.38	0.102	59.591	-1.034	38.412	-130	2746	0.012	-0.13	1	3	51328
17	39.54	25.29	868096.5	4387366.5	0	0	jun04	22.38	0.102	59.481	-1.08	38.41	-123	7010	0.01	0.13	0	3	44246
18	39.56	25.28	868196.9	4389120.0	0	0	jun04	22.5	0.104	59.5	-1.126	38.407	-117	7736	NA	NA	NA	3	58220
19	39.57	25.29	868134.4	4390970.0	0	0	jun04	22.5	0.106	59.548	-1.22	38.402	-112	8215	0.011	-1	1	2	57385
20	39.59	25.29	868007.2	4392811.5	0	0	jun04	22.5	0.104	59.604	-1.269	38.4	-108	15861	0.011	-0.88	1	2	71647
21	39.61	25.29	867889.1	4394660.0	0	0	jun04	22.5	0.103	59.707	-1.32	38.397	-107	1722	0.012	-0.63	1	2	33055
22	39.62	25.29	867760.6	4396633.0	0	0	jun04	22.5	0.102	59.739	-1.427	38.392	-106	6688	0.011	-0.63	1	2	46440
23	39.64	25.29	867541.8	4398329.0	110	38	jun04	22.5	0.103	59.746	-1.483	38.39	-106	1937	0.01	-0.88	1	3	81875
24	39.66	25.28	867441.1	4400182.0	0	97	jun04	22.5	0.105	59.655	-1.542	38.387	-105	3920	NA	NA	NA	4	121545
25	39.67	25.28	867359.1	4402029.5	0	0	jun04	22.63	0.109	59.565	-1.602	38.385	-103	5307	0	0.38	0	4	123635

\*LAT-LON (decimal degrees) and X-Y (meters): coordinates

ANCH, SARD, species (anchovy and sardine abundance acoustic index)

SST-DEP, monthly-averaged environmental variables and bathymetry; Dcoast, distance to coast (m); Chl-AN-SST-AN, environmental anomalies (indication of upwelling); MPH, presence/absence of marine productivity hotspots; SED, sediment types; Dfronts, distance to thermal fronts (m)

#### Data processing

Environmental and other habitat descriptor datasets can be inserted into GIS and projected under a common georeference system in order to extract a suite of environmental parameters for each sampling station. There are many tools available for this purpose (e.g. ArcGIS, MapInfo, etc) as well as a variety of data format conversion utilities for data communication among tools. For example, in the EnviEFH project, ESRI's ArcGIS software and Arc Macro Language (AML) programming language were used to create vector and raster layers of information (ESRI, 1994). Interpreted satellite images are processed as regular grids (ArcGIS GRID module) while fisheries data are placed in coverages of point topology (ArcGIS ARC module). Environmental data can be assigned to each sampling point of fisheries data by means of controlled cursors (pointers that move one-by-one through a selected set of geographic features) between vector and raster datasets (e.g. among selected sets of spatial point features and associated attribute tables and related remotely sensed parameter grids) using ArcGIS INFO/ TABLES and ARCPLOT modules. An important consideration is the extent of the buffer zone (area around each sampling point), which is used to calculate an average for environmental parameters, e.g. the SST associated with a given sample could be a weekly or monthly average within a range of anything from 1 km to several kms of latitude and longitude. Derived descriptors, such as closest distances from thermal and productivity-enhancing fronts, marine productivity hotspots, temperature and chlorophyll-a anomalies, sediment types (when available) as well as distances from coast and bathymetry zones, are quantified using ArcGIS embedded distance functions under the ARC module.

#### Approaches to essential fish habitat modelling

Nature is too complex and heterogeneous to be predicted accurately in every aspect of time and space from a single, although complex, model (Guisan & Zimmermann, 2000). Levins (1966) formulated the principle that only any two out of three desirable model properties (generality, reality, precision) can be improved simultaneously while the third property has to be sacrificed. According to this principle, models can be classified to analytical (Pickett et al., 1994), mechanistic (e.g. Prentice, 1986) and empirical (Decoursey, 1992; Korzukhin et al., 1996). According to Lehmann et al. (2002), mechanistic models may provide more robust predictions than statistical models but the former are much more difficult to develop. Methods used to make spatial predictions should meet several criteria; they should be general enough to deal with the wide variety of attributes that need to be predicted; they should be rigorous and data-defined to make predictions in an objective and defensible manner; they should be standardized to produce uniform results and streamlined to facilitate the required analyses.

Modelling methods depend on data accuracy as well as the type of data. We can discriminate among various types of data, for example presence only data and presence/absence data (i.e. binary presence/ absence 1:0). In the former case, we have available samples from locations that a species is found (1:presence) and in the latter we have samples from locations where a species is found as well as from those where it is not found (1:presence–0:absence). Abundance data (e.g. counts, catch rates) may sometimes be converted to presence only or presence/absence data depending on the biological and logistical constraints governing a conservation monitoring situation (Pollock, 2006).

With a short description provided later in the text, common methods for modelling presence data include ENFA, BIOCLIM, DOMAIN, GARP and MAXENT, while ANN, GLM, GAM and CART require accurate presence/absence data in order to generate statistical functions or discriminative rules that allow habitat suitability to be ranked according to distributions of presence and absence of species (Manel et al., 1999; Guisan & Zimmerman, 2000). Although a data-specific characteristic some of the latter methods could be used with presence only data

(Brotons et al., 2004). Other categories of spatial modelling, also using binary presence/absence data are implemented via Kriging and Simulation techniques. All together could be integrated with a hierarchical Bayesian approach thinking about the scientific method as an iterative process: First, a hypothesis is formulated, rooted in current knowledge. Then, data are collected against which the hypothesis can be tested. Finally, current knowledge is updated in light of the data, repeating the process as appropriate. The Bayesian paradigm is similar, replacing current knowledge with prior probability distributions, data with a likelihood, and updated knowledge with posterior probability distributions, which may now serve as prior probability distributions for future studies. Zaniewski et al. (2002) argue that pure presence-only methods (such as ENFA) are more likely to predict potential distributions that more closely resemble the fundamental niche of the species, whereas presence/absence modelling is more likely to reflect the present natural distribution derived from realized niche. However, both methods aim at predicting distributions by sampling real distributions, and therefore, providing different estimations of the realized niche of the species (Loehle & LeBlanc, 1996). MacLeod et al. (2008, this volume) compared the performance of several presence-only models with that of GLM and showed that, although the latter had the highest predictive power, presence-only models could perform almost as well. Where survey effort is very uneven, both presence only and presence-absence models can give biased results, but only in the latter case is it possible to correct for the bias, e.g. by using effort as a weighting variable. In both cases, inadequate coverage of the full range of habitat types could lead to biased models.

Applying a statistical model consists of various main steps: parameter estimation, model selection, uncertainty estimation, model validation, and generating and testing predictions. Several techniques can be used in each step. For example, hypothesis testing or information criteria like the Akaike Information Criterion (Akaike, 1974) or Bayesian Information Criterion (Schwarz, 1978) can be used for model selection, uncertainty estimation can be done with classical methods based on the Fisher information matrix or using bootstrapping and jackknife techniques (Efron & Tibshirani, 1991). Also for model validation, many methods are available to verify the underlying assumptions (e.g. auto-correlation and semi-variograms for testing the independence assumptions).

A common problem with ordinary least squares regression approaches for modelling species responses to environmental variables is a bias introduced due to unmeasured variables. Typically, since only some of the factors that affect a species distribution are measured and included in statistical models, the influence of an unmeasured factor could mask the predictive relationship between response and explanatory variables. Even by taking into account all factors, some systems include an unexplained stochastic component or show chaotic behaviour.

An alternative approach is to view explanatory variables as constraints rather than as correlates. This approach stems from a fundamental ecological principal, namely Liebig's law of the minimum. Conventional correlation and regression analyses are not based on the concept of limiting factors (Thompson et al., 1996; Cade et al., 1999). Quantile regression is based on this principle and quantifies the effects of limiting factors by fitting regression curves in quantiles near the maximum response (e.g. 0.90 regression quantile) (Eastwood et al., 2001; Cade & Noon, 2003; Hiddink, 2005). That way the effect of other measured or unmeasured factors is disregarded and only the cases when the tested factor has a limiting effect are taken into account. At the same time quantile regression reveals hidden bias and the existence of important processes that are not adequately represented by the measured variables (Cade et al., 2005). Another technique based on the fact that the upper boundary of the distribution of abundance reveals the limiting effect of a factor was developed by Blackburn et al. (1992). This method estimates the regression slope of the upper boundary by dividing the data into size classes and using the highest abundance for the calculations. Other techniques based on the law of the minimum have been proposed by Maller (1990), Kaiser et al. (1994) and Thompson et al. (1996). However, Liebig's law is open to criticism since resources might exhibit interactive effects, i.e. a factor can have a limiting effect only in the presence or absence of an other factor (Huisman & Weissing, 2002) or all the resources can be limiting simultaneously ('multiple limitation hypothesis', Rubio et al., 2003).

Austin (2007) in a critical review of current modelling approaches introduces structural equation models as an alternative offering the possibility to incorporate latent variables in the model. Structural equation models are a descendant of 'path analysis' developed by Wright (1921) to provide a mathematical description of a hypothetical causal scheme between traits of a species and abiotic/biotic environmental variables. Structural equation models are a contemporary fusion of factor analysis with path analysis, which is able of testing causal claims. The method is based on the fact that, although correlation does not imply causation, causation does necessarily imply particular types of statistical independencies and this constraint is what is tested. Shipley (1999) characterizes structural equation models as the most sophisticated method of performing statistical control on causal relationships. Its major disadvantages are the inevitable linearity of the relationships, the multivariate nature of the data, and the necessity for large sample sizes.

These methods have been developed in an attempt to solve technical problems associated with ordinary least squares regression, such as heteroscedasticity, extreme values, overdispersion and bias due to unmeasured explanatory variables, but most importantly to introduce biological thinking into statistical modelling. The lack of a biological basis for the most broadly used statistical methods leads to lack of interpretable results and, therefore, biological processes and causal relationships are being overlooked. Moreover results of null hypothesis testing on observational studies are arbitrary because of the lack of control over the response and predictor variables. The information-theoretic approach, namely the coupling of statistical tools with ecological theory to develop robust and interpretable models, has already started to dominate species distribution modelling (Rushton et al., 2004).

#### Presence-only models

ENFA (Ecological Niche Factor Analysis) compares the statistical distributions of the ecogeographical variables for a presence dataset consisting of locations where the species has been detected with the predictors' statistical distributions over a wider geographic area. Like principal component analysis (PCA), ENFA summarizes all predictors into a few uncorrelated factors retaining most of the information. However, in this case, the factors have specific ecological meanings: the first factor is the 'marginality', reflecting the direction and distance in which the species niche differs most from the available conditions in the wider area. Subsequent factors represent the 'specialisation'; they are extracted successively by computing the direction that maximizes the ratio of the variance of the global distribution to that of the species distribution (Hirzel et al., 2001; Dettki et al., 2003; Brotons et al., 2004). Although developed for modelling habitats of terres-

trial species, it has been recently applied to harbour porpoises on the west coast of Scotland (UK) (MacLeod et al., 2008, this volume).

BIOCLIM is an 'envelope' method that implements a bioclimatic envelope algorithm (Busby, 1991). Environmental envelopes are conceptually closely related to niche theory, as they strive to delineate the hyper-surface (or envelope) that best circumscribes suitable conditions within the niche hyper-space defined by the environmental variables. For each environmental variable the algorithm finds the mean and standard deviation (assuming normal distribution) associated with the occurrence of surveyed species presence points. Besides the envelope, each environmental variable has additional upper and lower limits taken from the maximum and minimum values related to the set of occurrence points.

DOMAIN (Carpenter et al., 1993) is a distancebased method that assesses new sites in terms of their environmental similarity to sites of known presence by transforming the known occurrences into an environmental space and computing the minimum distance in environmental space from any cell to a known presence of the species. The Genetic Algorithm for Rule-Set Prediction (GARP) use a genetic algorithm to select a set of rules (e.g. adaptations of regression and range specifications) that best predicts the species distribution (Stockwell & Peters, 1999). MAXENT estimates a target probability distribution by finding the probability distribution of maximum entropy (i.e. that is most spread out, or closest to uniform), subject to a set of constraints that represent incomplete information about the target distribution (Phillips et al., 2006).

# Presence/absence models

#### Classification and regression trees

Classification and regression trees (CART) function by way of recursive binary partitioning of data into increasingly homogenous groups with respect to the dependent variable. The two most homogenous groups of data with respect to the response variable are chosen (using the explanatory variables) and the resulting model is a tree-like structure consisting of a series of nodes (Lawler et al., 2004; Bourg et al., 2005).

In boosted regression trees (BRT), each of the individual models consists of a simple CART while the boosting algorithm uses an iterative method for developing a final model in a forward stage-wise fashion, progressively adding trees to the model by re-weighting the data to emphasize cases poorly predicted by the previous trees. Advantages offered by a BRT model include its ability to accommodate both different types of predictor variables and missing values, its immunity to the effects of extreme outliers and the inclusion of irrelevant predictors, and its facility for fitting interactions between predictors (Friedman & Meulman, 2003). Leathwick et al. (2006a, b) used BRT to analyze fish species richness, environmental parameters and trawl characteristics.

#### Multivariate adaptive regression splines

Multivariate adaptive regression splines (MARS) provide an alternative regression-based method for fitting non-linear responses, using piecewise linear fits rather than smooth functions (Friedman, 1991). MARS offer similar level of performance to other non-linear modelling techniques but may be extended by generalized boosted models (rarely used in ecological studies) where the estimation of the classifier's prediction is based on learning algorithms while systematically varying the training sample. For example, MARS were used to predict the distribution of freshwater diadromous freshwater fish in New Zealand (Leathwick et al., 2005).

# Generalized linear, additive and mixed models

Generalized linear models (GLM) are extensions of linear regression in the sense that they use different

distributions (e.g. the Poisson distribution for count data, the binomial distribution for binary and proportional data, the negative binomial distribution for overdispersed count data). Furthermore, they use a link function between the expected values of the response variable and explanatory variables that ensures that the fitted values make sense (e.g. larger than 0 for count data, or between 0 and 1 for binary data) (McCullagh & Nelder, 1989). In the context of EnviEFH, GLM were used with a predictive rather than inductive goal. In such circumstances accuracy of model predictions is more important than significance of particular ecogeographic variables (Legendre & Lengendre, 1998). Nishida and Chen (2004) applied GLM on yellowfin tuna CPUE data of the Japanese longline fisheries in the Indian Ocean.

Generalized additive models (GAM, Hastie & Tibshirani, 1990; Wood, 2006) are straightforward extensions of GLM, which allow linear and other parametric terms to be replaced by smoothing functions; they are now widely applied in fisheries science (e.g. Zuur et al., 2007). In a comparison of modelling techniques, Moisen & Frescino (2002) found that GAM built on real (as opposed to simulated) data, performed marginally better than other techniques (CART, ANN and GLM). In addition, GAM are well-suited to model continuous relationships, provided the samples are spread out over the entire measured gradient (GAM gives wide confidence bands when most observations have the same values for the explanatory variables, or if the explanatory variables have extreme observations). GAM is perhaps the most common and well developed method for modelling fish habitats. For example, Maravelias et al. (2007) used GAMs to identify the distribution of Morocco dentex (Dentex maroccanus) in the NE Mediterranean and the environmental factors that are related with species distribution. Giannoulaki et al. (2006) used GAMs to identify the relationship between anchovy presence and environmental variables. Francis et al. (2005) predicted small fish presence and abundance in northern New Zealand harbours. Many authors suggested several approaches to improve model fitting and prediction capacity in GAM. Ridge regression and lasso (Tibshirani, 1996; Harrell, 2001; Hastie et al., 2001) and model averaging (Burnham & Anderson, 2004; Johnson & Omland, 2004) are promising alternatives in a model stepwise procedure. 13

The use of CART techniques in a complementary way to GLM and GAM enables identification of ecologically meaningful interactions (Guisan et al., 2002).

Species distributional or trait data based on range map (extent-of-occurrence) or atlas survey data often display spatial autocorrelation, i.e. locations close to each other exhibit more similar values than those further apart. If this pattern remains present in the residuals of a statistical model based on such data, one of the key assumptions of standard statistical analyses, that residuals are independent and identically distributed, is violated. The violation of this assumption may bias parameter estimates and can increase type I error rates (falsely rejecting the null hypothesis of no effect) (Dorman et al., 2007). Often, spatial correlation is due to a missing covariate or interaction term in the model, the use of the wrong link function, or modelling a non-linear effect as linear. If refitting the model still gives residuals with spatial correlation, then a spatial correlation structure has to be incorporated in the model. It is also possible that due to the nature of the data, there is spatial correlation, in which case, a correlation structure has to be included anyway. Zuur et al. (2007) showed that falsely ignoring residual spatial autocorrelation, can give P-values that result in incorrect ecological interpretation. Including a spatial correlation structure provides more accurate predictions. In this case, modellers can quantify and integrate the spatial correlation structure (but should not ignore it).

Wagner & Fortin (2005) describe three different approaches to deal with spatial autocorrelation in models: (1) regression models incorporating a spatial term (autoregressive models: Keitt et al., 2002), (2) partialling-out of the spatial component in the species-environment relationship (variance partitioning: Legendre, 1993), and (3) residuals analysis (multiscale ordination, Maggini et al., 2006). Redfern et al. (2006) separated methods for addressing spatial autocorrelation into two general categories: (1) removing autocorrelation from the data and (2) explicitly accounting for autocorrelation in statistical tests and models. Fotheringham et al. (2002) discussed the approach of geographically weighted regression (similar to kernel regression) where spatial autocorrelation in parameter estimation is treated through the assignment of weights, such that those observations near the point in space where the parameter estimates are desired have more influence on the result than observations further away.

In Generalized Regression Analysis and Spatial Prediction (GRASP), which uses GAM for spatial predictions, improvement is achieved by using either cross-validation as a model selection method, or weighted absences, or limited absences, or predictors accounting for spatial autocorrelation, or a factor variable accounting for interactions between all predictors (Maggini et al., 2006). With regard to spatial autocorrelation, model performance and stability can be improved by incorporate large spatial trends, although better models are obtained by accounting for local spatial autocorrelation. Interaction factors built from a regression tree on residuals of a first environmental model proved to be an efficient way to account for interactions between all predictors but this can lead to some overfitting (Maggini et al., 2006). BRUTO provides a rapid method to identify both variables to be included and the degree of smoothing to be applied in a GAM (Leathwick et al., 2006a, b). The final choice of model strategy should always depend on the nature of the available data and the specific study aims (Maggini et al., 2006).

#### Artificial neural networks

Artificial neural networks (ANN) are non-linear mapping structures based on hundreds or thousands of simulated neurons connected together in much the same way as the brain's neurons. ANN learn from experience (not from programming) and their behaviour is defined by the way its individual computing elements are connected and by the strength of those connections (weights). ANN can be trained to recognize patterns, classify data, and forecast future events (Kohonen, 1996; Ripley, 1996; Bishop, 1997). They have been shown to be universal and highly flexible function approximations for any data and any data dependencies. These make powerful tools for models, especially when the underlying data relationships are unknown (Lek & Guegan, 1999). However, ANN are not very common for fish habitat modelling. Brosse et al. (1999) used ANN to assess fish abundance and occupancy in the littoral zone of the lake Pareloup (SW France). Lek & Guegan (1999) presented an introduction of ANN as a tool in ecological modelling.

#### Model comparisons

The development of validation tools for prediction methods provides comparison methods. Although validation and comparison of models depends on specific datasets, predictions based on presence/ absence data perform generally better than presence only data (Brotons et al., 2004) while presence/ absence models perform generally better than abundance models (Francis et al., 2005). Presence only models can perform as well if survey coverage is evenly and widely distributed (see MacLeod et al., 2008, this volume) but they contain no mechanism to control for biased sampling. Given effort data, effort can be used as a weighting factor to compensate for unevenly distributed survey effort, although compensation for inadequate survey coverage of the full range of habitats is not possible. In principle, abundance models should be more informative, however, their poor performance in practice relates to the fact that real abundance data rarely conform to standard distributions, thus violating model assumptions. The assumptions associated with presence/absence data (binary distribution) are more easily met.

Brotons et al. (2004) suggested that GLM with presence/absence data predict more accurately than ENFA (presence data), although MacLeod et al. (2008, this volume) show that the performance of the two classes of model is similar given good survey coverage. Elith et al. (2006) evaluated the prediction of eleven distinct models and sixteen approaches that use presence-only data. They classified the models in three performance categories. The first highest performing group includes MARS, BRT, generalized dissimilarity (GDM and GDM-SS) and maximum entropy (MAXENT and MAXENT-T) models. A second group of methods includes most of the standard regression methods (GAM/BRUTO, GLM, MARS and GARP). A third group includes the methods that use presence data only (BIOCLIM, DOMAIN and LIVES, Li & Hilbert, in press). Studies of presence-absence modelling methods suggest that several non-linear techniques (e.g. GAM, ANN and MARS) are comparable in terms of predictive ability and are often superior to methods such as traditional single decision trees (Ferrier & Watson, 1997; Elith & Burgman, 2002, Moisen & Frescino, 2002, Munoz & Felicisimo, 2004; Segurado & Araujo, 2004).

Among some available methods for predictions (e.g. GLM, GAM, ANN) and based on specific datasets, Lehmann et al. (2002) selected GAM because of the ecological interpretability of its non-parametric response curves and of the advantage of being statistically well defined, allowing good inference, but also flexible enough to fit the data closely. Leathwick et al. (2006a, b) fitted GAM and MARS models between the distributions of 15 freshwater fish species and their environment, and based on ROC values, results indicated little difference between the performances of both models. According to Olivier & Wotherspoon (2005), GLM classification accuracy on both test and training data was higher than that of CART and these authors finally suggested that the application of CART in a complementary way to GLM and GAM proved very useful in the model building phase as a guide to identify meaningful interactions using tree nodes.

# Essential fish habitat mapping

#### Prediction versus range

There are at least two ways to produce an EFH map from a model. The first one is based on the model's graphical and numerical output. Estimated regression parameters, their signs, and significance levels indicate the strength and (partial) effect on the response variable. Some methods also provide graphical output for the explanatory variable (e.g. GAMs), which can be used for assessing its (partial) effect. Application of these ranges within GIS grids generates maps and indicates areas where variable ranges simultaneously meet, as potential EFH. Environmental ranges extracted from a specific surveyed area (e.g. North Aegean Sea in Eastern Mediterranean) can be applied to satellite data that cover the whole region (e.g. the whole Mediterranean basin), thus providing potential EFH maps for the region of interest.

The other approach includes the use of either a new set of values (or the original ones) for the explanatory variables of a fitted GAM model, in order to produce predictions. In this case, the predicted values can directly be mapped. The interpretation of prediction maps depends on the model's response variable (e.g. predicted values from a GAM with a response variable in presence/absence format gives probabilities of presence). The extent and the resolution of the predicted area depend on the set of the values used as the explanatory variables.

### Use of satellite data

There are many advantages in using satellite datasets in prediction models. Due to the great spatial and temporal coverage of satellite data, it is easy to extract EFH maps that expand the sampling area. The outcome can sometimes lead to underestimated or biased predictions for the areas outside the sampling area. Since the model is based on environmental parameters within specific ranges at the sampling area, predictions out of those ranges might be unrealistic. Applying the models to a new area or different time period (prospective sampling) provides different results on habitat availability and this will usually result in a change in the model coefficients and apparent selection. However, one measure of the robustness of a habitat model is its capacity to be applied in other areas (Boyce et al., 2002; Olivier & Wotherspoon, 2005).

# Seasonal or pooled

Given seasonal data, GAM can be applied in each season or in the whole dataset. In each case, there are advantages and disadvantages. The final choice depends on the study's objectives (prediction or description). If the whole dataset is used, the model will have a wider applicability because of the wider range of values of the explanatory variables. If only one season is used, the model will describe accurately the specific season (better than the previous model) but would be weak to predict other seasons. As a general rule, although always depending on the nature of specific datasets, the use of whole year datasets is recommended for predictive models whereas seasonal datasets might be used for descriptive models. The same type of argument can be applied to data collected across several years or several areas. Boyce et al. (2002) concluded that an overall model (all-year pooled data) is generally not a good indicator for individual-year models.

# Model validation

There are several techniques to validate a model or to compare the accuracy of prediction among different models. Kappa statistics, Receiver Operating Characteristic (ROC), k-Fold cross validation, confusion matrices and classification tables are well described by Boyce et al. (2002) for presence/absence data. ROC statistics are preferable to Kappa, because, unlike Kappa, the ROC method avoids the problem of choosing a threshold value (Lehmann et al., 2002). For presence data, better model evaluation is achieved by withholding data (k-Fold partitioning) for testing model predictions or by comparing Resource Selection Function (RSF) predictions using models developed at other times and places (prospective sampling) (Boyce et al., 2002). One step towards improving evaluation of model performance in predicting distributions of species is to use independent, well structured presence-absence datasets for validation (Elith et al., 2006). On the other hand, Lehmann et al. (2002) indicated that crossvalidation is generally more practical because it creates relatively independent random subsets and allows the use of all available data in the modelling process. By using entirely independent datasets, there is a risk of comparing different sampling strategies instead of evaluating a model (Lehmann et al., 2002). In addition, adequate data for independent validation may be difficult to collect and modelers usually prefer to use all available data to fit their model (Araujo et al., 2005; Maggini et al., 2006). The jackknife is also used (Jaberg & Guisan, 2001) for model validation.

False positives and false negatives are the types of prediction errors in modelling based on presence/absence data. Some data partitioning methods for the allocation of cases to training and testing datasets are resubstitution (Stockwell, 1992), which tends to provide optimistic measures of prediction success, bootstrapping (Buckland & Elston, 1993) in which accuracy is usually reported as a mean and confidence limits, randomization and prospective sampling (Capen et al., 1986) that could be from a different region or time, k-fold partitioning and jackknife sampling (Fielding & Bell, 1997).

# Conclusions

We conclude this overview with the statement that the best model selection depends on the specific dataset and on the aims of the modelling process. In the EnviEFH project, the final objective was to produce essential fish habitat maps for small, large pelagic and demersal fish resources in the Mediterranean and adjacent seas, thus we focused more on the fact that different methods produce similar maps rather than examining in great detail the pros and cons of the statistics behind each model.

Published studies have moved from using simple correlation and regression (assuming normal distributions, homogeneity of variance and linear/nonlinear relationships) to techniques that can account for the effects and interactions of multiple explanatory variables, response variables with a range of different distributions, non-linear relationships, heteroscedasticity, time-lagged effects and temporal autocorrelation and, one of the less tractable of these issues, spatial autocorrelation. Particular attention should be given to ensuring adequate and representative sampling and robust model validation methods.

Acknowledgement This review was supported by the EU-FP6-SSP Action EnviEFH 'Environmental Approach to Essential Fish Habitat Designation' (Project No: 022466).

#### References

- Akaike, H., 1974. A new look at the statistical model identification. IEEE Transactions on Automatic Control 19: 716–723.
- Araujo, M. B., R. J. Whittaker, R. J. Ladle & M. Erhard, 2005. Reducing uncertainty in projections of extinction risk from climate change. Global Ecology and Biogeography 14: 529–528.
- Austin, M., 2007. Species distribution models and ecological theory: a critical assessment and some possible new approaches. Ecological Modelling 200: 1–19.
- Austin, M. P. & P. C. Heyligers, 1989. Vegetation survey design for conservation: gradsect sampling of forests in north-east New South Wales. Biological Conservation 50: 13–32.
- Austin, M. P. & P. C. Heyligers, 1991. New approach to vegetation survey design: gradsect sampling. In Margules, C. R. & M. P. Austin (eds), Nature Conservation: Cost Effective Biological Surveys and Data Analysis. CSIRO, Australia: 31–36.

- Behrouz, A.-N., A. St-Hilaire, M. Berube, E. Robichaud, N. Thiemonge & B. Bobee, 2006. A review of statistical methods for the evaluation of aquatic habitat suitability for instream flow assessment. River Research and Applications 22: 503–523.
- Bishop, C. M., 1997. Neural Networks for Pattern Recognition. Oxford University Press, New York: 484.
- Blackburn, T. M., J. H. Lawton & J. Perry, 1992. A method for estimating the slope of upper bounds in plots of body size and abundance in natural animal assemblages. Oikos 65: 107–112.
- Bourg, N. A., W. J. McShea & D. E. Gill, 2005. Putting a CART before the search: successful habitat prediction for a rare forest herb. Ecology 86: 2793–2804.
- Boyce, M. S., P. R. Vernier, S. E. Nielsen & F. K. A. Schmiegelow, 2002. Evaluating resource selection functions. Ecological Modelling 157: 281–300.
- Brosse, S., J. Guegan, J. Tourenq & S. Lek, 1999. The use of artificial neural networks to assess fish abundance and spatial occupancy in the littoral zone of a mesotrophic lake. Ecological Modelling 120: 299–311.
- Brotons, L., W. Thuiller, M. B. Araujo & A. H. Hirzel, 2004. Presence–absence versus presence-only modelling methods for predicting bird habitat suitability. Ecography 27: 437–448.
- Buckland, S. T. & D. A. Elston, 1993. Empirical models for the spatial distribution of wildlife. Journal of Applied Ecology 30: 478–495.
- Burnham, K. P. & D. R. Anderson, 2004. Multimodel inference – understanding AIC and BIC in model selection. Sociological Methods & Research 33: 261–304.
- Busby, J. R., 1991. BIOCLIM A bioclimate analysis and prediction system. In Margules, C. R. & M. P. Austin (eds), Nature Conservation: Cost effective biological surveys and data analysis. CSIRO, Australia: 64–68.
- Cade, B. S. & B. R. Noon, 2003. A gentle introduction to quantile regression for ecologists. Frontiers in Ecology and the Environment 1: 412–420.
- Cade, B. S., B. R. Noon & C. H. Flather, 2005. Quantile regression reveals hidden bias and uncertaintly in habitat models. Ecology 86: 786–800.
- Cade, B. S., J. W. Terrell & R. L. Schroeder, 1999. Estimating effects of limiting factors with regression quantiles. Ecology 80: 311–323.
- Capen, D. E., J. W. Fenwick, D. B. Inkley & A. C. Boynton, 1986. On the measurement of error: multivariate models of songbird habitat in New England forests. In Verner, J. A., M. L. Morrison & C. J. Ralph (eds), Wildlife 2000: Modelling Habitat Relationships of Terrestrial Vertebrates. University of Wisconsin Press, Madison: 171–175.
- Carpenter, G., A. N. Gillison & J. Winter, 1993. DOMAIN a flexible modelling procedure for mapping potential distributions of plants and animals. Biodiversity and Conservation 2: 667–680.
- Clark, S. J., 2005. Why environmental scientists are becoming Bayesians. Ecology Letters 8: 2–14.
- Decoursey, D. G., 1992. Developing models with more detail: do more algorithms give more truth? Weed Technology 6: 709–715.
- Dettki, H., R. Lofstrand & L. Edenius, 2003. Modelling habitat suitability for moose in coastal Northern Sweden:

empirical vs. process-oriented approaches. Ambio 32: 549-556.

- Dormann, C. F., J. M. McPherson, M. B. Araujo, R. Bivand, J. Bolliger, G. Carl, R. G. Davies, A. Hirzel, W. Jetz, W. D. Kissling, I. Kuhn, R. Ohlemuller, P. R. Peres-Neto, B. Reineking, B. Schroder, F. M. Schurr & R. Wilson, 2007. Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. Ecography 30: 609–628.
- Eastwood, P. D., G. J. Meaden & A. Grioche, 2001. Modelling spatial variations in spawning habitat suitability for the sole *Solea solea* using regression quantiles and GIS procedures. Marine Ecology Progress Series 224: 251–266.
- Efron, B. & R. Tibshirani, 1991. Statistical data analysis in the computer age. Science 253: 390–395.
- Elith, J. & M. A. Burgman, 2002. Predictions and their validation: rare plants in the Central Highlands, Victoria, Australia. In Scott, J. M. (ed.), Predicting Species occurrences: Issues of Accuracy and Scale. Island Press, Covelo CA: 303–314.
- Elith, J., C. H. Graham, R. P. Anderson, M. Dudik, S. Ferrier, A. Guisan, R. J. Hijmans, F. Huettmann, J. R. Leathwick, A. Lehmann, J. Li, L. G. Lohmann, B. A. Loiselle, G. Manion, C. Moritz, M. Nakamura, Y. Nakazawa, J. Mc C. Overton, A. T. Peterson, S. J. Phillips, K. S. Richardson, R. Scachetti-Pereira, R. E. Schapire, J. Soberon, S. Williams, M. S. Wisz & N. E. Zimmermann, 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography 29: 129–151.
- ESRI, 1994. ARC Macro Language. Environmental Systems Research Institute Inc. Redlands, CA, USA: 3–37.
- Ferguson, M. C., J. Barlowa, P. Fiedler, S. B. Reilly & T. Gerrodette, 2006. Spatial models of delphinid (family *Delphinidae*) encounter rate and group size in the eastern tropical Pacific Ocean. Ecological Modelling 193: 645– 662.
- Ferrier, S. & G. Watson, 1997. An evaluation of the effectiveness of environmental surrogates and modelling techniques in predicting the distribution of biological diversity. Environment, Australia Canberra.
- Fielding, A. H. & J. F. Bell, 1997. A review of methods for the assessment of prediction errors in conservation presence/ absence models. Environmental Conservation 24: 38–49.
- Fotheringham, A. S., C. Brunsdon & M. E. Charlton, 2002. Geographically Weighted Regression: The Analysis of Spatially Varying Relationships. Chichester, Wiley.
- Francis, M. P., M. A. Morrison, J. Leathwick, C. Walsh & C. Middleton, 2005. Predictive models of small fish presence and abundance in northern New Zealand harbours. Estuarine, Coastal and Shelf Science 64: 419–435.
- Friedman, J. H., 1991. Multivariate adaptive regression splines. Annals of Statistics 19: 1–141.
- Friedman, J. H. & J. J. Meulman, 2003. Multiple adaptive regression trees with application in epidemiology. Statistics in Medicine 22: 1365–1381.
- Giannoulaki, M., A. Machias, V. D. Valavanis, S. Somarakis, A. Palialexis & C. Papaconstantinou, 2006. Spatial modelling of the European anchovy habitat in the Eastern Mediterranean basin using GAMs and GIS technology. General Fisheries Commission for the Mediterranean Scientific Advisory Committee, Sub-Committee for Stock

Assessment Working Group on Small Pelagic Species FAO, Rome, 11–14 September 2006.

- Guisan, A., J. Edwards, C. Thomas & T. Hastie, 2002. Generalized linear and generalized additive models in studies of species distributions: setting the scene. Ecological Modelling 157: 89–100.
- Guisan, A. & N. E. Zimmermann, 2000. Predictive habitat distribution models in ecology. Ecological Modelling 135: 147–186.
- Harrell, F. E., 2001. Regression Modelling Strategies With Applications to Linear Models Logistic Regression and Survival Analysis. Springer-Verlag, New York.
- Hastie, T. & R. Tibshirani, 1990. Generalized additive models. Chapman and Hall, London.
- Hastie, T., R. Tibshirani & J. H. Friedman, 2001. The elements of statistical learning: data mining, inference and prediction. Springer-Verlag, New York.
- Heikkinen, R. K., M. Luoto, M. B. Araujo, R. Virkkala, W. Thuiller & M. T. Sykes, 2006. Methods and uncertainties in bioclimatic envelope modelling under climate change. Progress in Physical Geography 30: 1–27.
- Hiddink, J. G., 2005. Implications of Liebig's law of the minimum for the use of ecological indicators based on abundance. Ecography 28: 264–271.
- Hirzel, A. H. & R. Arlettaz, 2003. Modelling habitat suitability for complex species distributions by the environmentaldistance geometric mean. Environmental Management 32: 614–623.
- Hirzel, A. H. & A. Guisan, 2002. Which is the optimal sampling strategy for habitat suitability modelling. Ecological Modelling 157: 331–341.
- Hirzel, A. H., V. Helfer & F. Metral, 2001. Assessing habitat suitability models with a virtual species. Ecological Modelling 145: 111–121.
- Huisman, J. & F. J. Weissing, 2002. Oscillations and chaos generated by competition for interactively essential resources. Ecological Research 17: 175–181.
- Jaberg, C. & A. Guisan, 2001. Modelling the distribution of bats in relation to landscape structure in a temperate mountain environment. Journal of Applied Ecology 38: 1169–1181.
- Johnson, J. B. & K. S. Omland, 2004. Model selection in ecology and evolution. Trends in Ecology and Evolution 19: 101–108.
- Kaiser, M. S., P. L. Speckman & J. R. Jones, 1994. Statistical models for limiting nutrient relations in inland waters. Journal of the American Statistical Association 89: 410–423.
- Keitt, T. H., O. N. Bjornstad, P. M. Dixon & S. Citron-Pousty, 2002. Accounting for spatial pattern when modelling organism–environment interactions. Ecography 25: 616–625.
- Kohonen, T., 1996. Self-organizing Maps. Springer-Verlag, New York: 428.
- Korzukhin, M. D., M. T. Ter-Mikaelian & R. G. Wagner, 1996. Process versus empirical models: which approach for forest ecosystem management? Canadian Journal of Forest Research 26: 879–887.
- Kuhn, T. S., 1996. The Structure of Scientific Revolutions. University of Chicago Press, USA.
- Lakatos, I., 1970. Falsification and the methodology of scientific research programmes. In Lakatos, I. & A. Musgrave

(eds), Criticism and the Growth of Knowledge. Cambridge University Press, London: 91–195.

- Laurel, B. J., A. W. Stoner & T. P. Hurst, 2007. Densitydependent habitat selection in marine flatfish: the dynamic role of ontogeny and temperature. Marine Ecology Progress Series 338: 183–192.
- Lawler, J. J., R. J. O'Connor, C. T. Hunsaker, K. B. Jones, T. R. Loveland & D. White, 2004. The effects of habitat resolution on models of avian diversity and distributions: a comparison of two land-cover classifications. Landscape Ecology 19: 515–530.
- Leathwick, J. R., J. Elith, M. P. Francis, T. Hastie & P. Taylor, 2006a. Variation in demersal fish species richness in the oceans surrounding New Zealand: an analysis using boosted regression trees. Marine Ecology Progress Series 321: 267–281.
- Leathwick, J. R., J. Elith & T. Hastie, 2006b. Comparative performance of generalized additive models and multivariate adaptive regression splines for statistical modelling of species distributions. Ecological Modelling 199: 188–196.
- Leathwick, J. R., D. Rowe, J. Richardson, J. Elith & T. Hastie, 2005. Using multivariate adaptive regression splines to predict the distributions of New Zealand's freshwater diadromous fish. Freshwater Biology 50: 2034–2052.
- Legendre, P., 1993. Spatial autocorrelation: trouble or new paradigm? Ecology 74: 1659–1673.
- Legendre, P. & L. Legendre, 1998. Numerical Ecology. Elsevier.
- Lehmann, A., J. Mc, C. Overton & J. R. Leathwick, 2002. GRASP: generalized regression analysis and spatial prediction. Ecological Modelling 157: 189–207.
- Lek, S. & J. F. Guegan, 1999. Artificial neural networks as a tool in ecological modelling, an introduction. Ecological Modelling 120: 65–73.
- Levins, R., 1966. The strategy of model building in population ecology. American Scientist 54: 421–431.
- Li, J. & D. Hilbert, in press. A new predictive model, LIVES, for the potential distributions and habitats of species using presence-only data. Ecological Modelling (in press).
- Loehle, C. & D. LeBlanc, 1996. Model-based assessments of climate change effects on forests: a critical review. Ecological Modelling 90: 1–31.
- Lutchman, I., 2003. New technical approaches in fisheries management: the precautionary approach and the ecosystem approach. In De Fontaubert, C. & I. Lutchman (eds), Achieving Sustainable Fisheries: Implementing the New International Legal Regime. IUCN, The World Conservation Union: 31–45.
- MacLeod, C. D., L. Mandleberg, C. Schweder, S. M. Bannon & G. J. Pierce, 2008. A comparison of approaches to modelling the occurrence of marine animals. Hydrobiologia. doi:10.1007/s10750-008-9491-0.
- Maggini, R., A. Lehmann, N. E. Zimmermann & A. Guisan, 2006. Improving generalized regression analysis for the spatial prediction of forest communities. Journal of Biogeography 33: 1729–1749.
- Maller, R. A., 1990. Some aspects of a mixture model for estimating the boundary of a set of data. Journal du Conseil International pour l'exploration de la Mer 46: 140–147.

- Manel, S., J. M. Dias, S. T. Buckton & S. J. Ormerod, 1999. Alternative methods for predicting species distribution: an illustration with Himalayan river birds. Journal of Applied Ecology 36: 734–747.
- Maravelias, C. D., E. V. Tsitsika & C. Papaconstantinou, 2007. Evidence of Morocco dentex (*Dentex maroccanus*) distribution in the NE Mediterranean and relationships with environmental factors determined by Generalized Additive Modelling. Fisheries Oceanography 16: 294–302.
- McCullagh, P. & J. A. Nelder, 1989. Generalized Linear Models. Chapman & Hall, London.
- Moisen, G. G. & T. S. Frescino, 2002. Comparing five modelling techniques for predicting forest characteristics. Ecological Modelling 157: 209–225.
- Morrell, L. J. & R. James, 2008. Mechanisms for aggregation in animals: rule success depends on ecological variables. Behavioral Ecology 19: 193–201.
- Munoz, J. & A. M. Felicisimo, 2004. A comparison between some statistical methods commonly used in predictive modeling. Journal of Vegetation Science 15: 285–292.
- Nishida, T. & D. G. Chen, 2004. Incorporating spatial autocorrelation into the general linear model with an application to the yellowfin tuna (*Thunnus albacares*) longline CPUE data. Fisheries Research 70: 265–274.
- Olden, J. D. & D. A. Jackson, 2002. A comparison of statistical approaches for modelling fish species distributions. Freshwater Biology 47: 1976–1995.
- Olivier, F. & S. J. Wotherspoon, 2005. GIS-based application of resource selection functions to the prediction of snow petrel distribution and abundance in East Antarctica: comparing models at multiple scales. Ecological Modelling 189: 105–129.
- Perry, A. L., P. J. Low, J. R. Ellis & J. D. Reynolds, 2005. Climate change and distribution shifts in marine fishes. Science 308: 1912–1915.
- Phillips, S. J., R. P. Anderson & R. E. Schapire, 2006. Maximum entropy modelling of species geographic distributions. Ecological Modelling 190: 231–259.
- Pickett, S. T. A., G. Kolasa & C. G. Jones, 1994. Ecological Understanding: the Nature of Theory and the Theory of Nature. Academic Press, New York.
- Pierce, G. J., V. D. Valavanis, A. Guerra, P. Jereb, L. Orsi-Relini, J. M. Bellido, I. Katara, U. Piatkowski, J. Pereira, E. Balguerias, I. Sobrino, E. Lefkaditou, J. Wang, M. Santurtun, P. R. Boyle, L. C. Hastie, C. D. MacLeod, J. M. Smith, M. Viana, A. F. González & A. F. Zuur, 2008. A review of cephalopod-environment interactions in European Seas and other world areas. Hydrobiologia.
- Pierce, G. J., J. Wang & V. D. Valavanis, 2002. Application of GIS to cephalopod fisheries: workshop report. Bulletin of Marine Science 71: 35–46.
- Pierce, G. J., J. Wang, X. Zheng, J. M. Bellido, P. R. Boyle, V. Denis & J.-P. Robin, 2001. A cephalopod fishery GIS for the Northeast Atlantic: development and application. International Journal of Geographical Information Science 15: 763–784.
- Pollock, J. F., 2006. Detecting population declines over large areas with presence–absence, time-to-encounter, and count survey methods. Conservation Biology 20: 882–892.

- Popper, K. R., 1963. The Growth of Scientific Knowledge. Routledge, London.
- Prentice, I. C., 1986. Some concepts and objectives of forest dynamics research. In Fanta, J. (ed.), Forest Dynamics Research in Western and Central Europe. PUDOC, Wageningen: 32–41.
- Redfern, J. V., M. C. Ferguson, E. A. Becker, K. D. Hyrenbach, C. Good, J. Barlow, K. Kaschner, M. F. Baumgartner, K. A. Forney, L. T. Ballance, P. Fauchald, P. Halpin, T. Hamazaki, A. J. Pershing, S. S. Qian, A. Read, S. B. Reilly, L. Torres & F. Werner, 2006. Techniques for cetacean-habitat modelling. Marine Ecology Progress Series 310: 271–295.
- Ripley, B. D., 1996. Pattern Recognition and Neural Networks. Cambridge University Press, London: 416.
- Rubio, G., J. Zhu & J. P. Lynch, 2003. A critical test of the two prevailing theories of plant response to nutrient availability. American Journal of Botany 90: 143–152.
- Rushton, S. P., S. J. Ormerod & G. Kerby, 2004. New paradigms for modelling species distributions? Journal of Applied Ecology 41: 193–200.
- Schwarz, G., 1978. Estimating the dimension of a model. Annals of Statistics 6: 461–464.
- Segurado, P. & M. B. Araujo, 2004. An evaluation of methods for modelling species distributions. Journal of Biogeography 31: 1555–1568.
- Shipley, B., 1999. Testing causal explanations in organismal biology: causation, correlation and structural equation modelling. Oikos 86: 374–382.
- Stockwell, D. R. B., 1992. Machine learning and the problem of prediction and explanation in ecological modelling. Ph.D. Thesis, Australian National University.
- Stockwell, D. & D. Peters, 1999. The GARP modelling system: problems and solutions to automated spatial prediction. International Journal of Geographical Information Science 13: 143–158.
- Thompson, J. D., G. Weiblen, B. A. Thompson, S. Alfaro & P. Legendre, 1996. Untangling multiple factors in spatial distributions: lilies, gophers and rocks. Ecology 77: 1698–1715.
- Tibshirani, R., 1996. Regression shrinkage and selection via the lasso. Journal of the Royal Statistical Society 58: 267–288.
- Ullman, D. S. & P. C. Cornillon, 2000. Evaluation of front detection methods for satellite-derived SST data using in situ observations. Journal of Atmopheric and Oceanic Techology 17: 1667–1675.
- Valavanis, V. D., S. Georgakarakos, A. Kapantagakis, A. Palialexis & I. Katara, 2004. A GIS environmental modelling approach to Essential Fish Habitat Designation. Ecological Modelling 178: 417–427.
- Valavanis, V. D., S. Georgakarakos, D. Koutsoubas, C. Arvanitidis & J. Haralabous, 2002. Development of a marine information system for cephalopod fisheries in the Greek seas (eastern Mediterranean). Bulletin of Marine Science 71: 867–882.
- Valavanis, V. D., I. Katara & A. Palialexis, 2005. Marine GIS: identification of mesoscale oceanic thermal fronts. International Journal of Geographical Information Science 19: 1131–1147.

- Wagner, H. H. & M. J. Fortin, 2005. Spatial analysis of landscapes: concepts and statistics. Ecology 86: 1975– 1987.
- Wood, S. N., 2006. Generalized Additive Models: An Introduction with R. CRC Press, London.
- Wright, S., 1921. Correlation and causation. Journal of Agricultural Research 20: 557–585.
- Zaniewski, A. E., A. Lehman & J. Overton, 2002. Predicting species spatial distributions using presence-only data: a case study of native New Zealand ferns. Ecological Modelling 157: 261–280.
- Zuur, A. F., E. N. Ieno & G. M. Smith, 2007. Analysing Ecological Data. Springer Series: Statistics for Biology and Health.

# FISH HABITAT MAPPING

# A comparison of approaches for modelling the occurrence of marine animals

Colin D. MacLeod · Laura Mandleberg · Caroline Schweder · Sarah M. Bannon · Graham J. Pierce

© Springer Science+Business Media B.V. 2008

Abstract Approaches for modelling the distribution of animals in relation to their environment can be divided into two basic types, those which use records of absence as well as records of presence and those which use only presence records. For terrestrial species, presence-absence approaches have been found to produce models with greater predictive ability than presence-only approaches. This study compared the predictive ability of both approaches for a marine animal, the harbour porpoise (Phoceoena phocoena). Using data on the occurrence of harbour porpoises in the Sea of Hebrides, Scotland, the predictive abilities of one presence-absence approach (generalised linear modelling-GLM) and three presence-only approaches (Principal component analysis-PCA, ecological niche factor analysis-ENFA and genetic algorithm for rule-set prediction-GARP) were compared. When the predictive ability of the

Guest editor: V. D. Valavanis Essential Habitat Mapping in the Mediterranean

C. D. MacLeod (⊠) · L. Mandleberg · C. Schweder · S. M. Bannon · G. J. Pierce School of Biological Sciences (Zoology), University of Aberdeen, Tillydrone Avenue, AB24 2TX Aberdeen, UK e-mail: c.d.macleod@abdn.ac.uk

#### G. J. Pierce

Centro Oceanográfico de Vigo, Instituto Español de Oceanografía, P.O. Box 1552, 36200 Vigo, Spain

models was assessed using receiver operating characteristic (ROC) plots, the presence-absence approach (GLM) was found to have the greatest predictive ability. However, all approaches were found to produce models that predicted occurrence significantly better than a random model and the GLM model did not perform significantly better than ENFA and GARP. The PCA had a significantly lower predictive ability than GLM but not the other approaches. In addition, all models predicted a similar spatial distribution. Therefore, while models constructed using presence-absence approaches are likely to provide the best understanding of species distribution within a surveyed area, presence-only models can perform almost as well. However, careful consideration of the potential limitations and biases in the data, especially with regards to representativeness, is needed if the results of presence-only models are to be used for conservation and/or management purposes.

**Keywords** Species distribution modelling · Marine species · Harbour porpoise · GLM · ENFA · GARP

# Introduction

A detailed knowledge of species' distribution in relation to their environment is essential for understanding many aspects of their ecology, as well as for effective conservation, management and assessment of possible impacts from anthropogenic activities (Lindenmayer et al., 1991; Beerling et al., 1995; Schulze & Kunz, 1995; Austin et al., 1996). However, knowledge on the true distribution of many marine animals remains limited, especially for species that are hard to detect. In the marine environment, poor detectability is primarily a function of the fact that humans can only directly observe surface waters close to the coast with any ease and usually require expensive and complex equipment to conduct studies on species that occur only in waters far from shore (e.g. large research vessels) or below the surface (e.g. underwater vehicles and deep-water camera sleds—see Robison (2004)).

One solution to this lack of knowledge is to use mathematical approaches to model species distribution relative to various quantifiable aspects of their physical environment known as eco-geographic variables (EGVs). These modelled relationships can then be used to predict where species are most likely to occur and investigate ecological relationships between a species and its environment (Lindenmayer et al., 1991; Zaniewski et al., 2002). Many traditional modelling approaches require presence-absence data (Guisan & Zimmerman, 2000; Hirzel et al., 2001). That is, they require data on locations where a species is known not to occur (absence data) as well as data on locations where a species does occur (presence data). It is essential that any absence data used for such modelling are accurate and that none of the data points represent 'false' absences-locations where a species occurs but for some reason was not detected during data collection (Hirzel et al., 2002). For hardto-detect species, even in terrestrial environments, it can be difficult to obtain datasets that do not include a substantial number of false absences. In the marine environment, accurate absence data may be all but impossible to collect for many species, particularly those that occur at great depth, far from shore, are very mobile, avoid survey vessels or that are difficult to detect in other ways.

The problem of false absences has led to the development of modelling approaches that do not use absence data (e.g. Robertson et al., 2001; Hirzel et al., 2002; Ortega-Huerta & Peterson, 2004). Such presence-only approaches are generally based on constructing a model of a species' niche from locational records. This modelled niche can then be

used to predict distribution within the available environment.

The validity of such modelled niches is contingent on having unbiased distribution data available to build the models. If survey effort data are available, it is possible to both determine whether all habitat types have been adequately sampled and to correct for bias by using effort as a weighting factor in the model. However, as presence-only models do not take survey effort into account such models may be affected by biases in the collection of presence data. While this is less likely to be a problem with large numbers of records, as can often be available for terrestrial species from sources such as museum collections (e.g. Robertson et al., 2001; Reutter et al., 2003), this may be an issue when a small number of records is used to generate the model.

When presence-absence and presence-only modelling approaches have been compared using the same datasets, presence-absence models have generally been found to perform better and have higher predictive abilities (Hirzel et al., 2001; Brotons et al., 2004), leading to most researchers to prefer the use of presence-absence models whenever possible. However, these comparative studies have been limited to terrestrial species (Brotons et al., 2004) and theoretical populations (Hirzel et al., 2001) and it is not known whether the same relationship will hold in the marine environment where detectability of many species is much lower than for terrestrial species. Here, the abilities of presence-absence and presenceonly modelling approaches to predict the distribution of a marine species, the harbour porpoise (Phocoena phocoena Linnaeus 1758), in relation to EGVs are compared for the first time.

Harbour porpoises are one of the smallest members of the order Cetacea and are known to be hard to detect, particularly in rougher seas (Palka, 1996; Laake et al., 1997; Teilmann, 2003). This low detectability is primarily a function of small body size, small group sizes, boat avoidance and unobtrusive surface behaviours. Traditionally, problems with detectability have been dealt with by introducing a correction factor to estimate the number of animals missed, especially for abundance estimates (Teilmann, 2003). However, such correction factors can be difficult to calculate (Laake et al., 1997; Teilmann, 2003). In particular, visual detectability of harbour porpoises varies in relation to many factors, such as changes in group size with season (Bannon Pers. Obs.), behaviour, time of day and sea state (Palka, 1996).

Four modelling approaches were compared in this study. These were Generalised Linear Modelling (GLM), a widely used presence-absence technique (Sparholt et al., 1991; Guisan & Zimmerman, 2000; Garcia-Charton & Perez-Ruzafa, 2001; Guisan & Hofer, 2003; MacLeod et al., 2004; Evans & Hammond, 2004) which has been compared to presenceonly techniques in previous studies (Hirzel et al., 2001; Brotons et al., 2004), and three presence-only approaches: Ecological niche factor analysis (ENFA), Genetic algorithm for rule-set prediction (GARP) and a PCA-based approach. Presence-only techniques were selected based on their previous successful application in the terrestrial environment (Robertson et al., 2001; Hirzel et al., 2002; Stockwell & Peters, 1999; Ortega-Huerta & Peterson, 2004). Currently, there are no published applications of these presenceonly approaches to model the distribution of marine animals. The aim of this study was to directly compare the ability of these approaches to predict the occurrence of harbour porpoises within a surveyed area using a single data set, and, in particular, to explore the potential application of presence-only models to the marine environment.

#### Materials and methods

Study area and eco-geographic variables (EGVs)

This study was conducted in the Sea of Hebrides, an area of shelf waters to the west of Scotland, UK (Fig. 1). A geographic information system (GIS) consisting of 15,520 1 km<sup>2</sup> grid cells was created using ESRI Map Info software to cover this study area. Each cell was assigned a value for water depth, seabed slope, standard deviation of seabed slope, aspect of seabed and distance from the nearest coast using ESRI ARCView 3.2 software. The EGVs used in this study were primarily related to topography and included a number that are commonly used when studying the distribution of cetacean species (e.g. MacLeod et al., 2004; MacLeod & Zuur, 2005; Ingram et al., 2007) and that are known to be important for porpoise habitat use in the west of Scotland (MacLeod et al., 2007). While other variables, not included in this analysis, may also



Fig. 1 The study area used to investigate the ability of different modelling approaches to predict the occurrence of harbour porpoises in the Sea of Hebrides. Black lines indicate route travelled by ferries used to survey for harbour porpoise. Shading indicates water depth. Latitudes are in degrees north and longitude in degrees west

relate to porpoise distribution, the aim of this study was not to identify all factors that relate to porpoise distribution but rather to compare modelling approaches using the same variables. Therefore, while this limitation should be borne in mind when considering the actual habitat preferences identified by the models presented here, it will not affect the results in relation to the comparisons of the predictive abilities of the different modelling approaches using this standardised data set.

Water depth was interpolated from the ETOP02 global 2' elevation dataset (National Geophysical Data Centre 2001) at a 1 km by 1 km resolution, and slope, standard deviation of slope and aspect for each cell were derived using ARCView functions. In order to make aspect a suitable parameter for inclusion in the analysis, it was converted into two linear components: aspect easting (the sine of the aspect value) and aspect northing (the cosine of the aspect value). For all modelling approaches, the modelling process started with all six variables. However, the EGVs included in the final model were identified through the modelling process independently for each modelling approach. Finally, each grid cell was assigned a random number using the random grid function in ArcView.

# Data collection

Data on the occurrence of harbour porpoises were collected from repeated surveys along five fixed routes in the months of May to July 2003 and 2004 using passenger ferries as research platforms (Fig. 1). While these ferry routes may not cover a representative sample of habitat within the study area, the same data set was used for all four models and therefore allows a direct comparison of the predictive abilities of the different modelling approaches for the surveyed areas. In addition, the repeated coverage of these routes allowed a large number of grid cells to be surveyed on multiple occasions, a feature that was important for reducing the likelihood of false absences within the dataset, at low cost. The surveys were conducted by a single observer situated approximately 15 m above sea level to one side of the vessel. This gave a field of view that covered from 90 degrees on the observer's side of the bow to 20 degrees to the other side.

This field of view was continuously swept with  $7 \times 50$  reticulated binoculars and with the naked eye. At the start and end of each survey, as well as every 15 min during the surveys, the position, direction of travel and speed of the ship were recorded using a GPS receiver, along with environmental variables such as sea state. Assuming a straight line course between the locations of the ship recorded every 15 min allowed the ship's track between these two points to be plotted. When any harbour porpoises were detected, the distance to the animals was estimated with the reticules in the binoculars (following the trigonometric methods of Lerczak & Hobbs, 1998) and a relative bearing to the animals was recorded using a compass rose, along with the group size, the ship's position, course and speed. This information allowed the actual position of each group to be estimated, in terms of latitude and longitude, and plotted in the GIS.

In order to identify those cells that were surveyed, all 15-min track segments surveyed in sea states of Beaufort 3 or less were identified. Around these survey segments, a cut off point of 750 metres from the vessel was defined as the point beyond which the observer could not accurately detect harbour porpoise at the surface (although even within this distance animals that were underwater would still be missed). This distance was based on previous experience with surveys from these vessels, the binoculars used and the distances over which porpoises could be visually detected. Due to the restricted field of view, this resulted in a survey swath width of 1,000 m, 750 m on the side of the vessel where the observer was positioned and 250 m on the opposite side. Since results are not used to estimate absolute abundance of porpoises, no bias will result if the real swath width was not exactly 1,000 m. A cell was defined as surveyed if the survey swath covered a portion of the cell defined by a triangle with a hypotenuse of at least 500 m, or approximately one-eighth of the cell, although for the majority of surveyed cells the proportion of the cell within the survey swath was much greater than this. The total number of times each cell was surveyed throughout the study was then calculated. Finally, the sightings data associated with the 15-min segments conducted in sea states 3 or less were compared to the survey swathe and only those where the estimated position fell within it sightings for which used to identify which surveyed cells could be assigned as porpoise presence.

The surveyed cells within the study area were divided into a model construction dataset and a model testing dataset in a ratio of 2:1 using the random number assigned to each cell. Within each set, any cell where one or more groups of harbour porpoises were recorded were classified as 'presence', while all cells that were surveyed at least three times without recording any harbour porpoises were classified as 'absence'. This provided a relatively strict rule for classifying cells as 'absence' and reduced the likelihood of false absences (i.e. cells that are used by harbour porpoises but where they were not detected) within the datasets used for presence–absence modelling and intermodel comparisons.

# Model construction

# GLM

As the data were binary (presence/absence), a binomial regression was applied to the presence–absence data in the construction dataset. All linear and quadratic terms were included as potential predictors in the building of the model. Co-variance between each variable was assessed using pair plots and only variables with co-variance <0.8 were considered for the GLM. In order to select the model that explained the most variation using the fewest number of variables, a 'backwards stepwise' procedure was used (BRODGAR software, Highland Statistics Ltd). The statistic used to select the final linear model was the Akaike Information Criterion (AIC—Chambers & Hastie, 1997). For the final model, the probabilities of harbour porpoise occurrence were calculated for all grid cells in the study area by substituting the intercept value and the coefficients for each of the variable into the following equation:

Probability of occurrence  $= e^{g(x)}$ 

where g(x) is the regression equation from the GLM.

PCA

PCA-based modelling followed the method provided by Robertson et al. (2001). For presence cells within the model construction dataset, a mean and standard deviation was calculated for each EGV. The values for each EGV for each presence cell were then standardised by subtracting this mean and dividing by the standard deviation. Standard PCA analyses were conducted using Minitab statistical software (Minitab Ltd) on these standardised values using all possible combinations of three or more variables. For each PCA, the predicted likelihood of occurrence in each cell was calculated by first standardising the values for each EGV of every cell in the study area by dividing it by the species mean and subtracting the species standard deviation for that variable. Then a total eigen score was calculated for each cell for each principal component by weighting each EGV used to construct the model with its principal componentspecific eigen score. The total eigen score for each principal component was then divided by its eigen value. Finally, the resulting values for each principal component were squared and summed until the accumulated variation explained by the principal components was >90%. The Chi-squared distribution was then used to produce a likelihood of occurrence based on this value. The model-testing dataset was used to assess the predictive ability of all models using a receiver operating characteristic (ROC) plot.

ROC plots provide a threshold-independent method for assessing the predictive ability of ecological models and allow the predictive abilities of models constructed using different techniques to be directly compared (Fielding & Bell, 1997). For every possible threshold value for separating model predictions into predicted presence and predicted absence, sensitivity and specificity values were calculated. Sensitivity values indicate the proportion of cells where the model correctly predicted presence in relation to all presence cells in the testing dataset. Specificity values indicate the proportion of cells where the model correctly predicted absence in relation to all absence cells in the testing dataset. When one minus the specificity value (on the X-axis) and the sensitivity value (on the Y-axis) at every possible threshold value are plotted on a scatter plot, the area under curve (AUC) provides a measure of predictive ability. A random model (i.e. does not predict occurrence better than randomly selecting cells from the testing dataset) would be expected to have an AUC of 0.5, while a model that was in perfect agreement with the testing dataset would have an AUC of 1.0 (Fielding & Bell, 1997). The higher the AUC, the greater the predictive ability of the model under consideration and the further it differs from a random model.

ROC analysis was conducted using the Analyse-It 'Add-In' to Microsoft Excel produced by Analyse-It, LTD. The PCA model with the highest AUC was defined as the best PCA model of harbour porpoise occurrence within the study area.

#### ENFA

ENFA was conducted using Biomapper 3 software (Hirzel et al., 2000). An EGV grid for each variable was imported into the Biomapper programme along with a grid identifying which cells were classified as 'presence' within the model construction dataset. The EGV grids were standardised using a Box-Cox transformation. The broken stick rule was used to suggest how many niche factors should be used to construct the final habitat suitability map. This habitat suitability map classified cells on a scale of 0-100 based on its combination of values for the EGVs, weighting each one in a similar way to the PCA analysis. A cell with a habitat suitability value of zero would have the least suitable combination of values for all variables, while a cell with a value of 100 would have the most suitable combination. This habitat suitability map was then assessed using jackknife cross-validation and area-adjusted frequencies (Boyce et al., 2002).

# GARP

GARP was conducted using GARP Desk Top software (University of Kansas Centre for Research, Inc.). This software was set to automatically conduct 20 runs of every possible combination of the EGVs consisting of at least three EGVs and using four-fifths of the presence cells in the construction dataset. The final fifth was used for an assessment of each model to identify the best combination of EGVs based on the lowest mean omission error across the 20 runs. For the best model, the output maps of all 20 runs were imported into the GIS and summed. This resulted in a map that gave each cell a value between 0 and 20. A zero value meant that presence was not predicted in a cell in any of the 20 runs, while a value of 20 meant that presence was predicted in all 20 runs.

#### Intermodel comparison

ROC plots were calculated for each model using the testing dataset, allowing a direct comparison to be made between the predictive abilities of each model within the surveyed area (Fielding & Bell, 1997). In addition, the spatial predictions of the models were compared by using the models to predict species occurrence for all cells (including those not surveyed) within the study area. The study area was then divided into 12 sub-areas based on coarse oceano-graphic similarities and differences (Fig. 5). The average predicted occurrence for cells within these 12 sub-areas for each model was then compared using Pearsons correlation to assess whether each model was predicting relatively high and relatively low occurrences in the same spatial areas.

# Results

Harbour porpoises were recorded on 159 occasions in sea states of 3 or less, in 101 separate grid cells (Fig. 2). This surveyed area constitutes a substantial proportion of the Sea of Hebrides (around 10%), however all results presented below are only applied to the surveyed areas. Of these presence cells, 68 were partitioned into the model construction dataset and 33 into the testing dataset. Of the remaining cells in the study area, 965 were surveyed three times or



Fig. 2 Cells defined as surveyed during this study. Black cells where harbour porpoises were recorded; dark grey—Cells surveyed three or more times without harbour porpoises being recorded; Light grey—Cells surveyed only once or twice times without harbour porpoises being recorded

more. Of these, 679 were classified as absence data for model construction and 286 for model testing.

For GLM, all six variables considered were found to have a sufficiently low co-variance to be included in the model as separate terms. The model with the best 'fit' used three variables: (i) distance from coast (ii) standard deviation of slope and (iii) aspect northing. The AIC value for this model was 363.6. Both distance from coast (P = 0.004) and standard deviation of slope (P = 0.002) had highly significant effects, with porpoise presence decreasing with increasing distance from the coast (co-efficient: -0.0002537) and increasing with greater standard deviation of slope (co-efficient: 0.8957). Aspect northing had a positive effect on porpoise presence (co-efficient: 0.3642), but this was not significant (P > 0.05). However, including it increased the fit of the model as measured by the AIC. For the PCA, the model with the highest AUC used four EGVs: distance from the coast, water depth, and aspect easting and aspect northing. Four principal components were used to construct this model accounting for 100% of the variation in the presence data (Table 1). In the ENFA, four niche factors were selected accounting for 88.4% of the variation (Table 1). For GARP, the best model (the one with the lowest omission error for the internal testing

27

PCA	Variable	Component 1	Component 2	Component 3	Component 4
	Distance from coast	-0.645	0.153	-0.293	0.689
	Aspect easting	0.380	0.340	-0.856	-0.083
	Aspect northing	-0.139	0.916	0.322	-0.197
	Water depth	0.648	0.149	0.280	0.693
	Eigen Value	1.6089	1.0246	0.8808	0.4848
	Accumulated Variation Explained	0.402	0.659	0.879	1.000
ENFA	Variable	Niche Factor 1	Niche Factor 2	Niche Factor 3	Niche Factor 4
	Distance from coast	-0.599	0.694	-0.521	0.107
	Water depth	0.523	0.703	0.087	-0.279
	Aspect northing	0.107	-0.102	-0.357	-0.733
	Aspect easting	-0.016	-0.065	0.043	0.098
	Slope	0.157	0.035	0.395	-0.219
	Standard deviation slope	0.576	0.092	-0.661	0.563
	Eigen Value	6.805	2.943	1.116	1.046
	Accumulated Variation Explained	0.505	0.723	0.806	0.884

 Table 1
 Components and niche factors used for PCA and ENFA modelling of harbour porpoise distribution. The most important variable for each component/niche factor is highlighted in bold; the second most important is highlighted in italics

procedure) was produced using three EGVs, distance from coast, slope and standard deviation of slope.

The ROC plots revealed that all four models differ significantly from a random model (AUC = 0.5), indicating that all four approaches produced models that could predict harbour porpoise occurrence in relation to EGVs (Fig. 3). Of the four approaches, the GLM had the highest AUC (0.828) followed by the GARP model (0.773), PCA (0.746), and ENFA (0.745—Table 2).

While these comparisons showed that GLM had the greatest predictive ability, the only significant differences (at P = 0.05) were that the GLM had a significantly greater predictive ability than the PCA. However, multiple statistical comparisons were used to test the null hypothesis that there was no difference in the predictive ability between the modelling techniques. As a result, the Bonferroni correction (the usual threshold for significance divided by the number of statistical tests conducted) should probably be applied to reduce the chance of a type 1 error (but see Devlin et al., 2003; Garcia, 2004). This would shift the threshold P-value for a significant difference in predictive ability from 0.05 to 0.0083. At this corrected P-value, there were no significant differences in the predictive ability between any of the models (Table 3).



Fig. 3 Receiver operating characteristic (ROC) plots used to assess and compare the predictive abilities of the different modelling approaches (as recommended by Fielding & Bell, 1997). Black lines—ROC plots for individual models; Light grey line—Random model with area under curve (AUC) of 0.5. See Table 2 for AUC values of each model

In terms of the predicted spatial occurrence, all models predicted similar areas of high and low occurrence. For example, all four models predicted the highest likelihood of occurrence within shallow coastal areas, such as the Sound of Mull, and the

Table 2 Area under curve (AUC) for ROC plots of each model type, including the repeat of GARP for the testing dataset

	GLM	PCA	ENFA	GARP
Area under curve (AUC)	0.828 (0.762-0.895)	0.746 (0.676–0.816)	0.745 (0.667–0.823)	0.773 (0.701–0.846)

Numbers in brackets are 95% confidence intervals. All models differed significantly from a random model at P < 0.0001

 Table 3 Difference in predictive abilities of the models as measured by ROC plots

	Probability the	hat AUCs are differen	t due to chance		
Difference in	Model	GLM	PCA	ENFA	GARP
AUC	GLM	-	<i>P</i> = <b>0.0256</b>	P = 0.0810	P = 0.1472
	PCA	0.083	_	P = 0.9847	P = 0.4877
	ENFA	0.084	0.001	_	P = 0.4925
	GARP	0.055	0.028	0.029	-

Probabilities in bold indicate significant differences at P = 0.05. However, if the Bonferroni correction for multiple statistical tests of a null hypothesis is applied there is no significant difference for any pair-wise comparison at P = 0.0083

lowest likelihood of occurrence in deeper waters further from shore, such as the Sea of Hebrides (Fig. 4). This apparent similarity was confirmed by the correlation of the average predicted occurrence in the 12 sub-areas, as there was a strong and significant correlation between the spatial predictions of all four models (Table 4). Therefore, the relative spatial occurrence predicted by each model within the study area was very similar.

# Discussion

Ecological modelling offers the opportunity to investigate species distribution and to increase the understanding of the biology of individual species. However, while mathematically sound, modelling approaches can often be difficult to implement due to the imperfections and limitations of biological data. This can reduce the usefulness of a specific approach to model the distribution of a specific species. In particular, problems associated with detecting species can lead to errors in assigning locations into presence/absence categories (Hirzel et al., 2002; Williams, 2003) and violate assumptions of accurate absence data required for modelling approaches such as GLM (although it may be possible to use the amount of survey effort at a specific location as a weighting factor to at least partially control for the risk of 'false' absences within the dataset). This is likely to be an issue for many marine species that are inherently hard to detect due to problems associated with undertaking surveys for species presence in the marine environment. Therefore, modelling approaches that do not require accurate absence data would appear to offer a solution to these problems, provided that the survey coverage is adequate.

The results of this study suggest that presenceabsence approaches provide the best predictive ability, and therefore presumably the best understanding of species distribution, in relation to ecogeographic variables. As a result, when it is possible to implement them, such presence-absence approaches should be used. However, this study also suggests that when no sufficiently accurate and/or suitable absence data are available, presence-only approaches, such as ENFA, can potentially produce models of the distribution of marine species which perform significantly better than random models and that do not necessarily have a significantly poorer performance than presence-absence modelling approaches for the same surveyed area. In addition, the predicted spatial distributions of the presenceabsence model and the three presence-only models were similar, with all predicting the highest likelihoods of occurrence in similar areas. Therefore, while their application may be limited to specific data sets, these modelling approaches do appear to offer an opportunity to increase our understanding of the distribution of marine species.

The results of this study differ from previous studies, such as Brotons et al. (2004) that found a

57°00'



Fig. 4 Maps of predicted occurrence of harbour porpoises within the study area from each of the four modelling techniques. (A) GLM—Predicted probability of occurrence for individual cells ranging from 0 to a highest probability of 0.755; (B) PCA—Predicted likelihood of occurrence ranges from 0 for cells with habitat furthest from the centre of the calculated niche to 1.0 for cells with habitat closest to the

significant difference in the predictive ability of ENFA and GLM for forest-dwelling bird species. However, this significant difference was identified by comparing the combined outcomes of models for 30 different species rather than by directly comparing the models for individual species. In this study, only a single species was examined, so it may be that the differences between ENFA and GLM are only



7°00'

6°40'

6°20'

6°00'

0.8-1.0

0.6-0.8

0.4-0.6

0.2-0.4

0-0.2

centre; (C) ENFA—Habitat suitability index ranges from 0 for least suitable habitat to 100 for most suitable habitat based on niche preferences calculated during analysis; (D) GARP— Values range from 0 to 20 with 20 indicating that occurrence was predicted in all 20 runs and 0 that it was not predicted on any runs

significant when compared across a large number of species to take individual variation between species into account. Certainly, in over 20% of species modelled by Brotons et al. (2004) the AUCs of the GLM and ENFA models were similar (within 0.03) or the ENFA had the higher AUC, suggesting a degree of variation between species in the comparative predictive abilities of these approaches. The cause of

Scotland (see Fig. 5) GLM PCA ENFA GARP GLM 0.93 0.841 0.953 PCA 0.894 P < 0.0010.951 **ENFA** P < 0.001P = 0.001\_ 0.957 GARP P < 0.001P < 0.001P < 0.001

Table 4 Results of the correlation between mean predicted occurrences of cells within 12 sub-areas on the West Coast of

Statistical Test: Pearsons Correlation Coefficient (top right), *P* values (lower left)



Fig. 5 The 12 sub-areas used to compare the spatial predicted occurrence from the four modelling approaches. These sub-areas were assigned based on coarse oceanographic similarities. Shading shows water depth (white: 0-20 m, black: >300 m)

this variation is unclear, although the majority of these species (six out of seven) had low prevalence (were recorded in a relatively small number of grid cells in comparison to the total number surveyed) and high marginality (how the habitat occupied differed from the average habitat in the study area). As a result, Brotons et al. (2004) suggest that presenceonly approaches may be particularly useful for modelling the distribution of such species when absence data are not available. For this study, the ENFA found that the marginality of harbour porpoise was relatively high at 0.907 (see Hirzel et al., 2002 for how marginality is calculated), while the prevalence was relatively low (68 cells out of 679, or 0.10, within the model construction dataset).

However, there is another possible explanation for the difference between the results of this study and that of Brotons et al. (2004). Williams (2003) found that the predictive ability of some ecological modelling approaches varies with species detectability. While presence-absence approaches generally have higher predictive abilities for species with high detectability, they do not perform as well as presence-only approaches when detectability is low (Williams, 2003). Marine species, such as harbour porpoises, may have sufficiently low levels of detectability that the numbers of false absences within the model construction dataset are sufficient to violate the requirement of presence-absence approaches that all absence data are accurate. As a result, the predictive ability of any models generated using presence-absence approaches may be reduced in comparison to ones produced from datasets that do not contain such high numbers of false absences. If low detectability is the underlying reason for the difference between this study and previous comparative studies, this has important implications for modelling the distribution of other marine animals. While it is hard to detect in comparison to many terrestrial species, the harbour porpoise is relatively easy to detect when compared to many other marine species, including other cetaceans such as beaked whales (MacLeod, 2000; Barlow & Gisiner, 2006). However, further research is required to test if this is in fact the case.

Even though they may not perform as well as presence-absence approaches, all the presence-only models applied here provided models with significantly greater predictive ability than random models. In addition, the predicted spatial distribution of these models was very similar to that predicted from the Therefore. presence-absence model. these approaches could potentially allow presence data collected opportunistically, non-systematically or held in databases collated from surveys using incompatible methods to be used to investigate a species distribution. In particular, presence-only approaches may be useful when a species occurrence needs to be understood to allow potential environmental impacts to be assessed and conservation strategies developed in the short term rather than waiting for logistically complex, time-consuming and expensive systematic surveys to collect data of sufficient quality for presence-absence approaches to be applied. However, clearly due caution is necessary since models based on unrepresentative (biased) surveys could generate misleading results. This can be avoided, even if the quality of the survey is unknown, by adequate testing of the model's predictive ability, although assessing the accuracy of presence-only models can be problematic. The PCA approach requires absence data to test the predictive ability of the model and to identify the best combination of variables to use to model species distribution. This can be a sub-sample of the total available data and, if they can be identified, the most accurate absence data can be assigned to the testing dataset. For example, for harbour porpoises, it would be possible to use data collected under the best conditions, such as sea state zero, when they are most detectable and when absence data may be most accurate (Palka, 1996) to test the models, while still allowing presence data collected under poorer sightings conditions when detectability is lower to be used for model construction.

Neither ENFA nor GARP necessarily require any absence data and both rely on internal verification procedures to test whether a model has a high predictive ability (jack-knife cross validation) and as a result, there is always the possibility that models produced using these approaches, while internal verification suggests a good fit to the data, may not be biologically sensible due to unidentified biases in the presence data associated with the way they were collected. Both approaches assume that the presence data are representative of the species' niche in terms of the EGVs used in the model. If this is not the case, the model may under-predict species occurrence in some locations. While this is unlikely to be a problem with very large datasets, such as those used by Hirzel et al. (2002), this is more likely to be a problem with small datasets. Therefore, when applying these modelling approaches, particularly to the small datasets that likely be available for hard-to-detect marine species, it is important to consider this possibility and try to ensure that the presence data are likely to be representative of the species niche in terms of the EGVs to be used for modelling. If, for some reason, it is suspected that a certain EGV is under-represented in the presence data, it may be prudent to exclude that EGV from any presence-only modelling.

One possible solution to this limitation of using the results of presence-only models for conservation and/

or management purposes is to conduct surveys to specifically test the models' predictive ability. This could involve intensively sampling a representative, but small, portion of an area of interest in order to use the data to assess how any model performs. This combination of presence-only modelling followed by the collection of a data set to specifically test the models' performance from a more limited, but representative, area would potentially allow much greater use to be made of currently available data sets which contain only locational records, rather than presence-absence records, while still retaining a strong assessment criterion for the model's predictive ability. With specific reference to cetaceans, such surveys could be conducted from platforms of opportunity, such as passenger ferries or research vessels conducting other activities, as long as they pass through representative areas, and this would keep costs to a minimum.

However, there may be circumstances where these limitations of presence-only models are not as important. For example, presence-only models may be particularly useful for comparing the relative distributions of a number of species. If these data come from a single data set, it can be assumed that the survey coverage for each species was similar. Therefore, any detected differences in the distributions of species are likely to relate to real differences between them. This may be particularly useful when assessing whether marine protected areas for one species are likely to also protect areas that are important for other species.

Acknowledgements This project would not have been possible without the co-operation of the staff and crew of the Caledonian MacBrayne passenger ferries throughout summer 2003 and 2004. Fieldwork was conducted by both L. Mandleberg and C. Schweder as part of M.Res./M.Sc. degrees at Aberdeen University. S. Bannon and C.D. MacLeod initiated the ferry survey programme used to collect the data, while G. J. Pierce supervised these projects. L. Mandleberg was funded for this M.Sc. by a grant from the NERC. Funding for fieldwork in 2004 was provided by DSTL. G. J. Pierce was supported by the EU under the EnviEFH project (CEC FP6 Specific Support Action, 022466).

## References

Austin, G. E., C. J. Thomas, D. C. Houston & D. B. A. Thompson, 1996. Predicting the spatial distribution of buzzard *Buteo buteo* nesting areas using a Geographical Information System and Remote Sensing. Journal of Applied Ecology 33: 1541–1550.

- Barlow, J. & R. Gisiner, 2006. Mitigating, monitoring and assessing the effects of anthropogenic sound on beaked whales. Journal of Cetacean Research and Management 7: 239–250.
- Beerling, D. J., B. Huntley & J. P. Bailey, 1995. Climate and the distribution of *Fallopia japonica*: Use of an introduced species to test the predictive capacity of response surfaces. Journal of Vegetation Science 6: 269–282.
- Boyce, M. S., P. R. Vernier, S. E. Nielsen & F. K. A. Schmiegelow, 2002. Evaluating resource selection functions. Ecological Modelling 157: 281–300.
- Brotons, L., W. Thuiller, M. B. Araujo & A. H. Hirzel, 2004. Presence-absence versus presence-only modelling methods for predicting bird habitat suitability. Ecography 27: 437–448.
- Chambers, J. M. & T. J. Hastie, 1997. Statistical Models in Science. Chapman and Hall, New York.
- Devlin, B., K. Roeder & L. Wasserman, 2003. False discovery or missed discovery? Heredity 91: 537–538.
- Evans, P. G. H. & P. S. Hammond, 2004. Monitoring cetaceans in European waters. Mammal Review 34: 131–156.
- Fielding, A. H. & J. F. Bell, 1997. A review of methods for the assessment of prediction errors in conservation presence/ absence models. Environmental Conservation 24: 38–49.
- Garcia, L. V., 2004. Escaping the Bonferroni iron claw in ecological studies. Oikos 105: 657–663.
- Garcia-Charton, J. A. & A. Perez-Ruzafa, 2001. Spatial pattern and the habitat structure of a Mediterranean rocky reef fish local assemblage. Marine Biology 138: 917–934.
- Guisan, A. & U. Hofer, 2003. Predicting reptile distributions at the mesoscale: Relation to climate and topography. Journal of Biogeography 30: 1233–1243.
- Guisan, A. & N. E. Zimmerman, 2000. Predictive habitat distribution models in ecology. Ecological Modelling 135: 147–186.
- Hirzel, H. A., J. Hausser & N. Perrin, 2000. Biomapper 2.0. Laboratory for Conservation Biology, University of Lausanne.
- Hirzel, A. H., V. Helfer & F. Metral, 2001. Assessing habitatsuitability models with a virtual species. Ecological Modelling 145: 111–121.
- Hirzel, A. H., J. Hausser, D. Chessel & N. Perrin, 2002. Ecological Niche-factor analysis: How to compute habitat suitability maps without absence data? Ecology 83: 2027– 2036.
- Ingram, S. N., L. Walshe, D. Johnston & E. Rogan, 2007. Habitat partitioning and the influence of benthic topography and oceanography on the distribution of fin and minke whales in the Bay of Fundy, Canada. Journal of the Marine Biological Association of the United Kingdom 87: 149–156.
- Laake, J. L., J. Calambokidis, S. D. Osmek & D. J. Rugh, 1997. Probability of detecting harbor porpoise from aerial surveys: Estimating g(0). Journal of Wildlife Management 61: 63–75.
- Lerczak, J. A. & R. C. Hobbs, 1998. Calculating sightings distances from angular readings during shipboard, aerial and shore-based marine mammal surveys. Marine Mammal Science 14: 590–599.

- Lindenmayer, D. B., H. A. Nix, J. P. McMahon, M. F. Hutchinson & M. T. Tanton, 1991. The conservation of Leadbeater's possum, *Gymnobelideus leadbeateri* (McCoy): A case study of the use of bioclimatic modelling. Journal of Biogeography 8: 371–383.
- MacLeod, C. D., 2000. Review of the distribution of *Mesoplodon* species (order Cetacea, family Ziphiidae) in the North Atlantic. Mammal Review 30: 1–8.
- MacLeod, K., R. Fairbairns, A. Gill, B. Fairbairns, J. Gordon, C. Blair-Myers & E. C. M. Parsons, 2004. Seasonal distribution of minke whales *Balaenoptera acutorostrata* in relation to physiography and prey off the Isle of Mull, Scotland. Marine Ecology Progress Series 277: 263–274.
- MacLeod, C. D., C. R. Weir, C. Pierpoint & E. J. Harland, 2007. The habitat preferences of marine mammals west of Scotland (UK). Journal of the Marine Biological Association of the United Kingdom 87: 157–164.
- MacLeod, C. D. & A. F. Zuur, 2005. Habitat utilisation by Blainville's beaked whales off Great Abaco, Northern Bahamas, in relation to seabed topography. Marine Biology 147: 1–11.
- Ortega-Huerta, M. & A. T. Peterson, 2004. Modelling spatial patterns of biodiversity for conservation prioritisation in north-eastern Mexico. Diversity and Distributions 10: 39– 54.
- Palka, D., 1996. Effects of Beaufort Sea state on the sightability of harbour porpoises in the Gulf of Maine. Report of the International Whaling Commission 46: 575–582.
- Reutter, B. A., V. Helfer, A. H. Hirzel & P. Vogel, 2003. Modelling habitat-suitability on the base of museum collections: an example with three sympatric *Apodemus* species from the Alps. Journal of Biogeography 30: 581–590.
- Robertson, M. P., N. Caithness & M. H. Villet, 2001. A PCAbased modelling technique for predicting environmental suitability for organisms from presence records. Diversity and Distributions 7: 15–27.
- Robison, B. H., 2004. Deep pelagic biology. Journal of Experimental Marine Biology and Ecology 300: 253–272.
- Schulze, R. E. & R. P. Kunz, 1995. Potential shifts in optimum growth areas of selected commercial tree species and subtropical crops in southern Africa due to global warming. Journal of Biogeography 22: 679–688.
- Sparholt, H., E. Aro & J. Modin, 1991. The spatial distribution of cod *Gadus morhua* L. in the Baltic Sea. Dana 9: 45–56.
- Stockwell, D. & D. Peters, 1999. The GARP modelling system: problems and solutions to automated spatial prediction. International Journal of Geographical Information Science 13: 143–158.
- Teilmann, J., 2003. Influence of sea state on density estimates of harbour porpoises (*Phocoena phocoena*). Journal of Cetacean Research and Management 5: 85–92.
- Williams, A. K., 2003. The influence of probability of detection when modelling species occurrence using GIS and survey data. PhD thesis, Blacksburg University, Blacksburg, USA.
- Zaniewski, A. E., A. Lehman & J. M. Overton, 2002. Predicting species spatial distributions using presence-only data: a case study of the New Zealand ferns. Ecological Modelling 157: 261–280.

FISH HABITAT MAPPING

# Atmospheric forcing on chlorophyll concentration in the Mediterranean

Isidora Katara · Janine Illian · Graham J. Pierce · Beth Scott · Jianjun Wang

© Springer Science+Business Media B.V. 2008

Abstract Recent research suggests the coupling of climatic fluctuations and changes in biological indices that describe species richness, abundance and spatio-temporal distribution. In this study, large-scale modes of atmospheric variability over the northern hemisphere are associated with chlorophyll-a concentration in the Mediterranean. Sea level atmospheric pressure, air temperature, wind speed and precipitation are used to account for climatic and local weather effects, whereas sea surface temperature, sea surface height and salinity are employed to describe oceanic variation. Canonical Correlation Analysis was applied to relate chlorophyll concentration to the above-mentioned environmental variables, while correlation maps were also built to distinguish between localized

Guest editor: V. D. Valavanis Essential Fish Habitat Mapping in the Mediterranean

I. Katara (⊠) · G. J. Pierce · B. Scott · J. Wang School of Biological Sciences (Zoology), University of Aberdeen, Tillydrone Avenue, AB24 2TZ Aberdeen, UK e-mail: r02ik6@abdn.ac.uk

#### J. Illian

School of Mathematics and Statistics, University of St. Andrews, Observatory Buchanan Gardens, KY16 9LZ, St. Andrews, UK

#### G. J. Pierce

Centro Oceanográfico de Vigo, Instituto Español de Oceanográfía, P.O. Box 1552, 36200 Vigo, Spain and distant effects. Spectral analysis was used to identify common temporal cycles between chlorophyll concentration and each environmental variable. These cycles could be interpreted as mechanistic links between chlorophyll and large-scale atmospheric variability. Known teleconnection patterns such as the East Atlantic/Western Russian pattern, the North Atlantic Oscillation, the Polar/Eurasian pattern, the East Pacific/North Pacific, the East Atlantic jet and the Mediterranean Oscillation are found to be the most important modes of atmospheric variability related to chlorophyll-a concentration and distribution. The areas that are mostly affected are near the coasts and areas of upwelling and gyre formation. The results also suggest that this influence may arise either through local effects of teleconnection patterns on oceanic features or largescale changes superimposed onto the general circulation in the Mediterranean.

**Keywords** Teleconnection pattern · Canonical correlation analysis · Productivity

# Introduction

The distribution of phytoplankton biomass is defined by the availability of light and nutrients. These growth-limiting factors are in turn regulated by physical processes of ocean circulation, mixed layer dynamics, atmospheric dust deposition and the solar cycle. A common factor driving these processes is climate. A description of trends in primary production on a global scale is provided by Behrenfeld et al. (2006). In their study, satellite chlorophyll concentration records are linked to the Multivariate El Niño-Southern Oscillation (ENSO) index, a climatic index based on variables such as sea level pressure, surface wind, sea surface temperature, surface air temperature; and cloudiness fraction over the tropical Pacific, sea surface temperature (SST) and stratification intensity. The leading role of climate variability in determining primary productivity is illustrated.

On a less extensive scale, the most profound and best-studied large-scale, oceanic-atmospheric phenomenon, affecting phytoplankton concentration, is El Niño. The mechanisms proposed to link changes in the atmosphere to primary productivity during these events include the presence of upwelling favourable winds, the presence of macronutrients,  $CO_2$  flux (Chavez et al., 1999) and the turning off/recommencement of the iron-rich Equatorial Undercurrent (Murtugudde et al., 1999; Murakami et al., 2000; Wilson & Adamec, 2001).

Focusing on the northern hemisphere one of the prominent and therefore best-studied patterns of atmospheric variability is the North Atlantic Oscillation (NAO). NAO has been linked to changes in phytoplankton biomass (Lindhal et al., 1998; Reid et al., 1998; Barton et al., 2003; Pingree, 2005), species composition (Irigoien et al., 2000) and toxic algal blooms (Belgrano et al., 1999). However, in a review of the ecological effects of NAO, Ottersen et al. (2001) comment on the lack of evidence supporting the hypothesis on the causal mechanisms of the NAO-phytoplankton relationships, pointing out the need for mechanism-oriented studies.

Here, we focus on surface chlorophyll-a concentration in the Mediterranean, in an effort to disentangle its relationship with climatic patterns and describe possible mechanisms. The general hypothesis is that large scale atmospheric phenomena affect chlorophyll concentration, by inducing changes in local weather patterns and oceanic features. Therefore, the hypothesis is tested and the subsequent variable selection is based on known links between chlorophyll concentration and oceanic/local weather patterns and between oceanic/local weather patterns and large-scale atmospheric patterns. The Mediterranean appears to be the perfect candidate for the study of the effect of large-scale atmospheric patterns on the spatiotemporal distribution of chlorophyll. Despite its prevailing oligotrophy, the Mediterranean supports a large biomass of marine organisms, due to oceanographic features that locally maintain high levels of primary productivity. Therefore, it is expected that a large proportion of the spatial and temporal variability of primary production will depend on changes in oceanic conditions rather than on biological interactions. Trophic conditions vary, from oligotrophic to mesotrophic. The known oligotrophy in the area and the prominent seasonal cycle in the forcing concur in creating a dynamical environment where physical processes play a crucial role in conditioning the ecosystem functions. Oceanic circulation is in turn dependent to a great extent on climate.

A climatological synopsis of the trophic response to physical forcing in the Mediterranean Sea is provided by Crise et al. (1998, 1999). Permanent cyclonic features located at the north-western Mediterranean and the Levantine, unstable coastal fronts and gyres along the Algerian current and coastal effects such as upwelling and coastal boundary currents are considered to be the prevailing processes, importing nutrients into the euphotic zone.

A number of mechanisms for how weather and oceanic variability might affect productivity in the Mediterranean have been suggested in the literature. At the same time, atmospheric patterns of a global or hemispheric scale have been associated with weather patterns and oceanic variability. Combinations of meteorological, oceanographic and biological studies can evoke interesting hypotheses about how teleconnection patterns could drive phytoplankton abundance and distribution in the Mediterranean. For example, winds influence primary productivity in the Mediterranean especially through wind-induced upwelling (Bakun & Agostini, 2001), while wind patterns and Mediterranean cyclone tracks are associated with the East Atlantic Jet (Barnston & Livezey, 1987), the Asian monsoon region (Raicich et al., 2003; Rodwell & Hoskins, 1996) and the North Atlantic Oscillation. These findings lead to the hypothesis that wind could be the link between large-scale atmospheric patterns and primary production.

Precipitation is also a candidate for explaining the influence of atmospheric patterns on primary production. Freshwater input has an overriding effect on the dynamics of the Mediterranean ecosystem; it affects mesoscale circulation, deep-water formation, exchanges with the Atlantic, atmospheric deposition and the input of materials from land (Paerl, 1985; Paerl et al., 1990; Rohling & Bryden, 1992; Béthoux & Gentili, 1996; Roether et al., 1996; Martin & Milliman, 1997; Özsoy & Saydam, 2000; Arhonditsis et al., 2002), which in turn determine primary production. Duarte et al. (1999) commented on the importance of rainfall and the occurrence of storms as factors influencing the ecosystem and proposed the association of storms with high discharge of suspended material, which leads to a deterioration in conditions for phytoplankton growth, as a possible mechanism. Precipitation is also one of the beststudied variables in relation to teleconnection patterns. For the Mediterranean, precipitation has been linked to the East Atlantic pattern (Rodriguez-Puebla et al., 1998; Wibig, 1999), the East Atlantic/Western Russian (EA/WR) pattern, the East Atlantic (EA) jet (Dünkeloh & Jacobeit, 2003) and the NAO (Hurrell, 1995; Moulin et al., 1997).

Variables describing oceanic status, such as SST and Sea Surface Height (SSH), have also been associated with primary productivity. SST has been employed numerous times in efforts to identify areas of elevated primary production such as fronts, gyres and upwelling (e.g. Su & Sheng, 1999; Demarcq & Faure, 2000; Shaw & Vennell, 2000; Somayajulu et al., 2003; Valavanis et al., 2004; Sokolov et al., 2006), because of the cold water signature of these features. SSH can be seen either as an indication of the thermocline depth or can be used to identify tidally-induced and large-scale ocean circulation features (currents, eddies) (Fu & Cazenave, 2000). Furthermore, wave intensity is considered to be important for the development of blooms (Marchetti, 1992; Cacciamani et al., 1992; Cebrian et al., 1996). The link between planktonic variation and that of sea level and wave action does not result from a direct cause-effect relationship, but rather through the influence of these climatic factors on the proximal factors, such as nutrient inputs and water column stability, influencing planktonic organisms (Duarte et al., 1999). Both SST and SSH are highly dependent on atmospheric variability. The EA/WR pattern exerts its influence on wave height in the western Mediterranean in winter (Galati & Lionello, 2007). EA is also strongly and negatively correlated with wave height. Teleconnections with the Indian monsoon have been reported to affect the meridional circulation over the Mediterranean, winds and wave height (Lionello & Sanna, 2005). Raicich et al. (2003) found a negative correlation between sea-level anomalies at coastal stations in the eastern Mediterranean and the Indian monsoon index, due to changes in the wind structure.

The aim of this study is to reveal which large-scale atmospheric patterns over the northern hemisphere drive chlorophyll-a distribution in the Mediterranean. Furthermore, the role of regional weather/oceanic circulation patterns is described and possible mechanistic links between climatic indices and chlorophyll-a concentration are tested.

#### Materials and methods

Monthly data on sea level atmospheric pressure (SLP), air temperature, wind speed, precipitation, sea surface temperature (SST), sea surface height (SSH), salinity and chlorophyll-a concentration were analysed. Their temporal extent and sources are listed in Table 1. The spatial extent for all the datasets is the Mediterranean with the exception of sea level pressure data that extend over the northern hemisphere. All datasets were processed and organized in a GIS database, using Arc Info routines (ESRI, 1994), as monthly grid maps. The average for each map point for each month was computed and subtracted from the equivalent monthly maps, in order to remove seasonality from the data. The resulting anomalies were organized in a matrix, for each variable, with each column representing a month and each row a map point, and the matrices were introduced into MATLAB. All the analyses described below are applied to the anomaly datasets.

In a first exploratory approach, maps of correlations between chlorophyll and each of the explanatory variables were produced by calculating the Pearson correlation coefficient, and corresponding *P*-values, between the time series of the anomalies at each map point. Maps of statistically significant correlation coefficients were produced. A more sophisticated method, namely Canonical Correlation Analysis (CCA), was employed to analyse the joint variability, pair-wise, between chlorophyll concentration and the explanatory variables. The analysis was applied to Empirical Orthogonal Functions (EOF) space as

Parameter	Sensor/model	Units	Resolution	Source
Sea surface chlorophyll-a (CHLO)	SeaWiFS	mg/m <sup>3</sup>	9 km	www.oceancolor.gsfc.nasa.gov
Sea level pressure (SLP)	NCEP/NCAR Reanalysis	Millibars	2.5°	http://www.cdc.noaa.gov/ http://www.cdc/data.ncep.reanalysis
Air temperature (AIR)	NCEP/NCAR Reanalysis	°C	2.5°	http://www.cdc.noaa.gov/ cdc/data.ncep.reanalysis
Precipitation (PRE)	CPC Merged Analysis of Precipitation (CMAP)	mm/day	2.5°	http://www.iridl.ldeo.columbia.edu
Sea surface temperature (SST)	AVHRR	°C	1.1 km	http://www.eoweb.dlr.de:8080
Sea surface wind speed (WS)	QSCAT	m/sec and degree from N	0.25°	http://www.ssmi.com
Mean sea level anomaly (MSLA)	Merged Jason-1, Envisat, ERS-2, GFO, T/P	cm	0.25°	http://www.jason.oceanobs.com
Sea surface salinity	CARTON-GIESE SODA and CMA BCC GODAS models	psu	0.5°	http://www.iridl.ldeo.columbia.edu

 Table 1
 Datasets used, their units, resolution and sources

proposed by Barnett & Preisendorfer (1987). The Barnett Preisendorfer (BP-CCA) type CCA involves the application of an EOF analysis to the data prior to a classical CCA, and retaining only a few leading EOFs. The EOF analysis is in essence a type of filter that removes much of the small-scale noise. CCA is a long-standing multivariate statistical technique that finds linear combinations of two datasets of random variables, whose correlations are maximal (von Storch & Zwiers, 1999; Wikle, 2004). The aim of CCA is to identify and quantify the relationships between a pdimensional variable X and a q-dimensional random variable Y. The tables of each variable were produced by sampling the grid cells of each map so that each table will be organized in space (columns) and time (rows). We look for linear combinations aT X and bT Y of the original variables, having maximal correlation. Expressed in mathematical terms, CCA seeks vectors *a* and *b* such that:

$$(a,b) = \underset{a,b}{\operatorname{arg\,max}} |Corr(a^T X, b^T Y)|$$

The resulting univariate variables U = aT X and V = bT Y are then called canonical variates. Higher order canonical variates and correlations are defined as in the above equation, but now under the additional restriction that a canonical variate of order k, with  $1 < k \le \min(p; q)$ , should be uncorrelated with all canonical variates of lower order.

Therefore, CCA results for each pair of variables comprise a number of canonical variates that explain a large percentage of the coupled variability of the two datasets analysed. Each pair of canonical variates is a spatial (visualized in a map) and a temporal (time series) pattern for each variable that is maximally correlated. In this analysis, one of the matrices is always chlorophyll-a concentration and the other is one of the atmospheric/oceanic variables listed in Table 1. Therefore a time series of chlorophyll-a concentration index associated with an environmental parameter is produced from each CCA, and timeseries of chlorophyll-a concentration indices that explain a proportion of chlorophyll variability are produced from EOF analysis. Due to the different resolution of the data, the spatial patterns are more (finer resolution) or less (coarser resolution) detailed.

Cross correlation analysis (or Cross Correlation Functions—CCF) was applied to northern hemisphere teleconnection indices sourced from the NOAA/Climate Prediction Centre and the leading chlorophyll-a time series derived from the EOF analysis, in order to verify the CCA results. CCF is in essence the estimation of correlation coefficients between two time series at different time lags. The teleconnection indices were also correlated to chlorophyll-index time series derived through CCA. This analysis provided an insight into the relationship between atmospheric patterns and coupled modes of




**Fig. 2** Canonical pairs for wind speed and chlorophyll in the Mediterranean



variability for chlorophyll and led to the suggestion of various mechanisms that could potentially explain how large-scale atmospheric patterns influence chlorophyll distribution.

Climatic variations may take place at various spatial and temporal scales. Sometimes, the variations are due to oscillations which recur in periodic fashions. Cyclical patterns in the atmosphere might lead to cyclical variations in the ocean and vice versa. The analysis of such dependencies between two time series is the role of bivariate spectral analysis. Cross Spectral Analysis (CSA) was applied to detect common cycles between the chlorophyll-index time series derived from CCA and the northern hemisphere teleconnection indices. The purpose of CSA is to find out how the variability of the two time series is interrelated in the spectral domain; to determine the time scale at which the variability is related, as well as the characteristics of this co-variation. Thus, from cross spectral analysis, it is possible to obtain not only the coherence, which is the measure of correlation between two processes at each frequency, but also the phase spectrum, which measures the phase difference at each frequency.

# Results

# Correlation maps

Wind speed and precipitation present a positive correlation with chlorophyll-a while air temperature

**Fig. 3** Canonical pairs for air temperature and chlorophyll in the Mediterranean



presents a negative one. The relationship with SST is straightforward as well, with all statistically significant correlations being negative. However, the relationships become more complicated as we move to variables, such as SSH and salinity, that describe complex oceanic phenomena and features.

### Canonical correlation analysis

# Chlorophyll-a and sea level pressure over the northern hemisphere

For the first pair of canonical variates for SLP and chlorophyll, the SLP pattern for the northern hemisphere consists of a combination of the East Atlantic pattern (EA) and remnants of the East Atlantic/ Western Russian pattern (EA/WR), both in their positive phases (Fig. 1A). The pattern dominating the Pacific sector probably represents the negative phase of the East Pacific/North Pacific pattern. The corresponding pattern for chlorophyll-a concentration in the Mediterranean reveals higher than average values for the western and central parts of the Mediterranean and lower for the eastern part. This pattern accounts for 12% of the variability of chlorophyll concentration in the Mediterranean. The second CCA SLP pattern for the northern hemisphere explains 9% of the variability of chlorophyll-a concentration and the major feature identified corresponds to the East Atlantic Jet, the third primary mode of low frequency variability found over





the North Atlantic, in its negative phase (Fig. 1B). This pattern seems to positively influence chlorophyll in coastal areas of the Mediterranean; equivalently strong negative effects are observed near the strait of Gibraltar, the Balearic Sea and the Levantine. The third CCA spatial component for chlorophyll concentration (7.3% of variation explained) reveals localized correlations. The corresponding SLP CCA component can be interpreted as remnants of the North Atlantic Oscillation (NAO; positive phase) and the Mediterranean Oscillation (MO), which is related to the larger pattern of the NAO. Remnants of what could be interpreted as the Polar/Eurasian (POL) and the East Pacific/North Pacific (EP/NP) patterns can also be identified (Fig. 1C).

Chlorophyll-a and wind speed

A see-saw between the western part of the basin (positive values) and the central-eastern part (negative values) shapes the first CCA component for wind speed. The corresponding pattern for chlorophyll shows enhanced concentrations in most areas. The second pair of canonical variates shows a 'wave' form, i.e. an alternation of positive and negative centres with an east-west direction, for wind speed, inducing higher than average chlorophyll concentrations in the west and lower in the east. Two areas of opposite signs are identified for the third CCA mode for wind speed, with the negative values over the western part and the positive ones over the eastern **Fig. 5** Canonical pairs for sea surface temperature and chlorophyll in the Mediterranean



part of the basin. This pattern seems to have a negative effect on chlorophyll concentrations for the north-western Mediterranean and positive for the south-central and eastern parts of the basin (Fig. 2).

# Chlorophyll-a and air temperature

For the first pair of canonical variables a 'wave' form dominates the air temperature spatial pattern, while the corresponding chlorophyll pattern shows mostly negative anomaly values for the central and eastern Mediterranean (Fig. 3). The second CCA component for air temperature is a dipole between west (negative) and east (positive) that induces local influences on chlorophyll-a concentration. A dipole between north (positive values) and southwest (negative values) constitutes the air temperature pattern of the third pair of canonical variables and is associated with large areas of negative values for chlorophyll.

### Chlorophyll-a and precipitation

The CCA results for chlorophyll and precipitation show higher than average values of chlorophyll in the western Mediterranean and lower than average values in the eastern part for the first pair of variates. The corresponding precipitation pattern reveals two major poles, a negative one over the central-north Mediterranean and a positive one over the eastern-north Mediterranean (Fig. 4). The second CCA spatial





pattern reveals a positive precipitation pole over north-west Mediterranean and a negative one for the south-western part. This pattern is correlated with lower than average chlorophyll concentration in northern regions and positive anomaly values in southern regions. The third spatial pattern for precipitation has a 'wave' form with an east-west direction and affects chlorophyll mostly in the western part of the Mediterranean.

# Chlorophyll-a and sea surface temperature

Higher than average temperatures for the central part of the Mediterranean and lower values for the eastern comprise the first CCA mode for SST (Fig. 5). This pattern seems to affect mostly the western part of the basin as well as some small areas in the Levantine with higher than average chlorophyll concentrations. Low chlorophyll values are observed in the western part of the Alboran Sea, around the Balearic Islands and in the Sea of Sicily. In the second CCA component, SST represents mesoscale patterns. Negative chlorophyll concentration values are observed in the Adriatic, the northern Aegean and the western Mediterranean. A dipole between the northwest (positive) and southeast parts of the Mediterranean basin characterizes the third spatial pattern for SST and has diverse effects on chlorophyll in different areas. **Fig. 7** Canonical pairs for sea surface height and chlorophyll in the Mediterranean



#### Chlorophyll-a and salinity

A positive anomaly value centre, stretching from the Balearic Islands to the Libyan sea, and a negative gradient of salinity stemming from the Atlantic are the dominant patterns in the first salinity CCA pattern (Fig. 6). A similar salinity pattern, but with opposite signs, appears in the second CCA component. The third CCA component shows a similar pattern of salinity to the second, with the negative centre displaced to the north. The effect on chlorophyll is local.

# Chlorophyll-a and sea surface height

Higher than average SSH values are observed, in the first SSH CCA component, for the western Mediterranean and in particular for the path taken by the northern current (Fig. 7). However, negative values are also observed for the central-south and eastern Mediterranean with the exceptions of two cyclonic features offshore Libya and another mesoscale feature located near the eastern Levantine coasts, probably the Shikmona gyre. Negative chlorophyll anomalies are located in the western part of the basin and positive values in the central and eastern parts. For the second pair of canonical variables, higher than the average SSH values are observed mainly along the south coasts of the basin and at the western edge of Crete. The western sub-basin and the eastern part of the mid-Mediterranean jet present lower than average SSH values. Positive values in the Alboran Sea and for locations characterized by cyclonic circulation in the Levantine, and negative anomalies for areas of anticyclonic circulation in the Levantine comprise the second spatial pattern for chlorophyll. The pattern of the third pair of variates for chlorophyll shows higher than average values for the central Mediterranean and the coasts of the Greek mainland. The opposite sign is observed for the western part of the basin. The corresponding SSH pattern reveals mesoscale eddies.

### Time series analysis

#### Cross correlation functions

Statistically significant correlations between chlorophyll indices, derived from the CCAs, and the teleconnection indices for the northern hemisphere are estimated with CCF. SST-related chlorophyll indices appear to have the highest number of significant correlations followed by SSH-related chlorophyll indices. The most frequent time lags at which the correlations are statistically significant are 0 months for EA, PNA and POL, 2 for SCA and WP and 8 for NAO and EA/WR. Only PNA presents time lags of more than 2 years and only SCA does not present time lags of more than one year. Among the chlorophyll indices, precipitation-related ones appear mostly in correlations at lag 4, air temperature- and salinity-related at lag 2, and SSH-, SST- and WSrelated at 0 lag.

The EA pattern is correlated with WS- and SSTrelated chlorophyll indices, at different time lags, 0 and 20 months, respectively. The WP and POL patterns are associated with SST-related chlorophyll indices at lag 2, while correlations with the NAO and PNA are estimated for almost all the CCA-derived chlorophyll indices at varying time lags, the most frequent ones being from 0 to 8 months.

# Spectral analysis

The spectral analysis showed statistically significant correlations between chlorophyll-a EOF patterns and the EA, EA/WR, NAO and POL teleconnection indices as well as PNA and WP, from the Pacific sector. The periods of the common cycles extend from 2 months to more than a decade and their time intervals from 0 to 13 years. As for the correlation with the CCA-derived chlorophyll indices, the EA

pattern has common cycles with WS-related chlorophyll, the EA/WR with precipitation-related chlorophyll, and the NAO with salinity- and SSHrelated chlorophyll indices. PNA, SCA and WP also correlate with SSH-related chlorophyll indices. Tables 2 and 3 present the statistically significant correlations, the frequency/period of the common cycles and the phase/time interval between them.

# Discussion

The East Atlantic pattern, the East Atlantic/Western Russian pattern, the North Atlantic Oscillation and the East Atlantic Jet and the Mediterranean oscillation, appear to be the most important climatic patterns of the northern hemisphere driving chlorophyll-a variability in the Mediterranean.

The first pair of CCA patterns between chlorophyll and sea level pressure over the northern hemisphere reveals a dipole for chlorophyll, which could be interpreted either as an opposite/delayed effect of an external forcing on the western and eastern sub-basins or as an interaction between the two sub-basins. It could thus be hypothesized that chlorophyll-a distribution is linked to a phenomenon that 'moves' from west to east (or vice versa). Storm/ precipitation tracks that move from the Atlantic to eastern Mediterranean are such a phenomenon and, what is more, they are known to be regulated by the East Atlantic and the EA/WR patterns, the two dominant patterns seen in the SLP map of this first CCA pair of variates. Both patterns have been related to the transport of air masses from the Atlantic to the Eastern Mediterranean with a positive effect on precipitation of the EA in the western Mediterranean and a negative effect of the EA/WR on the eastern part of the basin. This hypothesis is further supported by the results of spectral analysis that suggest wind speed as the link between EA and chlorophyll and precipitation as the link between EA/WR and chlorophyll. A see-saw between east and west and what was described as a 'wave' in the results, namely alternation of positive and negative centres, also appear in wind speed, air temperature and precipitation CCA patterns, which further supports the abovementioned hypothesis.

The third CCA pattern of chlorophyll associated with SLP is related to the North Atlantic Oscillation.

**Table 2** Spectral analysis results between teleconnectionindices (1st column) and chlorophyll indices derived fromCCA for chlorophyll and wind speed (WS), precipitation(PRE), surface air temperature (AIR), sea surface temperature

(SST), surface salinity (SAL) and sea surface height (SSH) (2nd column). Numbers in parenthesis indicate the rank of the CCA pattern

Teleconnection index	CCA of CHLO with:	Coherency	Frequency	Phase	Period	Time interval
EA	WS(1)	0.81	0.39	1.20	2.56	0.49
EA	WS(3)	0.80	0.05	0.00	20.00	0.00
EA/WR	PRE(1)	0.80	0.00	0.00	10,000	0.00
EA/WR	PRE(3)	0.82	0.50	3.00	2.00	0.95
EP/NP	AIR(3)	0.83	0.40	0.80	2.50	0.32
EP/NP	SST(1)	0.80	0.00	3.00	0.00	0.00
NAO	SAL(2)	0.90	0.27	0.03	3.70	0.02
NAO	SSH(1)	0.88	0.02	1.00	50	7.96
PNA	SSH(1)	0.90	0.45	2.50	2.22	0.88
PNA	SSH(2)	0.90	0.18	1.50	5.56	1.33
POL	AIR(2)	0.83	0.48	2.70	2.08	0.90
POL	SSH(3)	0.85	0.00	3.00	10,000	4774.65
POL	SST(2)	0.82	0.05	0.20	20	0.64
POL	WS(2)	0.80	0.40	2.80	2.50	1.11
SCA	SSH(1)	0.80	0.01	0.00	100	0.00
WP	SSH(1)	0.80	0.13	2.00	7.69	2.45

Table 3 Spectral analysis						
results between						
teleconnection indices (1st						
column) and chlorophyll						
indices derived from EOF						
analysis (2nd column)						

Teleconnection index	Chlorophyll EOF index	Coherency	Frequency	Phase	Period	Time interval
EA	7	0.79	0.30	0.00	3.33	0.00
EA/WR	9	0.78	0.20	2.00	5.00	1.59
NAO	3	0.79	0.35	3.00	2.86	1.36
NAO	8	0.79	0.16	1.50	6.25	1.49
PNA	10	0.78	0.20	0.00	5.00	0.00
PNA	3	0.81	0.00	1.00	1,000	159.15
POL	10	0.80	0.23	3.00	4.35	2.08
POL	6	0.77	0.49	3.00	2.04	0.97
POL	8	0.80	0.36	0.00	2.78	0.00
POL	9	0.80	0.38	2.80	2.63	1.17
SCA	6	0.80	0.36	2.80	2.78	1.24
WP	10	0.77	0.05	0.20	20.00	0.64

NAO seems to be affecting areas of wind-induced upwelling and gyre formation. Chlorophyll patterns suggest that upwelling, probably induced by the westerlies along the northern coasts of the Mediterranean, are favoured during the positive NAO phase, leading to higher chlorophyll values. Other studies have shown that the EA/WR pattern often comes hand in hand with the NAO in regulating atmospheric phenomena and oceanic features in the Mediterranean (Rodríguez-Puebla et al., 2001). Below-normal precipitation over most of the Mediterranean region, with lowest values along the western coasts of the peninsulas and highest in the south-eastern part of the basin, correlates with NAO/ AO and EA/WR and the northward shifts of storm tracks from the Mediterranean towards western and northern Europe that produce the dryness over the Mediterranean (Xoplaki et al., 2004). It is therefore probable that abrupt changes in wind and precipitation intensity are mechanisms through which largescale atmospheric patterns disturb the mean status of chlorophyll concentration in the basin. The spectral analysis results also show EA and EA/WR patterns influencing chlorophyll through wind speed and precipitation at small time lags.

The second chlorophyll CCA pattern associated with SLP is a north-south dipole. This can be ascribed to changes in the inflow of Atlantic water through the strait of Gibraltar, which affect the southern part of the basin, or to the presence of strong westerlies that could affect both the currents carrying the Atlantic water and the upwelling forming along the northern coasts. The East Atlantic jet is the teleconnection pattern correlated with chlorophyll in this case. Its positive phase is associated with strong westerlies over Europe, and the negative phase with long-lived blocking anticyclones in the vicinity of Greenland and Great Britain. It is related to Mediterranean cyclone tracks in summer, which are mostly arranged from the western basin towards the Black Sea (Alpert et al., 1990; Trigo et al., 1999) and has been linked to summer precipitation in the northern Mediterranean (Dunkeloh & Jacobeit, 2003). It can therefore be concluded that the East Atlantic jet affects chlorophyll concentration through changes in wind and wind-induced circulation patterns.

Considering weather patterns, in general the CCA results reveal a combination of local and large-scale events influencing chlorophyll-a concentration. Local effects tend to produce positive correlations and can be attributed to the supply of nutrients through rainfall. On the other hand, negative correlations occur due to large scale weather and climatic patterns. The results also suggest that strong winds and rainfall might have a direct negative effect to phytoplankton growth, due to causing turbulence in the water column, but they favour chlorophyll concentration in the long run by importing nutrients into the euphotic zone.

The areas that are most affected by the atmospheric and oceanic regime are either coastal or areas of known upwellings such as the northwest coasts, the Alboran Sea, regions characterized by the influences of the inflow of water from the Atlantic and the southern coasts of Turkey, where the system is dominated by changes in the mid-Mediterranean jet and the Levantine Intermediate Water. The north Aegean, one of the most productive parts of the Mediterranean, also appears to be affected by the atmosphere mainly due to changes in the inflow of water from the Black Sea and from rivers.

The time series analysis on the other hand stresses the importance of sea surface temperature and sea surface height, as links between atmospheric patterns and chlorophyll. When SST is the intermediate link between chlorophyll and the atmosphere, the significant time lags are more than a year which could imply changes in the circulation regime. The inflow of water from the Atlantic, currents such as the Algerian current and the Asia Minor Current, and gyres located mainly in the Levantine, appear in the leading CCA patterns for the pairs Sea Surface Temperature—Chlorophyll and Sea Surface Height—Chlorophyll.

Patterns from the Pacific sector also produce significant correlations with chlorophyll, probably because they are related to other atmospheric patterns over Europe and the Atlantic or to ENSO-monsoon teleconnections that affect the eastern Mediterranean.

These analyses provide a reasonable means to generate hypotheses linking phytoplankton and climate-dependent physical factors. Nevertheless, conclusions based on relatively short time series are speculative and must be interpreted cautiously (Barton et al., 2003).

When CCA is applied on EOF space the amount of variability explained by the correlation between the variables depends on the amount of variability explained by the EOF. The small portion of chlorophyll variability captured by the EOF analysis, along with the patchiness of the spatial patterns derived for chlorophyll, depicts the unique characteristics of each area and the importance of local features. However, the results of this study suggest that some of the major features affecting chlorophyll concentration and distribution in the Mediterranean are driven by large-scale atmospheric patterns, and provide a basis to speculate on possible mechanisms. The role of precipitation and wind as links between large-scale atmospheric phenomena and mesoscale changes in chlorophyll concentration is pointed out, whereas oceanic variables such as SST and SSH seem to be influencing chlorophyll in different ways and according to each area's specific features. At the same time the complex nature of this system is inferred; more than one parameter affects chlorophyll simultaneously with a very diverse pattern as a result. In addition, relationships between biological indices and environmental factors tend to be non-linear, an aspect that was not considered in this analysis but is a subject for future studies. Lastly, much information can be derived from the seasonal component of the datasets. Seasonality is of utmost importance for the Mediterranean and incorporating it in the analysis would result in higher percentages of the variability being explained. However, the aim of this study was not to describe seasonal fluctuations but to see how the regime of chlorophyll is disturbed due to atmospheric forcing.

A number of known teleconnection patterns have been suggested to play some role in changes of the spatiotemporal patterns of chlorophyll-a in the Mediterranean. The prominent mechanism pertains to large-scale patterns causing air mass movements from the Atlantic to the Eastern Mediterranean that in turn affect oceanic features related to higher primary production.

Future work will focus on different spatial scales, in order to acquire information on how local characteristics interact with large-scale features, and on non-linear relationships between chlorophyll and atmospheric patterns. The complexity of the data suggests that different mechanisms of atmospheric forcing act on different areas at different temporal and spatial scales.

Acknowledgment I. Katara was funded by the "ECOSUMMER" Marie Curie training site (MEST-CT-2005-020501). G.J. Pierce was supported by the ANIMATE project (MEXC-CT-2006-042337).

#### References

- Alpert, P., B. U. Neeman & Y. Shay-El, 1990. Intermonthly variability of cyclone tracks in the Mediterranean. Journal of Climate 3: 1474–1478.
- Arhonditsis, G., G. Tsirtsis & M. Karydis, 2002. The effects of episodic rainfall events to the dynamics of coastal marine ecosystems: applications to a semi-enclosed gulf in the Mediterranean Sea. Journal of Marine Systems 35: 183– 205.
- Bakun, A. & V. N. Agostini, 2001. Seasonal patterns of winddriven upwelling/downwelling in the Mediterranean Sea. Scientia Marina 65: 243–257.
- Barnett, T. P. & R. Preisendorfer, 1987. Origins and levels of monthly and seasonal forecast skill for United States surface air temperatures determined by canonical correlation analysis. Monthly Weather Review 115: 1825– 1850.

- Barnston, G. & R. E. Livezey, 1987. Classification, seasonality and low-frequency atmospheric circulation patterns. Monthly Weather Review 115: 1083–1126.
- Barton, A. D., C. H. Greene, B. C. Monger & A. J. Pershing, 2003. The continuous plankton recorder survey and the North Atlantic oscillation: interannual- to multidecadalscale patterns of phytoplankton variability in the North Atlantic Ocean. Progress in Oceanography 58: 337–358.
- Behrenfeld, M. J., R. T. O'Malley, D. A. Siegel, C. R. McClain, J. L. Sarmiento, G. C. Feldman, A. J. Milligan, P. G. Falkowski, R. M. Letelier & E. S. Boss, 2006. Climatedriven trends in contemporary ocean productivity. Nature 444: 752–755.
- Belgrano, A., O. Lindahl & B. Hernroth, 1999. North Atlantic oscillation primary productivity and toxic phytoplankton in the Gullmar Fjord, Sweden (1985–1996). Proceedings of the Royal Society of London Series B 266: 425–430.
- Béthoux, J. P. & B. Gentili, 1996. The Mediterranean Sea, coastland deep-sea signatures of climatic and environmental changes. Journal of Marine Systems 7: 383–394.
- Cacciamani, C., S. Nanni, F. Nucciotti & T. Paccagnella, 1992. Analysis of meteorological parameters relating to Adriatic eutrophication. In Vollenweider, R. A., R. Marchetti & R. Viviani (eds), Marine coastal eutrophication. Regione Emilia Romagna, Elsevier: 159–170.
- Cebrian, J., C. M. Duarte, N. Marba, S. Enriquez, M. Gallegos & B. Olesen, 1996. Herbivory on *Posidonia oceanica* (L.) Delile: magnitude and variability in the Spanish Mediterranean. Marine Ecology Progress Series 130: 147–155.
- Chavez, F. P., P. G. Strutton, G. E. Friederich, R. A. Feely, G. C. Feldman, D. G. Foley & M. J. McPhaden, 1999. Biological and chemical response of the Equatorial Pacific Ocean to the 1997–98 El Niño. Science 286: 2126–2131.
- Crise, A., G. Crispi & E. Mauri, 1998. A seasonal threedimensional study of the nitrogen cycle in the Mediterranean Sea Part I. Model implementation and numerical results. Journal of Marine Systems 18: 287–312.
- Crise, A., J. I. Allen, J. Baretta, G. Crispi, R. Mosetti & C. Solidoro, 1999. The Mediterranean pelagic ecosystem response to physical forcing. Progress in Oceanography 44: 219–243.
- Demarcq, H. & V. Faure, 2000. Coastal upwelling and associated retention indices derived from satellite SST. Application to *Octopus vulgaris* recruitment. Oceanologica Acta 23: 391–408.
- Duarte, C. M., S. Agusti, H. Kennedy & D. Vaque, 1999. The Mediterranean climate as a template for Mediterranean marine ecosystems: the example of the northeast Spanish littoral. Progress in Oceanography 44: 245–270.
- Dünkeloh, A. & J. Jacobeit, 2003. Circulation dynamics of Mediterranean precipitation variability 1948–98. International Journal of Climatology 23: 1843–1866.
- ESRI, 1994. ARC Macro Language. Environmental Systems Research Institute Inc, Redlands, CA, USA: 1/3–5/37.
- Fu, L. L. & A. Cazenave, 2000. Satellite Altimetry and Earth Sciences: A Handbook of Techniques and Applications, Academic Press: 463.
- Galati, M. B. & P. Lionello, 2007. Influence of teleconnection patterns on the significant wave height distribution in the Mediterranean Sea. Second ESF MedCLIVAR workshop, La Londe les Maures, Toulon, France, 8–10 October 2007.

- Hurrell, J. W., 1995. Decadal trends in the North Atlantic Oscillation: regional temperatures and precipitation. Science 269: 676–679.
- Irigoien, X., R. P. Harris, R. N. Head & D. Harbour, 2000. North Atlantic Oscillation and spring bloom phytoplankton composition in the English Channel. Journal of Plankton Research 22: 2367–2371.
- Lionello, P. & A. Sanna, 2005. Mediterranean wave climate variability and its links with NAO and Indian Monsoon. Climate Dynamics 25: 611–623.
- Marchetti, R., 1992. The problem of the Emilia Romagna coastal waters: facts and interpretation. In Vollenweider, R. A., R. Marchetti & R. Viviani (eds), Marine coastal eutrophication. Elsevier, Regione Emilia Romagna: 21–33.
- Martin, J. M. & J. D. Milliman, 1997. EROS 2000 (European River Ocean System) the west Mediterranean: an introduction. Deep-Sea Research II 44: 521–529.
- Moulin, C., C. E. Lambert, F. Dulac & U. Dayan, 1997. Control of atmospheric export of dust from North Africa by the North Atlantic oscillation. Nature 387: 691–693.
- Murakami, H., J. Ishizaka & H. Kawamura, 2000. ADEOS observations of chlorophyll a concentration, sea surface temperature, and wind stress change in the equatorial Pacific during the 1997 El Niño onset. Journal of Geophysical Research 105: 19551–19559.
- Murtugudde, R. G., S. R. Signorini, J. R. Christian, A. J. Busalacchi, C. R. McClain & J. Picaut, 1999. Ocean color variability of the tropical Indo-Pacific basin observed by SeaWiFS during 1997–1998. Journal of Geophysical Research 104: 18351–18366.
- Ottersen, G., B. Planque, A. Belgrano, E. Post, P. C. Reid & N. C. Stenseth, 2001. Ecological effects of the North Atlantic Oscillation. Oceanologia 128: 1–14.
- Özsoy, T. & A. C. Saydam, 2000. Acidic and Alkaline precipitation in the Cilician Basin, northeastern Mediterranean Sea. Science of the Total Environment 253: 93–109.
- Paerl, H. W., 1985. Enhancement of marine primary production by nitrogen-enriched acid rain. Nature 315: 747–749.
- Paerl, H. W., J. Rudek & M. A. Mallin, 1990. Stimulation of phytoplankton production in coastal waters by natural rainfall inputs: nutritional and trophic implications. Marine Biology 107: 247–254.
- Pingree, R., 2005. North Atlantic and North Sea Climate Change: curl up, shut down, NAO and ocean colour. Journal of Marine Biological Association of the United Kingdom 85: 1301–1315.
- Rodriguez-Puebla, C., A. H. Enchinas, S. Nieto & J. Garmendia, 1998. Spatial and temporal patterns of annual precipitation variability over the Iberian Peninsula. International Journal of Climatology 18: 299–316.
- Rodríguez-Puebla, C., A. H. Enchinas & J. y Sáenz, 2001. Winter precipitation over the Iberian Peninsula and its relationships to circulation indices. Hydrology and Earth System Sciences 5: 233–244.

- Raicich, F., N. Pinardi & A. Navarra, 2003. Teleconnections between Indian Monsoon and Sahel rainfall and the Mediterranean International. Journal of Climatology 23: 173–186.
- Reid, P. C., B. Planque & M. Edwards, 1998. Is observed variability in the long-term results of the Continuous Plankton Recorder survey a response to climate change? Fisheries Oceanography 7: 282–288.
- Rodwell, M. J. & B. J. Hoskins, 1996. Monsoons and the dynamic of deserts. Quarterly Journal of the Royal Meteorological Society 122: 1385–1404.
- Roether, W., B. Manca & B. Klein, 1996. Recent changes in eastern Mediterranean deep waters. Science 271: 333– 335.
- Rohling, E. J. & H. L. Bryden, 1992. Man-induced salinity and temperature increases in Western Mediterranean deep water. Journal of Geophysical Research 97: 191–198.
- Shaw, A. G. P. & R. Vennell, 2000. A front-following algorithm for AVHRR SST imagery. Remote Sensing of Environment 72: 317–327.
- Sokolov, S., S. R. Rintoul & B. Wienecke, 2006. Tracking the Polar Front south of New Zealand using penguin dive data. Deep-Sea Research I 53: 591–607.
- Somayajulu, Y. K., V. S. N. Murty & Y. V. B. Sarma, 2003. Seasonal and inter-annual variability of surface circulation in the Bay of Bengal from TOPEX/Poseidon altimetry. Deep Sea Research Part II: Topical Studies in Oceanography 50: 867–880.
- Su, Y. & Y. Sheng, 1999. Visualizing upwelling at Monterey Bay in an integrated environment of GIS and scientific visualisation. Marine Geodesy 22: 93–104.
- Trigo, I. G., T. D. Davies & G. R. Bigg, 1999. Objective climatology of cyclones in the Mediterranean Region. Journal of Climate 12: 1685–1696.
- Valavanis, V. D., I. Katara & A. Palialexis, 2004. Critical regions: A GIS-based modelling approach for the mapping of marine productivity hotspots. Aquatic Science 36: 234–243.
- Von Storch, H. & F. W. Zwiers, 1999. Statistical Analysis in Climate Research. Cambridge University Press, Cambridge: 484.
- Wibig, J., 1999. Precipitation in Europe in relation to circulation patterns at the 500 hPa level. International Journal of Climatolology 19: 253–269.
- Wikle, C. K., 2004. Spatiotemporal methods in climatology. UNESCO Encyclopedia of Life Support Systems (EOLSS), Eolss Publishers, Oxford, UK.
- Wilson, C. & D. Adamec, 2001. Correlations between surface chlorophyll and sea surface height in the tropical Pacific during the 1997–1999 El Nino-Southern Oscillation event. Journal of Geophysical Research 106: 31175–31188.
- Xoplaki, E., J. F. Gonzalez-Rouco, J. Luterbacher & H. Wanner, 2004. Wet season Mediterranean precipitation variability: influence of large-scale dynamics and trends. Climate Dynamics 23: 63–78.

# FISH HABITAT MAPPING

# A review of cephalopod–environment interactions in European Seas

Graham J. Pierce · Vasilis D. Valavanis · Angel Guerra · Patricia Jereb · Lydia Orsi-Relini · Jose M. Bellido · Isidora Katara · Uwe Piatkowski · João Pereira · Eduardo Balguerias · Ignacio Sobrino · Eugenia Lefkaditou · Jianjun Wang · Marina Santurtun · Peter R. Boyle · Lee C. Hastie · Colin D. MacLeod · Jennifer M. Smith · Mafalda Viana · Angel F. González · Alain F. Zuur

© Springer Science+Business Media B.V. 2008

Abstract Cephalopods are highly sensitive to environmental conditions and changes at a range of spatial and temporal scales. Relationships documented between cephalopod stock dynamics and environmental conditions are of two main types: those concerning the geographic distribution of abundance, for which the mechanism is often unknown, and those relating to biological processes such as egg survival, growth,

Guest editor: V. D. Valavanis Essential Fish Habitat Mapping in the Mediterranean

G. J. Pierce (🖂)

Centro Oceanográfico de Vigo, Instituto Español de Oceanografía, P.O. Box 1552, 36200 Vigo, Spain e-mail: graham.pierce@vi.ieo.es

G. J. Pierce · I. Katara · J. Wang · P. R. Boyle · L. C. Hastie · C. D. MacLeod · J. M. Smith · M. Viana School of Biological Sciences (Zoology), University of Aberdeen, Tillydrone Avenue, AB24 2TX Aberdeen, UK

V. D. Valavanis

Marine GIS Laboratory, Institute of Marine Biological Resources, Hellenic Center for Marine Research, P.O. Box 2214, 71003 Heraklion Crete, Greece

A. Guerra · A. F. González ECOBIOMAR, Instituto de Investigaciones Marinas (CSIC), Eduardo Cabello 6, 36208 Vigo, Spain

### P. Jereb

Istituto Centrale per la Ricerca Scientifica e Tecnologica Applicata al Mare, Via di Casalotti 300, 00166 Rome, Italy recruitment and migration, where mechanisms are sometimes known and in a very few cases demonstrated by experimental evidence. Cephalopods seem to respond to environmental variation both 'actively' (e.g. migrating to areas with more favoured environmental conditions for feeding or spawning) and 'passively' (growth and survival vary according to conditions experienced, passive migration with prevailing currents). Environmental effects on early life stages can affect life history characteristics (growth and maturation rates) as well as distribution and

L. Orsi-Relini

Dipartimento per lo studio del Territorio e delle sue Risorse, Corso Europa 26, 16132 Genova, Italy

J. M. Bellido

Centro Oceanográfico de Murcia, Instituto Español de Oceanografía, C/ Varadero 1, Apdo 22, San Pedro del Pinatar, 30740 Murcia, Spain

#### U. Piatkowski

Leibniz-Institut fur Meereswissenschaften an der Universitat Kiel, Düsternbrooker Weg 20, 24105 Kiel, Germany

J. Pereira Instituto de Investigação das Pescas e do Mar, Av. de Brasília, 1449-006 Lisbon, Portugal

#### E. Balguerias

Centro Oceanografico de Canarias, Instituto Español de Oceanografia, Carretera de San Andrés Apdo 1373, 38120 Santa Cruz de Tenerife, Spain abundance. Both large-scale atmospheric and oceanic processes and local environmental variation appear to play important roles in species-environment interactions. While oceanographic conditions are of particular significance for mobile pelagic species such as the ommastrephid squids, the less widely ranging demersal and benthic species may be more dependent on other physical habitat characteristics (e.g. substrate and bathymetry). Coastal species may be impacted by variations in water quality and salinity (related to rainfall and river flow). Gaps in current knowledge and future research priorities are discussed. Key research goals include linking distribution and abundance to environmental effects on biological processes, and using such knowledge to provide environmental indicators and to underpin fishery management.

**Keywords** Cephalopods · Gulf Stream · North Atlantic Oscillation · Fisheries · Ocean processes · Ecology

#### Introduction

The abundance and distribution of the world's commercial cephalopod stocks present wide annual fluctuations, generally attributed to the species' short life cycles, characterized by non-overlapping generations and consequent lack of buffering of the population from the influence of varying environmental conditions on spawning and recruitment success (Boletzky, 1986; Boyle, 1990; Rodhouse, 2001; Piatkowski et al., 2001; Rocha et al., 2001; Guerra,

#### I. Sobrino

Unidad de Cádiz, Instituto Español de Oceanografía, Campus Universitario de Puerto Real, Institutos de Investigación—CACYTMAR, C/ República Saharaui, s/n, 11510 Puerto Real, Cádiz, Spain

#### E. Lefkaditou

Institute of Marine Biological Resources, Hellenic Centre for Marine Research, Aghios Kosmas, 16777 Helliniko, Athens, Greece

#### M. Santurtun

Department of Fisheries Resources, AZTI Foundation, Txatxarramendi ugartea, 48395 Sukarrieta, Spain

#### A. F. Zuur

Highland Statistics Ltd, 6 Laverock Road, AB41 6FN Newburgh, UK

2004; Boyle & Rodhouse, 2005). Experimental and modelling work on the influence of temperature on hatching dates, hatching success and paralarval survival and growth provide insights into possible mechanisms (Forsythe, 1993; Jackson, 2004), highlighting sensitivity to water temperature. Recent studies suggests that increased temperature may also have a negative impact on cephalopods due to a progressive transition of routine mantle metabolism to an anaerobic mode of energy production (Portner, 1994; Melzner et al., 2006). Consistent with these findings, in European waters, cephalopods appear to be highly influenced by environmental variation at all stages of their life history (e.g. Guerra & Rocha, 1994; Pierce et al., 1994; Balguerias et al., 2000; González et al., 2005; Otero, 2006; Guerra, 2006b).

The sensitivity of cephalopod species to environmental fluctuations is a potentially important factor to take into account in stock assessments and fishery management measures. It also suggests that cephalopods could act as indicators of environmental change and ecosystem conditions. As an important ecosystem component, cephalopods and their fluctuations influence the population dynamics of both higher predators and their own prey. It is generally agreed that the world's climate is currently experiencing unprecedented anthropogenically-induced directional change. Possible effects of climate change on the world's oceans include reduced salinity (due to ice melting), increased temperatures, increases in acidity due to absorption of carbon dioxide, shifts in current systems, changing patterns of upwelling and other cyclical phenomena and increased numbers of storms (see Robinson et al., 2005 for a recent review). The short generation time, plasticity of life history and high environmental sensitivity of cephalopods could prove to be a double-edged sword in the context of fishery exploitation, as already noted by Caddy & Rodhouse (1998). On the one hand, cephalopods may be more strongly and more rapidly affected than many longer-lived species by external drivers such as climate change, yet they may ultimately be quicker to recover from extreme environmental variations and better able to adapt to changing conditions.

Caddy (1983) and Rowell et al. (1985) were probably the first authors to suggest relationships between cephalopod distribution and abundance and the environment, although they did not give much consideration to the nature of such links. In the early 1990s, some authors started to describe relationships between temperature and distribution or abundance for various squid species, initially in South Africa (e.g. Augustyn, 1990, 1991; Sauer et al., 1991; Roberts & Sauer, 1994) and later in Europe (e.g. Rasero, 1994; Pierce et al., 1998; Waluda & Pierce, 1998).

The importance of oceanographic conditions as determinants of cephalopod distribution and abundance has been highlighted in particular in relation to studies on the pelagic squid family Ommastrephidae. Thus, Bakun & Csirke (1998) examined the physical processes affecting different aspects of the life-cycle of the genus Illex (enrichment, concentrating food and paralarvae, transporting eggs and juveniles and facilitating adult spawning migrations). Anderson & Rodhouse (2001) noted the importance of understanding the links between oceanographic variability and cephalopod life cycles, and the relative spatial and temporal scales at which different processes take place, giving examples related to the Ommastrephid squids Dosidicus gigas in the eastern Pacific, and Martialia gigas and Illex argentinus from the southwest Atlantic. Semmens et al. (2007) focussed on the pivotal role of movement, during all phases of cephalopod life history, in determining abundance and distribution, and the important effects of environmental parameters, such as sea temperature and oceanographic processes in influencing those movements, especially in oceanic squids.

51

Relatively recently, the role of global oceanographic phenomena, such as El Niño and La Niña, in determining the distribution and abundance of cephalopod species has become apparent (e.g. González et al., 1997; Waluda et al., 2006; Waluda & Rodhouse, 2006; Rodhouse et al., 2006; Chen et al., 2007). Such large-scale phenomena may be cyclic or occasional and are sometimes linked to dramatic fishery collapses (e.g. Peruvian anchovy). Understanding the role of such events is crucial to understanding the nature of relationships between cephalopods and the environment.

Here, we review and synthesize published literature on cephalopod-environment interactions and categorize cephalopod responses to environmental changes and processes, with particular focus on European Seas. In addition, we briefly review the various techniques, particularly in statistical modelling, used to identify and quantify such relationships and consider how recent advances in methodology may help to shape future research. The main part of the review is structured geographically, with the aim of highlighting differences between contrasting marine environments and different large marine ecosystems. The review focusses on European and adjacent seas (Fig. 1), which we have divided into four broad areas: the NE Atlantic (including the North Sea, the English Channel and the Bay of Biscay), the Iberian Peninsula (Galician and Portuguese waters and the Gulf of Cadiz), the Saharan

Fig. 1 Major oceanic processes affecting cephalopod geographic distribution in European waters (NAO: North Atlantic Oscillation, G.S.: Gulf Stream, C.C.: Canary Current, I.P.C.: Iberian Poleward Current, A.C.: Algerian Current). Areas: N.S.: North Sea, E.C.: English Channel, B.B.: Bay of Biscay, G.W.: Galician Waters, G.C.: Gulf of Cadiz, S.B.: Saharan Bank, W.M., C.M., E.M.: Western, Central, Eastern Mediterranean, A.S.: Aegean Sea



Bank and the Mediterranean Sea (Western/Central/ Eastern Mediterranean). We also provide a brief account of studies from the rest of the Atlantic Ocean and adjoining regions.

# Physical and oceanographic general characteristics of the study area

Recent reviews on the physical oceanographic conditions in European and adjacent seas of these areas include those by Van Aken & Becker (1996) for the NE Atlantic, Relvas et al. (2007) for the Iberian Peninsula, Lafuente & Ruiz (2007) for the Gulf of Cadiz, Barton et al. (2004) for the Saharan Bank and Millot (2005) for the Mediterranean Sea.

The northern part of the study area (NE Atlantic) is influenced by variations of the Gulf Stream/North Atlantic current that, seasonally, delivers Atlantic water into the North Sea and the English Channel. The southern part of the area (Iberian Peninsula and Saharan Bank) is influenced by seasonal upwelling and gyre formation. The northwestern part of Iberian Peninsula (Galicia) constitutes the northern boundary of the Iberian-Canary current upwelling system, which has been intensively studied from the oceanographic perspective, including physical oceanography, biogeochemical cycles and plankton ecology and productivity (reviewed by Aristegui et al., 2006). The Mediterranean Sea has a highly complex system of water mass circulation, mainly influenced by the Algerian Current (western basin) and Libyo-Egyptian Current (eastern basin), which generate anticyclonic eddies and gyres.

Biological processes (e.g. recruitment and migration) in European Seas and the northwestern African coast are influenced by the North Atlantic Oscillation (NAO) and other atmospheric and ocean processes (e.g. the East Atlantic/Western Russian pattern, the Polar/Eurasian pattern, the East Atlantic jet and the Mediterranean Oscillation) that create seasonal and annual changes in temperature distribution and precipitation levels and corresponding river run-off regimes. Continental shelf regions of varying extent from the coast, and with widely different bottom sediment types and biological assemblages, characterize the whole study area; these support different benthic cephalopod communities and a variety of ocean processes that affect pelagic communities.

#### Hypotheses, data and methods

# Types of questions asked

Studies on cephalopod-environment interactions are usually shaped by the type, resolution and scale of data available. Studies using post-recruit distribution and abundance are, implicitly, examining the cumulative effects of environmental conditions over the entire life history, whereas other studies may focus on particular stages and specific effects (e.g. the influence of temperature on embryonic development). These latter studies should ultimately provide a more detailed and mechanistic understanding of the broader post-recruitment cephalopod-environment relationships. Thus, studies may be divided into those focussing on the geographical distribution of abundance and those relating to specific biological processes such as spawning, embryonic development, hatching, growth, recruitment, maturation and migration, while recognizing that environmental effects on different life-cycle stages and processes are likely to result in changes in abundance and distribution.

Critical stages of cephalopod life cycle include spawning, hatching, early growth, recruitment to the population and to the fishery, and movements to and from the spawning grounds. The majority of studies focus on spatial and temporal patterns in distribution and abundance of the post-recruit stages of commercially exploited species. However, in principle, models of spatiotemporal variation can be fitted to data on distribution, abundance and life history parameters at all life stages, and indeed relationships may be more critical at the earlier stages. In many cephalopods, the paralarval (post-hatching) period tends to be the least well known but there have been several laboratory studies of environmental effects on eggs and paralarvae (Villanueva, 1995; Gowland, 2002; Craig & Overnell, 2003), modelling studies based on laboratory data (Forsythe, 1993) and also studies in the wild focussed on the influence of oceanographic regimes in the distribution and abundance of paralarvae (Rocha et al., 1999; Vecchione, 1999; González et al., 2005; Otero, 2006). It is also important to be aware of possible indirect environmental effects, e.g. operating through environmental effects on the predators, prey competitors or parasites of cephalopods (Otero et al., 2008). Pascual et al. (2007) review relationships between oceanographic processes and parasite recruitment in fish and cephalopods. They conclude that variability in recruitment of parasite communities tends to be associated with major current systems and that instability in water masses (e.g. due to turbulent mixing in upwelling systems) is associated with instability of trophic interactions over time, which in turn leads to less well-developed parasite communities.

# Sources of data on cephalopods

Data on cephalopods may arise from fisheries (landings, by-catch and discard records), trawl surveys (e.g. catch per unit effort (CPUE) and length– frequency distributions in survey trawl hauls), predator stomach contents and tagging or direct observation; obviously, all these sources have associated limitations and biases. Relevant considerations include availability, coverage and resolution (in time and space), and accuracy and precision of the data.

Cephalopod species of no commercial interest tend to be less well documented, with distribution often inferred from indirect evidence such as occurrence in predator stomachs (e.g. Clarke et al., 1980). Even most commercially exploited species are less well studied than many fish, because they are non-target species in large-scale fisheries and/or are targeted by littlemonitored artisanal fisheries, or simply because finfish catches are more economically important and attract most funding for routine data collection and research. Although this picture is changing in European waters as many traditional finfish species have been overexploited and fleets are seeking new target species such as cephalopods, many European countries do not regularly record cephalopod catches during fisheries surveys. Survey CPUE is generally regarded as measuring relative abundance in cephalopods, since gear selectivity is poorly known or unknown for most species in most gears (see, however, Bravo de Laguna & Balguerias, 1993; Hastie, 1996).

Commercial landings data are subject to the usual issues of under- and mis-reporting, and cephalopod landings are rarely identified to species, e.g. squid landings are usually classified as 'long-finned' (loliginid) or 'short-finned' (ommastrephid). Where market sampling occurs (e.g. for loliginid squid in Spain, Portugal and Greece), the typical monthly sampling regime is rather coarse for application to such short-lived species (Lourenço & Pereira, 2006). Life history data tend to be recorded only on a project basis with no long-term and established monitoring taking place in European waters.

Some alternative methodologies and models have been used to estimate catch and CPUE in small-scale fisheries. Among these, Gomez-Muñoz (1990) developed a simple model to estimate catch and CPUE in multispecies small-scale fisheries. This model has been applied in small-scale fisheries for squid and octopus and to larger scale fisheries for monkfish in NW Spain (Simon et al., 1996; Rocha et al., 2004; Otero et al., 2005) and to the fishery for squid in Scottish waters (Young et al., 2006a). In multispecies fisheries, this model can estimate catches of individual species for a specific gear (Rocha et al., 2004).

#### Environmental variables analyzed

Most cephalopods are benthic, demersal or vertically migrating pelagic species that spend relatively little time in surface waters, except planktonic paralarvae (Jereb & Roper, 2005). However, the ready availability of remotely-sensed ocean surface data, plus the known sensitivity of cephalopod growth to temperature and the presumed importance of primary productivity have led to many studies focussing on the influence of sea surface temperature (SST) and chlorophyll (Chl-a) on cephalopod distribution and abundance. Spatial patterns in these variables may also be used to infer the locations of ocean surface features (thermal fronts, gyres and upwelling), the high productivity of which may be exploited by cephalopods (Jereb et al., 2001; Valavanis et al., 2004; Wang et al., 2004). Surface conditions may also, implicitly or explicitly, be assumed to provide indirect information on sub-surface conditions, although such assumptions are risky without knowledge of local oceanographic conditions (e.g. concerning the degree of mixing of the water column or the existence of sub-surface currents).

Some studies also use sea surface salinity (SSS), e.g. as a proxy for water mass identity or sea surface height (SSH, also expressed as sea level anomaly, SLA) (Valavanis et al., 2002). Where survey environmental data (e.g. conductivity, temperature and depth (CTD) data) are available, studies may also consider sea bottom temperature (SBT) and salinity (SBS) or the temperature and salinity profile of the whole water column (Wang et al., 2003). However, in general, effects of sub-surface oceanographic conditions on cephalopod distribution and abundance remain poorly known.

Other relevant and readily available data include sea depth (bathymetry), since the distribution of most demersal and benthic species seem to be restricted to certain depth ranges. Loliginid squid may undertake inshore-offshore migrations, so that depth could be a useful predictor of location for particular life stages (e.g. Arkhipkin et al., 2000). Sea bed morphology (e.g. slope, aspect in relation to the direction of prevailing currents and depth variability or 'bumpiness') may also be important. In addition, several studies have analyzed surveyed meteorological (wind and Ekman transport data), thermohaline (CTD data) and chemistry (e.g. dissolved oxygen and nitrate, ammonium and phosphate concentration) variables (e.g. Cushing, 1975; Bakun & Csirke, 1998; Otero, 2006). Studies on Loligo reynaudii off South Africa highlight the importance of turbidity and dissolved oxygen in determining the location of spawning areas (e.g. Augustyn et al., 1994).

The known migratory routes of some oceanic squids (e.g. *Illex argentinus* in the southwest Atlantic, Rodhouse et al., 1994a, b, 1995; Waluda et al., 2002) suggest that measures of current direction and strength may be important predictor variables, albeit difficult to incorporate into spatial models. For demersal species, sea bed substrate is another important potential explanatory variable (e.g. for species that attach their eggs to the substratum), although these data are usually only available for coastal areas. The degree to which the substrate has been disturbed by trawling activity may also be important (De Alteris et al., 1998).

Lastly, for analyses of interannual variation in abundance, many studies have used large-scale ocean climate indicators such as the NAO Index. The NAO is the best readily available general index of oceanographic conditions in the NE Atlantic and is related to the strength of the Gulf Stream (Hurrell, 1995; Jones et al., 1997).

#### Methods of analysis

As there is no buffering effect of older age classes, environmental effects on the extant generation are a crucial feature of cephalopod population dynamics. Indeed, in terms of classical population dynamics, the stock-recruitment relationship (if one exists) and prespawning mortality may be the only relevant intrinsic population parameters (see Pierce & Guerra 1994; Pierce et al., 2006). This has led to a tendency to focus on empirical models of distribution and abundance rather than models rooted in classical population dynamics, such as those used in estimating the abundance of exploited teleost fish populations (e.g. Rochet, 2000). However, in other respects, the approaches to modelling cephalopod habitat requirements are in principle no different from those for other taxa: see, for example, Redfern et al. (2006) for a review of methods applied to data on marine mammals, and Valavanis et al. (2008, this volume), for a review of methods used in essential fish habitat modelling).

Models of cephalopod distribution, abundance and life history parameters can be classified in various ways, e.g. in relation to the species or life-stage to which they refer, whether they address temporal (diurnal, seasonal and interannual) or spatial variation (or some combination thereof), and according to the scale and resolution of the data available or the study area.

Some of the earliest empirical models of abundance (Fogarty, 1989) rely on simple uni-factorial linear regression or correlation. However, advances in statistical modelling have facilitated increasingly sophisticated approaches, taking account of the effects of multiple explanatory variables and their interactions (e.g. multiple linear regression, also ordination and classification methods such as redundancy analysis and regression trees), non-normality in the response variables (e.g. Generalized Linear Models-GLM), non-linearity and heteroscedasticity in the response to variation in explanatory variables (e.g. Generalized Additive Models-GAM), timelagged effects and temporal autocorrelation (e.g. Auto-Regressive Integrated Moving Average (AR-IMA) and other time-series techniques) and spatial autocorrelation (e.g. Generalized Additive Mixed Models-GAMM). Generic methodologies such as geostatistics, Geographic Information Systems (GIS), bootstrapping, artificial neural networks (ANN) and Bayesian models have also been applied as part of the modelling process (e.g. Georgakarakos et al., 2006).

The objectives of model fitting have been diverse. Often, the underlying purpose is some form of fishery forecasting, with the stated aim of extrapolating model results to either future years or to unexploited areas. However, models based on contemporaneous environmental conditions are of little use for forecasting, while the short life-cycle of cephalopods restricts the importance of time-lagged environmental effects, although Waluda et al. (1999) showed that SST anomalies associated with El Niño may be linked to recruitment of the ommastrephid squid Illex argentinus between 2 and 5 years later. In addition, often no explicit predictions are made since the entire data set is used for model fitting. Indeed, because of this, most published models remain hypotheses generated rather than hypotheses tested (although the development of cross-validation routines for model fitting partially answers this criticism). Other studies focus on individual species habitat requirements or the influence of particular environmental variables on particular life history events or stages (spawning, embryonic increment, hatching, growth, recruitment, maturation and migration). A particular recent focus in fisheries has been on the identification of critical habitats of various life-stages of exploited species, so-called Essential Fish Habitat (EFH), a concept that is readily extended to cephalopods (e.g. articles in this volume).

As indicated above, a particular concern for empirical models, although it could equally be applied to mechanistic models, is that they require adequate testing. Where this has not been done, it is worth keeping in mind the cautionary words of Solow (2001) about the 'fleeting nature of temporal relationships identified between short-time series', a comment that could equally be generalized to spatial extrapolation of studies based on small areas. Finally, even where a correlative relationship is established and can be shown to generate useful predictions, this does not indicate a direct causal link and further study of the underlying mechanism is desirable.

We cite several studies which infer environmental relationships from observed patterns of occurrence without the benefit of any formal statistical analysis. While careful observation of patterns in distribution and abundance is invaluable in defining testable hypotheses, particular caution is needed when interpreting seasonal patterns of distribution or seasonal migrations, since they will inevitably be correlated with seasonal patterns in some environmental variables. An indirect causal link is of course likely (since timing of breeding in many animal taxa is selected to ensure that the young experience favourable environmental conditions and a good food supply).

# Review of studies on a regional basis

NE Atlantic (including North Sea, English Channel and Bay of Biscay)

The oceanography of the northeastern Atlantic is strongly affected by the Gulf Stream/North Atlantic Current, which delivers Atlantic water into coastal seas such as the North Sea and English Channel and helps to maintain temperatures at levels higher than at equivalent latitudes elsewhere in the world, and by the NAO, the cycles of which generate substantial variation in temperature and precipitation over the area.

The best documented cephalopods in the NE Atlantic are probably the two Loligo species, L. vulgaris and L. forbesi. Around Scotland, L. vulgaris is relatively rare and fishery catches can generally be assumed to be almost exclusively L. forbesi. Further south, both species co-exist, although L. vulgaris increasingly dominates with decreasing latitude: it has been speculated that the balance between the two species is environmentally mediated (see Chen et al., 2006). These species appear to be patchily distributed in space and time. Many studies of life history, distribution and abundance have pointed to the complexity of population structure in UK, e.g., the existence of summer and winter breeders, as first proposed by Holme (1974). Nevertheless, throughout continental shelf waters, L. forbesi seems to comprise a single stock (Shaw et al., 1999) so that the substantial variations in life history parameters reported by numerous authors may be largely environmentally driven.

Making use of spatial and statistical tools, Bellido (2002) reported differences in spatial patterns of distribution of L. forbesi between seasons, and between the east and west coasts of Scotland. The separate analysis of data from these two areas revealed intra-annual variability in L. forbesi abundance, as later confirmed by Pierce & Boyle (2003) and Pierce et al. (2005a, b), and suggested a possible spatial migration from the west to the east in seasons of high abundance (see also Waluda & Pierce, 1998). Bellido (2002) suggests that the western area represents the main 'reservoir' of squid abundance, with a more or less stable spatial structure, while the east area is occupied seasonally (with a widespread coverage in seasons of high abundance) by a population made up of small, fast moving aggregations in which it is more difficult to see a clear spatial structure.

Information on detailed habitat preferences and ontogenetic migrations in *L. forbesi* can be inferred from anecdotal evidence provided by fishermen. Thus, in the Moray Firth (Northeast Scotland), fishermen have commented that early in the season (summer), catches are best close inshore around 10-m depth over hard ground. As the season progresses, and the squid increase in size, the squid and the fishery gradually move further offshore to sandy/muddy bottoms in waters of around 55-m depth. Better catches have also been reported in areas that experience stronger tidal currents (Young et al., 2006b).

Interannual variation in abundance of *Loligo* is related to SST, as well as a signal from the previous year's abundance (Pierce & Boyle, 2003). Similarly, *Loligo* landings from the English Channel are related to SST during the previous winter (Robin & Denis, 1999) and there is also evidence that recruitment of the English Channel *L. forbesi* stock is density-dependent (Challier et al., 2005).

The spatial distribution of *Loligo* spp. abundance in the North Sea in winter tends to be positively correlated with both SBT and SST, i.e. higher abundance is seen in areas with higher temperature, while abundance in summer is negatively spatially correlated with SST (Waluda & Pierce, 1998; Pierce et al., 2001). Analysis of survey abundance data from the North Sea in February suggests that squid avoid waters with SBT <7°C (Pierce et al., 1998). Bellido et al. (2001) found evidence that peaks of abundance in Scottish waters occur in the temperature range 8–13°C.

In the Bay of Biscay (ICES Div. VIII a,b,d), *Loligo* spp. catches appeared to be higher in months with lower SST while the spatial distribution of the catches for those cooler higher-catch months is associated with the coolest waters or with the frontal zones (Santurtun et al., 2004).

Both *L. forbesi* and *L. vulgaris* perform seasonal migrations in waters off south-west England. During the winter, *L. forbesi* adults spawn and die, and their eggs hatch in the western English Channel and the new cohort migrates east towards southern North Sea until the following winter (Holme, 1974; Sims et al., 2001). Sims et al. (2001) reported that *L. forbesi* movement in the English Channel is temperature-dependent, migrations occurring earlier in years when water temperatures were generally higher.

The relationships between abundance, movements and SST may be linked to larger-scale climatic variation, as shown by links with the NAO (Sims et al., 2001; Pierce & Boyle, 2003), and thus to Gulf Stream inflow into northeast Atlantic coastal waters. However, signals of both SST and NAO can be detected in the interannual variation of *Loligo* abundance, i.e. local scale variation and large-scale phenomena both play a role (Zuur & Pierce, 2004).

In Scotland, L. forbesi exhibits a clear annual abundance peak around October-December as the winter breeding season approaches (Bellido et al., 2001). Nevertheless, analysis by Pierce et al. (2005b) suggested that environmental conditions affect the timing of breeding and the size at maturity, and that (as revealed by changes over three decades in the seasonal pattern of fishery landings) the winter breeding peak may not always have been the dominant one. High autumn/winter temperatures (high winter NAO values) are associated with high squid abundance and precocious maturation and also tend to favour high abundance in the following year, along with increased body weight at length and a decrease in the proportion of animals breeding in December. High abundance in summer, conversely, leads to a fall of body weight at length in the following year. Thus, there may be alternation of precocious and slow maturation, and/or summer and winter breeding, driven by a combination of environmental conditions and intraspecific competition (Pierce et al., 2005b). Sensitivity to environmental triggers is however at least partially under intrinsic control, allowing maturation to begin one to two months earlier in males than in females, as highlighted in analysis by Smith et al. (2005). Boyle et al. (1995) suggested various scenarios under which variation in environmental conditions might affect the duration of the life-cycle and timing of breeding in L. forbesi.

The English Channel cuttlefish (*Sepia officinalis*) provides one of the highest cephalopod fishery yields in the NE Atlantic (Royer et al., 2006), spawning in spring on both north (English) and south (French) coasts (Dunn, 1999). Cuttlefish in the English Channel and French Atlantic coast expand their distribution during the spawning season. The centre of high abundance, as identified from fishery data, is located further north in warm years and further south in cooler years (Wang et al., 2003). While local environmental changes, e.g. in SST, affect the

location of peaks in abundance, the authors nevertheless note that it is hard to determine if this reflects any causal link.

There have been few studies on environmental relationships for other cephalopods in the NE Atlantic, although Hastie et al. (1994) noted that the high abundance of Todaropsis eblanae in the North Sea in 1990 appeared to be related to a positive salinity anomaly (these are generally associated with higher temperatures and stronger inflow of Atlantic water). De Heij & Baayen (2005) discuss the occurrence of various cephalopods in the central and southern North Sea in relation to environmental conditions, although their observations are not supported by any formal statistical analysis. They suggest that the central and southern North Sea is generally unsuitable habitat for cephalopods due to the shallow water. They note that the occurrence of individual species is restricted by water temperature or salinity requirements, as inferred from their seasonal migration patterns. Deep waters in the central and southern North Sea are cooler in summer and warmer in winter, while the reverse is the case in shallow waters and they argue that this explains the seasonal migration of the small loliginid squid Alloteuthis subulata, which is suggested to prefer relatively warm waters. Differences in the distribution of sepiids and sepiolids are related to differences in salinity tolerance. Thus, Rossia macrosoma is restricted to the northern part of the North Sea, because it requires high salinities, while S. officinalis and Sepiola atlantica both tolerate low salinities. The authors note that incidental findings of unusual cephalopod species in the North Sea (e.g. Onychoteuthis banksii) are likely to be the result of passive transport in the north Atlantic current.

The relationship between broad-scale distribution and sea depth is evident in various deep-water benthic and bentho-pelagic cephalopods in the northeast Atlantic. At shallower depths (150–500 m), sepiolids are the most abundant group, with *S. atlantica*, *Sepietta oweniana* and *Rondeletiola minor* restricted to waters <300 m and *Rossia macrosoma* (205–515 m) and *Neorossia caroli* (400–1,535 m) extending into deeper water. Among the incirrate octopods, *Eledone cirrhosa* occurs at depths of up to 500 m, while the genera *Benthoctopus* and *Bathypolypus* occur between 250 and 2,700 m and *Graneledone verrucosa* was caught at depths of 1,785–2,095 m. Cirrate octopods dominate cephalopod catches from the deepest areas, with species including *Opisthoteuthis massyae* (877–1,398 m), *O. grimaldii* (2,165– 2,287 m), *Stauroteuthis syrtensis* (1,425–3,100 m), *Cirroteuthis muelleri* (700–4,854 m), *Cirrothauma murrayi* (2,430–4,850 m) and *Grimpoteuthis* spp. (1,775–4,877 m) (Collins et al., 2001).

Relationships between distribution/abundance patterns and environmental factors in North European squid and cuttlefish are relatively well known but most studies do not consider spatial or temporal autocorrelation (e.g. Bellido et al., 2001; Zuur & Pierce, 2004; Pierce et al., 1998, 2005a, b). Bellido (2002) reported that squid abundance in Scotland is correlated over distances between 135 and 405 nautical miles, meaning a spatial correlation of over 5 to 14 ICES rectangles (one ICES rectangle is  $1 \times 0.5^{\circ}$ ). In the past few years, new statistical approaches to study interactions with the environment have emerged (e.g. mixed models, which can take into account temporal autocorrelation), and reanalysis of some of the published data sets would be useful to confirm whether the relationships previously described persist once autocorrelation is taken into account.

Atlantic waters off Iberian Peninsula (Northern Spain, Portugal and Gulf of Cadiz)

The Iberian Atlantic coast is characterized by a relatively limited continental shelf. The oceanography of the region is dominated by the seasonal upwelling/ relaxation pulses of Eastern North Atlantic Central Water (ENACW), linked to the Canary Current and the NAO. The upwelling results in nutrient enrichment and supports a high local biodiversity with at least 78 species of cephalopods recorded in Galician waters (Guerra, 1992). In 'relaxed' ENACW periods, the Iberian Poleward Current (IPC) dominates the area, creating appropriate conditions for the transfer of subtropical cephalopod species into northern regions (Guerra et al., 2002).

The upwelling pulses are associated with negative NAO index values and increase the productivity levels of the area, creating favourable conditions for increased paralarval survival in *Octopus vulgaris* (Otero et al., 2005). This influences the artisanal fishery for *O. vulgaris*, which is one of the main small-scale fisheries in the Galician region. This resource shows wide year-to-year fluctuations. Otero et al. (2008) have shown that the wind stress structure, in

both spring-summer (previous to the hatching peak) and autumn-winter, affects the planktonic stage of this species and subsequent recruitment, explaining up to 90% of the interannual variability of the adult catches. In the Ria de Vigo and the adjacent shelf, upwelling generates a succession of wind stress/relaxation cycles with a periodicity of 10 to 20 days. The associated short-term variation in water chemistry affects paralarval abundance and biomass (Otero, 2006). The decrease in nitrate, ammonium and chlorophyll during the relaxation phase of upwelling events can explain up to 88% of variation in paralarval abundance. During the relaxation phase, nutrient salts are consumed by primary producers to generate biogenic matter, which is retained in the system and transferred through the food web.

Spawning of *O. vulgaris* in this area extends from December to September with a single peak in spring months (Otero et al., 2007). For eggs laid at this peak, the embryonic phase is associated with low bottom temperatures and lasts around 4 months. Thus, the peak of early hatched paralarvae of *O. vulgaris* occurs at the end of the upwelling season, suggesting that the reproductive strategy is tightly linked to the seasonal dynamics of the major local environmental process (Otero, 2006).

Spawning and/or hatching during the upwelling period, as found in O. vulgaris in Galician waters, is a common reproductive strategy within other coastal upwelling ecosystems. Factors such as the formation of retention areas due to coastal topography, and the concomitant maintenance of higher productivity levels, play an important role in the determination of the frequency of spawning events, which can vary between different parts of the same upwelling system. Octopus vulgaris on the northwestern Portuguese coast displays two spawning peaks, one in March and another in July. This spawning pattern is similar to that found off NW Africa, in the Arguin bank and the South Senegalese coast (Demarcq & Faure 2000), but unlike that found to the north along the Galician coast (Otero, 2006) or to the south on the southwestern Portuguese coast (Pereira et al., unpublished data), all of which areas are within the Canary Current upwelling system.

Studies undertaken in Galician waters show that *O*. *vulgaris* and *Loligo vulgaris* paralarvae are markedly smaller than those collected in the wild in other areas and under rearing conditions at higher temperatures

(Villanueva, 1995, 2000; Sakaguchi et al., 1999). These size differences are explicable since temperature influences cephalopod growth rate throughout the life cycle. Hatchlings emerging at warmer temperatures have also experienced warmer incubation temperatures during embryonic development, and so hatch at larger sizes (Forsythe, 1993; Pecl et al., 2004). Another reason that could explain the differences in size would be the stress produced during the towing of the net when the animals were captured. However, studies on *L. vulgaris* paralarvae from the Mediterranean hatched in captivity, which were subjected to the same actions involving their capture, revealed that the paralarvae did not shrink substantially after these stressing activities (A. F. Gonzalez, unpublished data).

A positive correlation was observed between the upwelling index and *T. eblanae* abundance in Galician waters over 13 years (1973–1976, 1980–1986 and 1988–1989), suggesting that food availability (abundance of appropriate zooplankton prey, which is strongly related with primary production) during the planktonic phase of the species (paralarvae) is critical for the survival of hatchlings, and consistently, for the success of recruitment (Rasero, 1994).

The NAO index is positively correlated with *O. vulgaris* landings in the Algarve region (Erzini, 2005). Paralarvae of *O. vulgaris* are more abundant during summer (off the west coast) and autumn (off the south coast), while those of ommastrephid squids are abundant during autumn. Highest numbers for both groups are observed over a bathymetric range of 50 to 150 m in SST between 17 and 20°C (Moreno & Pereira, 1998).

Loliginid distribution along the Portuguese continental shelf is limited within SST 13-20°C, with higher catches between 13 and 16°C (Moreno & Sousa-Reis, 1995). A greater number of egg masses of L. vulgaris is observed on the south coast of Portugal when higher levels of zooplankton abundance (due to upwelling) are recorded (Villa et al., 1997). Loliginid early life stages are mainly concentrated around the 80-90-m isobath in winter and spring and at 60 m during summer and autumn, while they show a seasonal pattern of higher abundance during winter and spring along the northern Portuguese coast (Cunha et al., 1995). Loliginid and Sepiolid paralarvae are mostly found during winter and spring, in waters with SST less than 16°C and over a bathymetric range of 50 to 100 m (Moreno & Pereira, 1998). Off the Portuguese coast, higher SST during the first three months of life of the squid *L. vulgaris* was shown to favour somatic development before maturation, with putative effects on fecundity and, indirectly, on abundance (Moreno et al., 2007).

Sepia officinalis tolerates temperatures up to 30°C and the species is found in the lagoon system of the Ria Formosa (South Portugal), where the temperature reaches  $27 \pm 3$ °C in summer (Domingues et al., 2002, 2006). Depth tolerance in this species changes over the life cycle: larger cuttlefish implode between 150 and 200 m, whereas advanced embryonic specimens and newly hatched animals implode between 50 and 100 m (Guerra, 2006a).

Recent studies suggest that the distribution of some species around the Iberian Peninsula may be changing, possibly as a consequence of slow environmental trends. The musky octopus (Eledone moschata) was considered to be a Mediterranean species (Mangold, 1983) with a low or occasional occurrence in the Gulf of Cadiz (Guerra, 1992; Silva et al., 2004) and southern Portuguese coast, as confirmed by early anecdotal accounts and regular species monitoring surveys of Instituto de Investigacao das Pescas e do Mar (IPIMAR) from the early 1980s. Throughout the 1990s and the beginning of the 2000s, however, it became increasingly abundant and widespread to the north, and is currently well established with breeding populations found as far north as Lisbon (Lourenço et al., unpublished data). The same environmental change seems to have had the opposite consequence for L. forbesi, a more northerly species, which has contracted its former distribution to northern waters, becoming scarce or absent in western Iberian shores in the same period of time (Chen et al., 2006).

The analysis of the isotope composition of calcareous structures of marine organisms has proved useful in providing bio-ecological data. Analyses undertaken on the carbon- and oxygen-isotope composition of cuttlebone aragonite of wild and cultivated specimens of *S. officinalis* from NW Spain showed that the seasonal temperature changes inferred from isotope ratios were consistent with changes in the temperature of ambient sea water. The maximum life span of 2 years and variable growth rates among and within individuals can be inferred from isotopic signatures (Bettencourt & Guerra, 1999).

The Gulf of Cadiz is characterized by river discharges that affect SST distribution. Thus, rainfall

levels (in turn affected by NAO) play an important role in determining cephalopod abundance. Here, octopus abundance is highly correlated with levels of rainfall prior to the fishing season, river discharges in December and SST in May and June (Sobrino et al., 2002).

# Saharan Bank

The oceanography of the Saharan Bank, a highly productive ecosystem, is dominated by strong upwelling activity and gyre formation. Generally, these features increase the productivity levels in the area and create a variable SST distribution, although the intensity of these processes depends on depth. Cephalopod species in the area include *Loligo vulgaris*, *Octopus vulgaris* and *Sepia officinalis*, all of which are or have been important fishery resources and *Todarodes sagittatus*.

There are relatively few studies on the environmental relationships of cephalopods in this region. Balguerias et al. (2000) evaluated the history of fisheries in the area and the apparent replacement of finfish (due to overexploitation of the resource) by *O. vulgaris* and *S. officinalis* since the 1960s. They suggested that changes in the faunistic composition of the communities were caused by a combination of factors, including economic initiatives as well as oceanographic variation and competition for food.

In the Saharan Bank area, two distinct octopus stocks (north and south Saharan Bank) have been described. Annual abundance variability is related to depth and SST, with abundance reaching a maximum in October-November when SST is highest (Balguerias et al., 2002). Transient productive gyres of the Saharan Bank seem to trap octopus paralarvae, positively affecting their survival (Balguerias et al., 2000, 2002). Faraj & Bez (2007) showed that there are clear distinctions between the spatial distribution patterns of the spawning and recruitment phases of the Dakhla stock of O. vulgaris in relation to bathymetry: juveniles are more coastal, less spatially dispersed, patchier, and more anisotropically distributed.

In the Saharan Bank region, *Todarodes sagittatus* reaches maturity at younger ages and smaller sizes than in the Mediterranean (further north), while the latter attain larger sizes as a result of maintaining fast growth over a longer period and delaying maturation. Greater growth rates in juveniles from the Saharan

Bank could be explained by higher temperatures in this area than in the Mediterranean (Quetglas & Morales-Nin, 2004).

The common cuttlefish is not very tolerant of low oxygen concentrations. Low oxygen concentrations can account for the absence or low abundance of *S. officinalis* (Guerra, 2006a). The existence of cuttlefish fisheries in the upwelling areas off the NW African coast and the Northern Benguela current suggests continuous eutrophic scenarios in shallow waters in the cores of the southern upwelling cells (Guerra & Sanchez, 1985). This is where low oxygen concentrations are common, and they appear to be the most important limiting factor for the development of cuttlefish populations.

#### Mediterranean Sea

In this warm, oligotrophic body of water, the hydrological circulation is dominated by the continuous transformation of the Atlantic Water (AW) into Mediterranean Water (MW), and the formation of dense water masses, which sink offshore in specific northern zones of the western and eastern basins (see Millot & Taupier-Letage, 2004; Millot, 2005 for reviews). In particular, the highly unstable southern portions of the two main water gyres circulating in the western and eastern basin, also named the Algerian and Libyo-Egyptian Currents, meander and generate anticyclonic eddies and water masses at very different depths, resulting in rather complex circulating systems. River flows and discharge and wind systems represent additional important driving forces in the Mediterranean water circulation. Bottom diversity and the existence of widely contrasting bathymetries along the whole Mediterranean Sea contribute to make this a very interesting area to study cephalopod distribution and abundance in relation to environmental conditions.

Along the Iberian Mediterranean coast three main cephalopod communities are defined (González & Sanchez, 2002): the shelf community (<150 m), the middle slope community (>480 m) and a group of cephalopods that are widely distributed on the lower continental shelf-upper slope (150–480 m). In the Balearic Sea, there are two main cephalopod assemblages that are associated with the continental shelf (50–100 m) and the upper slope (600–800 m) respectively, separated by a wide transitional zone

(100–600 m) (Quetglas et al., 2000). Depth and shelf shape are among the factors affecting the spatial distribution and abundance of *Eledone cirrhosa* in the Aegean Sea, Western Mediterranean (French and Spanish waters) and coastal waters off Sardinia (Lefkaditou et al., 2000).

Known teleconnection patterns such as the East Atlantic/Western Russian pattern, NAO, the Polar/ Eurasian pattern, the East Pacific/North Pacific, the East Atlantic jet and the Mediterranean Oscillation all affect chlorophyll concentration in the Mediterranean, especially in coastal areas, areas of upwelling and regions with a gyre formation (Katara et al., 2008, this volume). In the Ligurian Sea, E. cirrhosa abundance, recorded during late spring-summer surveys, was positively related to the winter NAO index (Orsi Relini et al., 2006). In addition, river discharges and bathymetry play important roles in determining the distribution of cephalopods. In the Gulf of Lions and the Gulf of Roses-Cape Creus (France), E. cirrhosa, L. vulgaris and S. officinalis landings are positively correlated with run-off of the local Rhone and Muga rivers (Lloret et al., 2001).

In the Central Mediterranean between southern Sardinia and northern Tunisia off northwestern Sicily, the flow of the AW splits: one stream continues westwards and northwards, along the southwestern Tyrrhenian Sea, while the other flows southwards, through the Sicilian channel, towards the eastern Mediterranean basin. This central portion of the western Mediterranean is characterized by complex water circulation (e.g. Atzeni et al., 1997; Millot, 2005) with upwelling events and cyclonic meanders that are maintained both by the coastal topography and the intermediate flow of waters that goes from the eastern to the western basin, also named Mid-Mediterranean Jet (MMJ) (Rio et al., 2007). Jereb et al. (2005) investigated cephalopod abundance and distribution in Sardinian waters and showed a correlation between I. coindetii recruitment and environmental variation off the western Sardinian coast. A temporal shifting of the Algerian current, and consequently of the frontal zone off the western Sardinian coasts, during 1996 and 1998 was probably responsible for the unusually high pulse of recruitment observed for I. coindetii during 1997 (Cuccu et al., 2008). Anomalous SST values were observed corresponding to a shift in the Algerian Current, confirming the potential for using SST as an indirect indicator of biological conditions for squids (see also Dawe et al., 2000, 2001).

A similar correlation was hypothesized for *I. coindetii* in the Strait of Sicily (Jereb et al., 2001). In this area, two cyclonic meanders create a Western Sector with colder waters (16.9–20°C), an Eastern Sector with warmer waters (20–23.2°C), and a permanent upwelling along the southern Sicilian coasts (e.g. Piccioni et al., 1998; Mazzola et al., 2000). Here, the shift of the frontal zone resulting from the two opposing water masses of the western and eastern side was probably responsible for an unusual pulse of recruitment, and consequently, for the unusually high concentration of juveniles (Jereb et al., 2001).

In the Eastern Mediterranean, the area that supports the most important cephalopod fisheries (*L. vulgaris*, *I. coindetii*, *S. officinalis*, *O. vulgaris*, and *Eledone* spp.) is the North Aegean Sea (Lefkaditou et al., 2007). Here, environmental conditions and oceanic processes affect species recruitment timing, seasonal abundance and migration. In general, the positive correlation between loliginid landings and SST concerns nutrient-rich areas (North Aegean), while in oligotrophic areas (Central/South Aegean), higher production is attributed to the occurrence of seasonal, randomly distributed marine productivity hotspots, areas of below-average SST and above average chlorophyll concentration (Georgakarakos et al., 2002).

In Greek waters, it has been shown that SST may be used to forecast loliginid landings, but is inadequate to predict landings of ommastrephids, which occur in deep pelagic zones (Georgakarakos et al., 2006). Nevertheless, Arvanitidis et al. (2002) highlighted the importance of SST and Chl-a concentration in determining biological indices of I. coindetii in the Eastern Mediterranean. Analysis of bottom trawl data for the ommastrephid squid Todarodes sagittatus from the Western Mediterranean showed significant correlations between hatching success and temperature at 50-m depth (Quetglas & Morales-Nin, 2004). Mediterranean squids have wider embryonic increments in their statoliths than Atlantic squids due to higher water temperatures in the Mediterranean (Villanueva et al., 2003). In the early life stages, there is superior growth performance for I. coindetii and I. illecebrosus specimens hatched in warm conditions relative to specimens hatched in colder conditions (Ragonese et al., 2002).

In the North Aegean, Cyclades Plateau and Ionian Sea fishing grounds, the spatial distribution of *L. vulgaris* and *I. coindetii* CPUE was found to be positively correlated with the distribution of marine productivity hotspots (Valavanis et al., 2004) as well as with the distribution of mesoscale thermal fronts (Valavanis et al., 2005). Suitable habitat areas for *I. coindetii* are characterized by SST of 13 to  $29^{\circ}$ C, surface chlorophyll-a concentrations of 0.30 to 15.60 mg/m<sup>3</sup> and SSS values of 36.12 to 38.51‰ (Valavanis et al., 2002).

Movements of *L. vulgaris* into inshore fishing grounds are mainly related to seasonal variability of temperature in the NE Aegean Sea, whereas in coastal areas occupied by water masses of lower salinity, variation in CPUE of this species is also related to rainfall variability (Lefkaditou et al., 1998a). Recruitment timing and duration as well as the resulting seasonal demographic structure and abundance of *E. moschata* are associated with temporary upwelling and shelf topography in the insular area of the Southern Aegean Sea, which affect the productivity levels of this area that is generally characterized by oligotrophic waters (Lefkaditou et al., 1998b).

The reproductive strategies of cephalopod species that are found throughout the Mediterranean are seen to vary depending on the location of each population, suggesting a strong influence of environmental factors on significant biological traits such as the size and number of eggs produced by females (Laptikhovsky et al., 2008). Specimens found in the Western Mediterranean tend to be more similar to those found in adjacent areas of the Atlantic, whereas those found in the Eastern Mediterranean display adaptations which seem to bring the characteristics of the reproductive strategies of different species in the area closer to each other.

# Cephalopod-environment relationships in other areas

The SW Atlantic is a well-studied area due to the important fisheries for *Illex argentinus* and *Loligo gahi*. Many studies reveal links between the environment and the distribution and abundance of those cephalopods (e.g. Bakun & Csirke, 1998; Semmens et al., 2007).

Annual recruitment success in *I. argentinus* is related to SST in the region where the animals hatch, in particular to the proportion of the hatching grounds occupied by 'frontal' waters and favourable SST conditions (González et al., 1997; Waluda et al., 1999, 2001a). Waluda et al. (2001b) showed that the distribution of *I. argentinus* around the Falkland Islands was associated with areas of thermal gradients, commonly seen at the interface of Falkland Current and Patagonian shelf waters.

Sacau et al. (2005) described the spatio-temporal pattern of abundance of *I. argentinus*, demonstrating that higher catches and higher proportions of mature squid were related to warmer and deeper water. Waluda et al. (2008) studied the spatial dynamics of the *I. argentinus* fishery by tracking the powerful incandescent lights of the jigging vessels used to attract squid, noting that SST during June and July of 2003 and 2004 (the egg-hatching period) was 0.4 and 0.9°C warmer than average, respectively, which may have partially contributed to the reduced fishery yield during 2004 and 2005.

Hatfield (2000) showed that L. gahi hatched in the summer, i.e. at higher temperatures, were significantly larger than squid of the same age but hatched in the winter months. Agnew et al. (2000) showed a negative correlation between SST and the strength of the recruitment of L. gahi, with a delay of 6 months. Arkhipkin et al. (2004) studied the effects of the Falkland current inflows on the ontogenetic migrations of L. gahi and showed that stronger flows of the Falkland current onto the western part of the southern Falkland Shelf induce stronger outflows of warmer and less saline shelf waters, and correspondingly greater offshore movements of squid. Arkhipkin et al. (2006) identified the role of the Falkland current in the dispersal of L. gahi along the Patagonian shelf. They reported a good correspondence between the inshore movements of the current in May-July with the squid abundance in the following September-October. Inter-specific competition between I. argentinus and L. gahi is highly plausible as Arkhipkin & Middleton (2002) reported inverse patterns of abundance of these two species in Falkland waters.

In South African waters, the chokka squid *Loligo reynaudii* (formerly *Loligo vulgaris reynaudii*) has long been the focus of a directed fishery and associated studies (e.g. Augustyn, 1990, 1991; Sauer et al., 1991; Roberts & Sauer, 1994). Olyott et al. (2006) studied

spatio-temporal patterns in maturation of this species off the coast of South Africa, relating maturity cycles to environmental conditions, finding that squid matured smaller in winter/spring than in summer/ autumn and that squid in the east Agulhas Bank matured at a smaller size than squid in the west. Mqoqi et al. (2007) studied the influence of abiotic factors (depth, region, temperature, salinity and oxygen) on the abundance of the cuttlefish *Sepia australis* along the coast of South Africa, suggesting that abundance increases in areas with high temperature anomalies and along increasing bathymetry gradients.

Collins & Rodhouse (2006) reviewed the Southern Ocean cephalopod fauna, reporting the main biological and oceanographic factors related to those species. Rodhouse et al. (1994a, b, 1996) described some environmental relationships with cephalopod distribution and abundance, particularly related to the ommastrephid squid Martialia hyadesi. The appearance of M. hyadesi in the Falkland Islands fishery has been related to SST anomalies (Gonzalez et al., 1997). Teleconnections probably exist between these anomalies, El Niño Southern Oscillation (ENSO) events in the Pacific and sub-decadal oceanographic instability in the Antarctic. However, it is not clear at what stage in the life cycle of M. hyadesi these oceanographic events exert their effect. These authors proposed two alternative, but not mutually exclusive, hypotheses. Warm events prior to the appearance of M. hyadesi may favour reproductive success of the parent generation, giving rise to a strong recruitment, or alternatively this cool water species may extend its range to the edge of the Patagonian Shelf early in the development of cold oceanographic events. In either case, oceanographic effects are probably mediated via effects on the squids' prey. Rodhouse et al. (1996) described the mesoscale oceanography of the Antarctic Polar Front and how it affects cephalopod distribution and abundance.

# Conclusion and future concerns

Numerous studies reviewed here have underlined the high sensitivity of cephalopod species to local, regional and large-scale environmental conditions and changes. Clearly, spatiotemporal environmental variations strongly affect the biological processes and characteristics of cephalopods during their short life cycle. Cephalopods seem to respond to environmental variation both 'actively' (migrating to areas with more favoured environmental conditions) and 'passively' (using optimum environmental conditions to reach certain life stages at different growth rates between different generations).

In many demersal and benthic species, distribution range is related to bathymetry and different groups dominate at different depth ranges, with benthic octopus species tending to occur in the deepest waters. In some demersal species, notably cuttlefish and loliginid squids, inshore-offshore migrations are seen within the range of occurrence. The pelagic species, such as ommastrephid squids, tend to be highly migratory, and are likely to be strongly affected by changes in current systems (O'Dor, 1992) and large-scale oceanographic phenomena (e.g. El Niño). Coastal species may be impacted by variations in water quality (e.g. turbidity and oxygenation) and salinity (related to rainfall and river flow). Local abundance of many species, both demersal and pelagic, has been shown to be related to temperature and or productivity, although these links can often be displaced in both time and space, with conditions experienced by eggs and paralarvae affecting recruitment to the adult population, which may occur several months later in a completely different area. The timing of cephalopod life cycles can often be shown to be related to the seasonal cycle of environmental conditions, raising the issue that climatic change may result in a mismatch between the timing of critical life stages and optimum environmental conditions (Bakun & Csirke, 1998).

Besides the importance of environmental parameters in modulating the abundance of adult cephalopod resources, more attention should be given to the early stages of development, especially in those species with a planktonic stage. This part of most cephalopod life cycles is highly influenced by physical and chemical oceanographic factors, which when combined with the variation of prey abundance will lead to large variations in growth and mortality rates. There is evidently considerable plasticity in life-cycles, and consequently, changes in SST and productivity can affect the life-cycle in unexpected ways. For example, higher temperatures in early life will strongly affect growth rates. In some species, the animals may consequently reach a larger adult size and perhaps achieve greater reproductive success due to a positive relationship between adult body size and fecundity and/or egg size. For example, fecundity in female *Loligo forbesi* increases with body size (Boyle et al., 1995). However, in other species, faster early growth may paradoxically lead to more rapid maturation at a smaller adult body size. In addition, the timing of migration may be altered.

It is not clear for most species whether there is any density dependence in recruitment or spawning success. There is generally high variability in annual abundance of many cephalopods, suggesting that environmental effects on abundance at the population level tend to be transient: there is little evidence that consistently high or low abundance can be sustained over a substantial number of years. Cephalopods are intrinsically unpredictable fishery resources and links between abundance and environmental conditions often become clear only after the fact, although there clearly is scope to use conditions experienced by hatchlings as a means for forecasting fishery success when that generation matures. Based on this general perspective, future research should include a thorough examination and explanation of the environmental 'teleconnection' processes in European Seas (e.g. from NAO and Gulf Stream to local environmental variation) as well as an in-depth overview of the individual and population level responses of cephalopods to a combination of changing environmental habitat descriptors. We can also learn much about cephalopod habitat use from the experience of fishermen and much more use could be made of such 'anecdotal' sources of information, if only to suggest hypotheses that can be tested by future scientific studies.

The ability of environmental fishery models to forecast recruitment suggest that in the future it may be possible to set the level of fishing effort in some cephalopod fisheries (mainly targeted squid species) on the basis of scientifically predicted levels of abundance in advance of recruitment of the individuals into the fishery (Boyle & Rodhouse, 2005). For example, Agnew et al. (2002) have developed an approach that may allow for an increased catch while at the same time reducing the possibility of overexploiting the fishery.

Some questions that should be addressed in future research include:

1. Which environmental factors have the most important effects on individual life history and

population parameters of different cephalopod species, what are the mechanisms underlying these effects and how do they link to patterns of distribution and abundance?

- 2. To what extent do we need to revise our understanding of cephalopod–environment relationships as new data (e.g., on oceanographic phenomena, especially sub-surface phenomena) and analytical techniques (e.g. accounting for spatial and temporal autocorrelation) become available?
- 3. Are these effects observed consistently through time, in different areas and when other aspects of environmental conditions change, and can they be used in stock assessment and/or fishery forecasting for cephalopods?
- 4. What are the specific teleconnection mechanisms, between large scale meteo-oceanic phenomena and local environmental variation, that are relevant to cephalopods?
- 5. Can cephalopod populations be used as indicators of climate change?

Topics of this nature may be useful objectives for new research initiatives to facilitate our understanding of what determines the distribution of cephalopod habitats in an ever changing marine environment, to identify certain species as important environmental change indicators and to improve current stock assessment methods. Research contributions of this type will help to underpin any new management effort under both the ecosystem-based and precautionary approaches.

Acknowledgements This work was funded by the European Commission. It was initiated through FP5 Concerted Action 'CEPHSTOCK' (QLRT-2001-00962) as part of WP3 (Fisheries-Environment Interactions) and concluded under the FP6 Scientific Support to Policies Action 'EnviEFH' (SSA 022466). GJP would also like to acknowledge support from the ANIMATE project (MEXC-CT-2006-042337).

# References

- Agnew, D. J., J. R. Beddington & S. L. Hill, 2002. The potential use of environmental information to manage squid stocks. Canadian Journal of Fisheries and Aquatic Science 59: 1851–1857.
- Agnew, D. J., S. Hill & J. R. Beddington, 2000. Predicting the recruitment strength of an annual squid stock: *Loligo gahi* around the Falkland Islands. Canadian Journal of Fisheries and Aquatic Sciences 57: 2479–2487.
- 🖄 Springer

- Anderson, C. I. H. & P. G. Rodhouse, 2001. Life cycles, oceanography and variability: ommastrephid squid in variable oceanographic environments. Fisheries Research 54: 133–143.
- Aristegui, J., X. A. Alvarez-Salgado, E. D. Barton, F. G. Figueiras, S. Hernandez-Leon, C. Roy & A. M. P. Santos, 2006. Oceanography and fisheries of the Canary Current/ Iberian region of the eastern North Atlantic. In Robinson, A. R. & K. H. Brink (eds), The sea. Harvard University Press, Cambridge, MA: 877–931.
- Arkhipkin, A. I., P. Jereb & S. Ragonese, 2000. Growth and maturation in two successive seasonal groups of the shortfinned squid *Illex coindetii* from the Strait of Sicily (central Mediterranean). ICES Journal of Marine Science 57: 31–41.
- Arkhipkin, A. I., V. V. Laptikhovsky, A. M. Sirota & R. Grzebielec, 2006. The role of the Falkland Current in the dispersal of the squid *Loligo gahi* along the Patagonian Shelf. Estuarine, Coastal and Shelf Science 67: 198–204.
- Arkhipkin, A. I. & D. A. J. Middleton, 2002. Inverse patterns in abundance of *Illex argentinus* and *Loligo gahi* in Falkland waters: possible interspecific competition between squid? Fisheries Research 59: 181–196.
- Arkhipkin, A. I., D. A. J. Middleton, A. M. Sirota & R. Grzebielec, 2004. The effect of Falkland Current inflows on offshore ontogenetic migrations of the squid *Loligo gahi* on the southern shelf of the Falkland Islands. Estuarine, Coastal and Shelf Science 60: 11–22.
- Arvanitidis, C., D. Koutsoubas, J.-P. Robin, J. Pereira, A. Moreno, M. Cunha, V. D. Valavanis & A. Eleftheriou, 2002. A comparison of the fishery biology of three *Illex coindetii* Verany, 1839 (Cephalopoda: Ommastrephidae) populations from the European Atlantic and Mediterranean waters. Bulletin of Marine Science 71: 129–146.
- Atzeni, A., A. Balzano & G. Lai, 1997. Sulle correnti del Golfo di Cagliari: dipendenza dalle correnti del Mediterraneo e simulazione numerica dei regimi stagionali. Quaderni di ricerca del Dipartimento di Ingegneria del Territorio. Sezione di Ingegneria Idraulica: 27–79.
- Augustyn, C. J., 1990. Biological studies on the Chokker squid *Loligo vulgaris reynaudii* (Cephalopoda; Myopsida) on spawning grounds off the south-east coast of South Africa. South African Journal of Marine Science 9: 11–26.
- Augustyn, C. J., 1991. The biomass and ecology of chokka squid *Loligo vulgaris reynaudii* off the west coast of South Africa. South African Journal of Zoology 26: 164–181.
- Augustyn, C. J., M. R. Lipinski, W. H. H. Sauer, M. J. Roberts & B. A. Mitchell-Innes, 1994. Chokka squid on the Agulhas Bank: life history and ecology. South African Journal of Marine Science 90: 143–153.
- Bakun, A. & J. Csirke, 1998. Environmental processes and recruitment variability. In Rodhouse, P. G., E. G. Dawe & R. K. O'Dor (eds), Squid Recruitment Dynamics. The Genus *Illex* as a Model. The Commercial *Illex* Species. Influences on Variability, Vol. 376. FAO Fisheries Technology Paper: 273.
- Balguerias, E., C. Hernandez-Gonzalez & C. Perales-Raya, 2002. On the identity of *Octopus vulgaris* Cuvier, 1797 stocks in the Saharan Bank (Northwest Africa) and their spatiotemporal variations in abundance in relation to some

environmental factors. Bulletin of Marine Science 71: 147-163.

- Balguerias, E., M. E. Quintero & C. L. Hernandez-Gonzalez, 2000. The origin of the Saharan Bank cephalopod fishery. ICES Journal of Marine Science 57: 15–23.
- Barton, E., J. Aristegui, P. Tett & E. Navarro-Perez, 2004. Variability in the Canary Islands area of filament-eddy exchanges. Progress in Oceanography 62: 71–94.
- Bellido, J. M., 2002. Use of geographic information systems, spatial and environment-based models to study ecology and fishery of the veined squid (*Loligo forbesi* Steenstrup 1856) in Scottish waters. PhD Thesis. University of Aberdeen, United Kingdom: 183.
- Bellido, J. M., G. J. Pierce & J. Wang, 2001. Modelling intraannual variation in abundance of squid *Loligo forbesi* in Scottish waters using generalized additive models. Fisheries Research 52: 23–39.
- Bettencourt, V. & A. Guerra, 1999. Carbon- and oxygenisotope composition of the cuttlebone of *Sepia officinalis*: a tool for predicting ecological information? Marine Biology 133: 651–657.
- Boletzky, S. V., 1986. Reproductive strategies in cephalopods: variations and flexibility of life-history. Advances in Invertebrate Reproduction 4: 379–389.
- Boyle, P. R., 1990. Cephalopod biology in the fisheries context. Fisheries Research 8: 303–321.
- Boyle, P. R., G. J. Pierce & L. C. Hastie, 1995. Flexible reproductive strategies in the squid *Loligo forbesi*. Marine Biology 121: 501–508.
- Boyle, P. R. & P. G. Rodhouse, 2005. Cephalopods. Ecology and Fisheries, Blackwell Science Ltd, Oxford.
- Bravo de Laguna, J. & G. E. Balguerias, 1993. La pesqueria sahariana de cefalopodos: una breve revision. Boletin del Instituto Espanol de Oceanografia 9: 203–213.
- Caddy, J. F., 1983. The cephalopods: factors relevant to their population dynamics and to the assessment and management of stocks. In Caddy, J. F. (ed.), Advances in Assessment of World Cephalopod Resources, Vol. 231. FAO Fisheries Technical Paper, Rome: 416–449.
- Caddy, J. F. & P. G. Rodhouse, 1998. Cephalopod and groundfish landings: evidence for ecological change in global fisheries? Reviews in Fish Biology and Fisheries 8: 431–444.
- Challier, L., J. Royer, G. J. Pierce, N. Bailey, B. Roel & J. P. Robin, 2005. Environmental and stock effects on recruitment variability in the English Channel squid *Loligo forbesi*. Aquatic Living Resources 18: 353–360.
- Chen, C. S., G. J. Pierce, J. Wang, J. P. Robin, J. C. Poulard, J. Pereira, A. F. Zuur, P. R. Boyle, N. Bailey, D. J. Beare, P. Jereb, S. Ragonese, A. Mannini & L. Orsi-Relini, 2006. The apparent disappearance of *Loligo forbesi* from the south of its range in the 1990s: trends in *Loligo* spp. abundance in the northeast Atlantic and possible environmental influences. Fisheries Research 78: 44–54.
- Chen, X. J., X. H. Zhao & Y. Chen, 2007. Influence of El Nino/ La Nina on the western winter-spring cohort of neon flying squid (*Ommastrephes bartramii*) in the northwestern Pacific Ocean. ICES Journal of Marine Science 64: 1152–1160.
- Clarke, M. R., N. MacLeod, H. P. Castello & M. C. Pinedo, 1980. Cephalopod remains from the stomach of a sperm

whale stranded at Rio Grande do Sul in Brazil. Marine Biology 59: 235–239.

- Collins, M. A. & P. G. K. Rodhouse, 2006. Southern ocean cephalopods. Advances in Marine Biology 50: 191–265.
- Collins, M. A., C. Yau, A. Allcock & M. H. Thurston, 2001. Distribution of deep-water benthic and bentho-pelagic cephalopods from the north-east Atlantic. Journal of the Marine Biological Association of the UK 81: 105–117.
- Craig, S. & J. Overnell, 2003. Metals in squid, *Loligo forbesi*, adults, eggs and hatchlings. No evidence for a role for Cuor Zn-metallothionein. Comparative Biochemistry and Physiology Part C 134: 311–317.
- Cuccu, D., P. Jereb, S. Ragonese, N. Giovannini, S. Colella & A. Cau, 2008. On the abundance and spatial distribution of *Illex coindetii* and *Eledone moschata* in the Sardinian Seas (central-western Mediterranean)—A preliminary and qualitative investigation with special attention to some environmental constraints. Bollettino Malacologico 54: 15–25.
- Cunha, M. M., A. Moreno & J. M. F. Pereira, 1995. Spatial and temporal occurrences of *Loligo* spp. in Portuguese waters. ICES CM 1995/K:33.
- Cushing, D. H., 1975. Marine Ecology and Fisheries. Cambridge University Press, Cambridge: 271.
- Dawe, E. G., E. B. Colbourne & K. F. Drinkwater, 2000. Environmental effects on recruitment of shorth-finned squid (*Illex illecebrosus*). ICES Journal of Marine Science 57: 1002–1013.
- Dawe, E. G., L. C. Hendrickson, E. B. Colbourne, M. A. Showell, D. D. Jones & D. A. Methven, 2001. Squids as potential indicators species of environmental or ecosystem change in the Northwest Atlantic Ocean. ICES CM 2001/ K:07.
- De Alteris, J., L. Skrobe & C. Lipsky, 1998. Fish habitat: essential fish habitat and rehabilitation. American Fisheries Society Symposium Series 22: 224–237.
- De Heij, A. & R. P. Baayen, 2005. Seasonal distribution of cephalopod species living in the central and southern North Sea. Basteria 69: 91–119.
- Demarcq, H. & V. Faure, 2000. Coastal upwelling and associated retention indices derived from satellite SST. Application to *Octopus vulgaris* recruitment. Oceanologica Acta 23: 391–408.
- Domingues, P. M., V. Bettencourt & A. Guerra, 2006. Growth of *Sepia officinalis* in captivity and in nature. Vie et Milieu. Life and Environment 56: 109–120.
- Domingues, P. M., A. Sykes & J. P. Andrade, 2002. The effects of temperature in the life cycle of two consecutive generations of the cuttlefish *Sepia officinalis* L. cultured in the Algarve (South Portugal). Aquaculture International 10: 207–220.
- Dunn, M. R., 1999. Aspects of the stock dynamics and exploitation of cuttlefish, *Sepia officinalis* (Linnaeus, 1758), in the English Channel. Fisheries Research 40: 277–293.
- Erzini, K., 2005. Trends in NE Atlantic landings (southern Portugal): identifying the relative importance of fisheries and environmental variables. Fisheries Oceanography 14: 195–209.
- Faraj, A. & N. Bez, 2007. Spatial considerations for the Dakhla stock of Octopus vulgaris: indicators, patterns, and

fisheries interactions. ICES Journal of Marine Science 64: 1820–1828.

- Fogarty, M. J., 1989. Forecasting yield and abundance of exploited invertebrates. In Caddy, J. F. (ed.), Marine Invertebrate Fisheries: Their Assessment and Management. Wiley: 701–724.
- Forsythe, J. W., 1993. A working hypothesis of how seasonal temperature change may impact the field growth of young cephalopods. In Okutani, T., R. K. O'Dor & T. Kubodera (eds), Recent Advances in Cephalopod Fisheries Biology. Tokai University Press, Tokyo: 133–143.
- Georgakarakos, S., J. Haralabus, V. D. Valavanis, C. Arvanitidis & D. Koutsoubas, 2002. Prediction of fishery exploitation stocks of Loliginid and Ommastrephid squids in Greek waters (Eastern Mediterranean) using uni- and multivariate time series analysis techniques. Bulletin of Marine Science 71: 269–288.
- Georgakarakos, S., D. Koutsoubas & V. D. Valavanis, 2006. Time series analysis and forecasting techniques applied on Loliginid and Ommastrephid landings in Greek waters. Fisheries Research 78: 55–71.
- Gomez-Munoz, V. M., 1990. A model to estimate catches from a short fishery statistics survey. Bulletin of Marine Science 46: 719–722.
- González, A. F., J. Otero, A. Guerra, R. Prego, F. J. Rocha & A. W. Dale, 2005. Temporal variation of cephalopod paralarvae in a wind-driven upwelling area (Ria of Vigo, NW Spain). Journal of Plankton Research 27: 271–277.
- González, A. F., P. Trathan, C. Yau & P. G. Rodhouse, 1997. Interactions between oceanography, ecology and fishery biology of ommastrephid squid *Martialia hyadesi* in the South Atlantic. Marine Ecology Progress Series 152: 205– 215.
- González, M. & P. Sanchez, 2002. Cephalopod assemblages caught by trawling along the Iberian Peninsula Mediterranean coast. Scientia Marina 66: 199–208.
- Gowland, F. C., 2002. Developmental variability in loliginid squid (*Loligo forbesi* and *Sepioteuthis australis*). PhD Thesis, University of Aberdeen.
- Guerra, A., 1992. Mollusca, cephalopoda. In: Ramos, M. A., J. Alba, X. Bellés, J. Gosálbez, A. Guerra, E. Macpherson, F. Martín, J. Serrano & J. Templado (eds), Fauna Ibérica, Vol. 1. Museo Nacional de Ciencias Naturales, CSIC, Madrid: 327 pp.
- Guerra, A., 2004. Relaciones entre la oceanografia y los recursos marinos renovables. Revista de la Real Academia de Ciencias Exactas. Fisicas y Naturales 98: 77–88.
- Guerra, A., 2006a. Ecology of Sepia officinalis. Vie et Milieu. Life and Environment 56: 97–107.
- Guerra, A., 2006b. Estrategia evolutiva de los cefalopodos. Investigacion y Ciencia 355: 50–59.
- Guerra, A., A. F. González & F. Rocha, 2002. Appearance of the common paper nautilus *Argonauta argo* related to the increase of the sea surface temperature in the north-eastern Atlantic. Journal of Marine Biological Association of U.K. 82: 855–858.
- Guerra, A. & F. Rocha, 1994. The life history of *Loligo vulgaris* and *Loligo forbesi* (Cephalopoda: Loliginidae) in Galician waters (NW Spain). Fisheries Research 21: 43–69.
- Guerra, A. & P. Sanchez, 1985. Comparacion de las pesquerias de cefalopodos de dos areas de afloramiento de la costa

occidental africana. Simposio Internacional sobre Aflororamientos. Instituto de Investigaciones Pesqueras, Barcelona II: 749–760.

- Hastie, L. C., 1996. Estimation of trawl codend selectivity for squid (*Loligo forbesi*) based on Scottish research vessel survey data. ICES Journal of Marine Science 53: 741–744.
- Hastie, L. C., J. B. Joy, G. J. Pierce & C. Yau, 1994. Reproductive biology of *Todaropsis eblanae* (Cephalopoda: Ommastrephidae) in Scottish waters. Journal of the Marine Biological Association of the United Kingdom 74: 367–382.
- Hatfield, E. M. C., 2000. Do some like it hot? Temperature as a possible determinant of variability in the growth of the Patagonian squid, *Loligo gahi* (Cephalopoda: Loliginidae). Fisheries Research 47: 27–40.
- Holme, N. A., 1974. The biology of *Loligo forbesi* Steenstrup (Mollusca: Cephalopoda) in the Plymouth area. Journal of Marine Biological Association of the United Kingdom 54: 481–503.
- Hurrell, J. W., 1995. Decadal trends in the North Atlantic Oscillation: regional temperatures and precipitation. Science 269: 676–679.
- Jackson, G. D., 2004. Cephalopod growth: historical context and future directions. Marine and Freshwater Research 55: 327–330.
- Jereb, P., D. Cuccu, D. Giordano, P. Maiorano & S. Ragonese, 2005. Using historical series of trawl surveys data to investigate cephalopods: a new method of exploratory analysis. Biologia Marina Mediterranea 12: 526–530.
- Jereb, P., D. Massi, G. Norrito & F. Fiorentino, 2001. Preliminary observations of environmental effects on spatial distribution and abundance of *Eledone cirrhosa* and *Illex coindetii* in the Strait of Sicily (Central Mediterranean Sea). ICES CM 2001/K:34.
- Jereb, P. & C. F. E. Roper, 2005. Cephalopods of the World: An Annotated and Illustrated Catalogue of Cephalopod Species Known to Date. Vol. 1. Chambered Nautiluses and Sepioids (Nautilidae, Sepiidae, Sepiolidae, Sepiadariidae, Idiosepiidae and Spirulidae). FAO Species Catalogue for Fisheries Purposes, No 4, Vol. 1. FAO, Rome.
- Jones, P. D., T. Jonsson & D. Wheeler, 1997. Extension to the North Atlantic Oscillation using early instrumental pressure observations from Gibraltar and Southwest Iceland. International Journal of Climatolology 17: 1433–1450.
- Katara, I., J. Illian, G. J. Pierce, B. Scott & J. Wang, 2008. Atmospheric forcing on chlorophyll concentration in the Mediterranean. Hydrobiologia (this volume).
- Lafuente, J. G. & J. Ruiz, 2007. The Gulf of Cadiz pelagic ecosystem: a review. Progress in Oceanography 74: 228–251.
- Laptikhovsky, V., J. Pereira, A. Salman, A. Arkhipov & A. Costa, 2008. A habitat-dependence in cephalopod and pelagophil fish reproductive strategies in the Mediterranean Sea. Bollettino Malacologico (in press).
- Lefkaditou, E., P. Sanchez, A. Tsangridis & A. Adamidou, 1998a. A preliminary investigation on how meteorological changes may affect beach-seine catches of *Loligo vulgaris* in the Thracian Sea (Eastern Mediterranean). South African Journal of Marine Science 20: 453–461.
- Lefkaditou, E., A. Siapatis & C. Papaconstantinou, 1998b. Seasonal and spatial changes in the abundance and

distribution of *Eledone moschata* (Cephalopoda: Octopoda), in the South Aegean Sea (Eastern Mediterranean). ICES CM 1998/M:44.

- Lefkaditou, E., A. Souplet, N. Peristeraki, M. Gonzalez, S. Kavadas, P. Vidoris, D. Cuccu & C. Papaconstantinou, 2000. Preliminary investigation of factors affecting the spatial distribution and abundance of *Eledone cirrhosa* (Cephalopoda: Octopoda) in the Mediterranean Sea. In Bertrand, J. A. & G. Relini (eds), Demersal Resources in the Mediterranean. Actes de Colloques 26, Ifremer, Plouzane: 208–218.
- Lefkaditou E., G. Verriopoulos & V. Valavanis, 2007. Research on cephalopod resources in Hellas. In Papaconstantinou, C., A. Zenetos, V. Vassilopoulou & G. Tserpes (eds), State of Hellenic Fisheries. Hellenic Centre for Marine Research, Athens: 440–451.
- Lloret, J., J. Lleonart, I. Sole & J. M. Fromentin, 2001. Fluctuations of landings and environmental conditions in the North-Western Mediterranean Sea. Fisheries Oceanography 10: 33–50.
- Lourenço, S. & J. Pereira, 2006. Estimating standardised landings per unit effort for an octopus mixed components fishery. Fisheries Research 78: 89–95.
- Mangold, K., 1983. *Eledone moschata*. In Boyle, P. R. (ed.), Cephalopod Life Cycles. Species Accounts. Academic Press, New York: 387–400.
- Mazzola, S., A. Garcia & J. G. Lafuente, 2000. Distribution, Biology and Biomass Estimates of the Sicilian Channel Anchovy. Final Report. Commission of the European Communities. Directorate General for Fisheries (DG-XIV), Mimeo:152.
- Melzner, F., C. Bock & H.-O. Portner, 2006. Critical temperatures in the cephalopod *Sepia officinalis* investigated using in vivo 31P NMR spectroscopy. Journal of Experimental Biology 209: 891–906.
- Millot, C., 2005. Circulation in the Mediterranean Sea: evidences, databases and unanswered questions. Scientia marina 69: 5–21.
- Millot, C. & I. Taupier-Letage, 2004. Circulation in the Mediterranean Sea. The Handbook of Environmental Chemistry. The Natural Environment and the Biological Cycles 1: 1–30.
- Moreno, A., M. Azevedo, J. Pereira & G. J. Pierce, 2007. Growth strategies in the squid *Loligo vulgaris* from Portuguese waters. Marine Biology Research 3: 49–59.
- Moreno, A. & J. M. F. Pereira, 1998. Cephalopod paralarval distribution in Iberian Atlantic waters. ICES CM 1998/ M:42.
- Moreno, A. & C. Sousa-Reis, 1995. Seasonal distribution of loliginid early young stages in the Portuguese continental shelf. ICES CM 1995/K:32.
- Mqoqi, M., M. R. Lipinski & A. G. V. Salvanes, 2007. The ecology of *Sepia australis* (Cephalopoda: Sepiidae) along the south coast of South Africa. ICES Journal of Marine Science 64: 945–955.
- O'Dor, R. K., 1992. Big squid in big currents. South African Journal of Marine Science 12: 225–235.
- Olyott, L. J. H., W. H. H. Sauer & A. J. Booth, 2006. Spatiotemporal patterns in maturation of the chokka squid (*Loligo vulgaris reynaudii*) off the coast of South Africa. ICES Journal of Marine Science 63: 1649–1664.

- Orsi Relini, L., A. Mannini, F. Fiorentino, G. Palandri & G. Relini, 2006. Biology and fishery of *E. cirrhosa* in the Ligurian Sea. Fisheries Research 78: 72–88.
- Otero, J., 2006. Ecologia del pulpo comun (Octopus vulgaris Cuvier, 1797) en un area de afloramiento costero (Galicia, NE Atlántico). PhD Thesis, University of Vigo, Spain.
- Otero, J., X. A. Alvarez-Salgado, A. F. Gonzalez, A. Miranda, S. B. Groom, J. M. Cabanas, G. Casas, B. Wheatley & A. Guerra, 2008. Bottom-up and top-down controls of common octopus (*Octopus vulgaris*) in a wind-driven upwelling ecosystem (Galicia, NE Atlantic). Marine Ecology Progress Series. doi:10.3354/meps07437.
- Otero, J., A. F. Gonzalez, M. P. Sieiro & A. Guerra, 2007. Reproductive cycle and energy allocation of *Octopus vulgaris* in Galician waters, NE Atlantic. Fisheries Research 85: 122–129.
- Otero, J., F. Rocha, A. F. Gonzalez, J. Gracia & A. Guerra, 2005. Modelling artisanal coastal fisheries of Galicia (NW Spain) based on data obtained from fishers: the case of *Octopus vulgaris*. Scientia Marina 69: 577–585.
- Pascual, S., A. F. Gonzalez & A. Guerra, 2007. Parasite recruitment and oceanographic regime: evidence suggesting a relationship on a global scale. Biological Reviews 82: 257–263.
- Pecl, G. T., M. A. Steer & K. E. Hodgson, 2004. The role of hatchling size in generating the intrinsic size-at-age variability of cephalopods: extending the Forsythe Hypothesis. Marine and Freshwater Research 55: 387–394.
- Piatkowski, U., G. J. Pierce & M. Morais da Cunha, 2001. Impact of cephalopods in the food chain and their interaction with the environment and fisheries: an overview. Fisheries Research 52: 5–10.
- Piccioni, A., M. Gabriele, E. Salusti & E. Zambianchi, 1988. Wind-induced upwellings off the southern coast of Sicily. Oceanologica Acta 11: 309–314.
- Pierce, G. J., N. Bailey, Y. Stratoudakis & A. Newton, 1998. Distribution and abundance of the fished population of *Loligo forbesi* in Scottish waters: analysis of research cruise data. ICES Journal of Marine Science 55: 14–33.
- Pierce, G. J. & P. R. Boyle, 2003. Empirical modelling of interannual trends in abundance of squid (*Loligo forbesi*) in Scottish waters. Fisheries Research 59: 305–326.
- Pierce, G. J., P. R. Boyle, L. C. Hastie & M. B. Santos, 1994. Diets of squid *Loligo forbesi* and *Loligo vulgaris* in the northeast Atlantic. Fisheries Research 21: 149–164.
- Pierce, G. J. & A. Guerra, 1994. Stock assessment methods used for cephalopod fisheries. Fisheries Research 21: 255– 286.
- Pierce, G. J., M. B. Santos, C. D. MacLeod, J. Wang, V. D. Valavanis & A. F. Zuur, 2006. Modelling environmental influences on squid life history, distribution, and abundance. Proceedings of the GLOBEC-CLIOTOP Working Group 3 and the Pelagic Fisheries Research Program (PFRP) Workshop. Nov. 14–17, 2006, University of Hawaii, Honolulu.
- Pierce, G. J., G. Stowasser, C. D. MacLeod, T. Valinassab, M. B. Santos & J. Wang 2005a. Mapping and modelling spawning habitat for the squid *Loligo forbesi*. In The Third International Symposium on GIS/Spatial Analyses in Fishery and Aquatic Sciences, 22–26, 2005, Shanghai, China.

- Pierce, G. J., J. Wang, J. M. Bellido, C. M. Waluda, J. P. Robin, V. Denis, D. Koutsoubas, V. D. Valavanis & P. R. Boyle, 1998. Relationships between cephalopod abundance and environmental conditions in the Northeast Atlantic and Mediterranean as revealed by GIS. ICES CM 1998/M:20.
- Pierce, G. J., J. Wang, X. Zheng, J. M. Bellido, P. R. Boyle, V. Denis & J.-P. Robin, 2001. A cephalopod fishery GIS for the northeast Atlantic: development and application. International Journal of Geographical Information Science 15: 763–784.
- Pierce, G. J., A. F. Zuur, J. M. Smith, M. B. Santos, N. Bailey, C. S. Chena & P. R. Boyle, 2005b. Interannual variation in life-cycle characteristics of the veined squid (*Loligo forbesi*) in Scottish (UK) waters. Aquatic Living Resources 18: 327–340.
- Portner, H. O., 1994. Coordination of metabolism, acid-base regulation and haemocyanin function in cephalopods. In Portner, H. O., R. K. O'Dor & D. L. Macmillan (eds), Physiology of Cephalopod Molluscs: Lifestyle and Performance Adaptations. Gordon & Breach, Basel: 131–148.
- Quetglas, A., A. Carbonell & P. Sanchez, 2000. Demersal continental shelf and upper slope cephalopod assemblages from the Balearic Sea (North-Western Mediterranean): biological aspects of some deep-sea species. Estuarine, Coastal and Shelf Science 50: 739–749.
- Quetglas, A. & B. Morales-Nin, 2004. Age and growth of the Ommastrephid squid *Todarodes sagittatus* from the western Mediterranean Sea. Journal of the Marine Biological Association of the UK 84: 421–426.
- Ragonese, S., P. Jereb & E. Dawe, 2002. A comparison of growth performance across the squid genus *Illex* (Cephalopoda, Ommastrephidae) based on modelling weight-atlength and age data. Journal of Shellfish Research 21: 851–860.
- Rasero, M., 1994. Relationship between cephalopod abundance and upwelling: the case of *Todaropsis eblanae* (Cephalopoda: Ommastrephidae) in Galician waters (NW Spain). ICES CM 1994/K:40.
- Redfern, J. V., M. C. Ferguson, E. A. Becker, K. D. Hyrenbach, C. Good, J. Barlow, K. Kaschner, M. F. Baumgartner, K. A. Forney, L. T. Ballance, P. Fauchald, P. Halpin, T. Hamazaki, A. J. Pershing, S. S. Qian, A. Read, S. B. Reilly, L. F. Torres & F. Werner, 2006. Techniques for cetacean habitat modelling. Marine Ecology Progress Series 310: 271–295.
- Relvas, P., E. D. Barton, J. Dubert, P. B. Oliveira, A. Peliz, J. C. B. da Silva & A. M. P. Santos, 2007. Physical oceanography of the western Iberia ecosystem: Latest views and challenges. Progress in Oceanography 74: 149–173.
- Rio, M. H., P. M. Poulain, A. Pascual, E. Mauri, G. Larnicol & R. Santoleri, 2007. A mean dynamic topography of the Mediterranean Sea computed from altimetric data, in-situ measurements and a general circulation model. Journal of Marine Systems 65: 484–508.
- Roberts, M. J. & W. H. H. Sauer, 1994. Environment: the key to understanding the South African chokka squid (*Loligo* vulgaris reynaudii) life-cycle and fishery? Antarctic Science 6: 249–258.
- Robin, J. P. & V. Denis, 1999. Squid stock fluctuations and water temperature: temporal analysis of English Channel Loliginidae. Journal of Applied Ecology 36: 101–110.

- Robinson, R. A., J. A. Learmonth, A. M. Hutson, C. D. Macleod, T. H. Sparks, D. I. Leech, G. J. Pierce, M. M. Rehfisch & H. Q. P. Crick, 2005. Climate Change and Migratory Species: A Report for DEFRA on Research Contract CR0302. BTO Research Report 414, British Trust for Ornithology.
- Rochet, M.-J., 2000. A comparative approach to life-history strategies and tactics among four orders of teleost fish. ICES Journal of Marine Science 57: 228–239.
- Rocha, F., J. Gracia, A. F. Gonzalez, C. M. Jardon & A. Guerra, 2004. Reliability of a model based on a short fishery statistics survey: application to the Northeast Atlantic monkfish fishery. ICES Journal of Marine Science 61: 25–34.
- Rocha, F., A. Guerra & F. Gonzalez, 2001. A review of reproductive strategies in cephalopods. Biological Reviews 76: 291–304.
- Rocha, F., A. Guerra, R. Prego & U. Piatkowski, 1999. Cephalopod paralarvae and upwelling conditions off Galician waters (NW Spain). Journal of Plankton Research 21: 21–33.
- Rocha, F., J. Otero, R. Outeiral, A. F. Gonzalez, J. Gracia & A. Guerra, 2006. Modelling small-scale coastal fisheries of Galicia (NW Spain) based on data obtained from fisheries: the case of *Sepia officinalis*. Scientia Marina 70: 593–601.
- Rodhouse, P. G., 2001. Managing and forecasting squid fisheries in variable environments. Fisheries Research 54: 3–8.
- Rodhouse, P. G., J. Barton, E. M. C. Hatfield & C. Symon, 1995. *Illex argentinus*: life cycle, population structure and fishery. ICES Marine Science Symposium 199: 425–432.
- Rodhouse, P. G., U. Piatkowski & C. C. Lu, 1994a. Southern ocean cephalopods: life cycles and populations. Antarctic Science 6: 135–290.
- Rodhouse, P. G., P. A. Prince, P. N. Trathan, E. M. C. Hatfield, J. L. Watkins, D. G. Bone, E. J. Murphy & M. G. White, 1996. Cephalopods and mesoscale oceanography at the Antarctic Polar Front: satellite tracked predators locate pelagic trophic interactions. Marine Ecology Progress Series 136: 37–50.
- Rodhouse, P. G., K. Robinson, S. B. Gajdatsy, H. I. Daly & M. J. S. Ashmore, 1994b. Growth, Age structure and Environmental history in the cephalopod *Martialia hyadesi* (Teuthoidea, Ommastrephidae) at the Antarctic Polar Frontal zone and on the Patagonian Shelf Edge. Antarctic Science 6: 259–267.
- Rodhouse, P. G., C. M. Waluda, E. Morales-Bojorquez & A. Hernandez-Herrera, 2006. Fishery biology of the Humboldt squid, *Dosidicus gigas*, in the Eastern Pacific Ocean. Fisheries Research 79: 13–15.
- Rowell, T. W., J. H. Young, J. C. Poulard & J. P. Robin, 1985. Changes in the distribution and biological characteristics of *Illex illecebrosus* on the Scotian shelf, 1980–83. NAFO Scientific Council Studies 9: 11–26.
- Royer, J., G. J. Pierce, E. Foucher & J.-P. Robin, 2006. The English Channel stock of *Sepia officinalis*: Modelling variability in abundance and impact of the fishery. Fisheries Research 78: 96–106.
- Sacau, M., G. J. Pierce, J. Wang, A. I. Arkhipkin, J. Portela, P. Brickle, M. B. Santos & X. Cardoso, 2005. The spatiotemporal pattern of Argentine shortfin squid *Illex argentinus* abundance in the southwest Atlantic. Aquatic Living Resource 18: 361–372.

- Sakaguchi, H., T. Hamano & A. Nakazono, 1999. Occurrence of planktonic juveniles of *Octopus vulgaris* in eastern Iyo-Nada of the Seto Inland sea, Japan. Bulletin of the Japanese Society of Fisheries Oceanography 63: 181–187.
- Santurtun, M., Y. Sagarminaga, P. Lucio, I. Galparsoro, J. Quincoces & A. Iriondo, 2004. Interannual trends in catches of squid (*Loligo* spp.) in the Bay of Biscay (ICES Div. VIIIa, b, d) during 2000 in relation to oceanographic features. ICES CM 2004/CC.
- Sauer, W. H. H., W. S. Goschen & A. S. Koorts, 1991. A preliminary investigation of the effect of sea temperature fluctuations and wind direction on catches of Chokka squid *Loligo vulgaris reynaudii* off the Eastern Cape, South Africa. South African Journal of Marine Science 11: 467–473.
- Semmens, J. M., G. T. Pecl, B. M. Gillanders, C. M. Waluda, E. K. Shea, D. Jouffre, T. Ichii, K. Zumholz, O. N. Katugin, S. C. Leporati & P. W. Shaw, 2007. Approaches to resolving cephalopod movement and migration patterns. Reviews in Fish Biology and Fisheries 17: 401–423.
- Shaw, P. W., G. J. Pierce & P. R. Boyle, 1999. Subtle population structuring within a highly vagile marine invertebrate, the Veined Squid *Loligo forbesi*, demonstrated with microsatellite DNA markers. Molecular Ecology 8: 407–417.
- Silva, L., F. Ramos & I. Sobrino, 2004. Reproductive biology of *Eledone moschata* (Cephalopoda: Octopodidae) in the Gulf of Cádiz (south-western Spain, ICES Division IXa). Journal of the Marine Biological Association of the United Kingdom 84: 1221–1226.
- Simon, F., F. Rocha & A. Guerra, 1996. The small-scale squid hand-jig fishery off the northwestern Iberian Peninsula: application of a model based on a short survey of fishery statistics. Fisheries Research 25: 253–263.
- Sims, D. W., M. J. Genner, A. J. Southward & S. J. Hawkins, 2001. Timing of squid migration reflects North Atlantic climate variability. Proceedings of the Royal Society of London 268(1485): 2607–2611.
- Smith, J. M., G. J. Pierce, A. F. Zuur & P. R. Boyle, 2005. Seasonal patterns of investment in reproductive and somatic tissues in the squid *Loligo forbesi*. Aquatic Living Resources 18: 341–351.
- Sobrino, I., L. Silva, J. M. Bellido & F. Ramos, 2002. Rainfall, river discharges and sea temperature as factors affecting abundance of two coastal benthic cephalopod species in the Gulf of Cadiz. Bulletin of Marine Science 71: 851–866.
- Solow, A. R., 2001. Observation error and the detection of delayed density dependence. Ecology 82: 3263–3264.
- Valavanis, V. D., S. Georgakarakos, A. Kapantagakis, A. Palialexis & I. Katara, 2004. A GIS environmental modelling approach to essential fish habitat designation. Ecological Modelling 178: 417–427.
- Valavanis, V. D., S. Georgakarakos, D. Koutsoubas, C. Arvanitidis & J. Haralabous, 2002. Development of a marine information system for Cephalopod fisheries in the Greek Seas (Eastern Mediterranean). Bulletin of Marine Science 71: 867–882.
- Valavanis, V. D., I. Katara & A. Palialexis, 2005. Marine GIS: identification of mesoscale oceanic thermal fronts. International Journal of Geographical Information Science 19: 1131–1147.

- Valavanis, V. D., G. J. Pierce, A. F. Zuur, A. Palialexis, A. Saveliev, I. Katara & J. Wang, 2008. Modelling of essential fish habitat based on remote sensing, spatial analysis and GIS. Hydrobiologia (this volume).
- Van Aken, H. M. & G. Becker, 1996. Hydrography and through-flow in the north-eastern North Atlantic Ocean: the NANSEN project. Progress in Oceanography 38: 297– 346.
- Vecchione, M., 1999. Extraordinary abundance of squid paralarvae in the tropical eastern Pacific Ocean during El Niño of 1987. Fishery Bulletin 97: 1025–1030.
- Villa, H., J. Quintela, M. L. Coelho, J. D. Icely & J. P. Andrade, 1997. Phytoplankton biomass and zooplankton abundance on the south coast of Portugal (Sagres), with special reference to spawning of *Loligo vulgaris*. Scientia Marina 61: 123–129.
- Villanueva, R., 1995. Experimental rearing and growth of plancktonic *Octopus vulgaris* from hatching to settlement. Canadian Journal of Fisheries and Aquatic Sciences 52: 2639–2650.
- Villanueva, R., 2000. Effect of temperature on statolith growth of the European squid *Loligo vulgaris* during early life. Marine Biology 136: 449–460.
- Villanueva, R., A. Arkhipkin, P. Jereb, E. Lefkaditou, M. R. Lipinski, C. Perales-Raya, J. Riba & F. Rocha, 2003. Embryonic life of the Loliginid squid *Loligo vulgaris*: comparison between statoliths of Atlantic and Mediterranean populations. Marine Ecology Progress Series 253: 197–208.
- Waluda, C. M., H. J. Griffiths & P. G. Rodhouse, 2008. Remotely sensed spatial dynamics of the *Illex argentinus* fishery Southwest Atlantic. Fisheries Research 91: 196– 202.
- Waluda, C. M. & G. J. Pierce, 1998. Temporal and spatial patterns in the distribution of squid *Loligo* spp. in United Kingdom waters. South African Journal of Marine Science 20: 323–336.
- Waluda, C. M. & P. G. Rodhouse, 2006. Remotely sensed mesoscale oceanography of the Central Eastern Pacific and recruitment variability in *Dosidicus gigas*. Marine Ecology Progress Series 310: 25–32.
- Waluda, C. M, P. G. Rodhouse, G. P. Podestá, P. N. Trathan & G. J. Pierce. 2001a. Oceanography of *Illex argentinus* (Cephalopoda: Ommastrephidae) hatching and influences on recruitment variability. Marine Biology 139: 671–679.
- Waluda, C. M., P. G. Rodhouse, P. N. Trathan & G. J. Pierce, 2001b. Remotely sensed mesoscale oceanography and the distribution of *Illex argentinus* in the South Atlantic. Fisheries Oceanography 10: 207–216.
- Waluda, C. M., P. N. Trathan, C. D. Elvidge, V. R. Hobson & P. G. Rodhouse, 2002. Throwing light on straddling stocks of *Illex argentinus*: assessing fishing intensity with satellite imagery. Canadian Journal of Fisheries and Aquatic Science 59: 592–596.
- Waluda, C. M., P. N. Trathan & P. G. Rodhouse, 1999. Influence of oceanographic variability on recruitment in the *Illex argentinus* (Cephalopoda: Ommastrephidae) fishery in the South Atlantic. Marine Ecology Progress Series 183: 159–167.
- Waluda, C. M., C. Yamashiro & P. G. Rodhouse, 2006. Influence of the ENSO cycle on the light-fishery for

*Dosidicus gigas* in the Peru Current: an analysis of remotely sensed data. Fisheries Research 79: 56–63.

- Wang, J., G. J. Pierce, P. R. Boyle, V. Denis, J. P. Robin & J. M. Bellido, 2003. Spatial and temporal patterns of cuttlefish (*Sepia officinalis*) abundance and environmental influences: a case study using trawl fishery data in French Atlantic coastal, English Channel, and adjacent waters. ICES Journal of Marine Science 60: 1149–1158.
- Wang, J., G. J. Pierce, M. B. Santos & P. R. Boyle, 2004. Integration of GIS, remote sensing and statistical technologies for analysing and modelling cephalopod resources dynamics in the Northeast Atlantic waters. Littoral 2004, Seventh International Conference Delivering Sustainable

Coasts: Connecting Science and Policy. Sep. 20–22, 2004. Aberdeen, Scotland, UK.

- Young, I. A., G. J. Pierce, J. Murphy, H. I. Daly & N. Bailey, 2006a. Application of the Gomez- Muñoz model to estimate catch and effort in squid fisheries in Scotland. Fisheries Research 78: 26–38.
- Young, I. A. G., G. J. Pierce, G. Stowasser, M. B. Santos, J. Wang, P. R. Boyle, P. W. Shaw, N. Bailey, I. Tuck & M. A. Collins, 2006b. The Moray Firth directed squid fishery. Fisheries Research 78: 39-43.
- Zuur, A. F. & G. J. Pierce, 2004. Common trends in northeast Atlantic squid time series. Journal of Sea Research 52: 57–72.

# FISH HABITAT MAPPING

# Influences of environmental variability on the population structure and distribution patterns of the short-fin squid *Illex coindetii* (Cephalopoda: Ommastrephidae) in the Eastern Ionian Sea

Eugenia Lefkaditou · Chrissi-Yianna Politou · Andreas Palialexis · John Dokos · Panayota Cosmopoulos · Vasilis D. Valavanis

© Springer Science+Business Media B.V. 2008

Abstract Illex coindetii is the most common benthic ommastrephid squid exploited by bottom trawl in the Mediterranean Sea. A recent study examining trends in population metrics based on data from the International Bottom Trawl Surveys in the Mediterranean (MEDITS) has shown an increasing trend in average lengths of I. coindetii sampled in the eastern Ionian Sea, suggesting that this is possibly due to the thermoaline circulation reversal and the warming of the entire water column in this area after 1998 because of the Eastern Mediterranean Transient (EMT). In this study, spatial and inter-annual variability of the population structure and the distribution patterns of I. coindetii in the eastern Ionian is investigated in relation to environmental characteristics. Datasets used include demographical and biological data derived from the MEDITS surveys carried out during the summers of 1994-2006 and environmental

Guest editor: V. D. Valavanis Essential Fish Habitat Mapping in the Mediterranean

E. Lefkaditou (⊠) · C.-Y. Politou · J. Dokos · P. Cosmopoulos Institute of Marine Biological Resources, Hellenic Centre for Marine Research, Ag. Kosmas, 16777 Helliniko, Athens, Greece e-mail: teuthis@ath.hcmr.gr

A. Palialexis · V. D. Valavanis Marine GIS Laboratory, Institute of Marine Biological Resources, Hellenic Centre for Marine Research, Thalassocosmos, 71003 Heraklion Crete, Greece parameters obtained through CTD sampling and remotely sensed imagery. Analyses performed include descriptive methods like the length frequency analyses and GIS mapping of standardized densities, as well as habitat modelling of presence data for different life stages of I. coindetii (based on generalized additive models and maximum entropy). An increasing trend in frequency of occurrence and density indices for all life stages has been detected during the studied period, being more evident after 1999. At the same time a temporal shift in seasonal maturation was also evidenced, coinciding to the warming of eastern Ionian waters due to EMT effects. Spawning aggregations occurred steadily on the upper slope of the relatively more protected area west of the Kefalonia Island, extending also over the lower shelf of the Patraikos Gulf in summers with lower upwelling activity. The inter-annual variability observed in the location of main recruitment areas could be related to mechanisms affecting post-hatching dispersal during late winter and spring, when maximum intensity of surface mesoscale activity has been observed. Depth was found the principal variable associated with the distribution of *I. coindetii* in the study area. Anomalies of surface temperature and chlorophyll-a, as well as distances from coast and thermal fronts were also selected for the final set of response variables without, however, showing any clear trend particularly in the case of recruits. The results of this study highlight the importance of a more comprehensive study of both environmental processes and I. *coindetii* life history in the Ionian Sea, in order to improve the understanding of its dynamics and the links with environmental variability.

**Keywords** *Illex coindetii* · Distribution patterns · Mediterranean · Eastern Ionian Sea ·

Generalized additive models · Maximum entropy · Environmental effects

# Introduction

The short-fin squid *Illex coindetii* is a widely spread amphi-Atlantic species, extending from off the coast of Virginia (37°N) to the north-western coast of Venezuela (09°N) in the western Atlantic (Roper et al., 1998), from as far north as Oslo Fjord at approximately 60°N (Lu, 1973), southward to Namibia (17°S) (Clarke, 1966) and 30°W (Gonzalez et al., 1994) in the Eastern Atlantic, throughout the Mediterranean Sea (Mangold & Boletzky, 1987) and in the south-western part of the Sea of Marmara (E < 28°20') (Katagan et al., 1993).

*Illex coindetii* is the species of ommastrephids mainly exploited by trawlers as by-catches in the Mediterranean Sea (Jereb & Ragonese, 1991; Sánchez & Martin, 1993; Lefkaditou et al., 2002; Ceriola et al., 2006), the Bay of Biscay (Henry et al., 1998; Iriondol et al., 2007), off northwest Africa (Hernández-García, 1991) and off Portuguese coast (Cunha & Moreno, 1994), whereas its landings from trawl fishery off NW Spain is currently at the same levels with that of *Todaropsis eblanae*, which was the most abundant ommastrephid before 1983 in this area (González et al., 1994).

*Illex coindetii* has been recorded up to 1100 m of depth (Guerra, 1992), being more abundant on the lower shelf and upper slope, where it has been also found among the main dominant species of cephalopod assemblages (Sánchez et al., 1998a; Quetglas et al., 2000; Krstulovic-Sifner et al., 2005; Lefkaditou, 2006). Variations in its bathymetric distribution have been observed between different geographic regions but also in a certain region depending on season and life stage (Sánchez et al., 1998b). According to available information from commercial and experimental fishing with different gears, juveniles seem to be dispersed in the water column,

whereas larger individuals occur closer to the bottom during the day and undergo vertical migrations during the night remaining, however, below the thermocline (Sánchez et al., 1998b).

Recruits and fully mature individuals appear in catches throughout the year, presenting seasonal peaks that may vary widely between years and geographic areas across its distributional range (Arvanitidis et al., 2002). In the Mediterranean Sea, the population structure of the short-living (7-18 months life span according to direct age estimations summarized by Arvanitidis et al., 2002) I. coindetii presents two main modal components that overlap with small individuals mainly concentrating over the continental shelf and larger ones dispersed in a wider range of depths (Sánchez et al., 1998b; Ceriola et al., 2006). Apart from depth, oceanographic processes have been supposed to be related with the abundance and distribution of I. coindetii recruits in the western Mediterranean (Jereb & Ragonese, 1991; Jereb et al., 2001; Cuccu et al., 2008). Furthermore, the spatiotemporal variation of I. coindetii daily commercial catches has been found to be correlated to the distribution of mesoscale thermal fronts and marine productivity hotspots in the Aegean and the eastern Ionian Sea (Valavanis et al., 2004, 2005).

The objective of this article is to describe the distribution and demography of *I. coindetii* population in the Eastern Ionian Sea during summer and investigate correlations with the environmental characteristics and mesoscale oceanographic processes in the region. Moreover, among the main goals of this study is to examine in more detail how the changes in the thermoaline circulation of the Ionian Sea after 1998, due to the Eastern Mediterranean Transient (EMT), have affected the population structure of *I. coindetii* as hypothesized by recent studies based on MEDITS data (Rochet et al., 2007).

# Materials and methods

# Study area

The Eastern Ionian Sea is characterized by a narrow (2–10 nautical miles) continental shelf and very steep slope (Ramfos et al., 2006) known as the deep Hellenic Trench with a maximum depth of 5121 m, lying off the submarine valley system of seven

islands extending parallel to the western Hellenic coast. The eastern part of the study area includes a semi-enclosed basin with the relatively shallow Patraikos Gulf (maximum depth of 120 m) in its opening, which is connected through the narrow strait of Rio-Antirio with the deep Corinthiakos gulf (maximum depth of 800 m) (Fig. 1).

Three water masses are distinguished in the Ionian Sea: (a) the upper layer-surface water mass of lower salinity (38.4–38.6 psu) and higher temperature, namely Modified Atlantic Water (MAW), (b) the Levantine Intermediate Water (LIW) lying under the surface layer (60–140 m) and extending down to 800–900 m, traced by the subsurface salinity maximum, the depth of which increases from south to north and (c) the Eastern Mediterranean Deep Water (EMDW), which extends further down to the bottom, with its upper part (between 700 and 1600 m) considered as Transitional Modified Water (TMW) by LIW. EMDW is formed in the northern Ionian Sea during winter by the mixing of deep and cold Adriatic

water entering from the Otrando Strait, with transformed LIW and deep Cretan waters, which are warmer, more saline and richer in oxygen (Stergiou et al., 1997). The semi-enclosed Patraikos gulf receives surface waters from the Ionian Sea and fresh waters input from small rivers located along its north and south coasts, while its bottom layer is influenced by the Corintiakos Gulf water masses (Friligos et al., 1985).

The general circulation in the Ionian Sea is characterized by a cyclonic component in the central region surrounded by a series of anticyclones (Drakopoulos & Lascaratos, 1999). A permanent cyclone is located in the northeastern Ionian Sea, adjacent to the Hellenic coastline, determining the pathway of the mixed Adriatic surface water/Ionian surface water (Mallanote-Rizzoli et al., 1997). A well known permanent anticyclonic feature is the double-centred Pelops gyre off the southwest coast of Peloponnesus, the northern part of which usually does not appear in sea-surface but it is present in deeper layers



Fig. 1 Map of the area investigated showing the stations of MEDITS hauls in the Eastern Ionian Sea
(Theocharis et al., 2002). This water-trapping gyre dominates the eastern Ionian from 1998 onwards, driving the Cretan Intermediate Waters that come from the Aegean Sea, northwards along the eastern slope of the Ionian. Prior to 1998 (late 1980s and up to 1997), the mid-Ionian southward current, associated with the large anticyclonic system of the western Ionian Sea, was stronger (Manca, 2000). These changes in the area during the past two decades regarding deep and intermediate thermoaline circulation (EMT) and the main site of EMDW formation from the Adriatic to the Aegean Sea were related to a transient effect of climate forcing (Theocharis et al., 1992; Roether et al., 2007). The changes were salinity driven during the first period of anomaly (1987-1992) while during the second period (1992-1995) they were driven by temperature variations (Souvermezoglou & Krasakopoulou, 1999).

Furthermore, hydrographic analyses in Eastern Ionian on the comparison of water mass structures in 1995, during the mature status of the transient, and those observed in 1999, revealed: (a) an influence of Aegean origin waters, characterized by temperature  $(\sim 13.8^{\circ}C)$  and salinity  $(\sim 38.85 \text{ psu})$ , higher than those of the EMDW of Adriatic origin, in the water column below 800 m, (b) an increase of salinity and temperature in the intermediate layer (150-800 m) due to highly saline Cretan Intermediate Water (CIW) and (c) a change of the dynamics in the upper layers (0-150 m) from an anticyclonic to a cyclonic flow, with warmer but less saline ( $\sim$  38.5 psu) MAW more pronounced than previously (Manca et al., 2002). Although the surface circulation variability in the Ionian Sea is mainly affected by the reversal of the circulation in 1998-1999, high-frequency eddy kinetic energy has been disclosed to be strongly correlated with seasonal wind stress variations (Poulain et al., 2000; Pujol & Larnicol, 2005).

Finally, Casotti et al. (2003) characterized the Eastern Ionian Sea as a highly oligotrophic environment, where phytoplankton growth depends mainly on regenerated nutrients. With respect to the zooplankton abundance, higher levels (up to 992 ind/m<sup>3</sup>) have been reported in the north-eastern Ionian, compared to those in the central and southern areas that are considered among the most oligotrophic regions of the Hellenic waters (Stergiou et al., 1997). Upraise of the nutrient rich-oxygen poor TMW in the intermediate layers due to the upward displacement of old EMDW, affected

dramatically the vertical distribution of oxygen and nutrients in 1994–1995, with nutricline ascending in cyclonic regions up to the base of euphotic zone and contributing to the increase of primary production (Souvermezoglou & Krasakopoulou, 1999; Souvermezoglou, 2003). Opposite patterns in the upper thermoaline circulation, reversed in 1998 from an anticyclonic to a cyclonic flow, have been suggested to affect the abundance and composition of epipelagic mesozooplankton (Mazzocchi et al., 2003).

#### MEDITS survey data

The data analysed in the present study were collected during summer from 1994 to 2006 excluding 2002 (Table 1), in the framework of the International Bottom Trawl Survey in the Mediterranean (MED-ITS). Hauls were performed during daytime, at predefined locations, using a French synthetic bottom trawl net GOC 73 with high vertical opening and 20 mm stretched mesh size at the cod-end. The investigated area covered all trawlable areas from 10 to 800 m depth. Details on the sampling protocol are described by Bertrand et al. (2000). The total weight and number of individuals were recorded for all species found at each station and for target cephalopod species, including Illex coindetii, mantle length (ML) measurements, sex and gonad maturation stage (0: immature of undetermined sex, 1: immature, 2: maturing, 3: mature) were also assigned on-board, following the **MEDITS** common protocol

 Table 1
 Number of valid hauls and dates of the MEDITS

 surveys carried out in the Eastern Ionian Sea

Year	No of stations	Days/Month
1994	11	17-22/8
1995	14	22-28/7
1996	22	26/7-3/8
1997	18	9-14/8
1998	32	24/6-10/7
1999	31	20/6-7/7
2000	31	25/6-8/7
2001	30	10-24/6
2003	32	25/7-9/8
2004	31	25/6-10/7
2005	31	27/7-13/8
2006	30	28/6-13/7

(Anonymous, 1998). At each station, vertical profiles of temperature and salinity were taken using a SBE-19 plus Conductivity-Temperature-Depth (CTD) system, from 1999 onwards.

#### Environmental data

The study area is well monitored in terms of monthly satellite imagery. Sea surface temperature distribution (SST in °C) were obtained through the German Aerospace Agency's (DLR) satellite data archive (EOWEB) while sea surface chlorophyll concentration (CHLO in mg/m<sup>3</sup>) was downloaded through Oceancolor Web, NASA's online Distributed Active Archive Centre, for the period 1998–2006. Bathymetry (DEP) was calculated through processing (kriging) of a point dataset derived from a blending of depth soundings collected from ships with detailed gravity anomaly information obtained from the Geosat and ERS-1 satellite altimetry missions (Smith & Sandwell, 1997).

# Catch data

In order to investigate the spatio-temporal variability in *I. coindetii* distribution and taking into account preliminary analysis of the species mantle length composition by depth stratum during the MEDITS surveys and the habitat preferences in different stages of its life (Sánchez et al., 1998b), catch data were standardized to a trawled surface unit (km<sup>2</sup>), considering the total number of collected specimen per haul as well as the number of collected specimen for three life stages: immature individuals (maturity stage 0 and 1, as defined by the MEDITS protocol) with ML smaller than 10 cm (named juveniles hereafter), immature and maturing individuals (maturity stage 1 and 2) with ML greater than 10 cm (named adults), and mature individuals (maturity stage 3).

The obtained datasets were processed in order to compute density indices (number of individuals/km<sup>2</sup>) for each life stage per year. In order to identify annual trends, the standardized annual density estimates were log transformed and the significance of their trends by year of sampling was tested by regression analysis. In order to detect any geographical constraints in the distribution of the different life stages, GIS maps showing the density of *I. coindetii* per station by year of sampling and life stage were drawn, while frequency of occurrence of each life stage was also

calculated by year and 50 m depth zones, as a first approximation for the investigation of the different life stages depth preferences. In order to identify interannual variability of recruitment strength and population structure in the studied area, ML frequency distributions were constructed by year, considering 1 cm size intervals. The percentages of each maturity stage per year were also estimated in order to take into account the reproductive activity. As lower size-atmaturity has been observed mostly during the main spawning season in squid species with prolonged spawning period (Moreno et al., 2002; Lefkaditou, 2006) and consequently considered as indicator of reproduction intensity during the sampling period, ML<sub>50</sub> was also determined for males and females by year, using the logistic function (Fryer, 1991):

$$P = \frac{e^{(v_1 + v_2 \text{ ML})}}{1 + e^{(v_1 + v_2 \text{ ML})}}$$

where  $v_1$  represents the intercept and  $v_2$  the slope of the logistic curve after applying a log transformation and *P* is the probability of a specimen to be mature. The value of ML<sub>50</sub> can then be estimated from the following expression: ML<sub>50</sub> =  $\frac{v_1}{v_2}$ . The parameters  $v_1$ and  $v_2$  were calculated using the likelihood method (Fryer, 1991) as adopted in the algorithm developed by Petrakis & Stergiou (1997).

#### Environmental data analyses

Vertical profiles of temperature were constructed by CTD station and their mean values were calculated considering sampled stations by year, in four sub-areas: Corinthiakos and SW Patraikos Gulf, the region enclosed by the arc of Eptanisos (Lefkada-Kefalonia-Zakynthos) islands, the area northwest of Lefkada island and SE Ionian (south of 37°45′).

In order to incorporate environmental data into a common georeference system (ArcInfo GIS GRID software version 8.0.2, ESRI, 1994), monthly averaged satellite images were processed as regular grids while MEDITS data were processed as vector coverages of point topology (Valavanis et al., 1998). GIS routines were used to calculate mesoscale thermal front distributions (Valavanis et al., 2005) and SST/CHLO anomalies (Valavanis et al., 2004). Nearest distances of MEDITS point data to the coastline and thermal fronts were calculated using standard GIS distance routines (e.g. NEAR ArcInfo GIS command).

#### Habitat modelling

Model developments were performed for the period 1998-2006 during which remotely sensed environmental data were available. Analysis of all datasets included two independent methods, one using development of Generalized Additive Models (GAM, Hastie & Tibshirani, 1990) and another using the maximum entropy (MAXENT) approach to species distribution (Phillips et al., 2004, 2006). GAM (nonparametric generalizations of multiple linear regressions) can deal with non-linear relationships between a dependent variable and multiple predictors in the same model where a pre-defined link function is related to predictor variables by scatter-plot smoothers of least-squares fits. On the other hand, MAXENT models the probability distribution of maximum entropy (e.g. that is most spread out or closest to uniform) and is applied as a general approach for presence-only modelling of species distributions making predictions from incomplete information in a study area. In both methods, predictor variables (e.g. environmental data, bathymetry and distances) should not have inherent any spatial autocorrelation (Zuur et al., 2007).

As mentioned above, the GAM and MAXENT methods were used independently in order to examine the similarity of I. coindetii distribution maps derived from both methods. GAMs were developed using the 'mgcv' library in the R statistical software (R Development Core Team, 2005). An extended data exploration process was performed to deal with basic GAM assumptions (collinearity and outliers, Zuur et al., 2007). When modelled in GAMs, abundance data do not provide probability maps. Thus, in order to compare GAM output probabilities with those of MAXENT model (probability maps, only), we used presence/absence data in GAMs, as well. Since the response variable was in a presence/absence format, a binomial error distribution was used. The natural cubic spline smoother was chosen as appropriate for the explanatory variables. Although not shown here, each smoothed fit was rated with regards to the level of deviance explained (0-100%; the higher the better, Olivier & Wotherspoon, 2005), the Un-biased Risk estimator (UBRE, the lower the better), the Akaike Information Criterion (AIC (Akaike, 1973), the lower the better) and the confidence region for the smooth (that should not include zero throughout the range of the predictor). The degree of smoothing was also chosen based on the observed data and the Generalized Cross Validation method suggested by Wood (2006) and incorporated in the 'mgcv' library. The base model was constructed using a stepwise forward selection method, in order to maintain a simple model and avoid collinearity. After the selection of the base model, all first order interactions were examined by using the criteria mentioned above. Spatial autocorrelation is the norm for ecological data (Lennon, 2000), so model's residuals were examined for spatial patterns in order to measure the autocorrelation structure (Augustin et al., 1996; Keitt et al., 2002) that indicates spatial autocorrelation, but there was no evidence of the latter. The final GAM model was used with the predict.gam function of mgcv library and the output included possibilities of presence at the sampling area. The predictive ability of the final model was evaluated with Receiver Operating Characteristic (ROC)-plots (Fieldings & Bell, 1997; Guisan & Zimmerman, 2000; Elith et al., 2006) and the Area Under Curve (AUC) was estimated with the presence/absence library of the R statistical software. In MAXENT models based on presence-only datasets, MEDITS stations with surveyed I. coindetii individuals only, were inserted in MAXENT 3.1.0 (Phillips et al., 2006). The output presence probability maps and variable response curves were calculated as part of MAXENT cumulative output.

# Results

Population structure and biological characteristics

Mantle length ranged from 3 to 23 cm during the investigated period (Fig. 2). In the size frequency distributions, two main modal components were generally present, the second of which appeared as a tail on the right side of the distribution in some years. The first mode of recruits, peaking at 5–6 cm, dominated the catches in most years of sampling except in 1994 and 2005. Density indices, estimated for recently recruited juveniles as well as for individuals larger than 10 cm ML, showed a significant increasing trend (P < 0.05) through the years of sampling (Fig. 3). Only a few individuals with ML more than 10 cm appeared in the samples collected from 1994 to 1997 (Fig. 2). ML<sub>50</sub> estimates ranged

**Fig. 2** Mantle length frequency distribution by year of MEDITS sampling in the Eastern Ionian Sea



from 12 to 15.2 cm for males and 14 to 18.7 cm for females, showing similar annual fluctuation for the two sexes. Minimum  $ML_{50}$  values were observed for 2001 and 2006 surveys, during which the mature large females (ML > 10 cm) had the highest percentages (Fig. 4).

Depth and sub-areas variations in distribution

*Illex coindetii* was recorded between 40 and 600 m. Its distribution in the studied area was patchy in general, with higher frequency of occurrence in hauls performed on lower shelf and upper slope (100–400 m).



• 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 • 000 •

 $\cap$ 

Fig. 3 Standardized in density estimates (in number of individuals per km<sup>2</sup>) of *Illex coindetii* juveniles (immature ML < 10 cm) and adults (ML > 10 cm), in the Eastern Ionian Sea 1994–2006



Fig. 4 Variation of  $ML_{50}$  (top) and percentage of matures among individuals with ML more than 10 cm (bottom), estimated for *Illex coindetii* males and females sampled during the MEDITS surveys 1998–2006

Juveniles were exclusively caught shallower than 400 m, occurring at over 85% of hauls between 100 and 300 m (Table 3). Larger individuals were found over the whole depth range of the species with mature individuals more frequently caught at 200–400 m of depth and mainly in the region of the Ionian enclosed by the arc of Lefkada-Kefalonia-Zakynthos islands, as shown by mapping of standardized catches (Fig. 5d). Concerning the geographic distribution of juveniles, a change in the main recruitment areas is noted within the period studied, with recruitment occurring mainly

in Corinthiakos and Patraikos gulfs during 1994–1997 (Fig. 5a) while during most surveys after 1998 higher densities of juveniles were recorded in the NE Ionian (Fig. 5b), except in 1999 and 2005 when juveniles appeared more abundant in the region enclosed by the three islands (Fig. 5c). Adults with immature gonads were more frequently found at depths ranging between 200–300 m (Table 3) showing no particular geographic pattern of distribution.

Temperature and primary production variability

Temperature profiles, available for the surveys 1998 onwards, show an important variation at the vertical distribution of temperature in the upper 50 m water layer between years, as well as between the geographical sub-areas (Fig. 6). Spatial variability is mainly due to the different degree of upper layer warming from south to north during early summer, as well as to the variation of upwelling activity, which generally appears more intensive in the northernmost part (region 3) of the study area. An homogenized surface layer of stable temperature has been observed throughout the studied area only in 2003, while during the rest of the surveys the thermocline reached the sea surface, indicating upwelling activity being more pronounced in 1999, 2000, 2001 and 2004. CTD sampling in neighboring stations at a time interval of about a week in 2001, revealed a significant change at the height of mixed surface layer and thermocline, indicating that upwelling activity may vary significantly within only a few days during summer in the study area. The distinction of the water masses occupying the 50-100 m layer in the Corinthiakos gulf from those in the rest sub-areas was evident during all years of CTD sampling. Slightly higher temperature was observed at 50-100 m of Corinthiakos gulf in 2001, probably indicating a higher ventilation of the waters of this almost closed deep water basin. Satellite data on SST and CHLO show that during summer months, thermal and Chl-a gradients are generally observed closer to the continental and island coastlines while an area of trapped highly productive and warm waters is located west of Kefalonia Island.

#### Habitats modelling

Although both GAM and MAXENT methods were developed separately, the final selected set of response



Fig. 5 Standardized catch data of *Illex coindetii* juveniles during MEDITS surveys of 1996 (a), 2001 (b), 2005 (c) and for mature individuals during 2005 survey (d), in the Eastern Ionian Sea

variables for the best-fitting models was the same: depth (DEP natural logarithm for GAM) and chlorophyll anomaly (CHLAN) used as main-effect variables for the overall (IC\_ALL) presence/absence of *I. coindetii*. For mature individuals only (IC\_MATURE), the main-effect variables included DEP (natural logarithm for GAM), CHLAN and distance from fronts (DFRONTS). Finally, for the juveniles (IC\_JUVENILE) model, DEP (natural logarithm for GAM), distance from coast (DCOAST, square root of DCOAST for GAM) and sea surface temperature anomaly (SSTAN) were included as main effects. All environmental variables were significant (*P*-value <0.05) although some of the GAM smoothers show weak trends. The presence probability maps are shown in Figs. 7–10.

Probability maps derived from GAM are not directly comparable with those from MAXENT

because of the resulted different probability scales, due mainly to the inherent discriminative (GAM) and generative (MAXENT) methods (Elith et al., 2006; Phillips et al., 2006). MAXENT produced maps with the same probability scale though in GAMs, the mean probability of each map depends on the presence-absence ratio. The listing of AUC for GAM and MAXENT (Table 2) reflect these differences but both models predicted their higher presence probabilities in similar areas (Fig. 7-10). Average GAM and MAXENT probabilities of presence and surveyed frequency of I. coindetii occurrence per bathymetric zone are presented in Table 3 showing similar trends. Finally, Pearson correlation coefficients between observed sampled frequencies (FREQ) and GAM-MAXENT predictions in the whole study area are shown in Table 4.

Fig. 6 Vertical profiles of temperature from 5 to 100 m depth in Corinthiakos and SW Patraikos Gulf, region enclosed by the arc of Eptanisos (Lefkada-Kefalonia-Zakynthos) islands, NE Ionian northwest of Lefkada island, and SE Ionian (south of 37°45')



_	AUC-GAM	AUC-MAXENT
Juveniles	0.68	0.90
Adult	0.82	0.92
Mature	0.77	0.87
All	0.79	0.86

 Table 2
 Area under curve (AUC) estimates for GAM and

 MAXENT models for different *Illex coindetii* life stages

#### Discussion

# Variation in population structure and size-at-maturity

Illex coindetii is the most abundant ommastrephid squid in the Eastern Ionian Sea, playing also an important role in the cephalopod communities of the lower shelf and upper slope (Krstulovic-Sifner et al., 2005). Nevertheless, its life history in this area has not yet been adequately studied and the limited available information concerns seasonal composition of experimental catches only on the slope, the upper part (250-500) of which was not sufficiently sampled during all seasons (Lefkaditou et al., 2003). Recent analyses of length-based population metrics for species sampled and measured during the MEDITS surveys carried out over the period 1995-2006, have detected a statistically significant increasing trend in average lengths of I. coindetii in the Eastern Ionian Sea (Rochet et al., 2007), which is due to the absence of individuals

 
 Table 4
 Pearson correlation coefficients between observed sampled frequencies (FREQ) and GAM-MAXENT predictions for different *Illex coindetii* life stages

	All	MAT	JUVEN	Adult
FREQ-MAXENT	0.70	0.75	0.78	0.81
FREQ-GAM	0.87	0.78	0.92	0.43
GAM-MAXENT	0.83	0.96	0.79	0.70

larger than 15 cm in ML from the samples collected before 1998 as shown by the present study (Fig. 2). The analyses performed in the present study show an increasing trend in frequency of occurrence and density indices for all life stages along the studied period, being more evident after 1999. The poor representation of mature individuals in the samples collected from 1994 to 1997, suggests that during this period the peak of the species reproduction occurred later in autumn, as similarly observed in the north Aegean Sea in the early 1990s (Lefkaditou, 2006). The increase of occurrence of mature individuals after 1998, coinciding with the warming of Eastern Ionian waters due to EMT effects (Manca et al., 2002), points to a temporal shift in seasonal maturation with peak occurring earlier during summer. This confirms the suggestion by González et al. (1996) on the flexibility in the reproductive peaks of I. coindetii, linked to environmental conditions.

 $ML_{50}$  estimates in the Eastern Ionian Sea were similar to those previously reported for *I. coindetii* in the Eastern (Arvanitidis et al., 2002; Lefkaditou,

Table 3 Mean probability estimates (%) for GAM and MAXENT in various bathymetric zones as compared to the observed frequency of *Illex coindetii* in sampled stations

Depth MAX		MAXENT			GAM			Observed				
Zone All	Adult	MAT	JUVEN	All	Adult	MAT	JUVEN	All	Adult	MAT	JUVEN	
<50	23.13	9.27	21.79	16.53	49.26	24.00	17.97	42.52	21.88	6.25	18.75	12.50
50-100	42.69	29.08	35.30	38.63	78.96	19.53	22.04	67.55	70.19	38.46	28.85	53.85
100-150	42.89	25.83	25.93	41.45	86.92	8.16	21.85	77.01	90.70	41.86	30.23	88.37
150-200	23.39	16.03	28.22	22.03	87.79	6.75	21.04	78.61	100.0	54.55	27.27	90.91
200–250	32.98	23.32	39.57	24.13	86.77	14.50	37.31	80.85	85.71	71.43	42.86	71.43
250-300	57.59	41.49	67.52	28.66	82.54	29.04	63.27	71.75	92.31	73.08	69.23	88.46
300-350	36.37	26.00	48.83	14.17	70.99	15.82	45.47	64.02	77.42	48.39	61.29	35.48
350-400	15.34	10.98	23.44	6.39	56.94	7.32	21.61	40.95	83.33	33.33	66.67	33.33
400-500	9.06	6.75	13.67	4.97	45.48	4.25	12.89	26.08	0.00	0.00	0.00	0.00
500-550	3.20	3.76	6.57	5.00	30.38	4.67	11.35	12.34	29.41	17.65	23.53	0.00
550-600	4.04	3.99	6.73	8.15	24.9	3.71	10.78	10.62	11.11	11.11	11.11	0.00



Fig. 7 General MAXENT (top) and GAM (bottom) probability map estimates for adult *Illex coindetii* using summer surveyed MEDITS data 1998–2006

 $\overline{\textcircled{D}}$  Springer



Fig. 8 General MAXENT (top) and GAM (bottom) probability map estimates for immature *Illex coindetii* using summer surveyed MEDITS data 1998–2006



Fig. 9 General MAXENT (top) and GAM (bottom) probability map estimates for mature *Illex coindetii* using summer surveyed MEDITS data 1998–2006

D Springer



Fig. 10 General MAXENT (top) and GAM (bottom) probability map estimates for both juvenile and adults (including mature) *Illex* coindetii using summer surveyed MEDITS data 1998–2006

2006) Central (Jereb & Ragonese, 1995; Ceriola et al., 2006) and Western Mediterranean (Sánchez et al., 1998b) and off the western coasts of Iberian Peninsula (Gonzalez & Guerra, 1996; Arvanitidis et al., 2002). However, they were lower than those calculated for the Eastern Atlantic off NW Africa (Hernández-García, 2002) and north of Spain (Arvanitidis et al., 2002), where greater ML sizes were also attained, being in consistency with relatively higher growth rates estimated in these areas (Arkhipkin, 1996; González et al., 1996) than in the Mediterranean Sea (Sánchez, 1995; Arkhipkin et al., 2000; Lefkaditou, 2006).

Temperature, food availability and photo-period, occurring particularly during the early juvenile phase, have been considered as the most important environmental factors that influence maturation process, growth rate and hence size-at-maturity (Mangold, 1987), for both myopsid squids inhabiting the highly variable neritic environment (Jackson, 2004) and the ommastrephids, the early stages of which are assumed to be concentrated in the epipelagic zone (Arkhipkin et al., 2000). The latitudinal variability reported for the size at maturity of I. coindetii off NWest Africa (Hernández-García, 2002) as well as the seasonal variability observed in population sampled from the Strait of Sicily (Arkhipkin et al., 2000) were attributed to temperature variability affecting both size and ageat-maturity. The interranual variability of ML<sub>50</sub>, fluctuating in a similar manner for both males and females of I. coindetii, shown in the present study, is most probably reflecting variation in spawning intensity during the sampling period, since minimum ML<sub>50</sub> values were estimated in the years that higher percentages of mature males and females among large individuals (ML > 10 cm) have been observed (Fig. 4). Interannual variation in the peak and intensity of spawning for the neritic Loligo vulgaris, has been suggested to be related to the progress of sea water warming, presenting more pronounced peaks during years of earlier water warming as well as to the age structure of the population with fast-growing younger individuals maturing at a relatively wider range of sizes than the older slower-growing ones during the main breeding season (Lefkaditou, 2006). For species of the genus Illex, variation in the size of adults in different seasonal cohorts has been attributed to seasonal changes in water temperature during the juvenile ontogenetic phase (Arkhipkin, 1996).

Considering a mean age of about one year for mature individuals, according to direct age estimations for *I. coindetii* in the Eastern Mediterranean (Lefkaditou, 2006), minimum  $ML_{50}$  values appearing during 2001 and 2006 surveys, have been attained by individuals hatched in the relatively warmer summers of 2000 and 2005 (Fig. 6). Direct and long-term ageing studies are needed to confirm this hypothesis, which combined with systematic collection of environmental data will highlight how growth and life histories of this common in the Mediterranean Sea ommastrephid species respond to temporal and spatial environmental variability and may establish the extent to which it may serve as indicator of ecosystem change.

#### Habitats of different life stages

Illex coindetii is generally considered as less oceanic species (than its sympatric I. illecebrosus and I. argentinus) occurring in relatively stable habitats associated with solid sea bottom substrates (Bakun & Csirke, 1998). In consistency with the above considerations our GAM and MAXENT analyses revealed that depth is the principal variable associated with distribution of I. coindetii, showing diversification of recently recruited juveniles and immature individuals depth preferences. For mature individuals, a higher probability of presence at depths ranging between 200 and 330 m, in greater distances from thermal fronts and in locations characterized by highly positive surface chlorophyll-a anomaly was demonstrated.

The GIS maps obtained for mature individuals by year, have shown that particularly mature females concentrate steadily on the upper slope west of the Kefalonia island, extending also over the lower shelf of the Patraikos gulf during summer of 2005 and 2006, in which lower upwelling activity was identified during the sampling period. High abundance of *I. argentinus* was found to be associated with a lower proportion of frontal waters within the inferred hatching area of the species along the Patagonian shelf (SW Atlantic) in the precedent year (Waluda et al., 2001). Supposing that hatching areas are close to the spawning areas, the concentration of spawning females on the relatively more protected area enclosed by the Lefkada-Kefalonia-Zakynthos islands is probably related to the 'spatial protection' of paralarvae survival and successful

recruitment. Such a speculative hypothesis should obviously be confirmed by further investigation targeting the seasonal distribution of early planktonic stages of the species in the study area.

For juveniles, GAM resulted in mean probability values closer to the observed frequency of occurrence in the different bathymetric intervals examined, and indicated that, apart from the depth-effect, the distance from coast and SST anomaly were significant explanatory variables, although showing no trend, a pattern that is probably related to the intervention of some other factors (e.g. the availability of the species' preferable prey). Mechanisms influencing the distribution of recently recruited juveniles in the Eastern Ionian Sea may involve aggregation and retention of paralarvae and their prey species. Taking into account likely growth rates estimated for I. coindetii in the NE Mediterranean (Lefkaditou, 2006), recruited juveniles presumably hatched from eggs spawned the semester prior to the MEDITS surveys. Thus, the variability observed in the main areas of I. coindetii recruitment across the period of MEDITS sampling, is most probably related to surface mesoscale activity in late winter and spring, during which the maximum intensity and interannual variability of eddy kinetic energy, due partly to wind stress variations, has been observed (Pujol & Larnicol, 2005).

Higher densities of juveniles recorded in the northernmost region of the study area after 1998 are probably associated to a permanent cyclonic eddy located in the area (Mallanote-Rizzoli et al., 1997). The reversal in the upper thermoaline circulation of the Ionian Sea from an anticyclonic to a cyclonic flow, occurred in 1998 and resulting in the relatively deeper concentration of zooplankton abundance at the 50–100 m (Mazzocchi et al., 2003), might have favoured the survival of *I. coindetii* rynchoteuthions that like those of other ommastrephid species, are probably concentrating beneath the thermocline during daytime (Piatkowski, 1998).

Recruitment and overall abundance variability

The MEDITS recruitment patterns represent only part of the general recruitment processes of *I. coindetii* population in the Eastern Ionian, given the temporal limits of the MEDITS surveys and the variation of reproductive and recruitment intensity of the species in the Mediterranean (Sánchez et al., 1998a, b). Thus, it is not easy to distinguish if increasing abundance of recruited juveniles is due to a shift of seasonal recruitment peak or to the increase of the species overall abundance. Nevertheless, it may be considered that warming of upper and intermediate layer water masses in the Eastern Ionian from 1998 onwards (Manca et al., 2002) has favoured the reproductive success of the parent generations and/or the survival of the early life stages of the recruited generations.

Finally, the results of this study highlight the importance of a more systematic collection of both environmental data and *I. coindetii* samples, including those of early planktonic stages, during the whole year in the study area, in order to improve the understanding of population dynamics and the links with environmental variability. Given that a west-east gradient of oligotrophy has been reported for the Ionian Sea (Mazzocchi et al., 2003), a comparison of *I. coindetii* interannual recruitment variation in the western and eastern part would also be of interest.

Acknowledgements Andreas Palialexis and Panayota Cosmopoulos were supported by the EU FP6 Scientific Support to Policies Action EnviEFH (Environmental Approach to Essential Fish Habitat Designation).

#### References

- Akaike, H., 1973. Information theory as an extension of the maximum likelihood principle. In Petrov, N. B. & F. Csaki (eds), Second International Symposium on Information Theory. Akademiai Kiado, Budapest.
- Anonymous, 1998. MEDITS. Manuel de protocols. Biologia Marina Mediterranea 5: 515–572.
- Arkhipkin, A. I., 1996. Geographical variation in growth and maturation of the squid *Illex coindetii* (Oegopsida. Ommastrephidae) off the North-West African coast. Journal of the Marine Biological Association of the United Kingdom 76: 1091–1106.
- Arkhipkin, A. I., P. Jereb & S. Ragonese, 2000. Growth and maturation in two successive seasonal groups of the shortfinned squid, *Illex coindetii* from the Strait of Sicily (Central Mediterranean). ICES Journal of Marine Science 57: 31–41.
- Arvanitidis, C., D. Koutsoubas, J.-P. Robin, J. Pereira, A. Moreno, M. M. Cunha, V. Valavanis & A. Eleftheriou, 2002. A comparison of the fishery biology of three *Illex coindetii* (Vérany 1839) (Cephalopoda: Ommastrephidae) populations from the European Atlantic and Mediterranean waters. Bulletin of Marine Science 71: 129–146.
- Augustin, N. H., M. A. Mugglestone & S. T. Buckland, 1996. An autologistic model for the spatial distribution of wildlife. Journal of Applied Ecology 33: 339–347.

- Bakun, A. & J. Csirke, 1998. Environmental processes and recruitment variability. In Rodhouse, P. G., E. G Dawe & R. K. O'Dor (eds), Squid Recruitment Dynamics. The Genus *Illex* as a Model, the Commercial *Illex* Species and Influences on Variability. FAO Fisheries Technical Paper 376: 105–124.
- Bertrand, J., L. Gil de Sola, C. Papaconstantinou, G. Relini & A. Souplet, 2000. An international bottom trawl survey in the Mediterranean: the MEDITS programme. In Bertrand, J. A. & G. Relini (eds), Demersal Resources in the Mediterranean. Actes de Colloques 26: 76–93.
- Casotti, R., A. Landolfi, C. Brunet, F. D'Ortenzio, O. Mangoni, M. R. d'Alcala & M. Denis, 2003. Composition and dynamics of the phytoplankton of the Ionian Sea (Eastern Mediterranean). Journal of Geophysical Research Oceans 108: 8116.
- Ceriola, L., N. Ungaro & F. Toteda, 2006. Some information on the biology of *Illex coindetii* Verany, 1839 (Cephalopoda, Ommastrephidae) in the South-Western Adriatic Sea (Central Mediterranean). Fisheries Research 82: 41– 49.
- Clarke, M. R., 1966. A review of systematics and biology of oceanic squids. (Ommastrephidae). Advances Marine Biology 4: 91–300.
- Cuccu, D., P. Jereb, S. Ragonese, N. Giovannini, S. Colella & A. Cau, 2008. On the abundance and spatial distribution of *Illex coindetii* and *Eledone moschata* in the Sardinian Seas (central-western Mediterranean): a preliminary and qualitative investigation with special attention to some environmental constraints. Bollettino Malacologico (in press).
- Cunha, M. M. & A. Moreno, 1994. Recent trends in the Portuguese squid fishery. Fisheries Research 21: 231–241.
- Drakopoulos, P. G. & A. Lascaratos, 1999. Modelling the Mediterranean Sea: climatological forcing. Journal of Marine Systems 20: 157–173.
- Elith, J., C. H. Graham, R. P. Anderson, M. Dudik, S. Ferrier, A. Guisan, R. J. Hijmans, F. Huettmann, J. R. Leathwick, A. Lehmann, J. Li, L. G. Lohmann, B. A. Loiselle, G. Manion, C. Moritz, M. Nakamura, Y. Nakazawa, J. Mc. C. Overton, A. T. Peterson, S. J. Phillips, K. S. Richardson, R. Scachetti-Pereira, R. E. Schapire, J. Soberon, S. Williams, M. S. Wisz & N. E. Zimmermann, 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography 29: 129–151.
- ESRI, 1994. ARC Macro Language. Environmental Systems Research Institute Inc., Redlands CA, USA: 3–37.
- Fielding, A. H. & J. F. Bell, 1997. A review of methods for the assessment of prediction errors in conservation presence/ absence models. Environmental Conservation 24: 38–49.
- Friligos, N., A. Theocharis & D. Georgopoulos, 1985. Preliminary physical and chemical observations during summer 1980 on a silled embayment in the Ionian Sea. Vie Millieu 35: 115–125.
- Fryer, R. G., 1991. A model between haul variation in selectivity. ICES Journal of Marine Science 48: 281–290.
- González, A. F. & A. Guerra, 1996. Reproductive biology of the shot-finned squid *Illex coindetii* (Cephalopoda: Ommastrephilae) of the Northeasten Atlantic. Sarsia 81: 107–118.
- González, A. F., B. G. Castro & A. Guerra, 1996. Age and growth of the shortfinned squid *Illex coindetii* in Galician

Deringer

waters (NW Spain) based on statolith analysis. ICES Journal of Marine Science 53:802-810.

- González, A. F., M. Rasero & A. Guerra, 1994. Preliminary study of *Illex coindetii* and *Todaropsis eblanae* (Cephalopoda: Ommastrephidae) in northern Spanish Atlantic waters. Fisheries Research 21: 115–126.
- Guerra, A., 1992. Mollusca, Cephalopoda. In Ramos, M. A. (ed.), Fauna Ibérica. Museo Nacional de Ciencias Naturales, CSIC Madrid: 327.
- Guisan, A. & N. E. Zimmermann, 2000. Predictive habitat distribution models in ecology. Ecological Modelling 135: 147–186.
- Hastie, T. J. & R. J. Tibshirani, 1990. Generalized Additive Models. Chapman & Hall, London: 335.
- Henry, K., V. Denis & J.-P. Robin, 1998. Ommastrephid squids exploited by French trawlers: preliminary analysis of stock structure based on Southern Brittany landings. ICES CM1998/M: 24.
- Hernández-García, V., 1991. Distribution of flying squids (Cephalopoda teuthoidea) in the CECAF area (Preliminary results). ICES CM1991/K: 24.
- Hernández-García, V., 2002. Reproductive Biology of *Illex coindetii* and *Tadaropsis eblanae* (Cephalopoda: Ommastrephidae) off Northwest Africa (4°N, 35°N). Bulletin of Marine Science 71: 347–366.
- Iriondol, A., M. Santurtun & I. Artexte, 2007. The Basque cephalopod fishery in the northeasten Atlantic waters during the period 1994–2006. ICES CM2007/LRC: 15.
- Jackson, G. D., 2004. Advances in defining the life histories of myopsid squid. Marine and Freshwater Research 55: 457– 365.
- Jereb, P., D. Massi, G. Norrito & F. Fiorentino, 2001. Preliminary observations of environmental effects on spatial distribution and abundance of *Eledone cirrhosa* and *Illex coindetii* in the Strait of Sicily (Central Mediterranean Sea). ICES CM2001/K: 34.
- Jereb, P. & S. Ragonese, 1991. Distribution and reproductive biology of the squid *Illex coindetii* (Mollusca, Cephalopoda) in the Sicilian Channel. Bulletin of Marine Science 49: 664.
- Jereb, P. & S. Ragonese, 1995. An outline of the biology of the squid *Illex coindetii* in the Sicilian channel (Central Mediterranean). Journal of the Marine Biological Association of the United Kingdom 75: 373–390.
- Katagan, T., A. Salman & H. A. Benli, 1993. The cephalopod fauna of the Sea of Marmara. Israel Journal of Zoology 39: 255–261.
- Keitt, T., O. Bjornstad, P. Dixon & S. Citron-Pousty, 2002. Accounting for spatial pattern when modelling organismenvironment interactions. Ecography 25: 616–625.
- Krstulovic-Sifner, S., E. Lefkaditou, N. Ungaro, L. Ceriola, K. Osmani, S. Kavadas & N. Vrgoc, 2005. Composition and distribution of the cephalopod fauna in the eastern Adriatic and eastern Ionian Sea. Israel Journal of Zoology 51: 315–330.
- Lefkaditou, E., 2006. Taxonomy and biology of Cephalopods in the North Aegean Sea. PhD thesis, University of Patras, Patras, Greece: 298.
- Lefkaditou, E., S. Kavadas & C. Papaconstantinou, 2002. Cephalopod fisheries statistics in Greek waters (NE Mediterranean). ICES CM1999/G: 4.

- Lefkaditou, E., C. Mytilineou, P. Maiorano & G. D'Onghia, 2003. Cephalopod species captured by deep-water exploratory trawling in the northeastern Ionian Sea. Journal of Northwest Atlantic Fisheries Science 31: 431–440.
- Lennon, J. J., 2000. Red-shifts and red herrings in geographical ecology. Ecography 23: 101–113.
- Lu, C. C., 1973. Systematics and Zoogeography of the Squid Genus *Illex* (Oegopsida: Cephalopoda). Ph.D. Thesis, Memorial University of Newfoundland, Canada: 389.
- Mallanote-Rizzoli, P., B. B. Manca, M. Ribera d'Alcala, A. Theocharis, A. Bergamasco, D. Bregant, G. Budillon, G. Civitarese, D. Georgopoulos, A. Michelato, E. Sansone, P. Scarazzato & E. Souvermezoglou, 1997. A synthesis of the Ionian Sea hydrography, circulation and water mass pathways during POEM-Phase I. Progress in Oceanography 39: 153–204.
- Manca, B., 2000. Recent changes in dynamics of the Eastern Mediterranean affecting the water characteristics of the adjacent basins. In Briand, F. (ed.), The Eastern Mediterranean Transient. CIESM Workshop Series 10: 27–31.
- Manca, B. B., L. Ursella & P. Scarazzato, 2002. New development of Eastern Mediterranean Circulation based on hydrological observations and current measurements. Marine Ecology 23: 237–257.
- Mangold, K., 1987. Reproduction. In Boyle, P. R. (ed.), Cephalopod Life Cycles. Academic Press, London: 157– 200.
- Mangold, K. & S. Boletzky, 1987. Cephalopodes. Méditeranée et mer Noire. Zone de Pêche 37: 633–714.
- Mazzocchi, M. G., D. Nervegna, G. D'Elia, I. D. Capua, L. Aguzzi & A. Boldrin, 2003. Spring mesozooplankton communities in the epipelagic Ionian Sea in relation to the Eastern Mediterranean Transient. Journal of Geophysical Research Oceans 108: C9.
- Moreno, A., J. Pereira, C. Arvanitidis, J.-P. Robin, D. Koutsoubas, C. Perales-Raya, M. M. Cunha, E. Balguerias & V. Denis, 2002. Biological variation of *Loligo vulgaris* (Cephalopoda: Loliginidae) in the eastern Atlantic and Mediterranean. Bulletin of Marine Science 71: 515–534.
- Olivier, F. & S. J. Wotherspoon, 2005. GIS-based application of resource selection functions to the prediction of snow petrel distribution and abundance in East Antarctica: comparing models at multiple scales. Ecological Modelling 189: 105–129.
- Petrakis, G. & K. Stergiou, 1997. Size selectivity of diamond and square mesh cod ends for four commercial Mediterranean fish species. ICES Journal of Marine Science 54: 13–23.
- Piatkowski, U., 1998. Modern target sampling techniques provide new insights into the biology of early life stages of pelagic cephalopods. Biologia Marina Mediterranea 5: 260–272.
- Phillips, S. J., R. P. Anderson & R. E. Schapire, 2006. Maximum entropy modelling of species geographic distributions. Ecological Modelling 190: 231–259.
- Phillips, S. J., M. Dudik & R. E. Schapire, 2004. A maximum entropy approach to species distribution modelling. Proceedings of the 21st International Conference on Machine Learning. Banff, Canada.
- Poulain, P., J. M. Leitz & P. Flament, 2000. Sea Surface Temperature in the Ionian Sea: satellite and drifter

observations between May and October 1995. Aquatic Pollution and Environmental Quality: OS32A-14.

- Pujol, M.-I. & G. Larnicol, 2005. Mediterranean sea eddy kinetic energy variability from 11 years of altimetric data. Journal of Marine Systems 58: 121–142.
- Quetglas, A., A. Carbonell & P. Sanchez, 2000. Demersal continental shelf and upper slope cephalopod assemblages from the Balearic Sea (north-western Mediterranean). Biological aspects of some deep-sea species. Estuarine, Coastal and Shelf Science 50: 739–749.
- R Development Core Team, 2005. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, http://www.R -project.org.
- Ramfos, A., S. Isari, S. Somarakis, D. Georgopoulos, C. Koutsikopoulos & N. Fragopoulou, 2006. Mesozooplankton community structure in offshore and coastal of the Ionian Sea (Eastern Mediterranean) during mixed and stratified conditions. Marine Biology 150: 29–44.
- Rochet, M.-J., V. M. Trenkel, L. Gil de Sola, C.-Y. Politou, G. Tserpes & J. A. Bertrand, 2007. Do population and community metrics tell the same story about recent changes in Northern Mediterranean fish communities? ICES CM2007/D: 16.
- Roether, W., B. Klein, B. B. Manca, A. Theocharis & S. Kioroglou, 2007. Transient Eastern Mediterranean deep waters in response to the massive dense-water output of the Aegean Sea in the 1990s. Progress in Oceanography 74: 540–571.
- Roper, C. F. E., C. C. Lu & M. Vecchione, 1998. A revision of the systematics and distribution of *Illex* species (Cephalopoda: Ommastrephidae). In Voss, N. A., M. Vecchione, R. B. Toll & M. J. Sweeney (eds), Systematics and Biogeography of Cephalopods. Smithsonian Contributions to Zoology 586: 405–423.
- Sánchez P., 1995. Age and growth of *Illex coindetii*. ICES Marine Science Symposia 199:441–444.
- Sánchez, P., P. Belcari & P. Sartor, 1998a. Composition and spatial distribution of cephalopods in two north-western Mediterranean areas. South African Journal of Marine Science 20: 17–24.
- Sánchez, P., A. F. Gonzalez, P. Jereb, V. V. Laptikhovsky, K. M. Mangold, C. M. Nigmatulin & S. Ragonese, 1998b. *Illex coindetii*. In Rodhhouse, P. G., E. G. Dawe & R. K. O'Dor (eds), Squid Recruitment Dynamics. FAO Fisheries Technical Paper 376: 59–76.
- Sánchez, P. & P. Martin, 1993. Population dynamics of the exploited cephalopod species of the Catalan Sea (NW Mediterranean). Scientia Marina 57: 153–159.
- Smith, W. H. F. & D. T. Sandwell, 1997. Global sea floor topography from satellite altimetry and ship depth soundings. Science 277: 1956–1962.
- Souvermezoglou, E., 2003. The influence of thermoaline circulation variability in the Eastern Mediterranean on the distribution of the chemical parameters in the Ionian Sea (possible impact on the ecosystem). 7th Hellenic Symposium on Oceanography and Fisheries. Chersonissos, Abstracts volume: 107.
- Souvermezoglou, E. & E. Krasakopoulou, 1999. The effect of physical processes on the distribution of nutrients and oxygen in the NW Levantine Sea. In Malanotte-Rizzoli, P.

& V. N. Eremeev (eds), The Eastern Mediterranean as a laboratory Basin for the Assessment of Contrasting Ecosystems. NATO ARW Series. Kluwer Academic Publishers, Netherlands: 225–240.

- Stergiou, K. I., E. D. Christou, D. Georgopoulos, A. Zenetos & C. Souvermezoglou, 1997. In Ansell, A. D., R. N. Gibson & M. Barnes (eds), The Hellenic Seas: Physics, Chemistry, Biology and Fisheries. Oceanography and Marine Biology: Annual Review 1997. UCL Press: 415–538.
- Theocharis, A., D. Georgopoulos, P. Karagevrekis, A. Iona, L. Perivoliotis & N. Charalambidis, 1992. Aegean influence in the deep layers of the Eastern Ionian Sea. Rapports Commision International Mer Méditerranée 33: 235.
- Theocharis, A., B. Klein, K. Nittis & W. Roether, 2002. Evolution and status of the Eastern Mediterranean Transient (1997–1999). Journal of Marine Systems 33–34: 91– 116.
- Valavanis, V. D., S. Georgakarakos & J. Haralabous, 1998. A methodology for GIS interfacing of marine data. Proceedings of GIS PLANET 98: International Conference

and Exhibition on Geographic Information, Lisbon, Portugal, 7–11 September 1998. IMERSIVA CD-ROM.

- Valavanis, V. D., A. Kapantagakis, I. Katara & A. Palialexis, 2004. Critical regions: a GIS-based model of marine productivity hotspots. Aquatic Sciences 66: 139–148.
- Valavanis, V. D., I. Katara & A. Palialexis, 2005. Marine GIS: identification of mesoscale oceanic thermal fronts. International Journal of Geographical Information Science 19: 1131–1147.
- Waluda, C. M., P. G. Rodhouse, G. P. Podesta, P. N. Trathan & G. J. Pierce, 2001. Surface oceanography of the inferred hatching grounds of *Illex argentinus* (Cephalopoda: Ommastrephidae) and influences on recruitment variability. Marine Biology 139: 671–679.
- Wood, S. N., 2006. Generalized Additive Models. An Introduction with R. Chapman & Hall, London.
- Zuur, A. F., E. N. Ieno & G. M. Smith, 2007. Analysing Ecological Data. Springer Series: Statistics for Biology and Health, Springer.

# FISH HABITAT MAPPING

# Combining GIS and GAMs to identify potential habitats of squid *Loligo vulgaris* in the Northwestern Mediterranean

Pilar Sanchez · Montserrat Demestre · Laura Recasens · Francesc Maynou · Paloma Martin

© Springer Science+Business Media B.V. 2008

Abstract We characterised the most productive areas for the commercial squid Loligo vulgaris off the Catalan Coast based on the combined integration of SST and PAR satellite data. We present the distribution of these areas during the most productive months in relation to the spatiotemporal presence of paralarvae of this species off the Catalan Coast. The work is based on Generalised Additive Models (GAMs) that combine the simultaneous analysis of the effect of different environmental explanatory variables from satellite imagery data to obtain the optimal model for paralarvae of the squid. The proposed model helped define the potential Essential Fish Habitat (EFH) for squid paralarvae recruitment, based on the best environmental conditions and is consistent with the higher LPUE observed four months later. The EFH defined for paralarvae recruitment by the model was detected every year in May in the areas both north and central of the Catalan Coast, the same areas where fishing ports evidence the highest commercial yield of squid.

P. Sanchez ( $\boxtimes$ ) · M. Demestre · L. Recasens ·

F. Maynou · P. Martin

Institut de Ciències del Mar, Consejo Superior de Investigaciones Científicas, P. Marítim de la Barceloneta 37-49, 08003 Barcelona, Spain e-mail: pilar@cmima.csic.es **Keywords** Loligo vulgaris · NW Mediterranean · GIS · GAM · Squid LPUE · Environment

# Introduction

The relationship among the environmental characteristics, the distribution and the reproductive and feeding behaviour of marine organisms are a key research priority that should be investigated to build quantitative predictive models of complex marine ecosystems. Specific habitats for species where they can feed, grow, mature and spawn to sustain their populations are commonly named as Essential Fish Habitat (EFH) as defined by the EC Habitats Directive (Council Directive 92/43/EEC of 21 May 1992 on the Conservation of Natural Habitats and of Wild Fauna and Flora). The characteristics of bottom sediments together with the oceanographic properties of the water are the key points defining the distribution and abundance of species in different marine environments (Valavanis et al., 2004). Knowledge of EFH is very important for the maintenance of sustainable fisheries with a fundamental relationship between quality of habitats and quality of fisheries resources (Benaka, 1999). In order to sustain longterm fisheries production, the protection of EFH is a challenge to be considered by fishery management.

*Loligo vulgaris* is a valuable resource exploited with three types of fishing gear in the Catalan coast.

Guest editor: V. D. Valavanis Essential Fish Habitat Mapping in the Mediterranean

Bottom trawl comprises about 90% of total catches of the species while purse seine and different artisanal gear are used for the rest of the catches (Guerra et al., 1994). The distribution of *L. vulgaris* extends along the eastern Atlantic, from the North Sea and British Isles ( $55^{\circ}$  N) to the south-western coast of Africa ( $20^{\circ}$  S), and also throughout the Mediterranean Sea (Guerra, 1992). In the Mediterranean, it is more abundant in waters shallower than 100 m. Generally, it inhabits temperate waters ranging between 12.5 and 20°C and in rather low salinities (Mangold-Wirz, 1963). The species occurs generally within salinity range of 30–36 psu in the North Atlantic (Tinbergen and Verwey, 1945) and slightly higher (37.7–38.15 psu) in the Mediterranean (Salat et al., 1978).

The maturation occurs during the whole year, but may be particularly important in some periods of the year (winter and summer) further south in the Eastern Atlantic, from the Northwest Spanish coast to the Western Sahara (Guerra & Rocha, 1994; Moreno et al., 1994; Raya et al., 1999). In concrete, Mangold-Wirz (1963) found that L. vulgaris spawns in the Western Mediterranean during the whole year but with a peak in March-April. The duration of the embryonic development is highly dependent on environmental conditions, mainly temperature and oxygenation (Worms, 1983), and it is usually around 30 days. According to different experimental works, hatching occurs 125 days after spawning at 13°C, 40-45 days after spawning in 12-14°C and 26-27 days after spawning at 22°C (Boletzky, 1979) or 30 days at 17°C according to Mangold-Wirz (1963). The paralarvae of this species have a planktonic life style that lasts around two months (Mangold-Wirz, 1963). Growth of paralarvae is exponential and growth rates are highly influenced by temperature (Villanueva, 2000). Natsukari & Komine (1992) by examination of statolith increments of Mediterranean specimens of Loligo vulgaris found that the life span is probably about one year. Lately Arkhipkin (1995) studied the age and growth of Loligo vulgaris also by examination of statolith increments from the west Saharan shelf. The author found that maximum age was 396 days (498-mm mantle length).

Taking into account the life cycle described in the works above, together with our own data, we can assume that the peak of spawning period for the squid in the Catalan coast is basically in March–April, and taking into consideration the prevailing water temperature, hatching of paralarvae will occur mainly in May. The presence of paralarvae in May would contribute to the main peak of landings four months later (September–October).

Fisheries production data have been frequently used to try to identify the general distribution and habitat requirements for both recruitment and spawning areas of the resources to achieve sustainable fisheries within an ecosystem-based approach to management (Sanchez & Martin, 1993; Boyle & Pierce, 1994; Pierce & Guerra, 1994; Sakurai et al., 2000; Denis et al., 2002; Chen et al., 2006). On the other hand, the species requirements on environmental variables that control or limit the above-mentioned life history data deserves serious consideration to integrate the species life cycle and the ecological function.

Monthly landings of *L. vulgaris* show a marked seasonality in Atlantic and Mediterranean areas (Sanchez & Martin, 1993; Guerra et al., 1994). The results of these papers showed that landings were much more increased in summer and autumn than in winter and spring during 1981–1991 and the largest catch was generally obtained in October in the NW Mediterranean. Therefore, the individuals caught in summer-autumn come from the spring hatching. The landings are strongly dependent on the annual recruitment of paralarvae and more specifically on a combination of environmental factors that control paralarvae distribution and abundance within EFH areas where growth and reproduction occurs.

The use of Geographical Information System (GIS) appears as a potential and powerful tool in fisheries management and ecosystem studies to analyse and map the distribution of species and allows combining their biological characteristics, mainly spawning and recruitment, with the environmental features, as shown by several studies (Valavanis et al., 2002, 2004). GIS have been considered to define and characterise the EFH for a great number of marine species (Meaden & Do Chi 1996; Sakurai et al., 2000; Eastwood et al., 2001; Pertierra et al., 2001; Pierce et al., 2002; Valavanis et al., 2004; Koubbi et al., 2006). Development of Generalised Additive Models (GAMs) provides the possibility to model different environmental scenarios, including non-linear responses of biological variables to environmental forcing variables, and to define the optimal areas of potential distribution for the particular stages of the species life **Fig. 1** Location of the study area with the name of the 16 fishing ports where the LPUE are recorded



cycle, e.g. areas of larval development and recruits and adults grounds.

The aim of the present work is to study the relationship between some environmental variables, during the months when paralarvae are more abundant, and the maximum LPUE of *L. vulgaris* in the Catalan coast.

#### Material and methods

# Study area

The Catalan coast within the north-western Mediterranean supports 16 commercial fishing ports where squid are landed. The coast presents a latitudinal temperature gradient with colder waters in the northern part and the southern region starts warming in spring. In general the coast has a narrow continental shelf except in the south around the Ebre Delta (Fig. 1).

#### Environmental data

Environmental data were collated from internet-based sources by the Hellenic Centre for Marine Research (Brown et al. 2006), and then processed into files suitable for use in a GIS. ArcGIS software was chosen to represent the maps of environmental preferences defining the EFH for squid paralarvae, following the methodology of Valavanis et al. (2002, 2004). The monthly environmental data, for the period January 2000–December 2005, considered for the analyses were: Sea Surface Temperature (SST in °C), Chlorophyll-a (CHLO in mg/m<sup>3</sup>), Sea Level Anomaly (SLA in cm) and Photosynthetic Active Radiation (PAR in einstein/m<sup>2</sup>/day).

# LPUE data

The landings-per-unit-effort (LPUE data) were obtained from the DGPAM (General Direction of Fishing and Maritime Affairs) of the Catalan Government for the period 2000–2005 on a monthly basis. The analysis of the trends in time series of squid LPUE allowed the identification of the best month of squid landings in the Catalan Coast, and the ports with higher yields.

Generalised Additive Models (GAMs) were applied in a quantitative approach on LPUE data for squid L. vulgaris at the Catalan Coast (North-Western Mediterranean) using monthly data of the 16 most important ports. The GAMs developed in this work were implemented in R (using Brodgar software package, Highland Statistics Ltd., http://www.brodgar.com). We specified a gamma distribution function for the error structure of the dependent variable (LPUE) with a log link relating the dependent variable to the predictors. The predictor variables were modelled as cubic splines, with a degree of smoothing estimated by the routine mgcv (Wood, 2000). In order to decide which model best fitted the data we used Akaike's Information Criterion (AIC) as goodness-of-fit statistic (Zuur & Pierce, 2004). GAMs were fitted between environmental variables data in spring, when the hatching of paralarvae occurs and the LPUE for the month of peak catches for the period 2000-2005, usually September or October. Three set of environmental variables (April, May and June) were considered to run the model.

#### Results

In order to test the hypothesis proposed in the present study considering that LPUE (response variable) depends on the environment characteristics of the post-hatching period when paralarvae are present, GAM techniques were used to model squid abundance

**Table 1** Environmental variables: SST, Sea Surface Temper-<br/>ature; PAR, Photosynthetic Active Radiation; CHLO,<br/>Chlorophyll-a. DF, Degrees Freedom; n.s., no significant; DE,<br/>Deviance Explained; AIC, function

Month	DF	Variables (P-value)	DE	AIC
April	74	SST ( <i>P</i> < 0.05), PAR (n.s.)	0.19	560.66
May	74	SST ( $P < 0.001$ ), PAR ( $P < 0.05$ )	0.39	531.16
June	74	SST ( <i>P</i> < 0.05), CHLO (n.s.)	0.37	534.10

(LPUE) as a function of the climatic variables in spring. The LPUE data series showed a clear seasonal pattern, with a strong autumn peak centred mainly in September.

Model results are summarised in Table 1. The AIC function indicates a better fit of the response variable at the month of peak catches with May climatic parameters. GAM explained 39% of the deviance of the abundance of the squid. Two explanatory variables were significant: SST (P < 0.001) and PAR (P < 0.05) (Fig. 2). SST was the most important explanatory variable, as it represented 32% of the explained deviance. The range of positive values for this parameter is between 15.18 and 17.53°C. SST showed a strong negative effect at temperatures higher than 17.53°C. The favourable range for PAR is between 43.94 and 52.89 einstein/m<sup>2</sup>/day. The other environmental variables were not significant.

The inter-annual variations on squid EFH, defined as areas where the positive effects of SST and PAR overlapped in May for 2000-2005, were obtained by combining the SST and PAR layers with GIS (Fig. 3). The best climatic conditions for squid recruitment were predicted in both the north and the central part of the study area every year, from the ports of Llançà to Cambrils (see Fig. 1), while these optimal conditions only appeared in the Ebre delta area in the years 2002, 2004 and, less evidently, in 2005. In accordance with our hypothesis, these conditions were reflected in the historical LPUE data (Fig. 4). North and central ports showed higher LPUE than those closer to Ebre delta. Nevertheless, a slightly higher LPUE was reported in the south area (Fig. 4) during years 2002, 2004 and 2005, in agreement with the climatic pattern found in the study area (Fig. 3). Despite the differences on yield between northern and southern areas, LPUE data



**Fig. 2** GAM plot for *Loligo vulgaris* LPUE showing the effect of (a) May SST (Sea Surface Temperature) and (b) May PAR (Photosynthetic Active Radiation) on squid abundance (maximum LPUE)

series showed a clear seasonal pattern characteristic of the species, with a strong autumn peak centred mainly in September in both areas (Fig. 4).

## Discussion

The study characterised the most productive regions for the commercial squid *Loligo vulgaris* off the Catalan Coast based on the combined integration of



Fig. 3 GIS-based EFH maps of paralarvae *Loligo vulgaris* in Catalan coast (NW Mediterranean) in May 2000–2005



Fig. 4 Monthly *Loligo vulgaris* LPUE for 2000–2005 to the north and central fishing ports, Llançà to Cambrils (a) and to the Ebre River ports (b)

SST and PAR satellite data. The variability in abundance of fishery species may be attributed to several factors. However, in short-lived species such as cephalopods, abundance is highly influenced by the environmental conditions, which affect recruitment (Boyle & Rodhouse, 2005). The average temperature on March in the studied period is 12.87°C and at this temperature hatching would be 40-45 days (according to Boletzky, 1979), after spawning occurred, in March-April (Mangold-Wirz, 1963). Therefore, the temperature in May, month in which the paralarvae would hatch, is crucial for the success of the annual recruitment, reflected in the maximum catches in autumn. The seasonal variation in fisheries catches depends mainly on survival during the pre-recruitment months (Denis et al. 2002). Lloret & Lleonart (2002) found, in the north part of the same study area, that strong seasonal pattern in recruitment of L. vulgaris (about 12 cm mantle length) is reflected by high seasonal landings.

Due to their short life span and rapid growth rates, cephalopods growth and abundance are thought to be especially sensitive to changes in environmental conditions such as sea water temperature (Boyle & Pierce, 1994). The optimal range of PAR found in the present study is high (43.9–52.9 einstein/m<sup>2</sup>/day). The expression PAR designates the spectral range of solar light that is useful to terrestrial plants in the process of photosynthesis. PAR measurements are also used to calculate the euphotic depth in the ocean. The depth of the euphotic zone can be greatly affected by seasonal turbidity. *Loligo vulgaris*, as other cephalopods, is a visual predator (Messenger, 1968; Boucher-Rodoni et al., 1987) meaning that the species would prefer clear water to live in and grow. In the study area, the most turbid area is defined by the influence of Ebre River that is also the area with lower landings and PAR.

The range of temperatures found in May suggested that less warm weather conditions favour subsequent landing in autumn. The model shows a negative effect with values of temperature higher than 17.53°C in agreement with the result found by Challier et al. (2005) for L. forbesi. In some areas, such as in the coastal waters of the Thracian Sea (Eastern Mediterranean), temperature has been found to be highly significant for beach-seine catches of L. vulgaris, conditioning inshore-offshore movements of the species during autumn and winter (Lefkaditou et al., 1998). Valavanis et al. (2002) found that geodistribution of potential spawning grounds in selected areas suggested that the species prefer to spawn closer to the coast when sharp-rocky coastline is present and away from the coast when a smoothsandy beach is present. In the present study, the species presented higher LPUE in the north and central coast of the study area. The north area and part of the central consists mainly of a rocky coast with dominant sand and sandy-muddy bottom substrates (Fig. 1).

Loligo vulgaris couples their life pattern with the environmental features and takes also advantages from the hydrographic characteristic of the area. The fishing grounds for squids are mainly located in the north and central part of the Catalan coast where the EFH for paralarvae are optimal. The reported low LPUE in the south part could be related with the exportation/migration of paralarvae from north to south following the north–south current water that circulates parallel to the coast (Sabates & Maso, 1990).

Acknowledgements We thank the Directorate of Fisheries of the Autonomous Government of Catalonia (DGPAM) for access to their fisheries production database. This study was funded by the EU Project EnviEFH (FF6-SSP8-022466).

#### References

- Arkhipkin, A. I., 1995. Age, growth and maturation of the European squid *Loligo vulgaris* (Myopsidae, Loliginidae) on the west Saharan Shelf. Journal of the Marine Biological Association of the United Kingdom 75: 593–604.
- Benaka, L., 1999. Fish Habitat: Essential Fish Habitat and Rehabilitation. American Fisheries Society, Bethesda Maryland.
- Boletzky, S. V., 1979. Observations on early post-embryonic development of *Loligo vulgaris* (Mollusca, Cephalopoda). Rapport Commission Internationale Mer Méditerranée 25/ 26: 10.
- Boucher-Rodoni, R., E. Boucaud-Camou & K. Mangold, 1987. Feeding and digestion. In Boyle, P. R. (ed.), Cephalopod Life Cycles. Comparative reviews II. Academic Press, London: 85–108.
- Boyle, P. R. & G. J. Pierce, 1994. Fishery biology of Northeast Atlantic squid: An overview. Fisheries Research 21: 1–15.
- Boyle, P. & P. Rodhouse, 2005. Cephalopods: Ecology and Fisheries. Blackwell Books, London.
- Brown, A. M., J. M. Bellido, V. D. Valavanis & A. Giraldez, 2006. Investigating the distribution of small pelagic fish in Spanish Maditerranean waterns using environmental modelling and essential fish habitat mapping. ICES CM 2006/O:13.
- Challier, L., J. Royer, G. J. Pierce, N. Bailey, B. Roel & J. P. Robin, 2005. Environmental and stock effects on recruitment variability in the English Channel squid *Loligo forbesi*. Aquatic Living Resources 18: 353–360.
- Chen, C. S., G. J. Pierce, J. Wang, J. P. Robin, J. C. Poulard, J. Pereira, A. F. Zuur, P. R. Boyle, N. Bailey, D. J. Beare, P. Jereb, S. Ragonese, A. Mannini & L. Orsi-Relini, 2006. The apparent disappearance of *Loligo forbesi* from the south of its range in the 1990s: Trends in *Loligo* spp abundance in the northeast Atlantic and possible environmental influences. Fisheries Research 78: 44–54.
- Denis, V., J. Lejeune & J. P. Robin, 2002. Spatio-temporal analysis of commercial trawler data using General Additive Models: Patterns of Loliginid squid abundance in the northeast Atlantic. ICES Journal of Marine Science 59: 633–648.
- Eastwood, P. D., G. J. Meaden & A. Grioche, 2001. Modelling spatial variation in spawning habitat suitability for the sole *Solea solea* using regression quintiles and GIS procedures. Marine Ecology Progress Series 224: 251–266.
- Guerra, A., 1992. Mollusca, Cephalopoda. Fauna Ibérica, Museo Nacional de Ciencias Naturales, Madrid: 327.
- Guerra, A. & F. Rocha, 1994. The life history of *Loligo vulgaris* and *Loligo forbesi* (Cephalopoda: Loliginidae) in Galician waters (NW Spain). Fisheries Research 21: 43–69.
- Guerra, A., P. Sanchez & F. Rocha, 1994. The Spanish fishery for Loligo: Recent trends. Fisheries Research 21: 217–230.
- Koubbi, P., C. Loots, G. Cotonnec, X. Harlay, A. Grioche, S. Vaz, C. Martin, M. Walkey & A. Carpentier, 2006. Spatial patterns and GIS habitat modelling of *Solea solea*, *Pleuronectes flesus* and *Limanda limanda* fish larvae in the

eastern English Channel during the spring. Scientia Marina 70: 147–157.

- Lefkaditou, E., P. Sanchez, A. Tsangidis & A. Adamidou, 1998. A preliminary investigation on how meteorological changes may affect beach-seine catches of *Loligo vulgaris* in the Thracian Sea (Eastern Mediterranean). South African Journal of Marine Science 20: 453–461.
- Lloret, J. & J. Lleonart, 2002. Recruitment dynamics of eight fisheries species in the nortwestern Mediterranean Sea. Scientia Marina 66: 77–88.
- Mangold-Wirz, K., 1963. Biologie des Cephalopodes benthiques et nectoniques de la Mer Catalane. Vie et Millieu 13: 285.
- Meaden, G. J. & T. Do Chi, 1996. Geographical Information Systems. Applications to Marine Fisheries. FAO Fisheries Techical Paper 356, FAO, Rome.
- Messenger, J. B., 1968. The visual attack of the cuttlefish *Sepia* officinalis. Animal Behaviour 16: 342–357.
- Moreno, A., M. M. Cunha & J. M. F. Pereira, 1994. Population biology of the veined squid (*Loligo forbesi*) and European squid (*Loligo vulgaris*) from the Portuguese coast. Fisheries Research 21: 71–86.
- Natsukari, Y. & N. Komine, 1992. Age and growth estimation of the European squid *Loligo vulgaris*, based on statolith microstructure. Journal of the Marine Biological Association of the United Kingdom 72: 271–280.
- Pertierra, J. P., L. Recasens & V. D. Valavanis, 2001. Development of a GIS platform for the compilation and analysis of demersal species biomass indices off the Catalan coast (NW Mediterranean Sea). In Nishida, T., P. J. Kailola, C. E. Hollingworth (eds), Proceedings of the First International Symposium on Geographic Information Systems (GIS) in Fishery Science. Seattle Washington: 134–142.
- Pierce, G. J. & A. Guerra, 1994. Stock assessment methods used for cephalopods fisheries. Fisheries Research 21: 255–285.
- Pierce, G. J., J. Wang & V. D. Valavanis, 2002. Application of GIS Cephalopod fisheries: Workshop report. Bulletin of Marine Science 71: 35–46.
- Raya, C. P., E. Balguerias, M. M. Fernández-Núñez & G. J. Pierce, 1999. On the reproduction and age of the squid *Loligo vulgaris* from the Saharan Bank (north-west African coast). Journal of the Marine Biological Association of the United Kingdom 79: 111–120.
- Sabates, A. & M. Maso, 1990. Effect of a shelf-slope front on spatial distribution of mesopelagic fish larvae in the Western Mediterranean. Deep Sea Research 37: 1085–1098.
- Sakurai, Y., H. Kiyofuji, S. Saitoh, T. Goto & Y. Hiyama, 2000. Changes in inferred spawning areas of *Todarodes pacificus* (Cephalopoda Ommastrephidae) due to changing environmental conditions. ICES Journal of Marine Science 57: 24–30.
- Salat, J., J. Font & A. Cruzado, 1978. Datos oceanográficos frente a Barcelona (1975–1976). Datos Informativos Instituto Investigaciones Pesqueras 5: 73.
- Sanchez, P. & P. Martin, 1993. Population dynamics of the exploited cephalopod species of the Catalan Sea (NW Mediterranean). Scientia Marina 57: 153–159.
- Tinbergen, L. & J. Verwey, 1945. The biology of *Loligo vulgaris* Lam. Translation Services Fisheries Research Board of Canada 2733: 35.

- Valavanis, V. D., S. Georgakarakos, D. Koutsoubas, C. Arvanitidis & J. Haralabous, 2002. Development of a marine information system for cephalopod fisheries in Eastern Mediterranean. Bulletin of Marine Science 71: 867–882.
- Valavanis, V. D., S. Georgakarakos, A. Kapantagakis, A. Palialexis & I. Katara, 2004. A GIS environmental modelling approach to essential fish habitat designation. Ecological Modelling 178: 417–427.
- Villanueva, R., 2000. Effect of temperature on statolith growth of the European squid *Loligo vulgaris* during early life. Marine Biology 136: 449–460.
- Wood, S. N., 2000. Modelling and smoothing parameter estimation with multiple quadratic penalties. Journal of the Royal Statistical Society 62: 413–428.
- Worms, J., 1983. Loligo vulgaris. In Boyle, P. R. (ed.), Cephalopods Life Cycle, Vol. I. Species Account. Academic Press, London: 143–157.
- Zuur, A. F. & G. J. Pierce, 2004. Common trends in Northeast Atlantic Squid time series. Journal of Sea Research 52: 57–72.

# FISH HABITAT MAPPING

# Identification of deep-water pink shrimp abundance distribution patterns and nursery grounds in the eastern Mediterranean by means of generalized additive modelling

Chrissi-Yianna Politou · George Tserpes · John Dokos

© Springer Science+Business Media B.V. 2008

Abstract Generalized Additive Modelling (GAM) techniques were used to model the time series of abundance data of deep-water pink shrimp, collected during the MEDITS bottom trawl surveys carried out in the Greek seas from 1996 to 2006, as functions of the sampling location (longitude-latitude), depth and year. The life stages of the species were taken into account. All variables were highly significant, although latitude and depth had always the highest explanatory power. The total abundance was higher between 100 and 400 m of depth, with juveniles and adults being more abundant in the 100-200 m and 200-400 m depth strata, respectively. GAM prediction maps showed high abundance concentration areas for all life stages mainly in the Aegean Sea. The most important nursery ground identified was located in the Saronikos Gulf and a secondary in the Thracian Sea. Concerning the concentration areas of the adult

Guest Editor: V. D. Valavanis Essential Fish Habitat Mapping in the Mediterranean

C.-Y. Politou (⊠) · J. Dokos Institute of Marine Biological Resources, Hellenic Centre for Marine Research, Aghios Kosmas, 16777 Helliniko, Greece e-mail: c-y@ath.hcmr.gr

G. Tserpes

Institute of Marine Biological Resources, Hellenic Centre for Marine Research, Thalassocosmos, 71003 Heraklion Crete, Greece specimens, they are located mainly in the Saronikos Gulf, the Thracian Sea, the Thermaikos Gulf, the Cretan Sea and the eastern part of the Aegean.

**Keywords** Deep-water pink shrimp · Mediterranean · Distribution · Nurseries · Generalized Additive Models

# Introduction

The deep-water pink shrimp *Parapenaeus longirostris* (Lucas, 1846) is a species of wide geographical distribution extending from the eastern Atlantic, in the north of Spain to the southern waters of Angola, to the whole of Mediterranean and its adjacent seas (Sea of Marmara) (Holthuis, 1980; Pérez Farfante & Kensley, 1997; Sobrino et al., 2005).

In the Mediterranean Sea, the bathymetric distribution of the deep-water pink shrimp ranges from 20 to 840 m (Tom et al., 1988; Politou et al., 2005). However, sandy-muddy bottoms between 100 and 400 m constitute the main distribution areas of the species (Holthuis, 1980; Sobrino et al., 2005). A size-related bathymetric distribution was observed for the deep-water pink shrimp, with juveniles (<20 mm Carapace Length) settling at shallower waters (mostly around 100–200 m) and larger individuals moving towards deeper waters (Mori et al., 1986; Ardizzone

et al., 1990; D'Onghia et al., 1998; Politou et al., 2000; Abelló et al., 2002).

This species is the main target of a large fishing fleet operating in the eastern Atlantic. In the Mediterranean Sea, it is the fifth crustacean species in biomass landed and it is fished almost exclusively by trawl (Stamatopoulos, 1993). In Greece, it is widely fished in all the country and it presents the highest mean annual crustacean landings (1227 t) (Kapiris et al., 2007).

Due to its high commercial importance, a lot of information exists on its biology and ecology, which is summarized in Sobrino et al., 2005. However, there is a great lack of knowledge on the biological, ecological and exploitation aspects of the species in the Greek waters. Some information comes from experimental trawl surveys and it concerns its abundance, distribution, size structure, growth and mortality (MEDITS 1994-2006, INTERREG II Italy-Greece 1999-2001 and RESHIO 2000-2002 projects reports; Politou et al., 2000; Abelló et al., 2002) as well as its feeding habits (Labropoulou & Kostikas, 1999; Kapiris, 2004). The deep-water pink shrimp is a short-living epibenthic species with high abundance in the Greek waters (mainly in 100-500 m depth), and biomass usually higher in the 200-500 m depth stratum than in the 100-200 m stratum, in accordance with its depth related size trend. Its growth is fast, although comparatively slower to other Mediterranean areas (Sobrino et al., 2005), and its total mortality rate high. The presence of younger individuals in almost all seasons reinforces the hypothesis of continuous reproductive activity. Its diet is characterized by a large variety of preys, mainly small fishes, cephalopods and crustaceans. An evaluation of the exploitation state of this resource in the Greek waters indicates a general over- or full-exploitation (Kapiris et al., 2007; MEDITS, 2007). In order to contribute to a sustainable exploitation of the resource, the identification of its main nursery areas was recently attempted, based on nominal values obtained from a series of experimental bottom-trawl surveys (Fiorentino et al., 2002; Politou et al., 2006).

Within the same context and aiming to better understand the factors that might determine the spatial distribution and abundance of the deep-water pink shrimp, the present article focuses on the identification and analysis of the quantitative relationships between the abundance/distribution data time series and abiotic factors in the totality of the Greek waters, using Generalized Additive Modelling (GAM) techniques. The different life stages of the species are taken into account, and potential nursery grounds and adult concentration areas are mapped using the GAM estimates.

## Materials and methods

Data were collected in the frames of the MEDITS program (International bottom trawl survey in the Mediterranean) carried out in the Greek seas (Aegean and Ionian Sea) from 1994 to 2006 (with the exception of 2002) and included density indices (DI) per trawling station expressed in terms of number of animals per square km (n/km<sup>2</sup>). The first 2 years were not included in our analysis, since the sampling methods were not completely standardized. The MEDITS survey is accomplished once per year (summer) and covers all trawlable areas from 10 to 800 m of the Aegean and Ionian Sea with pre-defined sampling stations. Further details on the sampling protocol can be found in Bertrand et al. (2000, 2002). Based on literature information on size at first maturity (Sobrino et al., 2005), density indices were also estimated separately for adults (>20 mm CL) and juveniles.

The effects of trawling location and depth on DI (total, adult and juveniles) were examined by means of Generalized Additive models (GAMs). GAMs, which are able to deal with non-linear relationships between a dependent variable and multiple predictors in the same model, are non-parametric generalizations of multiple linear regression that are less restrictive in assumptions about the underlying distribution of data (Hastie & Tibshirani, 1990). In GAMs, a pre-defined link function is related to predictor variables by scatter-plot smoothers in lieu of least-squares fits.

In the present case, our non-linear components were fitted with a locally weighted regression scatterplot smoother (*loess* smoother, Cleveland & Devlin, 1988) by means of the S-PLUS software package following Venables & Ripley (1997). Based on the diagnostic residual plots of preliminary runs we assumed a Poisson distribution accompanied by its canonical log-link function. Apart from trawling location and the depth, the year parameter was also modelled as a categorical variable. Hence, four variables were included in the analysis: Year, Latitude (Lat), Longitude (Lon) and Depth. The GAM model was of the form:

$$DI = a + Year + \log(Lat) + \log(Lon) + \log(Depth) + e,$$

where a is a constant,  $lo_i$  is the *loess* smoother function of the corresponding independent variable and e is a random error term.

Variable selection proceeded by a stepwise forward entry and the Akaike Information Criterion (AIC) (Akaike, 1978) was used to detect the relative importance of each variable in explaining variations and determine the order of those that should be included in the final model. This approach resulted in parsimonious models that included only the most important variables, in terms of explanatory power. In addition, collinearity problems were avoided, as correlated variables were not included in the final models (Crawley, 2005). The AIC statistic accounts simultaneously for the degrees of freedom used and the goodness of fit. A smaller AIC statistic corresponds to a better model in the sense of smaller residual deviance penalized by the number of parameters that are estimated in fitting the model. At each stage of the forward entry, the AIC was computed for every candidate predictor not yet entered. The variable resulting in the highest AIC decrease was entered into the model. Forward entry continued until additional variables no longer yielded reductions in the AIC statistic. Significant levels for the added predictors were estimated by means of Chi-square tests and the level of significance was set at 95%.

The predicted DI values from the GAM analysis were used to construct density distribution maps for the pink shrimp in the Greek seas. Maps were generated using the SURFER software (Golden Software, 2002) and interpolation was made by means of the "inverse distance to a power" gridding method (Davis, 1986).

#### Results

Data from 1716 hauls were analyzed (Fig. 1). The three stepwise GAMs (total, adult and juveniles)



Fig. 1 Map showing the distribution of the sampling stations of the MEDITS surveys 1996–2006 in the Greek waters

Explanatory variable	Residual d.f.	Residual deviance	Cumulative variance explained DI
Total			
Mean	1715.00	13982750	
Latitude	1705.27	10998030	21.35
Depth	1696.33	8340559	40.35
Longitude	1686.41	7531263	46.14
Year	1677.40	7270476	48.00
Adults			
Mean	1715.00	7015614	
Depth	1706.01	5687683	18.93
Latitude	1696.44	4181988	40.39
Longitude	1686.45	3816384	45.60
Year	1677.45	3768221	46.29
Juveniles			
Mean	1715.00	8853561	
Latitude	1705.11	6622754	25.20
Depth	1696.14	5417116	38.81
Longitude	1686.28	4870400	44.99
Year	1677.22	4400700	50.29

 Table 1
 Analysis of deviance for the GAMs fitted to the pink shrimp DI data

explained 46–50% of the total variation (Table 1) and all variables were highly significant (P < 0.0001). Latitude and depth had always the highest explanatory power ranging from 38 to 40%.

The effect (loess plot) of the predictors on DI is shown on the y-axis for different values of the predictor (x-axis) (Figs. 2-4). The zero line indicates mean DI estimated by the model, while the y-axis is a relative scale where the effect of different values of the predictors on the response variable is shown. Hence, negative values on the y-axis indicate that at the corresponding levels of the predictor (x-axis), the model estimates that DI is lower than the mean, while the opposite holds for positive values on the y-axis. In that sense, loess plots did not reveal any trend in the yearly abundance variations, mostly referring to the adults. Yearly fluctuations in juvenile abundance, however, were much higher than those of the adults, probably reflecting recruitment variations. These were more limited after 2001 with the abundance remaining at a relatively higher lever than previously. This change can also be observed, in a lower degree, in the total population. All abundances decreased sharply below 400 m and adult abundance had an increasing trend up to 200 m. In general, the highest adult abundance occurred in depths from about 200 to 380 m, while juveniles seemed to prefer shallower waters. Juvenile abundance decreased after 200 m with the decrease being more abrupt after 400 m. In all cases, the graphs of latitude suggested that, with the exception of a peak around 38°N, abundances were higher in the southern and northern parts of the examined area. Longitude graphs had several local peaks with the highest ones around 23 and 28°E.

The density distribution maps that were built based on the GAM estimates indicated that relatively higher abundances, both for totals and juveniles, are expected in the Saronikos Gulf and the Thracian Sea. Adult distribution pattern was rather patchy with several local abundance maxima. Apart from the aforementioned locations, there were additional areas, mostly in the Cretan Sea, the eastern part of the Aegean and the outer part of Thermaikos Gulf, with relatively high adult densities (Figs. 5–7).

# Discussion

Our results reveal a wide bathymetric distribution (from 26 to 757 m) for *P. longirostris* in the Greek waters, with a higher abundance from 100 to 400 m. This observation is in agreement with previous findings for the Mediterranean area, which are summarized in Sobrino et al. (2005).

On the other hand, our results confirm the primordial role that depth plays in the distribution of the different life stages of the deep-water pink shrimp. The shallower distribution of juveniles (<20 mm CL), mostly in 100–200 m with their abundance decreasing deeper, and the preference of large individuals to depths of about 200–400 m is in accordance to earlier observations for the Greek waters (Politou et al., 2000) and other Mediterranean areas (e.g. central Tyrrhenian Sea: Ardizzone et al., 1990).

Concerning the year effect, there was indication of an amelioration of the recruitment during the last years, whereas no high variation or time trend was observed for the abundance of the adult population. Recent analyses of MEDITS data using population and community indicators have shown an increasing





**Fig. 3** GAM derived effects on the adult pink shrimp DI. Each plot represents the contribution of the corresponding variable to the fitted predictor. The fitted values are adjusted to average zero and the broken lines indicate two standard errors. The relative density of data points is shown by the "rug" on the *x*-axis

trend in the abundance of the deep-water pink shrimp in the Greek Ionian Sea for the period 1994–2004. No changes in abundance were found for the Aegean Sea during the same period, however, an increasing trend was observed after 2000 (MEDITS, 2007). The fisheries management measures imposed in the Greek waters (reduction of the fishing effort, increase of cod-end mesh size) during the last years could have decreased the fishing impact on the species and led to an increase of abundance, observed mainly in the Ionian Sea. However, environmental changes are also susceptible to be the factor that has affected the fisheries production. According to Rochet et al. (2007), an increased recruitment was detected at both population and community levels of demersal species in the Eastern Ionian. This was attributed to the recent changes in the water circulation in the area (Klein et al., 1999; Manca et al., 2002) that have contributed to an increase in biological production (Souvermezoglou & Krasakopoulou, 2005) **Fig. 4** GAM derived effects on the juvenile pink shrimp DI. Each plot represents the contribution of the corresponding variable to the fitted predictor. The fitted values are adjusted to average zero and the broken lines indicate two standard errors. The relative density of data points is shown by the "rug" on the *x*-axis



**Fig. 5** Map of the total pink shrimp distribution. DI is expressed in terms of n/km<sup>2</sup>. Interpolation was made by means of the "inverse distance to a power" gridding method

The geographical location (latitude, longitude) also had a consistent effect on the abundance of the different life stages of the deep-water pink shrimp. The maps built, based on the GAM predictions, showed high abundance concentration areas for all life stages mainly in the Aegean Sea. The most important nursery ground identified was located in the Saronikos Gulf and a secondary in the Thracian Sea. According to Fiorentino et al. (2002), the Aegean Sea was one of the areas where the main nursery grounds of the species, in terms of abundance of juveniles, were encountered in a Mediterranean level. Politou et al. (2006) identified the nuclei stations of its nursery grounds, which were found to occur mainly in the Saronikos Gulf and also in the Thracian Sea and the northern-eastern part of Crete. These findings are in general accordance with our results. Concerning the concentration areas of the adult specimens of the pink shrimp, according to our maps, they are located mainly in the Saronikos Gulf, the Thracian Sea, the Thermaikos Gulf, the Cretan Sea and the eastern part of the Aegean. These results





**Fig. 7** Map of the juvenile pink shrimp distribution. DI is expressed in terms of n/km<sup>2</sup>. Interpolation was made by means of the "inverse distance to a power" gridding method

are in good agreement to the pink shrimp catch data reported by the National Statistical Service of Greece (Kapiris et al., 2007). The density distribution map of the total population was more similar to that of the juveniles, which seems natural for a short-living species with a lifespan of 2–3 years and high mortality.

Over the last years, GAM techniques have been repeatedly used for the examination of marine species abundance in relation to environmental and spatiotemporal variables (e.g. Bigelow et al., 1999; Daskalov, 1999; Walsh & Kleiber, 2001; Maravelias & Papaconstantinou, 2003). In the current study, GAMs explained a relatively high percentage of abundance variations and allowed direct spatiotemporal comparisons by removing effects that could bias nominal indices.

Mapping of the spatial distribution of the different life stages of the species using the GAM estimates gave reasonable results and the predicted abundance variations were in good agreement with already existing observations. The performance of the models could be without doubt improved by including more parameters, which were not currently available, such as bottom type and temperature, water circulation and productivity. Nevertheless, the present approach gave a quantitative basis for the identification of the essential habitats of the pink shrimp in the Greek waters. Taking into account that the management of the demersal fisheries resources in the Mediterranean is based on technical measures, such as licence limitations, gear restrictions and closed seasons/areas, this information may contribute to the sustainable exploitation of the resource. Further research programs are clearly needed in order to investigate seasonal variations or to obtain results in a finer-local scale.

Acknowledgement The authors wish to express their appreciation to all participants in the MEDITS-GR cruises and the working groups involved in the project.

# References

- Abelló, P., A. Abella, A. Adamidou, S. Jukic-Peladic, P. Maiorano & M. T. Spedicato, 2002. Geographical patterns in abundance and population structure of *Nephrops norvegicus* and *Parapenaeus longirostris* (Crustacea Decapoda) along the European Mediterranean coasts. Scientia Marina 66: 125–141.
- Akaike, H., 1978. A Bayesian analysis of the minimum AIC procedure. Annals of the Institute of Statistical Mathematics 30: 9–14.
- Ardizzone, G. D., M. F. Gravina, A. Belluscio & P. Schintu, 1990. Depth-size distribution pattern of *Parapenaeus longirostris* (Lucas, 1846) (Decapoda) in the central Mediterranean Sea. Journal of Crustacean Biology 10: 139–147.
- Bertrand, J. A., L. Gil de Sola, C. Papaconstantinou, G. Relini & A. Souplet, 2000. An international bottom trawl survey in the Mediterranean: the MEDITS programme. In Bertrand, J. & G. Relini (eds), Demersal Resources in the Mediterranean. Actes de colloques 26, IFREMER, Plouzane France: 76–93.
- Bertrand, J. A., L. G. de Sola, C. Papaconstantinou, A. Relini & A. Souplet, 2002. The general specifications of the MEDITS surveys. Scientia Marina 66: 9–17.
- Bigelow, K. A., C. H. Boggs & X. He, 1999. Environmental effects on swordfish and blue shark catch rates in the US North Pacific longline fishery. Fisheries Oceanography 8: 178–198.
- Cleveland, W. S. & S. J. Devlin, 1988. Locally-weighted regression: an approach to regression analysis by local fitting. Journal of American Statistical Association 83: 596–610.
- Crawley, M. J., 2005. Statistical Computing: An Introduction to Data Analysis Using S-Plus. John Wiley & Sons, Chichester, West Sussex.
- Davis, J. C., 1986. Statistics and Data Analysis in Geology. John Wiley and Sons, New York.

- Daskalov, G., 1999. Relating fish recruitment to stock biomass and physical environment in the Black Sea using generalised additive models. Fisheries Research 41: 1–23.
- D'Onghia, G., A. Matarrese, P. Maiorano & F. Perri, 1998. Valutazione di *Parapenaeus longirostris* (Lucas, 1846) (Crustacea, Decapoda) nel Mar Ionio. Biologia Marina Mediterranea 5: 273–283.
- Fiorentino, F., J. A. Bertrand, E. Ferrandis, G. Garofalo, M. Gonzalez & C.-Y. Politou, 2002. Identifying the main nurseries of hake, greater fork-beard, deep water pink shrimp and broadtail shortfin squid in the Mediterranean using MEDITS trawl survey data. In Bertand, J. (ed.), International Bottom Trawl Survey in the Mediterranean. MEDITS – Survey 2000. Final report. IFREMER/IMBC/ NCMR/IEO.
- Golden Software, 2002. SURFER, Version 8, Golden Software Inc., Golden, Colorado.
- Hastie, T. J. & R. J. Tibshirani, 1990. Generalized Additive Models. Chapman and Hall, London.
- Holthuis, L. B., 1980. FAO Species Catalogue. Volume 1. Shrimps and Prawns of the World. An annotated catalogue of species of interest to fisheries. FAO Fisheries Sinopsis No125.
- Kapiris, K., 2004. Feeding ecology of *Parapenaeus longirostris* (Lucas, 1846) (Decapoda: Penaeidae) from the Ionian Sea (Central and Eastern Mediterranean Sea). Scientia Marina 68: 247–256.
- Kapiris, K., Ch. Mytilineou, C.-Y. Politou, S. Kavadas & A. Conides, 2007. Research on shrimps' resources and fishery in Hellenic waters. In: Papaconstantinou, C., A. Zenetos, V. Vassilopoulou & G. Tserpes (eds), State of Hellenic Fisheries. HCMR, Institute of Marine Biological Resources, Athens: 421–432.
- Klein, B., W. Roether, B. Manca, D. Bregant, V. Beitzel, V. Kovacevic & A. Luchetta, 1999. The large deep transient in the Eastern Mediterranean. Deep-Sea Research 46: 371–414.
- Labropoulou, M. & I. Kostikas, 1999. Patterns of resource use in deep-water decapods. Marine Ecology Progress Series 184: 171–182.
- Manca, B., L. Ursella & P. Scarazzato, 2002. New development of Eastern Mediterranean circulation based on hydrological observations and current measurements. Marine Ecology 23: 237–257.
- Maravelias, C. D. & C. Papaconstantinou, 2003. Size-related habitat use, aggregation patterns and abundance of anglerfish (*Lophius budegassa*) in the Mediterranean Sea determined by generalized additive modeling. Journal of Marine Biological Association of the U.K. 83: 1171– 1178.
- MEDITS, 2007. Assessment of indicator trends related to exploited demersal fish populations and communities in the Mediterranean. DCR Medits Working group. Nantes (France), 15–18 March 2005 and Kavala (Greece), 2–6 April 2006. http://www.ifremer.fr/docelec/default-en.jsp
- Mori, M., P. Belcari & F. Biagi, 1986. Distributione e sex-ratio di *Parapenaeus longirostris* (Lucas) nel Tirreno settentrionale. Nova Thalassia 8: 623–625.
- Pérez Farfante, I. & B. Kensley, 1997. Penaeoid and sergestoid shrimps and prawns of the world. Keys and diagnoses for

the families and genera. Mémoires du Muséum Nationale d'Histoire Naturelle: 175.

- Politou, C.-Y., A. Chilari, J. Dokos, A. Kallianiotis, G. Tserpes & P. Peristeraki, 2006. Identification of the nurseries of hake and deep-water pink shrimp in the Greek waters using trawl survey data. Working paper for STECF/ SGMED-06-01 sub-group meeting on Sensitive and Essential Fish Habitats in the Mediterranean, Rome, March 6–10, 2006.
- Politou, C.-Y., M. Karkani & J. Dokos, 2000. Distribution of Decapods caught during MEDITS surveys in Greek waters. In: Bertrand, J. & G. Relini (eds), Demersal Resources in the Mediterranean. Actes de colloques 26, IFREMER, Plouzané France: 196–207.
- Politou, C.-Y., P. Maiorano, G. D'Onghia & Ch. Mytilineou, 2005. Deep-water decapod crustacean fauna of the Eastern Ionian Sea. Belgian Journal of Zoology 135: 235–241.
- Rochet, M.-J., V. M. Trenkel, L. Gil de Sola, C.-Y. Politou, G. Tserpes & J. Bertrand, 2007. Do population and community metrics tell the same story about recent changes in Northern Mediterranean fish communities? ICES CM 2007/D:16.

- Sobrino, I., C. Silva, M. Sbrana & K. Kapiris, 2005. A review of the biology and fisheries of the deep water rose shrimp, *Parapenaeus longirostris*, in European Atlantic and Mediterranean waters (Decapoda, Dendrobranchiata, Penaeidae). Crustaceana 78: 1153–1184.
- Souvermezoglou, A. & E. Krasakopoulou, 2005. Nutrients in deep seas. In Papathanasiou, E. & A. Zenetos (eds.), State of the Hellenic Marine Environment. HCMR, Institute of Oceanography, Athens: 137–145.
- Stamatopoulos, C., 1993. Trends in the catches and landings. Mediterranean and Black Sea fisheries: 1972–1991. FAO Fisheries Circular 855. 4:1–177.
- Tom, M., M. Gorem & M. Ovadia, 1988. The benthic phases of life cycle of *Parapenaeus longirostris* (Crustacea, Decapoda, Penaeidae) along the Mediterranean coast of Israel. Hydrobiologia 169: 339–352.
- Venables, W. N. & B. D. Ripley, 1997. Modern Applied Statistics with S-PLUS, 2nd edn. Springer.
- Walsh, A. & P. Kleiber, 2001. Generalized additive model and regression tree analyses of blue shark (*Prionace glauca*) catch rates by the Hawaii-based commercial longline fishery. Fisheries Research 53: 115–131.

# FISH HABITAT MAPPING

# Salinity and temperature as factors controlling the spawning and catch of *Parapenaeus longirostris* along the Moroccan Atlantic Ocean

Said Benchoucha · Abdellatif Berraho · Hocein Bazairi · Isidora Katara · Salah Benchrifi · Vasilis D. Valavanis

© Springer Science+Business Media B.V. 2008

Abstract The deep-water rose shrimp, *Parapenaeus longirostris* (Lucas 1846, Decapoda: Penaeidae) is one of the main target species of the demersal fishery in the Moroccan Atlantic region. However, in the last decade, there is a severe decline of shrimp fisheries in the area without the existence of any management plan. The purpose of this article is to investigate the relationships between the spawning of the deep-water rose shrimp and environmental factors in order to provide basic information for any future management measure. The spatial distribution of mature females is investigated through statistical techniques on data collected in the Moroccan Atlantic

Guest editor: V. D. Valavanis Essential Fish Habitat Mapping in the Mediterranean

S. Benchoucha (⊠) · A. Berraho · S. Benchrifi Institut National de Recherche Halieutique, 2 rue de Tiznit, Casablanca, Morocco e-mail: bench2468@yahoo.fr

#### H. Bazairi

Faculté des Sciences, Université Hassan II Aïn Chock, Km 7, Route El Jadida, Casablanca, Morocco

#### I. Katara

School of Biological Sciences (Zoology), University of Aberdeen, Tillydrone Avenue, Aberdeen AB24 2TX, UK

#### V. D. Valavanis

Marine GIS Laboratory, Institute of Marine Biological Resources, Hellenic Centre for Marine Research, Thalassocosmos, 71003 Heraklion, Crete, Greece Ocean from bottom trawl surveys during 1981–2004. The geographic distribution of mature females is jointly analyzed in association to the spatial distribution of salinity and temperature at the depth of species catch. The study reveals a strong relationship between locations of spawning females and high salinity. Most spawning occurrences are observed in high salinity 'islands' (35.6–36.5 psu) or in the boundaries of higher-lower salinity patterns in the specific range of 36.2–36.4 psu in shallower (75–200 m) and deeper zones (250–500 m). Spawning occurs mostly in the shallower zone from spring to summer while during winter, it occurs in both depth zones. Temperature seems to be important on catch levels of the species.

**Keywords** Deep-water rose shrimp · Environment · Ecology · Atlantic · Morocco

# Introduction

The deep-water rose shrimp, *Parapenaeus longirostris*, thereafter rose shrimp, is one of the three species of the genus *Parapenaeus* that inhabits the Atlantic Ocean (Perez-Farfante & Kensley, 1997). It has a wide geographical distribution in the Eastern Atlantic, from the north of Spain (Olaso, 1990) to south Angola (Crosnier et al., 1968), as well as in the Mediterranean and its adjacent seas (Karlovac, 1949; Maurin, 1960; Massuti, 1963; Audoin, 1965). Rose shrimp is targeted by a large fishing fleet in eastern Atlantic waters, south of Spain and Portugal (Pestana, 1991; Sobrino et al., 1994), Morocco, Mauritania, Senegal, Guinea Bissau, Gabon, and Angola (Cervantes & Goni, 1986; Cervantes et al., 1991; Sobrino & Garcia, 1991, 1992a, b).

In Moroccan waters, rose shrimp is one of the main target species of the Moroccan Atlantic demersal fisheries representing one of the most valuable species in fishery markets. The species is targeted by a coastal fleet operating between the coast and 150 m and by a deep sea fleet operating between 150 and 700 m. The catch of the coastal fishery is always landed fresh for local consumption mainly in Casablanca, Larache, and Agadir. The catch of the deep sea fishery is landed frozen in Tangier and Agadir ports and it is exported to Europe. The rose shrimp represents 98% of the landing species of the deep sea fishery. During the last decade, the shrimp fisheries in Moroccan Atlantic fishing grounds have been characterized by a severe decline (FAO, 2004, 2005). However, the exploitation pattern of this species has not been defined within a management plan (Belvèze et al., 1982; Benchoucha, 2005).

Although the commercial importance of this resource is high and despite being a species with wide geographical distribution, especially in African Atlantic fishing grounds, studies on the biology, ecology, and exploitation aspects of the rose shrimp are limited and fragmented. Based on multiyear sampling (1988-1994), obtained from Spanish fishing fleet landings at Spanish ports but operating in Moroccan Atlantic waters, the rose shrimp showed a continuous spawning during the year with two spawning peaks, one at early summer and another at the beginning of autumn (Sobrino & Garcia, 1994). This spawning pattern is similar to that found in the south of Portugal by Ribeiro-Cascalho & Arrobas (1983), who reported two peaks, one in June and another in October. In more recent studies (Ribeiro-Cascalho & Arrobas, 1987; Pestana, 1991), spawning peaks were established between June and July and between January and February by obtaining a first maturity size of 26 mm cephalothorax length (sexual maturity length), for the fishing grounds exploited to the south Portugal. This area is influenced by Mediterranean outflow, indicating species growth at smaller sizes during the gonadal maturation process. Length-weight ratio is similar at minor sizes, nevertheless, beyond a certain value, females at the same size weigh more than males; this deviation starts at around 24 mm of cephalothorax length. The rose shrimp prefers sandy and muddy bottom substrates and its size and male presence are positively correlated with depth (Froglia, 1982). Sobrino et al., (2000) and Relini et al., (1999) reported that mature females are generally present in all seasons with reproduction starting in winter and maturity reached in autumn and early winter.

In the Gulf of Cadiz, spawning of rose shrimp occurs throughout the year with two peak periods in late spring and early autumn. Here, the species is characterized by a differential growth pattern, with females reaching a larger size, having a life cycle of 2-3 years. Individuals reach sexual maturity at 8-10 months at varying sizes, depending on the area (cephalothorax length 20-28 mm in females) and have an average fecundity of 90,000 eggs. The species feeds on a great variety of prey with main preference in annelid worms (polychaetes) and foraminiferans (Sobrino et al., 2005). In the Mediterranean, (centralsouthern Tyrrhenian coasts), the species has been caught between 61 and 587 m with higher abundance indices observed from 200 to 450 m and average cephalothorax length increasing significantly with depth (Spedicato et al., 1996). Similar results were also reported by D'Onghia et al. (1998) for the Ionian Sea (Central Mediterranean). In the Sea of Marmara (located between the Mediterranean and the Black Sea), the mature individuals of the species with fully developed eggs were found throughout the year with the highest gonadosomatic index values obtained in September, October, December, April, and May. The total length at which 50% of the population reaches maturity is calculated to be 9.7 cm. Among the individuals caught, females at 10-11 cm and males at 9-10 cm formed the dominant size groups (Bayhan et al., 2005). In Egypt, spawning occurs throughout the year in deep waters, with pick occurrence during November. Immature individuals were found from January to September (Abdel Razek et al., 2006).

In 2003, the Moroccan production of rose shrimp reached 10,866 tones in weight and 60,947,250 USD in value (4,917 tones and 14,702,250 USD by the coastal fleet and 5,949 tones and 46245000 USD by the deep-water fleet) (Official statistics, ONP-Morocco). The abundance of rose shrimp constitutes 57% of all shrimp species occurring in Morocco. The
number of females (63%) is far larger than that of males (37%). Cephalothorax length is 23.44 mm corresponding to 6.41 g weight and 0.44 years of age. Stock evaluation shows that rose shrimp is dramatically over exploited, the stock is deteriorated and the biomass is continually decreasing with most exploited sizes belonging to juveniles (FAO, 2007).

Based on long-term data from experimental trawling along the north Atlantic Moroccan coast, the aims of this study are to provide knowledge on the bathymetric distribution of the species and catch areas and to investigate the relationship between environmental factors (salinity and temperature) and rose shrimp spawning and catch in the Moroccan Atlantic waters aiming to contribute to any future and informed management decisions.

#### Materials and methods

9°30

35°00

The investigated area (Fig. 1) is located in the eastern part of the subtropical North Atlantic gyre off Morocco (NW Africa) influenced by the connection of the Gulf Stream via the Azores Current and the Canary Current with the North Equatorial Current. The study area belongs to one of the major eastern boundary upwelling systems of the world (Carr,

8°00

2002). Upwelling is predominant in summer and early fall due to the trade wind belt that is intensified during summer (Abrantes et al., 2002).

Fisheries data were collected during 40 experimental trawl surveys carried out during 1981–2004 in the North Moroccan Atlantic waters at a depth range 20–1,000 m. The duration of each survey was between 15 and 20 days. All stations were sampled during day-time in order to avoid rose shrimp considerable upward migrations during night-time. Two similar research vessels were used, 'Ibn Sina' during 1981–1986 and 'Charif Al Idrissi' during 1987–2004 surveys (Table 1). The two vessels were equipped with a trawl of 40 mm stretched mesh size at the cod-end.

The investigations covered two study areas: Larache–El Jadida (north zone) and Essaouira–Agadir (south zone) (Fig. 1). The bottom type in the region between these two zones is rocky, thus no investigation by trawling occurred there. The depth covered by the surveys was ranging from the coast (20 m) to 1,000 m depth with stratums of 0–100, 101–200, 201–500 and 501–1,000 m considered. Surface area (km<sup>2</sup>) for each sampling stratum is shown in Table 2.

A stratified random sampling design (Fig. 1) was adopted with allocation of hauls proportional to the area of the strata (Cochran, 1963; Fogarty, 1985).

10\*00

9930

9\*00

32900

31 30

31 000

100 200 500

11\*00

ATLANTIOUE

10%30



32°

31°30

31 000

35°00

Fig. 1 Map of the study area Moroccan Eastern Atlantic: Stratified sampling adopted in each survey (a): North zone (Larache–El Jadida) and (b): south Zone (Essaouira–Agadir)

Table 1Calendar of allParapenaeus longirostrissurveys realized during1981–2004

Time	Research vessel	Type of trawl	Type of panel	Zones investigated	Sampling
Dec81	Ibn Sina	Calypso	Morgeres	North–South	16
Apr82	Ibn Sina	Calypso	Morgeres	North-South	33
Oct82	Ibn Sina	Calypso	Morgeres	South	6
Dec82	Ibn Sina	Calypso	Morgeres	South	4
Apr83	Ibn Sina	Calypso	Morgeres	North-South	18
Aug83	Ibn Sina	Calypso	Morgeres	North-South	29
Dec83	Ibn Sina	Calypso	Morgeres	North-South	29
Mar84	Ibn Sina	Calypso	Morgeres	North-South	66
Dec84	Ibn Sina	Calypso	Morgeres	North-South	40
May85	Ibn Sina	Calypso	Morgeres	North-South	40
Sep85	Ibn Sina	Calypso	Morgeres	North-South	37
Apr86	Ibn Sina	Calypso	Morgeres	North-South	33
Nov86	Ibn Sina	Calypso	Morgeres	North-South	36
Nov87	Charif Al Idrissi	Shrimp	Japenese	North-South	39
Mar88	Charif Al Idrissi	Shrimp	Japenese	North-South	40
Jun89	Charif Al Idrissi	Shrimp	Japenese	North-South	35
May91	Charif Al Idrissi	Shrimp	Japenese	North	16
July92	Charif Al Idrissi	Shrimp	Morgeres	North-South	24
Dec92	Charif Al Idrissi	Shrimp	Japenese	North	8
Apr93	Charif Al Idrissi	Shrimp	Morgeres	North-South	44
Jun94	Charif Al Idrissi	Shrimp	Morgeres	North-South	53
Sep94	Charif Al Idrissi	Shrimp	Morgeres	North-South	37
Dec94	Charif Al Idrissi	Shrimp	Morgeres	North	25
Apr95	Charif Al Idrissi	Shrimp	Morgeres	North-South	48
July95	Charif Al Idrissi	Shrimp	Morgeres	North-South	67
Dec95	Charif Al Idrissi	Shrimp	Morgeres	North	54
May96	Charif Al Idrissi	Shrimp	Morgeres	North-South	70
July97	Charif Al Idrissi	Shrimp	Thyboron	North	52
Dec97	Charif Al Idrissi	Shrimp	Thyboron	North-South	77
July98	Charif Al Idrissi	Shrimp	Thyboron	North	53
Dec98	Charif Al Idrissi	Shrimp	Thyboron	North-South	71
Mar99	Charif Al Idrissi	Shrimp	Thyboron	North-South	50
Nov99	Charif Al Idrissi	Shrimp	Thyboron	North-South	68
Nov00	Charif Al Idrissi	Shrimp	Thyboron	North-South	72
Apr01	Charif Al Idrissi	Shrimp	Thyboron	North-South	82
Nov01	Charif Al Idrissi	Shrimp	Thyboron	North-South	70
May02	Charif Al Idrissi	Shrimp	Thyboron	North-South	76
June03	Charif Al Idrissi	Shrimp	Thyboron	North-South	83
June04	Charif Al Idrissi	Shrimp	Thyboron	North-South	80

Generally, a range of 50–84 30-min hauls were carried out during each survey. The vessel speed, measured by GPS, was maintained at 3.0 knots. The horizontal net opening (20 m) was measured by means of a SCANMAR sonar system. For each

station, the zoological collection has been sorted to species and length measurements were made. The abundance index (in kg/h) by zone or by stratum was calculated as the mean of the catch by species for all hauls in the zone or in the stratum.

**Table 2** Surfaces (in km<sup>2</sup>)of zones investigated

Bathymetry zone	North zone		South zone	
	Strata	Surface (km <sup>2</sup> )	Strata	Surface (km <sup>2</sup> )
0–100 m	Stratum 1	3254.574	Stratum 5	1583.148
101–200 m	Stratum 2	6296.902	Stratum 6	1462.023
201–500 m	Stratum 3	2435.297	Stratum 7	1553.021
501–1000 m	Stratum 4	5402.358	Stratum 8	3029.324

Table 3	Deep-water	pink shrimp	o females'	stages scale	(Laborator	y of	Invertebrates,	Russian	Institute)
---------	------------	-------------	------------	--------------	------------	------	----------------	---------	------------

Stage I	Juvenile stage, ovaries are completely transparent or hardly discernible the other organs.
Stage II	Ovaries are fine or relatively big very detachable the other parts of the body. They are flasks, semi transparent, letting suspect the other organs.
Stage III	Ovaries are big, opaque, can be of slightly greenish color or blue; these can be distinguished by transparency through the shell. The previous digitations of ovaries do not recover the stomach.
Stage IV	Previous stage of spawning, the ovaries are big, opaque, of green color. Gonads are visible through the shell. The previous digitations of ovaries recover the lateral parts of the stomach.
Stage V	Stage of spawning. At this stage, the ovaries distinguish themselves from the precedent only by their color which oscillates between the brown and the dark green.

Rose shrimp cephalothorax length was measured (in mm) from rear of ocular indent to posterior dorsal margin of cephalothorax. Sex and maturity stage were assigned according to the Atlantniro Russian Institute scale (Laboratory of Invertebrates) (Table 3). Female maturity stages were considered as immature (stages I and II) and mature (stages III–V). In order to depict the geographic distribution of mature females, we selected those halls where both more than 50% of females and more than 50% of mature females were present and assumed as spawning females.

In order to examine the effect of environmental factors (salinity and temperature) on the spawning distribution of rose shrimp, we obtained 3-dimensional environmental data through NOAA's National Oceanographic Data Center (NODC) website (http:// www.nodc.noaa.gov/OC5/WOA01/qd\_ts01.html). The environmental data source is the high resolution  $(1/4^\circ)$ temperature and salinity analyses (climatology) of the world's oceans (Boyer et al., 2005). Environmental data were processed under a Geographic Information System (GIS) environment and were superimposed to the distribution of spawning females of the species. Each spawning location was assigned an environmental value according to sampled month and depth. In order to examine whether factors such as depth and time (month, year or a combination of both) affect spawning frequency or catch, we used the analysis of variance (ANOVA) and in case of violation of the assumptions of ANOVA, its non parametric equivalent, the Kruskall-Wallis test. The Pearson and Spearman correlation coefficients were used to check for linear relationships between the catch or spawning variables and the environmental variables. Generalized additive (GAM) and linear regression models were also built to assess the influence of the environment and the relative importance of the variables. All statistical analyses were implemented in R language (R Development Core Team, 2005).

The study of the spatial distribution of spawning females was carried out under the implicit assumption of statistics that the structure of the investigated variable was stable in time, at least for the duration of each survey. This hypothesis seems to be realistic, considering the greater speed of the survey with respect to some possible biomass displacements. Moreover, catchability was not structured through space as the daylight sampling guaranteed that the catches were not affected by vertical migratory movements (Pestana & Ribeiro-Cascalho, 1991).

## Results

The study area and the distribution of all haul surveys as well as the distribution of spawning females are shown in Fig. 2. Rose shrimp population shows a wide distribution as it was present at almost 80% among all



Fig. 2 Moroccan Atlantic Ocean: geographic distribution of all surveys (left) and distribution of *Parapenaeus longirostris* spawning females (right)

stations sampled. Spawning females in all surveys are distributed in various depths and throughout the year. Maximum spawning occurs in the region of Loukkos and deeper in the north of Agadir city, where sand and mud dominate the seabed. Spawning occurs generally between the isobaths of 100 and 500 m.

The distribution of the abundance index of rose shrimp for the surveys May 2002, June 2003, and June 2004 is shown in Fig. 3. Although some differences in abundance levels of rose shrimp among the years are observed, two sub-areas with high density of the species are observed. The geographical areas characterized by a high level of abundance are mainly localized between Moulay Bousselham and Rabat and in Agadir surrounding region, at depths ranging from 20 to 500 m, with some intrusions in the deeper levels. However, the maximum of abundance is always situated in the Loukkos region (Larache-Kénitra).

The spatial distribution of spawning females is superimposed to the spatial distribution of salinity distribution at catch depth. Salinity-spawning distributions in various depth zones are shown in Fig. 4. In most cases, spawning occurrences are observed in high-salinity 'islands' or in the boundaries of higherlower salinity patterns.

The distribution of the spawning and its associated salinity is shown in Fig. 5. Most spawning occurrences

are observed in the salinity range of 36.2–36.4 psu (the general salinity range for spawning is 35.6–36.5 psu). The case of June 2003 presents a tongue of homogeneous salinity range and 3 cases of high spawning occurrences in 150, 300 and 500 m depth zones. Overall, there are 2 depth zones where spawning is mostly observed. These are the shallower zone (75–200 m) and the deeper zone (250–500 m). Spawning occurs mostly in the shallower zone from spring to summer (March–July) while during winter (November–December) it occurs in both depth zones.

In an exploratory approach, statistically significant linear correlations were observed between catch variables (frequency, min, max, mean, and sum) and the variability (standard deviation—std) of temperature, as well as between min catch and min temperature, and min catch and std of salinity. The spawning frequency showed a statistically significant correlation to maximum salinity (Table 4, Fig. 6a and b).

A generalized additive model describes the relationship between landings and the environmental parameters. Temperature, along with depth and timerelated variables (year and month) explain 15% of the variability of landings. An interaction between temperature and month was also statistically significant in this model (Fig. 7). Maximum salinity performs better than its minimum and mean values in terms of Akaike



Fig. 3 Geographic distribution of the abundance index (kg/h) of Parapenaeus longirostris in Moroccan Atlantic Ocean during selected surveys

Information Criterion (AIC, Akaike, 1973; Burnham & Anderson, 2002) and percentage of the variability explained. A better proportion of the variability of the number of spawning females, namely 33%, is explained by means of a linear model that uses salinity and depth as explanatory variables (Fig. 8).

## Discussion

As in any marine resource, the knowledge of the biology and the ecology of the rose shrimp constitute a fundamental asset for the management of the species. In spite of the economic importance,



Fig. 4 Geographical distribution of salinity and Parapenaeus longirostris spawning occurrences in various depth zones



Fig. 5 Spatial distribution of spawning Parapenaeus longirostris (left) and associated salinity (right) during all surveys

Table 4 Linear correlation	ons (statistically signi	ficant in bold) betw	een catch, spawn	ing and environmental	variables		
A							
Pearson correlation coeffi ( <i>P</i> -value)	cient Depth	Minimum salinity	Maximum salinity	Standard deviation salinity	Minimum temperature	Maximum temperature	Standard deviation temperature
Frequency	-0.344(0.2	28) 0.075 (0.8)	0.412 (0.14)	0.145 (0.62)		0.17 (0.59)	
Min catch Max catch	-0.2 (0.47) -0.33 (0.24)	(11.0) $(0.445)$ $(0.11)$ $(1.0)$ $(1.0)$ $(1.0)$	-0.07 (0.8) 0.42 (0.14)	-0.42(0.13) 0.18(0.53)	<b>0.69 (0.006)</b> -0.48 (0.08)	0.23 (0.41) -0.05 (0.85)	0.636 (0.014) -0.746 (0.002)
Mean catch	-0.48 (0.08	0.25 (0.38)	0.323 (0.26)	-0.15(0.6)	-0.255 (0.38)	0.085 (0.77)	-0.549 (0.042)
Sum catch	-0.39 (0.17	) 0.14 (0.62)	0.39 (0.17)	$0.04 \ (0.89)$	-0.38 (0.17)	0.18 (0.52)	-0.757 (0.0017)
В							
Spearman rank correlations ( <i>P</i> -value)	Standard deviation temperature	Standard deviation temperature	Standard deviation temperature	Minimum temperature	Standard deviation salinity	Standard deviation temperature	Standard deviation temperature
Frequency Maximum catch Mean catch Minimum catch Minimum catch Minimum catch Sum catch C Spearman rank correlation Spawning Spawning	-0.7511 (0.0068) ns ( <i>P</i> -value)	-0.7152 (0.0099) Minimum salinity -0.0384 (0.686)	-0.6425 (0.	0205) 0.6273 (0.02 imum salinity 5 (0.0064)	37) -0.718 (0.0 Mean salinity	0.6786 (0.0	144) -0.7239 (0.0091)
opawning					0.11 (0.240)		

D Springer



Fig. 6 (a) Analysis of variance and Kruskall-Wallis test P-values between catch and time-depth variables. (b) Analysis of variance and Kruskall-Wallis test P-values between spawning and time-depth variables

published papers on the rose shrimp are mainly based on commercial sampling in landings ports. The present study, based on multiannual data obtained by experimental trawling surveys brings useful elements for the management of this marine resource in Morocco.

The rose shrimp shows a wide geographical distribution in the study area with a bathymetric distribution related to size due to the migration of juveniles from the continental shelf to the slope, a pattern that is, however, common in many species of the family Penaeidae (Heldt, 1938). In Moroccan Atlantic, the distribution of rose shrimp is reported

between 20 and 700 m, though the species is more abundant between 70 and 400 m (Holthuis, 1987), with adults mainly observed between 150 and 350 m and juveniles between 100 and 180 m (Ardizzone et al., 1990). Generally, smaller specimens are more frequently caught on the upper part of the continental shelf (50–200 m) while larger ones are mainly distributed along the slope at depths exceeding 200 m (Ribeiro-Cascalho & Arrobas, 1987).

Geographic areas characterized by high level of abundance are mainly located between Moulay Bousselham and Rabat and in Agadir surrounding region, at depths ranging from 20 to 500 m, with











Fig. 6 continued

some intrusions in the deeper levels. Such distribution of the abundance of the rose shrimp might indicate a catch composition in which small sized shrimps prevail in some areas, as it can be argued by the knowledge on the bathymetrical partitioning of the different fractions (juveniles and adults) of the species population in the same basin (Ardizzone et al., 1990; Spedicato et al., 1996). Rose shrimp abounds in two zones: Larache–El Jadida and Essaouira–Agadir (Fig. 3). Maximum species abundance is always situated in the Loukkos region (Larache-Kénitra), probably due to the presence of ANOVA P-value: 0.0237 Kruskall-Wallis test P-value: 0.035



ANOVA P-value: 0.0553 Kruskall-Wallis test P-value: 0.065



extended muddy seabed and the increased productivity in this area, and consequently, the abundance of food. Benthic bio-sedimentary characterization of the north Atlantic Moroccan shelf between Tangier and El Jaida revealed an extended central region of mud, bounded on the coastal side by medium or fine sands and offshore by biogenic muddy or coral formations. An increased gradient in terms of biomass was highlighted with pure mud or sandy mud being highly productive (Bayed & Glémarec, 1987).

The spawning of the species occurs in the entire Moroccan coast throughout the year as it is shown by







Fig. 8 Linear regression model between maximum salinity and spawning females of *Parapenaeus longirostris* in the Moroccan Eastern Atlantic

the wide distribution of mature females along the Moroccan Atlantic coast. However, two spawning zones are observed: the coastal spawning band where the depth is between 75 and 200 m and the deeper spawning band where the depth ranges from 250 to 500 m. Female rose shrimp comprise the major proportion of the catch. Individuals in stage I have a smaller mean size, than stage II, which are smaller than those of stage III. This indicates that there is

growth at smaller sizes during the gonadal maturation process (Ashton, 1972).

As the spectrum of climatic variability is not identical at the equatorial and tropical or moderate zones, abundance of the stocks of shrimps in these regions varies considerably. Our intention here is to draw the attention on the diverse types of possible variations and their combinations because the consequences on fisheries management and research programmes for an optimal strategy of resource exploitation are different. Several laboratory and survey studies depict this. Charmantier-Daures et al. (1988), conducted laboratory experiments on survival under different salinity-temperature combinations using post-larvae of Penaeus japonicus and P. chinensis. Low temperature (10-14°C) decreases the tolerance of P. japonicus post-larvae to low salinity levels while this influence is less important in P. chinensis. Williams (1969) showed the relation between the 'thermal contents' of 1 year and the abundance of shrimps. Warm years correspond sharply to high species catch. In fact, the global abundance of shrimps is proportional to the species annual thermal balance sheet. Berry & Baxter (1969) showed the existing connection between the timing of the peak annual migration of juvenile P. aztecus toward offshore areas and air temperature in April of the same year. In addition, Barrett & Gillespie (1973, 1975) indicated that the catch of *P. aztecus* during May depends on the temperature in April. Perez-Farfante (1982) underlined the relationship between shrimp catches and rainfall (as indication of salinity levels). Such studies show that temperature influences the survival of larvae and post-larvae by increasing or decreasing the rate of metabolic processes for the absorption of food. However, the complex behavior of shrimps in relation to temperature and salinity variations remains unknown. It is evident that any study on the effect of environmental factors on the physiological and biological processes would allow the improvement of any management measures. In Morocco, the maximum of spawning is observed in the salinity range of 36.2-36.4 psu. In June, the observed gradient of salinity appears homogeneous, possibly as a result of increased riverine outflow in the region. Thus, in June 2003, the spawning occurrences are observed in various depths: 150, 300 and 500 m.

The main environmental factor governing the spawning of deep-water shrimp is salinity while temperature seems to be important on catch levels. A statistically significant linear correlation is observed between the catch variables (frequency, minimum, maximum, mean and sun) and the standard deviation coefficient of the temperature. A high linear correlation is also observed between the minimal catch and the standard deviation of the temperature and the salinity. The catch is low when the temperature is minimal. The minimal catches also depend on the variation of the salinity. The frequency and the maximum of spawning are strongly correlated and depend mainly on the maximal salinity. The spawning is maximal when the salinity is maximal. The frequency of the spawning seems to be affected by the depth and by the combination year-month but it is not affected by the year and the month taken separately. The catches are affected by all the examined factors.

The studying of the spatial correlations of the distribution of mature females and salinity-temperature variables can provide useful information for a better understanding of the biology of the rose shrimp and its stock assessment and comprise a distinct indication for suggesting advice to fisheries management. The protection of spawning areas, as well as the nursery areas, through limitation of the fishing pressure throughout the year could be considered as an effective, complementary regulation tool for a short-lived species like the rose shrimp. In fact, information on the spatial distribution of abundance index and of spawning females, if coupled with analysis of the geographical distribution of salinity and temperature, could be of importance in stock assessment, allowing some variant application of the composite surplus production models (Munro, 1980; Caddy & Garcia, 1982). Such an approach may help evaluating the status of resources exploitation in regions where multiyear time series of abundance data are available (Relini & Piccinetti, 1996; Bertrand et al., 1997).

## Conclusion

This study revealed the high relationship between the spawning females of the deep-water rose shrimp (*Parapenaeus longirostris*) and the high salinity levels in Moroccan Atlantic Ocean. High salinity levels seem to activate spawning of this species while temperature seems to affect the catch levels of the species. These results provide useful information for a better understanding of the biology of the rose shrimp, for improvements in stock assessment while comprising a distinct indication for suggesting advice to fisheries management.

## References

- Abdel Razek, F. A., S. S. El-Sherief, S. M. Taha & E. G. Muhamad, 2006. Some biological studies of *Parapenaeus longirostris* (Lucas, 1846) (Crustacea: Decapoda) in the Mediterranean coast of Egypt. Egyptian Journal of Aquatic Research 32: 385–400.
- Abrantes, F., H. Meggers, S. Nave, J. Bollmann, S. Palme, C. Sprengel, J. Henderiks, A. Spies, E. Salgueiro, T. Moita & S. Neuer, 2002. Fluxes of micro-organisms along a productivity gradient in the Canary Islands region (29° N): implications for paleoreconstructions. Deep-Sea Research II 49: 3599–3629.
- Akaike, H., 1973. Information theory and an extension of the maximum likelihood principle. In Petrov, B. N. & F. Csaki (eds), Proceedings of the 2nd International Symposium on Information Theory. Publishing House of the Hungarian Academy of Sciences, Budapest: 268–281.
- Ardizzone, G. D., M. F. Gravina, A. Belluscio & P. Schintu, 1990. Depth-size distribution pattern of *Parapenaeus longirostris* (Lucas, 1846) (Decapoda) in the central Mediterranean Sea. Journal of Crustacean Biology 10: 139–147.
- Ashton, W. D., 1972. The Logit Transformation with Special Reference to its Uses in Bioassay. Charles Griffin & Co. Ltd, London, England.

- Audoin, J., 1965. Répartition bathymétrique des crevettes sur les côtes algériennes entre les îles Zaffarines et les îles Habibats. Rapports Commission Internationale pour l'Exploration Scientifique de la Mer Méditerranée 18/518: 171–174.
- Barrett, B. B. & M. C. Gillespie, 1973. Primary factors which influence commercial shrimp production in coastal Louisiana. Wildlife and Fisheries Communication Technical Bulletin 9: 1–28.
- Barrett, B. B. & M. C. Gillespie, 1975. Environmental conditions relative to shrimp production in coastal Louisiana. Wildlife and Fisheries Communication Technical Bulletin 15: 1–22.
- Bayed, A. & M. Glémarec, 1987. La plate-forme continentale Atlantique nord-Marocaine: Bionomie et Zoogéographie. Oceanologica Acta 10: 111–121.
- Bayhan, K., T. Unluer & M. Akkaya, 2005. Some biological aspects of *Parapenaeus longirostries* (Lucas, 1846) (Crustacea, Decopoda) inhabiting the Sea of Marmara. Turkish Journal of Veterinary and Animal Science 29: 853–856.
- Belvèze, H., A. Berraho, A. Chaali, A. Idelhaj & A. Lahlou, 1982. Périodes et zones de reproduction des principales espèces halieutiques dans les eaux Marocaines et possibilités éventuelles d'aménagement. Note d'information, Institute Pêches Maritime, Maroc, Casablanca: 2–22.
- Benchoucha, S., 2005. Etude de la biologie de la crevette rose du large (Parapenaeus longirostris, Lucas, 1846) de la côte Atlantique marocaine. Mémoire DESA. Université Hassan II, Aïn Chock, Casablanca.
- Berry, R. J. & K. N. Baxter, 1969. Predicting brown shrimp abundance in the northwestern Gulf of Mexico. FOA Fisheries Report 3: 776–798.
- Bertrand, J., L. G. De Sola, C. Papaconstantinou & G. Relini, 1997. An international bottom trawl survey in the Mediterranean: the MEDITS Programme. ICES Annual Science Conference Y:03: 1–7.
- Boyer, T., S. Levitus, H. Garcia, R. A. Locarnini, C. Stephens & J. Antonov, 2005. Objective analyses of annual, seasonal, and monthly temperature and salinity for the World Ocean on a 0.25° grid. International Journal of Climatology 25: 931–945.
- Burnham, K. P. & D. R. Anderson, 2002. Model Selection and Multimodel Inference: A Practical Information-theoretic Approach. Springer-Verlag, New York.
- Caddy, J. F. & S. Garcia, 1982. Production modelling without long data series. FAO Fisheries Report 238: 309–313.
- Carr, M.-E., 2002. Estimation of potential productivity in eastern boundary currents using remote sensing. Deep-Sea Research II 49: 59–80.
- Cervantes, A. & R. Goni, 1986. Composición por tallas de la captura española de la Gamba blanca (*Parapenaeus longirostris* Lucas, 1846) en el área de CECAF. Division 34.1.1 COPACE/PACE Series 86/33: 240–245.
- Cervantes, A., I. Sobrino, A. Ramos & L. Fernandez, 1991. Descripción y análisis de los datos de las pesquerías de merluza y gamba de la flota española que faeno al fresco en África noroccidental durante el periodo 1983–1988. Informes Técnicos Instituto Español de Oceanografía 111: 85.
- Charmantier-Daures, M., P. Thuet, G. Charmantier & J. P. Trilles, 1988. Tolérance à la salinité et osmorégulation

🖄 Springer

chez les post-larves de *Penaeus japonicus* et *Penaeus chinensis*. Effet de la température. Aquatic Living Resources 1: 267–276.

- Cochran, W. G., 1963. Sampling Techniques. John Wiley & Sons, New York.
- Crosnier, A., E. De Bondy & S. Lefèvere, 1968. Les crevettes commercialisables de la côte ouest de l'Afrique intertropicale. Etat de nos connaissances sur leur biologie et leur pêche en juillet 1967. Rapports Scientifiques et Techniques. Sciences de la Mer. Biologie marine. Centre de Noumea ORSTOM 7: 60.
- D'Onghia, G., F. Mastrototaro, P. Maiorano & M. Basanisi, 1998. Selettività della rete a strascico utilizzata sui fondi di scarpata (250–750 m) dello Ionio (Mediterraneo Centrale). Biologico Mare Mediterranea 5: 437–448.
- FAO, 2004. FAO Statistical Yearbook. Statistics Division. FAO, Rome: 318.
- FAO, 2005. The State of Food Insecurity in the World 2005. FAO Economic and Social Department. FAO, Rome: 40.
- FAO, 2007. Guide to Bycatch Reduction in Tropical Shrimp-Trawl Fisheries. FAO, Rome: 120.
- Fogarty, M. J., 1985. Statistical considerations in the design of the trawl-survey. FAO Fisheries Circular 786: 1–21.
- Froglia, C., 1982. Contribution to the knowledge of the biology of *Parapenaeus longirostris* (Lucas) (Decapoda, Penaeidae). Quaderni del Laboratorio di Tecnologia della Pesca 3: 163–168.
- Heldt, J. H., 1938. La reproduction chez les crustacés décapodes de la famille des Pénéidés. Annales de l'Institut Océanographique 18: 31–206.
- Holthuis, L. B., 1987. Crevettes. In Fischer, W., M. Schneider & M. L. Bauchot (eds), Fiches FAO d'identification des espèces pour les besoins le la pêche. Méditerranée et Mer Noire. Zone de pêche 37. Végétaux et invertébrés: 271– 272.
- Karlovac, O., 1949. Le *Parapenaeus longirostris* (H. Lucas) de la haute Adriatique. Acta Adriatica 3: 407–416.
- Massuti, M., 1963. La pêche des crustacés aux Baléares (Méditerranée occidentale) et dans l'Atlantique sud (Golfe de Cadix). C.G.P.M. Débats et Document Technique 7: 191–202.
- Maurin, C., 1960. Les crevettes profondes du littoral français de la Méditerranée. Répartition selon la profondeur. Notes biométriques. Rapports Commission Internationale pour l'Exploration Scientifique de la Mer Méditerranée 15: 147–154.
- Munro, J. L., 1980. Stock assessment models: applicability and utility in tropical small-scale fisheries. In Saila S. B. & P. H. Roedel (eds), Stock assessment for tropical smallscale fisheries. Proc. Intern. Workshop Sept. 1979, Univ. Rhode Island. Int. Cent. Mar. Res. Dev. Kingston, R.L.: 1–198.
- Olaso, I., 1990. Distribución y abundancia del megabentos invertebrado en fondos de la plataforma Cantábrica. Publicaciones Especiales Instituto Español de Oceanografía 5: 1–128.
- Perez-Farfante, I., 1982. The geminate shrimps species Parapenaeus longirostris and Parapenaeus politus. Quaderni del Laboratorio di Tecnologia della Pesca 3: 187–205.
- Perez-Farfante, I. & B. Kensley, 1997. Penaeoid and Sergestoid shrimp and prawns of the world. Key and diagnose

for the families and genera. Memoires du Museum National d'histoire Naturelle 175: 1–233.

- Pestana, G., 1991. Stock assessment of deep water rose shrimp (*Parapenaeus longirostris*) from the southern Portugal (ICES Division IXA). ICES CM1991/K/46: 29.
- Pestana, G. & A. Ribeiro-Cascalho, 1991. Effects of changing trawl mesh size and fishing effort of deep water rose shrimp (*Parapenaeus longirostris*) from the southern Portugal (ICES, Division IXa). ICES CM1991/K/45: 18.
- R Development Core Team, 2005. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna. http://www.R-project.org.
- Relini, G., J. Bertrand & A. Zamboni, 1999. Synthesis of the knowledge on bottom fishery resources in central Mediterranean, Italy and Corsica. Biologia Maritima Mediterranea 6: 868.
- Relini, G. & C. Piccinetti, 1996. Ten years of trawl surveys in Italian seas (1985–1995). FAO Fisheries Report 533: 21–41.
- Ribeiro-Cascalho, A. & I. Arrobas, 1983. Further contributions to the knowledge about biology and fishery of *Parapenaeus longirostris* (Lucas, 1846) of South Portuguese coast. ICES CM1983/K/26: 26.
- Ribeiro-Cascalho, A. & I. Arrobas, 1987. Observations on the biology of *Parapenaeus longirostris* (Lucas, 1846) from the south coast of Portugal. Investigacion Pesquera 51: 201–212.
- Sobrino, I. & T. Garcia, 1991. Analisis y descripcion de las pesquerias de crustaceos decapodos en aguas de la Republica Islamica de Mauritania durante el periodo 1987– 1990. Informes Tecnicos Instituto Espanol de Oceanografia 112: 1–38.
- Sobrino, I. & T. Garcia, 1992a. Análisis y descripción de la actividad de la flota española en las pesquerías de

crustáceos decapodos profundos en aguas de la Republica de Senegal durante el periodo 1987–1990. Informes Técnicos Instituto Español de Oceanografía 125: 1–37.

- Sobrino, I. & T. Garcia, 1992b. Análisis y descripción de las pesquerías españolas de crustáceos decapodos en aguas de la Republica de Guinea Bissau durante el periodo 1987– 1991. Informes Técnicos Instituto Español de Oceanografía 135: 1–38.
- Sobrino, I. & T. Garcia, 1994. Biology and fishery of the deep water rose shrimp *Parapenaeus longirostris* (Lukas, 1846) from the Atlantic Moroccan coast. Scientia Marina 58: 299–305.
- Sobrino, I., T. Garcia & J. Baro, 2000. Trawl gear selectivity and the effect mesh size on the deep water rose shrimp (*Parapenaeus longirostris*, Lucas, 1846) fishery off the Gulf of Cadiz (SW Spain). Fisheries Research 44: 235– 245.
- Sobrino, I., A. Garcia, E. Garcia-Isarch, L. Silva, J. Baro & J. Mas, 2005. Estudio previo para la delimitacion de una reserva de pesca en la desembocadura del Guadalquivir. Junta de Andalucía, Consejería de Agricultura y Pesca: 205.
- Sobrino, I., M. P. Jiménez, F. Ramos & J. Baro, 1994. Descripción de las pesquerías demersales de la región sur atlántica española. Informes Técnicos Instituto Español de Oceanografía 151: 79.
- Spedicato, M. T., G. Lembo, T. Silecchia & P. Carbonara, 1996. Distribuzione e biologia di *Parapenaeus longirostris* nel Tirreno Centro-Meridionale. Biologia Maritima Mediterranea 3: 579–581.
- Williams, A. B., 1969. A ten-year study of meroplankton in North Carolina estuaries: cycles of occurrence among penaeidean shrimps. Chesapeake Science 10: 36–47.

## FISH HABITAT MAPPING

# Identification of hake distribution pattern and nursery grounds in the Hellenic seas by means of generalized additive models

George Tserpes · Chrissi-Yianna Politou · Panagiota Peristeraki · Argyris Kallianiotis · Costas Papaconstantinou

© Springer Science+Business Media B.V. 2008

**Abstract** A time series of hake abundance data obtained from the "MEDITS" experimental surveys carried out in the Greek seas from 1996 to 2006 have been modeled by means of Generalized Additive Models (GAMs), as functions of spatial and temporal variables, including sampling position (latitude–longitude interaction), depth, and year. All variables were highly significant but most of the variation was explained by the sampling position and the depth. Total abundance was higher in the 100–450 m depth zone, while juveniles showed preference for shallower waters, being more abundant from 100 to 320 m. Model predictions were used to generate density distributions maps, which revealed that total abundance is relatively higher in the western part of the

Guest editor: V. D. Valavanis Essential Fish Habitat Mapping in the Mediterranean

G. Tserpes (⊠) · P. Peristeraki Hellenic Centre for Marine Research, Institute of Marine Biological Resources, P. O. Box 2214, 71003 Iraklion, Greece e-mail: gtserpes@her.hcmr.gr

C.-Y. Politou · C. Papaconstantinou Hellenic Centre for Marine Research, Institute of Marine Biological Resources, Aghios Kosmas, 16604 Helliniko, Greece

A. Kallianiotis Fisheries Research Institute-NAGREF, 64007 N. Peramos, Greece Aegean Sea and in the eastern part of the Cretan Sea, while its maximum values are expected in the Saronikos Gulf. Nursery grounds are restricted in specific regions with the most important of them being in the Saronikos Gulf and its surrounding area.

**Keywords** Hake · Mediterranean · Distribution · Nursery · Generalized Additive Models

## Introduction

European hake, *Merluccius merluccius* L., 1758, is a demersal fish species distributed throughout the Mediterranean Sea and in the eastern Atlantic from the Barents Sea to the Mauritanian coast (Whitehead et al., 1984). In the Mediterranean, hake is a species of high economic importance as it is one of the main target species of most bottom-trawl fisheries (Papaconstantinou & Farrugio, 2000).

Genetic studies have shown that a clear genetic difference exists between the Atlantic and the Mediterranean hake (Pla et al., 1991; Roldan et al., 1998). Morphometric studies and preliminary findings of genetic studies support the hypothesis that differences also exist among western, central, and eastern Mediterranean hakes (Inada, 1981; Lo Brutto et al., 1998).

Studies on the bathymetric distribution of the species in the Mediterranean indicated that hake inhabits a wide depth range from 20 to 1,000 m,

depending on the area and the size of the fish (Oliver & Massutí, 1995; Papaconstantinou & Stergiou, 1995). Information, however, on the spatial distribution pattern of the species in relation to its biological cycle is limited to a few studies carried out mostly in the central and western Mediterranean, which have indicated the existence of nursery grounds in certain areas such as the Ligurian Sea and the Gulf of Lions (Orsi Relini et al., 1989; Campillo et al., 1991; Recasens et al., 1998; Orsi Relini et al., 2002). In the eastern Mediterranean, information from various local surveys has suggested the existence of hake nursery grounds in specific region of the Aegean and Ionian seas (Tsimenides et al., 1978; Papaconstantinou & Stergiou 1995; Maravelias & Papaconstantinou, 2006; Maravelias et al., 2007). However, not any quantitative estimate has been provided.

In the present work, we attempt to model bottomtrawl survey abundance data as functions of spatial and temporal variables, in order to identify spatiotemporal trends and built abundance density maps demonstrating on a quantitative basis the hake distribution in the Aegean and Ionian seas. The data we are using are coming from the Mediterranean International Trawl Survey (MEDITS) carried out in several parts of the Mediterranean Sea since 1994 (Bertrand et al., 2000, 2002). Abundances were modeled by means of Generalized Additive models (GAM) techniques (Hastie & Tibshirani, 1990), as functions of longitude, latitude, sampling year, and water depth.

## Materials and methods

Within the frames of the "MEDITS" project, a series of annual bottom trawl surveys are performed in various areas of the Mediterranean Sea since 1994. The surveys, which mainly aimed to obtain estimates of abundance indices and length frequency distributions for a series of target species, were accomplished from late spring to middle summer and included sampling at predefined stations. Further details on the sampling protocol can be found elsewhere (Bertrand et al., 2000, 2002). Since 1996, the sampling scheme of the Greek MEDITS survey is consistent covering annually (with the exception of 2002, when the survey was not accomplished) a total of about 180 stations distributed all over the Aegean and Ionian seas (Fig. 1).

In the present study, we analyzed hake abundance data by station from the surveys carried out in the 1996–2006 period. The examined abundance indices considered the total hake biomass and the number of juveniles. Abundance indices were expressed in terms of kg and number, respectively, per square km of swept area (kg/km<sup>2</sup>, *n*/km<sup>2</sup>). As juveniles, were conventionally considered all immature virgin



Fig. 1 Distribution of the sampling stations over the 50–100, 100–200, 200–500 and 500–800 bathymetric zones

individuals (gonads belonging to stage 0 and 1 according to MEDITS scale for maturity).

The effects of the station position and depth on both, the total and juvenile abundances were examined by means of GAMs. The latter, which are able to deal with non-linear relationships between a dependent variable and multiple predictors in the same model, are nonparametric generalizations of multiple linear regression that are less restrictive in assumptions about the underlying distribution of data (Hastie & Tibshirani, 1990). In GAMs, a predefined link function is related to predictor variables by scatterplot smoothers in lieu of least-squares fits.

In the present case, our nonlinear components were fitted with a locally weighted regression scatterplot smoother (*loess* smoother, Cleveland & Devlin, 1988) by means of the S-PLUS software package, in the way described by Venables & Ripley (1997). Apart from the trawling position and the depth, the year parameter was also modeled as a categorical variable. Hence, the following variables were included in the analysis: Year, Position (entered as the latitude–longitude interaction) and Depth. The general GAM model was of the form:

Abundance = 
$$a + \text{Year} + \text{lo}_1(\text{Position}) + \text{lo}_2(\text{Depth}) + e$$
,

where a is a constant,  $lo_i$  is the *loess* smoother function of the corresponding independent variable and e is a random error term.

Based on the diagnostic residual plots of preliminary runs we assumed a Poisson distribution accompanied by its canonical log-link function for the analysis of the total abundance.

In the case of the juvenile abundance, due to the high frequency of zero values in the data set, a Delta-X error-model was employed, which makes possible to treat separately the question of whether an abundance rate is zero or not, and the size of a rate given that it is non-zero (Vignaux, 1996). For the purposes of this analysis, the Bernoulli-type 0/1 measurements for each abundance index were recorded by assigning the value 0 in stations not having juveniles and the value 1 to the positive ones. The obtained measurements were assumed to follow a binomial distribution, where the estimated probability is a linear function of the predictor variables. The logit function was used as a link between the linear factor component and the binomial error. In this way the probability of having

juveniles was estimated for the different combinations of predictor variables. Since the data are 0/1 measurements, the deviance follows a  $\chi^2$ -distribution; hence a  $\chi^2$  statistic was used to test for the significance of the predictor variables (Ye et al., 2001).

The choice of the most appropriate link function and error distribution for the analysis of the nonzero juvenile abundance rates was made on the basis of residual plots. A poisson model accompanied by a log link function was found to be adequate in this case.

After obtaining model predicted values for the sampled stations for: (a) the probability, P, of nonzero rate, and (b) for the expected rate,  $\mu$ , conditional on it being positive, the unconditional abundance of each station is given by  $P\mu$  (Ye et al., 2001).

In all GAMs, variable selection proceeded by a stepwise forward entry and the Akaike Information Criterion (AIC) was used to detect the relative importance of each variable in explaining variations and determine the order of those that should be included in the final model. The AIC statistic accounts simultaneously for the degrees of freedom used and the goodness of fit, whereas a smaller AIC statistic corresponds to a better model in the sense of smaller residual deviance penalized by the number of parameters that are estimated in fitting the model. At each stage of the forward entry, the AIC was computed for every candidate predictor not yet entered. The variable resulting in the highest AIC decrease was entered into the model. Forward entry continued until additional variables no longer yielded reductions in the AIC statistic. Significant levels for the added predictors were estimated by means of the chi-square test and the level of significance was set at 95%.

The predicted abundance indices from the GAM analysis were used to construct density distribution maps for the total and juvenile abundance, respectively. Maps were generated using the SURFER software (Golden Software, 2002) and interpolation was made by means of the "inverse distance to a power" gridding method, adjusting properly the R parameter to avoid predictions in areas not covered by the survey (Davis, 1986).

## Results

Data from 1,714 trawling operations were analyzed (Fig. 1). The three stepwise GAMs explained 36–53%

Table 1 Analysis of
deviance for the GAM
models fitted to the hake
abundance data

Explanatory variable	Residual d.f.	Residual deviance	Cumulative variance explained in CPUE
Total abundance			
Mean	1,713	180,021	
Position	1695.28	136,594	24.12
Depth	1689.11	118,243	34.32
Year	1680.11	113,803	36.78
Juvenile presence (binon	nial model)		
Mean	1,713	2,165	
Depth	1707.01	1,824	15.75
Position	1688.95	1,643	24.14
Year	1679.95	1,597	26.24
Juvenile abundance (posi	itive values)		
Mean	1,151	3,832,741	
Position	1132.33	2,211,842	42.29
Depth	1126.01	1,936,595	49.47
Year	1116.98	1,782,956	53.48

of the total variation (Table 1) and all variables were highly significant (P < 0.0001). The sampling position had the highest explanatory power both, for the total and juvenile abundance, explaining 24.12% and 42.29%, respectively. Depth was the most important explanatory variable in the case of the juvenile presence binomial GAM, explaining as much as 15.75% of the total variance. The effect (loess plot) of the predictors on abundance, or probability of juvenile presence in the case of the binomial model, is shown on the y-axis (z-axis, in the case of "position") for different values of the predictor (x-axis) (Figs. 2–4). The zero line indicates mean model estimates, while the y (or z)-axis is a relative scale where the effect of different values of the predictors on the response variable is shown. Hence,

**Fig. 2** GAM derived effects on the total hake abundance index. Each plot represents the contribution of the corresponding variable to the fitted predictor. The fitted values are adjusted to average zero and the broken lines indicate two standard errors. The relative density of data points is shown by the "rug" on the *x*-axis



**Fig. 3** GAM derived effects on the probability of presence of juvenile hake. Each plot represents the contribution of the corresponding variable to the fitted predictor. The fitted values are adjusted to average zero and the broken lines indicate two standard errors. The relative density of data points is shown by the "rug" on the *x*-axis



**Fig. 4** GAM derived effects on the juvenile abundance index. Each plot represents the contribution of the corresponding variable to the fitted predictor. The fitted values are adjusted to average zero and the broken lines indicate two standard errors. The relative density of data points is shown by the "rug" on the *x*-axis

negative values on the y (or z)-axis indicate that at the corresponding levels of the predictor (x-axis), the model estimates abundance/probability that is lower than the mean, while the opposite holds for positive values on the y (or z)-axis.

In that sense, loess plots revealed that total abundance drops drastically after about 450 m while both, juvenile abundance and probability of finding juveniles drop after about 320 m. Total abundance is higher in the 100–450 m bathymetric zone, having two major peaks around 100 and 400 m, respectively. The major peak regarding juvenile abundance was around to 100 m. All indices and the probability of finding juveniles were increasing with depth, up to 100 m.

The "year" loess plots suggest the existence of an increasing trend for both, the total and juvenile abundances from 2001 onwards. The corresponding





latitude-longitude loess plots have quite similar patterns suggesting the presence of certain local maxima with the highest one being around  $23-24^{\circ}$  E and  $38-39^{\circ}$  N. The latitude–longitude loess plot of the binomial model, suggest that the probability of finding juveniles is higher in the northern part of the examined area.

The density distribution maps that were built based on the GAM estimates, indicate that total hake abundance is relatively higher in the western part of the Aegean Sea and in the eastern part of the Cretan Sea, with the maximum values expected in the Saronikos Gulf (Fig. 5).

The juvenile abundance map suggested the presence of certain major nursery grounds in specific regions. The most important of them is located in the Saronikos Gulf and its surrounding area, while relatively high juvenile abundances are estimated for an area off the eastern part of the Cretan coast. A few other nurseries of much less importance are found in the northern part of the Aegean and in the Ionian seas (Fig. 6).



## Discussion

The present study gives a global picture of the hake distribution in the Greek seas based on a time series of data obtained through the "MEDITS" experimental survey, which is carried out on a regular basis following the same sampling protocol. Such standardized surveys are able to provide estimates that are independent of factors, as for instance the behavior of the fisheries, which may bias commercial data.

The use of GAM techniques for the examination of population abundance indices in relation to environmental and spatiotemporal variables is gaining popularity among fisheries scientists over the last years, (e.g., Bigelow et al., 1999; Daskalov, 1999; Walsh & Kleiber, 2001; Maravelias & Papaconstantinou, 2003). In the current study, GAMs explained a relatively high percentage of the abundance variations confirming their suitability in addressing non-linear trends that cannot be easily captured through linear models (Borchers et al., 1997). This methodological approach permitted direct spatiotemporal comparisons as it removed effects that could bias nominal indices and provided a quantitative basis for the study of hake distribution in the Greek seas. Certainly, the analysis did not fully consider the complex geomorphology of the examined area (e.g., enclosures and islands), but the depth parameter included in the models, incorporates certain geomorphological features.

Our analysis revealed that hake is generally more abundant in the 100–450 m bathymetric zone. This is in agreement with the findings of previous studies in different Mediterranean areas, such as the Gulf of Lions (Campillo et al., 1991; Recasens et al., 1998), the Ionian (Vassilopoulou & Papaconstantinou, 1987), the Adriatic (Zupanovic & Jardas, 1986) and the Ligurian seas (Orsi Relini et al., 1989). Although the presence of juveniles affects the total abundance estimates, the fact that the corresponding distribution maps and GAM graphs do not show similar patterns, suggests that total abundance is not largely driven by the abundance of juveniles.

Juveniles seem to prefer somehow shallower waters than adults, being more abundant from 100 to 320 m and having their major abundance peak around 100 m. Most probably, the first total abundance peak, occurring around to 100 m (Fig. 2), is due to the high presence of juveniles in that depth. In general, juveniles seem to be mostly distributed over the continental shelf (depths up to 200–300 m) as it happens all over the Mediterranean (Orsi Relini et al., 2002). Similarly to our results, Orsi Relini et al. (1989), has reported that the main concentration of juveniles in the Ligurian Sea is around to 100 m.

Our analysis indicated the presence of an increasing trend in the examined abundance indices over the last five years and this finding is in agreement with the reported total catch levels of hake of the Greek fisheries that show a similar trend (Tserpes et al., 2007). A previous analysis based on MEDITS survey data from the south Aegean Sea covering the 1994–2000 period did not reveal the presence of any abundance trend over time (Tserpes & Peristeraki, 2002).

In general, the Mediterranean demersal stocks are considered to be over-exploited (Papaconstantinou & Farrugio, 2000). A recent assessment of hake in the Greek seas suggested that the current stock biomass levels are about 30-40% lower than the optimum ones (B<sub>msy</sub>), although an increasing stock biomass trend was observed over the 1999-2003 period (Tserpes et al., 2007). The progressive reduction of the total Greek fleet capacity, accompanied by the increase of the trawl-net mesh size over the past 10 years, may have resulted in stock level increases that are reflected in the MEDITS survey abundance indices. Environmental changes such as water temperature increase due to global warming may have also favored hake recruitment, and consequently stock size increase. Studies in the Adriatic support this hypothesis as they have shown a positive relationship among sea surface temperature during spring, and hake larval abundance (Zupanovic & Jardas, 1986). However, this hypothesis cannot be confirmed in the current case due to lack of relevant data.

The density maps revealed that hake is widely distributed over the examined area, but it is relatively more abundant in the western part of the Aegean Sea and in the eastern part of the Cretan Sea. They have also indicated quantitatively the location of the most important nursery grounds.

Papaconstantinou & Stergiou (1995) suggested specific areas of the Aegean and Ionian seas as hake nursery grounds, without, however, providing any quantitative estimate. In general, their suggestions agree with our findings apart from the area off the Cretan coast that they did not mention at all, probably due to lack of relevant data. Our study, however, has shown that the identified nursery grounds are not all of the same importance and that the Saronikos Gulf is by far the most significant one. It seems that the prevailing abiotic and/or biotic factors in Saronikos Gulf, an area of high fishing activity, favor the hake distribution in the area. Certain fishery closures that are locally applied may be also in favor of hake juvenile survival.

Considering that the Mediterranean demersal stocks are managed through control effort regimes, spatiotemporal closures and technical measures, our findings can provide useful information for spatial management purposes. The present results, however, are based on surveys carried out in a specific season; hence they do not take into account possible seasonal migrations. In case that hake in the Greek seas undertake seasonal migrations, as it has been suggested by Zupanovic & Jardas (1986) for the Adriatic and Recasens et al., 1998 for the Gulf of Lions, further studies are needed to confirm the consistency of the currently suggested distribution pattern throughout the year.

#### References

- Bertrand, J. A., L. Gil de Sola, C. Papaconstantinou, G. Relini & A. Souplet, 2000. An international bottom trawl survey in the Mediterranean: the MEDITS programme. In Bertrand, J. A. & G. Relini (eds), Demersal Resources in the Mediterranean. Actes de Colloques 26, Ifremer, Plouzané France: 76–93.
- Bertrand, J. A., L. Gil de Sola, C. Papaconstantinou, G. Relini & A. Souplet, 2002. The general specifications of the Medits surveys. Scientia Marina 66: 9–17.
- Bigelow, K. A., C. H. Boggs & X. He, 1999. Environmental effects on swordfish and blue shark catch rates in the US North Pacific longline fishery. Fisheries Oceanography 8: 178–198.
- Borchers, D. L., S. T. Buckland, I. G. Priede & S. Ahmadi, 1997. Improving the precision of the daily egg production method using generalised additive models. Canadian Journal Fisheries Aquatic Science 54: 2727–2742.
- Campillo, A., Y. Aldebert, J. L. Bigot & B. Liorzou, 1991. Repartition des principales especes commerciales du Golfe du Lion en fonction des saisons (et plus particulierement des groupes 0 et 1). FAO Fisheries Report 447: 103–118.
- Cleveland, W. S. & S. J. Devlin, 1988. Locally-weighted regression: an approach to regression analysis by local fitting. Journal of American Statistical Association 83: 596–610.
- Davis, J. C., 1986. Statistics and Data Analysis in Geology. John Wiley and Sons, New York.
- Daskalov, G., 1999. Relating fish recruitment to stock biomass and physical environment in the Black Sea using generalised additive models. Fisheries Research 41: 1–23.

- Golden Software, 2002. SURFER Version 8. Golden Software Inc., Golden, Colorado.
- Hastie, T. J. & R. J. Tibshirani, 1990. Generalized Additive Models. Chapman and Hall, London: 335 pp.
- Inada, T., 1981. Studies on the Merlucciid fish. Far Seas Fisheries Research Laboratory Bulletin 18: 1–172.
- Lo Brutto, S., M. Arculeo, A. Mauro, M. Scalisi, M. Cammarata & N. Parrinello, 1998. Allozymic variation in Mediterranean hake *Merluccius merluccius* (Gadidae). Italian Journal of Zoology 65: 49–52.
- Maravelias, C. D. & C. Papaconstantinou, 2003. Size-related habitat use, aggregation patterns and abundance of anglerfish (*Lophius budegassa*) in the Mediterranean Sea determined by generalized additive modeling. Journal of Marine Biological Association of the United Kingdom 83: 1171–1178.
- Maravelias, C. D. & C. Papaconstantinou, 2006. Geographic, seasonal and bathymetric distribution of demersal fish species in the eastern Mediterranean. Journal Applied Ichthyology 22: 35–42.
- Maravelias, C. D., E. V. Tsitsika & C. Papaconstantinou, 2007. Environmental influences on the spatial distribution of European hake (*Merluccius merluccius*) and red mullet (*Mullus barbatus*) in the Mediterranean. Ecological Research 22: 678–685.
- Oliver, P. & E. Massutí, 1995. Biology and fisheries of western Mediterranean hake (*M. merluccius*). In Alheit, J. & T. J. Pitcher (eds), Hake. Fisheries, Ecology and Markets. Fish and Fisheries Series 15. Chapman & Hall, London: 181–202.
- Orsi Relini, L., M. Cappanera & F. Florentino, 1989. Spatialtemporal distribution and growth of *Merluccius merluccius* recruits in the Ligurian Sea. Observations on the 0 Group. Cybium 13: 263–270.
- Orsi Relini, L., C. Papaconstantinou, S. Jukic-Peladic, A. Souplet, L. Gil de Sola, C. Piccinetti, S. Kavadas & M. Rossi, 2002. Distribution of the Mediterranean hake populations (*Merluccius merluccius smiridus* Rafinesque, 1810) (Osteichthyes: Gadiformes) based on six years monitoring by trawl-surveys: some implications for management. Scientia Marina 66: 21–38.
- Papaconstantinou, C. & H. Farrugio, 2000. Fisheries in the Mediterranean. Mediterranean Marine Science 1: 5–18.
- Papaconstantinou, C. & K. I. Stergiou, 1995. Biology and fisheries of eastern Mediterranean hake (*M. merluccius*).
  In Alheit, J. & T. J. Pitcher (eds), Hake. Fisheries, Ecology and Markets. Fish and Fisheries Series 15. Chapman & Hall, London: 149–180.
- Pla, C., A. Vila & J. L. Garcia-Marin, 1991. Differentiation de stocks de merlu (*Merluccius merluccius*) par l'analyse genetique: comparation de plusiers populations mediterraneennes et atlantiques du littoral espagnol. FAO Fisheries Report 447: 87–93.
- Recasens, L., A. Lombarte, B. Morales-Nin & G. J. Torres, 1998. Spatiotemporal variation in the population structure of the European hake in the NW Mediterranean. Journal Fish Biology 53: 387–401.
- Roldan, M. I., J. L. Garcia-Marin, M. F. Utter & C. Pla, 1998. Population genetic structure of European hake, *Merluccius merluccius*. Heredity 81: 327–334.

- Tserpes, G. & P. Peristeraki, 2002. Trends in the abundance of demersal species in the southern Aegean Sea. Scientia Marina 66: 243–252.
- Tserpes, G., J. Haralabous & C. Maravelias, 2007. A non-equilibrium surplus production model approach utilizing MEDITS data. GFCM Workshop on Trawl Survey Based Monitoring Fishery System in the Mediterranean, Rome, 26–28 March 2007. http://www.icm.csic.es/rec/projectes/ scsa/WS%202007%20Trawl%20Surveys/Selected%20 documents/prod\_mod.pdf.
- Tsimenides, N., C. Papaconstantinou & C. Daoulas, 1978. Age and growth of hake (*Merluccius merluccius*) in the Saronikos and Thermaikos gulfs. Thalassographica 2: 27–56.
- Vassilopoulou, V. & C. Papaconstantinou, 1987. Distribution and catches per unit effort of the hake and the red mullet in the western coasts of Greece. FAO Fisheries Report 394: 174–180.
- Venables, W. N. & B. D. Ripley, 1997. Modern Applied Statistics with S-PLUS, 2nd edn. Springer, New York.

- Vignaux, M., 1996. Analysis of spatial structure in fish distribution using commercial catch and effort data from the New Zealand hoki fishery. Canadian Journal of Fisheries and Aquatic Science 53: 963–973.
- Walsh, A. & P. Kleiber, 2001. Generalized additive model and regression tree analyses of blue shark (*Prionace glauca*) catch rates by the Hawaii-based commercial longline fishery. Fisheries Research 53: 115–131.
- Whitehead, P. J. P., M. L. Bauchot, J. C. Hureau, J. Nielsen & E. Tortonese, 1984. Fishes of the North-eastern Atlantic and the Mediterranean, Vol. II. UNESCO, Paris.
- Ye, Y., M. A. Hisaini & A. A. Baz, 2001. Use of generalized linear models to analyse catch rates having zero values: the Kuwait driftnet fishery. Fisheries Research 53: 151–168.
- Zupanovic, S. & I. Jardas, 1986. A contribution to the study of biology and population dynamics of the Adriatic hake, *Merluccius merluccius* (L). Acta Adriatica 27: 97–146.

## FISH HABITAT MAPPING

# Spatial patterns and GIS habitat modelling of fish in two French Mediterranean coastal areas

Romain Crec'hriou · Patrick Bonhomme · Géraldine Criquet · Gwenaël Cadiou · Philippe Lenfant · Guillaume Bernard · Erwan Roussel · Laurence Le Diréach · Serge Planes

© Springer Science+Business Media B.V. 2008

Abstract The spring and summer distribution of adults and larval fish stages of Sparids and Scorpaenids was studied in two sites in the western Mediterranean. Fish adults and larvae of those two taxa were identified and sorted according to their life stages in order to study their distribution and develop suitable habitat maps. Study areas were located on French coastal waters, the "Côte Bleue" Marine Park (CBMP) has an east-west orientation with substratum dominated by Posidonia beds and the Marine Reserve of Cerbère-Banyuls (MRCB) runs north-south and is dominated by rocky substrates. Generalised Additive Models (GAM) combined with Geographic Information System (GIS), were used to model the suitable habitats for fish larvae and adults. During spring months, waters exhibit low Sea Surface Temperatures (SST), low

Guest editor: V. D. Valavanis Essential Fish Habitat Mapping in the Mediterranean

R. Crec'hriou (⊠) · G. Criquet · P. Lenfant ·
E. Roussel · S. Planes
Laboratoire Ecosystèmes Aquatiques Tropicaux et
Méditerranéens, UMR 5244 CNRS-EPHE-UPVD
Biologie et Ecologie tropicale et méditerranéenne
CBETM, Université de Perpignan, 52 Avenue Paul Alduy,
Perpignan 66860, France
e-mail: crecrom@univ-perp.fr

P. Bonhomme · G. Cadiou · G. Bernard · L. Le Diréach GIS Posidonie, Centre d'Océanologie de Marseille, Parc Scientifique et Technologique de Luminy - Case 901, Marseille 13288, France Photosynthetically Active Radiation (PAR), high values of Sea Surface Chlorophyll-a concentration (Chl-a), and mostly negative values of Sea Level Anomaly (SLA) indicating anticyclonic eddies. During summer months, waters have higher values of SST, lower values of Chl-a and positive values of SLA indicating cyclonic eddies. The results revealed different environmental responses in the distribution of fish adults and larvae in the CBMP and MRCB. Suitable habitats for adult were mainly dependent on the substrate types (*Posidonia* meadows and sand) and they were found close to the coast, whereas fish larvae were dependent on environmental cues (Chl-a, SLA, SST) with a sparse spatial distribution.

**Keywords** Fish · Adults · Larvae · Suitable habitat · Essential fish habitat · GAM · GIS · Western Mediterranean

## Introduction

Habitat loss and degradation threaten the ability of marine coastal areas to support artisanal fisheries. The habitat utilised by species changes with life history stage, density, competition with other species and environmental variability in time and space. During their early life stages, many species occur in coastal waters in essential spawning and nursery habitats such as seagrass beds (Boudouresque et al., 2006), rocky bottoms (Guidetti, 2000, Vanderklif &

Jacoby, 2003) or soft shallow bottoms for flatfishes (Eastwood et al., 2001, Koubbi et al., 2006, Le Pape et al., 2007). These studies emphasised the ecological importance and the protection provided by such habitats in relation to their crucial role as nurseries for many fish species and their overall importance in maintaining littoral fish populations and species diversity. When different life stages of fish species are dependent on specific coastal habitats for development and growth, thorough knowledge of such habitats is a necessary component for improvements in fisheries management.

With an aim to develop sustainable fisheries, the Magnuson-Stevens act (NMFS 1996) reinforced the need to unify coastal land management with fisheries management by the creation of "Essential Fish Habitats" (EFH). The identification of EFH, defined as "those waters and substrate necessary for fish for spawning, feeding or growth to maturity", is important for management and conservational purposes. In 2002, European Community, following the statement in the Green Paper on the Future of the Common Fisheries Policy (European Commission, 2001), took similar initiative by including Habitat directive and Marine strategy directive as bases of reform of CFP. Coastal habitats of fish are combination of environmental factors that explain their distribution, with a presence link to suitable conditions and density to an optimum environmental conditions (Koubbi et al., 2006). Favourable conditions for fish development are linked to biological and physical factors. Location of spawning sites is influenced by bathymetry, substrate type and diversity of adult fish habitats as well as mechanisms conditioning the primary production of the region. However, physical processes (e.g. shelf-slope density front and associated current, continental water inflows, winter mixing and stratification of the water column) influence the final distribution patterns of fish eggs and larvae (Alemany et al., 2006; Sabatés et al., 2007). As the recruitment success of species depends on physical processes, the management of fish populations cannot be considered independently of their environment (Parsons and Harrison, 2000), and as such, habitat protection is a vital part of ecosystem-based approaches to fisheries management. Geostatistics is employed in fisheries, to optimise sampling strategies (Petitgas, 1996) and to estimate fish biomass and corresponding variances, by taking into account the existence of spatial structures (Maynou, 1998), as well as to map estimated distributions and spatial patterns of organisms (Stelzenmüller et al., 2004). Further, geostatistical tools can be used to assess the effects of trends on catch data (Rufino et al., 2006), such as the importance of factors including habitat association of species and spatial survey scales (Stelzenmüller et al., 2005) or type of fishing gears (Stelzenmüller et al., 2006) on spatial estimations of the distribution patterns of marine resources. Data on species–environment associations have been used to provide such spatially explicit models of habitat suitability by using Geographic Information System (GIS) (Guisan & Zimmermann, 2000; Stoner et al., 2004).

In Mediterranean coastal fishery systems, sparids are an important part of local marine resources, and various aspects of their distribution, life history, reproductive cycle, feeding ecology and fisheries have been studied (Bell, 1983; Santos et al., 1995; Petrakis & Stergiou, 1995; Pajuelo & Lorenzo, 1998; Vigliola et al., 1998; Planes et al., 1999; Catalán et al., 2006; Mariani, 2006; Stelzenmüller et al., 2007). A study in MRCB focused on the conditions, feeding and reproductive potential of white seabream (Diplodus sargus) as indicators of habitat quality (Lloret & Planes, 2003). Unexpected initially, this study proposed that unprotected rocky areas contribute more to production of white seabream than the unprotected sandy coasts and are, therefore, potentially essential fish habitats for this specie. Similarly, scorpaenids also have an important place in the littoral fish community and their distribution, life history and fisheries aspect have been studied in the Mediterranean (Santos et al., 2002; Deudero et al., 2008; Stergiou & Erzini, 2002; La Mesa et al., 2005).

In this study, we aimed to estimate the suitable habitats for two important fish taxa, at both adult and larval stage of development, in two French coastal areas. Our study was focused on two target and marketable taxa characteristic of the artisanal Mediterranean fishery, the sparids (*Pagellus erythrinus, Pagellus acarne* and *Diplodus spp., Sparus aurata*) and scorpaenids (*Scorpaena porcus* and *Scorpaena scrofa*). We combined geostatistical and GIS tools: (1) to characterise the distribution of the different life stages of fish and (2) to define suitable habitats (EFH) by investigating relationships between fish taxa and environmental conditions. Thus, we proposed an approach to assess the effect of habitat on the distribution of fish in heterogeneous coastal areas that can be used for further fisheries management.

## Materials and methods

## Study area

Marine Reserve of Cerbère-Banyuls (France): Established in 1974, the Marine Reserve of Cerbère-Banyuls (MRCB) extends over 1.85 square nautical miles, of which 0.185 square nautical miles are no-take (Fig. 1-1B). Adult fish community has been studied for over 20 years (since Bell, 1983). The area consists of a rocky shore 20 km long, orientated more or less along a north–south axis. Bays and capes divide the area into three topographic regions also characterised by different habitats, from north to south: (1) a continuous coast to Cape Bear with steep underwater rocky slopes; (2) the Bay of Banyuls mainly composed of sand and *Posidonia*  meadows; and (3) a continuous coast made of little embayments and capes from Cape l'Abeille to Cape Cerbère, with a mixed habitat of meadows: rocks in shallow waters and rocks and coralligen in deeper waters.

Côte Bleue "Marine Park (France): Located in the French north-western Mediterranean, the "Côte Bleue" Marine Park (CBMP) was established in 1983. CBMP is made of two effectively enforced notake reserves: Carry-le-Rouet MPA (0.248 square nautical miles), established in 1983, and Couronne MPA (0.612 square nautical miles), established later in 1995 (Fig. 1-2C). In addition to the reserves, artificial reefs, mainly for protection against illegal trawling and for biomass production, were deployed in the park in 1983, several of them being set at the border of the two reserves to ensure trawling exclusion. The area is made of a rocky shore 16 km long, orientated along an east-west axis, and it is covered with Posidonia meadows (total of 3.207 square nautical miles), rocky substrates and sand.



**Fig. 1** Location of *Marine Reserve of Cerbère-Banyuls* (1) and "*Côte Bleue*" *Marine Park* (2) with Adult sampling stations (A and D) and larvae sampling stations (B and C). Spring stations are represented by (+) and summer stations are represented by  $(\diamond)$ 

3.20

3.20

3.15

3.15



Fig. 2 IPUE results in *Marine Reserve of Cerbère-Banyuls* or adult sparids (A and B) and for adult scorpaenids (C and D), in spring (A and C) and in summer (B and D). IPUEs are in

#### **Biological sampling**

#### Adults

The artisanal fishing fleet in MRCB uses a whole range of fixed or mobile gear, such as gillnets, trammel nets and bottom longlines. Target species vary according to season and belong mostly to Sparidae (*Pagellus erythrinus, Pagellus acarne, Diplodus* spp.) and Scorpaenidae (*Scorpaena scrofa, Scorpaena porcus,*).

The fishing gears commonly used in CBMP include trammel nets, gillnets, bottom longlines and tuna nets. Target species vary according to season and belong mostly to Sparidae (*Diplodus* spp., *Sparus aurata*, *Dentex dentex*) and Scorpaenidae families (*Scorpaena scrofa*, *S. porcus*), together with significant catch of

number of fish per 100 m of net per day. Grey area between coast and sea delimits hard (Rock and *Posidonia* meadow) from soft bottom (Sand)

lobster (*Palinurus elephas*), *Mullus surmuletus, Merluccius merluccius* and Soleidae.

Assessment of suitable habitat, in the case of MRCB, was based on catch positions and Individual Per Unit of Effort data (IPUE, Number of individual per 100 m of net per day) for Sparidae and Scorpaenidae families recorded from 197 onboard samplings in 2000, 2001, 2003 and 2004 (Fig. 1-1A). In the case of CBMP, the assessment was based on catch positions and IPUE for the Sparidae and Scorpaenidae families, recorded from 119 onboard samplings from 2003 to 2004, between April and November (Fig. 1-1D).

#### Larvae

Data are issued from sampling conducted in surrounding areas of the MRCB from 2000 to 2003, between April and September (Fig. 1-1B). A Bongo net with a mesh size of 300 µm and MIK nets with a mesh size of 1 mm were used to collect fish larvae and eggs from oblique tows performed during daytime from the bottom to the surface. Stepwise oblique tows of 5-min duration each were made at three depth levels (20, 10 and 5 m) to facilitate catching more eggs and larvae of coastal fishes as they are reported to be more abundant in subsurface waters (Olivar & Sabatés, 1997). Sampling conducted in the vicinity of CBMP in spring and summer 2003 (Fig. 1-1C) used Bongo net following the same sampling protocol as previously described for MRCB.

Assessment of suitable habitat was based on catch positions and density of larvae (number of larvae per  $1000 \text{ m}^3$ ) for the Sparidae and Scorpaenidae families, resulting from 333 and 195 samples, respectively, in MRCB and CBMP.

## Environmental sampling

Four types of environmental data were collected from internet-based sources by the Hellenic Centre for Marine Research: (1) Photosynthetically Active Radiation (PAR), (2) Sea Level Anomaly (SLA), (3) Sea Surface Temperature (SST), and (4) Sea Surface Chlorophyll-a concentration (Chl-a). Data were processed for use with a GIS (Table 1). Fisheries and ichtyoplankton samples were combined together with environmental grids for each sampling date to extract environmental values for each sample. Substratum data, namely differentiating *Posidonia*  *meadows* (POS), rocky bottom (ROC) and sandy bottom (SAN), were extracted from results of Natura 2000 programs (FR9101482—Herbier de Posidonie de la côte des Albères) and calculated by applying a buffer area of 500 m in diameter to each sampling point with each substratum layer crossing this buffer in a certain percentage of coverage. Depth was extracted from the SHOM map (map No. 6843) for each sampling point.

#### Data analysis

Generalised Additive Models (GAMs) (Hastie & Tibshirani, 1990) are the non-parametric counterpart of Generalised Linear Models (GLMs). GIS, GAM and GLM were used to map habitat, and, in combination with geostatistical tools, to model species potential distribution and habitat. The models for different life stages, for species and for seasons were established using biological data (larval density and IPUE) together with environmental factors (SST, PAR, SLA, Chl-a, POS, ROC, SAN and depth). The data exploration process provided a clear graphical inclusion of explanatory variables that were themselves uncorrelated to avoid effect of collinearity. If a high degree of collinearity exists between two variables (more than 80%), those variables with the least collinearity with other variables were retained in the model. For each station, GAMs were used to model the spatial relationships between presence/absence and density of two taxa and the selected environmental variables per season (spring and summer). This method estimated the relationships between the response

 Table 1
 Sources and description of environmental data used in Model

Variable	Units	Source	Sensor/Model	Resolution
Photosynthetically Active Radiation (PAR)	E/m2/d	Oceancolor WEB, GSFC/NASA, USA	SeaWiFS	1.1 km
Sea Level Anomaly (SLA)	cm	Live Access Server	Merged (TOPEX/Poseidon, Jason-1, ERS-1/2, Envisat)	5 km
Sea Surface Temperature (SST)	°C	DLR EOWEB,Germany	AVHRR SST	1 km
Sea Surface Chlorophyll-a Concentration (CHL-A)	mg/m <sup>3</sup>	Oceancolor WEB, GSFC/NASA, USA	SeaWiFS	1.1 km
Posidonia meadow (POS)	%	Natura 2000, France		5 m
Rock (ROC)	%	Natura 2000, France		5 m
Sand (SAN)	%	Natura 2000, France		5 m
Bathymetry (Depth)	m	Echosounding, Shom France		1 m

variables and predictors, by fitting non-parametric functions to the data using smoothing operations. In this study, adult IPUE and larval density or presence/ absence were the response variables, while SST, PAR, SLA, Chl-a, POS, ROC, SAN, and depth were the selected uncorrelated predictors. The GAM stepwise procedures were used to automatically select the best predictors from a list of pre-specified possible predictors in terms of the Akanke's Information Criterion (AIC, Akaike, 1973). Akaike (1974) proposed a rule to select the order of the filter based on a generalisation of the maximum likelihood criterion. AIC was computed as a measure of the "goodness-of-fit" to select the most suitable model. For each biological group, the models associated with the lowest AIC were chosen from a number of fitted models. For each stage, taxa and season, two models were computed: one with presence/ absence (description of combination of environmental factors for presence in suitable conditions) and another with density values (description of combination of environmental factors for survival and a highest density in optimum condition). These two values were multiplied, resulting in a predicted value of density or IPUE that took into account the presence/absence probability. From each model, GAM plots were used to show the effect of environmental variable on density and presence/absence and to determine the threshold value, a value for which the effect became positive. These models were performed using R software (R Development Core Team, 2007).

## Mapping

MAPINFO professional 7.5 (Geographic information system from MapInfo Corporation) and Vertical Mapper were used to map data. The best models were then used to predict the value of density or IPUE that took into account the presence/absence probability for each season. Predicted data were interpolated, by use of Natural Neighbourhood methods, mapped to visualise their distribution and deduct their suitable habitat.

Natural Neighbourhood are built around data points using Delaunay triangulation. A network of Thiessen polygons is generated from the point locations creating what is called a Voronoi diagram. By calculating the area of the Thiessen polygon encompassing each point, attaching that area as an attribute to the point, and generating a grid of the new point files through interpolation, a representative density surface grid can be produced.

## Results

Environmental data description

Two distinct periods are shown in Tables 2 and 3: Spring is characterised by stable SST with values between 17.446  $\pm$  3.769°C and 19.097  $\pm$  3.353°C, and high values of Chl-a concentration (between 0.393  $\pm$  0.191 mg/m<sup>3</sup> and 0.674  $\pm$  0.681 mg/m<sup>3</sup>), high values of PAR (between 48.817  $\pm$  11.420 and 52.279  $\pm$  9.269) and mostly negative values of SLA (between -4.078  $\pm$  2.919 cm and -2.355  $\pm$ 2.026 cm) indicating anticyclonic eddies (e.g. convergence area).

In summer, SST is higher and more variable between  $20.442 \pm 2.321$ °C and  $24.751 \pm 1.964$ °C, values of Chl-a concentration are lower (between  $0.174 \pm 0.049 \text{ mg/m}^3$  and  $0.368 \pm 0.164 \text{ mg/m}^3$ ), the range of PAR is larger (between  $51.544 \pm 7.169$  and  $55.153 \pm 3.899$ ) and SLA values are mostly positive (between  $2.615 \pm 2.920$  cm and  $3.440 \pm 2.364$  cm) indicating cyclonic eddies (e.g. divergence area).

Table 2 Mean and standard deviation (SD) of environmental variable and IPUE concerning adult sampling for both species and area

		SST		CHL-/	4	PAR		SLA		IPUE of sparids		IPUE of	f Scorpaenids
		Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
MRCB	Spring	17.856	±3.363	0.431	±0.185	48.817	±11.420	-2.355	±2.026	1.685	±2.625	0.067	±0.235
	Summer	22.518	$\pm 1.593$	0.214	$\pm 0.066$	53.075	$\pm 6.542$	3.440	$\pm 2.364$	1.827	$\pm 9.233$	0.024	$\pm 0.091$
CBMP	Spring	17.446	$\pm 3.769$	0.674	$\pm 0.681$	52.279	±9.269	-3.878	$\pm 3.891$	5.560	$\pm 6.571$	3.506	$\pm 6.564$
	Summer	20.442	$\pm 2.321$	0.368	$\pm 0.164$	51.544	±7.169	2.615	$\pm 2.920$	5.732	$\pm 9.768$	3.313	$\pm 5.825$

Mean and SD were calculated from data resulting from Adult sampling effort

 Table 3 Mean and standard deviation (SD) of environmental variable and density concerning larvae sampling for both species and area

		SST		CHL-A	4	PAR		SLA		Density	of Sparids	Density o	f Scorpaenids
		Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
MRCB	Spring	17.621	±3.161	0.462	±0.202	49.302	±6.567	-4.078	±2.919	27.956	$\pm 65.000$	0.119	±0.700
	Summer	24.751	$\pm 1.964$	0.174	$\pm 0.049$	54.492	$\pm 4.011$	2.850	$\pm 2.365$	92.931	$\pm 606.893$	1.627	$\pm 0.889$
CBMP	Spring	19.097	$\pm 3.353$	0.393	±0.19	52.1	$\pm 7.348$	-2.95	$\pm 3.23$	21.128	±31.743	0.184	$\pm 0.559$
	Summer	23.972	$\pm 2.451$	0.248	$\pm 0.18$	55.15	±3.9	2.631	±2.15	3.171	$\pm 5.107$	0.657	±1.559

Mean and SD were calculated from data resulting from Larvae sampling effort

#### Adult stage

Adult scorpaenids (Tables 2 and 3) were caught in both areas and periods. In MRCB, the mean IPUE of adult was greater during spring (0.067  $\pm$  0.235) than in summer (0.024  $\pm$  0.091). The IPUE of adults were higher in coastal stations (20–40 m depth) than offshore, and the distribution of adults was homogeneous with an IPUE of 0.22 between Cape Béar and Cape Cerbère in spring (Fig. 2A) with the exception of a Bay under Cape Bear whose IPUE peaked at 2.2. In summer, the presence of adults was more sporadic and localised in the northern part of the MPA (Fig. 2B). At CBMP, the mean IPUE of

adults was similar between spring  $(3.506 \pm 6.564)$  and summer periods  $(3.313 \pm 5.825)$ . As in MRCB, the IPUEs of adults were higher in coastal stations than offshore (Fig. 3A, B).

Adult sparids were caught in both areas and periods. In MRCB, the mean IPUE was greater during summer (1.685  $\pm$  2.625) than in spring (1.827  $\pm$  9.233). Adults occurred in coastal stations rather than offshore (Fig. 2C, D). Higher density was located north in spring and summer, while a peak of adults was observed near the MPA border, at Cape "1'Abeille". In CBMP, the mean IPUE was smaller in spring (5.560  $\pm$  6.571) than in summer (5.732  $\pm$ 



Fig. 3 IPUE results in "*Côte Bleue*" *Marine Park* for adult sparids (A and B) and for adult scorpaenids (C and D), in spring (A and C) and in summer (B and D). IPUEs are in

number of fish per 100 m of net per day. Grey area between coast and sea delimited hard (Rock and *Posidonia* meadow) from soft bottom (Sand)

9.768). A density gradient was observed between the coastal station, middle shore and off-shore stations (Fig. 3C, D).

#### Larval stage

Scorpaenids larvae were caught in both areas and periods. In MRCB, mean larval density was greater in summer  $(1.627 \pm 0.889 \text{ larvae}/1000 \text{ m}^3)$  than in spring  $(0.119 \pm 0.700 \text{ larvae}/1000 \text{ m}^3)$ . Larvae were concentrated in coastal stations (20–40 m depth) than offshore, with a peak in the north of Cape Béar and in the north of Cape Cerbère in spring (Fig. 4A). A more widespread distribution was observed along the coast in summer (Fig. 4B). The relative importance of mid-shore stations is striking in spring as compared to the total absence of larvae in mid- and offshore stations in summer. In CBMP, mean larval density was higher in summer (0.184  $\pm$  0.559 larvae/

1000 m<sup>3</sup>) than in spring  $(0.657 \pm 1.559 \text{ larvae/} 1000 \text{ m}^3)$ . As in MRCB, larvae were more abundant in coastal stations than offshore (Fig. 5A, B).

Sparid larvae were caught in both areas and periods. In MRCB, mean larval density was greater in summer  $(92.931 \pm 606.893 \text{ larvae}/1000 \text{ m}^3)$  than in spring  $(27.956 \pm 65.000 \text{ larvae}/1000 \text{ m}^3)$ . Larvae were more abundant in coastal stations than offshore even if substantial densities were observed offshore. Overall higher densities were located along the 20 m isobaths in spring with a peak at Cape Béar station (Fig. 4C), and along the 40 m isobaths in summer with a peak near MPA limits (Fig. 4D). In CBMP, mean larval density was greater in spring  $(21.128 \pm 31.743 \text{ larvae}/1000 \text{ m}^3)$  than in summer  $(3.171 \pm 5.107 \text{ larvae}/1000 \text{ m}^3)$ . In summer, a density gradient was observed from coastal stations to middle and offshore stations (Fig. 5C, D), with higher densities in coastal stations.



Fig. 4 Density in *Marine Reserve of Cerbère-Banyuls* for sparid larvae (A and B) and scorpaenids larvae (C and D), in spring (A and C) and in summer (B and D). Densities are in



number of larvae per 1000 m<sup>3</sup>. Grey area between coast and sea delimits hard (Rock and *Posidonia* meadow) from soft bottom (Sand)



Fig. 5 Density in "*Côte Bleue*" *Marine Park* for sparid larvae (A and B) and scorpaenids larvae (C and D), in spring (A and C) and in summer (B and D). Densities are in number of larvae

# Suitable habitat

The environmental parameters used in each model are given in Tables 4 and 5. Standardised maps of larval and adult modelled suitable habitat are shown in Figs. 6, 7, 8 and 9.

#### Presence/absence

The presence/absence model explained between 14.1% (larvae of sparids groups) and 29.8% (adults of scorpaenids groups) of deviance in the presence/ absence of fish (Tables 4 and 5). In terms of life stages, the greatest proportion of deviance was explained for adults with 29.8% and 18.4% (from 316 samples) followed by larvae (19.3% and 14.1%, from 528 samples). In terms of taxa, the greatest proportion of deviance was explained for scorpaenids with 29.8% and 19.3% followed by sparids (18.4% and 14.1%).



per 1000 m<sup>3</sup>. Grey area between coast and sea delimits hard (Rock and *Posidonia* meadow) from soft bottom (Sand)

## Adult habitat

In MRCB (Table 4), adult Sparids models explained between 16.9% and 99.5% of deviance, negatively correlated with PAR in spring with a threshold value (TV) at 50 (Table 6), resulting in a relatively extended coastal suitable habitat (Fig. 6C). In summer, distribution was explained by the percentage of Posidonia cover (TV = 2% and 4%), and showed a positive correlation with Chl-a concentration and SLA (TV at 0.34 mg/m<sup>3</sup>, 3 cm, respectively) and a negative correlation with percentage of sand cover (TV = at 40%). Habitat is mainly located in protected areas (Fig. 6D). In CBMP, models explained between 34.8% and 51.4% of deviance. In spring, the IPUE was positively correlated with Chl-a concentration and negatively correlated with SLA with TV of 0.6 mg/m<sup>3</sup> and -2 cm, respectively. In summer, IPUE of adult was positively linked with the percentage of sand cover (TV = 30%). Our results

Stage	Location	Data type	Season	Variables (P-value)	Deviance explained	Ν
Adult	MRCB + CBMP	P/A		s(PAR) (<0.05) + s(POS) (<0.01) + s(CHL-A) (0.84) + s(SLA) (<0.05)	18.4%	316
	MRCB	IPUE	Spring	s(PAR) (<0.01) + s(DEP) (0.071)	16.9%	122
			Summer	s(POS) (<0.01) + s(CHL-A) (<0.01) + s(SLA) (<0.01) + s(SAN) (<0.01)	99.5%	75
	CBMP	IPUE	Spring	s(CHL-A) (<0.05) + s(SLA) (<0.05)	34.8%	48
			Summer	s(SAN) (<0.01) + s(SST) (0.077) + s(CHL-A) (0.152) + s(SLA) (0.083)	51.4%	71
Larvae	MRCB + CBMP	P/A		s(SLA) (<0.01) + s(ROC) (<0.01) + s(CHL-A w) (<0.01)	14.1%	528
	MRCB	Density	Spring	s(SST, CHL-A, SAN) (<0.01)	58.4%	204
			Summer	s(CHL-A) (<0.01) + s(SLA, SAN) (<0.01) + s(SST) (<0.01)	69.6%	129
	CBMP	Density	Spring	s(SAN, PAR) (<0.01)	56.0%	125
			Summer	s(SAN) (<0.01)	32.8%	70

Table 4 Sparid GAM results showing the best model for each stage and each area

Variables are ordered according to their importance in the model, based on results from AIC, from left most important to right less important. Non-significant variables are highlighted in bold

Table 5 Scorpaenids GAM results showing the best model for each stage and each area

Stage	Location	Data type	Season	Variables (P-value)	Deviance explained	Ν
Adult	MRCB + CBMP	P/A		s(POS) (0.058) + s(SAN) (<0.05) + s(SLA) (<0.01) + s(DEP) (<0.01)	29.8%	316
	MRCB	IPUE	Spring	s(POS) (<0.01) + s(ROC) (0.146) + s(DEP) (<0.05)	74.2%	122
			Summer	s(POS) (<0.01) + s(ROC) (<0.01)	71.3%	75
	CBMP	IPUE	Spring	s(SST) (<0.01) + s(POS) (<0.01) + s(PAR) (<0.01)	91.8%	48
			Summer	s(DEP) (<0.01) + s(PAR) (0.0689) + s(POS) (<0.05)	59.5%	71
Larvae	MRCB + CBMP	P/A		s(CHL-A) (<0.01)	19.3%	528
	MRCB	Density	Spring	s(CHL-A) (<0.01)	10.7%	204
			Summer	s(CHL-A) (<0.01)	5.14%	129
	CBMP	Density	Spring	s(CHL-A) (<0.01) + s(PAR) (0.078)	11.4%	125
		2		s(SLA) (<0.01) + s(POS) (<0.05)	35.9%	70

Variables are ordered according to their importance in the model, based on results from AIC, from left most important to right less important. Non-significant variables are highlighted in bold

show that some suitable habitat is concentrated in areas that are less coastal than previously thought (Fig. 7C, D).

In MRCB, models explained between 71.3% and 74.2% of deviance (Table 5), and the percentage of *Posidonia* and rocky bottoms cover were highly significant (Table 6). The relationship between the IPUE of adults and the percentage of *Posidonia* cover was positive for both seasons (TV = 12% in spring

and 3.5% in summer). The relationship between IPUE of adults and the percentage of rocky bottoms was negative in spring and positive in summer, with a common TV at 5%. (Fig. 6A, B). In CBMP, models explained between 59.5% and 91.8% of deviance. The relationship between IPUE of adults and SST, percentage of *Posidonia* cover and PAR was positive in spring (TV =  $21^{\circ}$ C, 40% and 60%, respectively). In summer, the relationship between IPUE of adult



Fig. 6 Suitable habitats in *Marine Reserve of Cerbère-Banyuls* for adult sparids (A and B) and for adult scorpaenids (C and D), in spring (A and C) and in summer (B and D).

and bathymetry was negative (TV = 25 m) and positive for percentage of *Posidonia* (TV = 45%), resulting in a coastal suitable habitat (Fig. 7A, B).

## Larval habitat

In MRCB, sparids larval models explained between 58.4% and 69.6% of deviance (Table 4) with a positive correlation with SST ( $13^{\circ}C < TV < 15^{\circ}C$  and  $TV > 19^{\circ}C$ ), Chl-a concentration (negative Slope,  $TV = 0.48 \text{ mg/m}^3$ ) (Table 6) and the percentage of sand (negative Slope, TV = 80%) in spring. The summer situation was explained by the distribution of Chl-a concentration (positive slope,  $TV = 0.18 \text{ mg/m}^3$ ), SLA (positive Slope, TV = 1.5 cm), percentage of sand (positive Slope, TV = 75%) and SST (positive Slope,  $TV = 23^{\circ}C$ ). The resulting suitable habitat was close to the coast during both seasons (Fig. 8C, D). In CBMP, models explained between 32.8% and 56.0% of deviance. In both seasons, larvae were positively correlated



White dotted line area between coast and sea delimits hard (Rock and *Posidonia* meadow) from soft bottom (Sand)

with the percentage of sand (TV = 45%) and in spring with PAR (negative slope, TV = 57). Suitable habitat resulted in a gradient of density from the coast to offshore stations during both seasons (Fig. 9C, D).

In MRCB, Scorpaenids larvae models explained between 5.14% and 10.7% of deviance (Table 5), with Chl-a concentration highly significant and positive in spring but negative in summer (TV = of  $0.55 \text{ mg/m}^3$ and 0.18 mg/m<sup>3</sup>, respectively) (Table 6). Suitable habitats were concentrated in middle shore areas in the spring but were more coastal in the summer (Fig. 8A, B). In CBMP, models explained between 11.4% and 35.9% of the deviance. The relationship between larval density and Chl-a concentration was negative in spring (TV of  $0.03 \text{ mg/m}^3$ ). In the summer, larval density was negatively correlated with SLA (TV = 1.7 cm) and positively correlated with the percentage of Posidonia (TV = 55%). Suitable habitat resulted in a gradient of density from the coast to offshore stations in spring, with an opposite trend in the summer (Fig. 9A, B).



Fig. 7 Suitable habitats in "*Côte Bleue*" Marine Park for adult sparids (A and B) and for adult scorpaenids (C and D), in spring (A and C) and in summer (B and D). White dotted line



area between coast and sea delimits hard (Rock and *Posidonia* meadow) from soft bottom (Sand)

## Discussion

We have combined GIS, statistical and geostatistical tools to understand the potential distribution for the different life stages of fish and define the suitable habitat by using a GIS-based environmental modelling approach to investigate relationships between sparids, scorpaenids and environmental conditions. Based on this approach, we estimated the suitable habitats of two target taxa characteristic of the artisanal Mediterranean fishery for both adult and larvae stages of development in two French coastal areas.

#### Habitat characterisation

Habitat characteristics were recorded as percentages of rock, sand and *Posidonia* meadows equivalent to measure habitat heterogeneity and link to taxa distribution. Habitat structure is known as one of the main factors that explain the variability of Mediterranean fish assemblages (García-Charton & Pérez-Ruzafa 1998, 2001; García-Charton et al., 2004). The complexity and the heterogeneity of the habitat lead, in some cases, to more diverse and abundant ichthyofauna than protection through an MPA (García-Charton et al., 2004).

In our study, adults scorpaenids are significantly linked to the percentage of Posidonia meadow and the percentage of rock together with depth, SST and PAR, whereas sparids are linked to the percentage of Posidonia meadow, sand and Chl-a, PAR and SLA. Regarding larvae, scorpaenids are directly linked to Chl-a and SLA and sparids with Chl-a, SST, SLA and the percentage of sand. In comparison to other models describing the presence/absence or density of juveniles (Stoner et al., 2007: 15 to 52%) or adults (Brown et al., 2006: 2.03 to 51.5%) to their environmental descriptors, high values of explained variances are obtained in the majority of our models (excepted for scorpaenids larvae and sparids adults in MRCB in the spring) leading to detailed definition of suitable habitat. The high explanatory power of the environmental variables used explains high values of results and indicates the way to reach better fitting models.

*Posidonia oceanica* seagrass meadows have been extensively studied in the Mediterranean as habitat structuring adult fish community structure (Harmelin-Vivien, 1984) or fish larval assemblage (Pilar Russo



Fig. 8 Suitable habitats in *Marine Reserve of Cerbère-Banyuls* for sparid larvae (A and B) and scorpaenids larvae (C and D), in spring (A and C) and in summer (B and D).

& Bayle Sempere, 2006), spatial and temporal variations (Francour, 1997, Deudero et al., 2008), comparisons with other inshore habitats (Guidetti, 2000) and the effect of protection (Francour, 2000, Macpherson et al., 2002). Most of these works have emphasised the importance of this habitat on fish structure, sustaining our results regarding *Posidonia* meadows as a major environmental parameter (such as minimum or maximum threshold values) in describing suitable habitats for adult of the two taxa.

SST, Chl-a and SLA are also identified as major environmental factors. In spring, SST becomes high due to an increase in solar heating and also creates a stratification of the water column in summer. This change between spring and summer has been observed in other Mediterranean areas as well. (Olivar et al., 2003; Sabatés et al., 2007). Most north-western Mediterranean fish reproduce during the spring–summer stratification period, when Chl-a concentration is at a maximum. However, for Mediterranean coastal area species (Tremblay & Sinclair, 1984), egg-stage duration is generally very short (24–36 h), and this may be



White dotted line area between coast and sea delimits hard (Rock and *Posidonia* meadow) from soft bottom (Sand)

reflected in the timing of spawning by adults to ensure optimum environmental conditions, for example when higher zooplankton biomass becomes available for larvae (Sabatés et al., 2007). SLA is an especially significant factor in summer (positively for MRCB and negatively for CBMP). On the coast of MRCB, SLA has highest values in coastal areas due to cyclonic eddies which create divergence and upwelling. Cold and less saline waters that arrive from the west with north-western winds create favourable conditions for this stratification (Bakun, 2006). Other stratifications in CBMP are linked to negative values of SLA on offshore areas, indicating convergence from coast to offshore areas and inducing an upwelling phenomenon along the coast that provokes the rise of deep cold waters when winds are pushing warmer surface waters offshore (Bakun, 2006). This effect makes CBMP an important source of larvae in southern nearby areas. This SLA patterns must also be linked with wind and current directions, key elements in structuring the ichthyoplankton community. In the case of winddriven current circulation, which occurs in most



Fig. 9 Suitable habitats in "*Côte Bleue*" Marine Park for sparid larvae (A and B) and scorpaenids larvae (C and D), in spring (A and C) and in summer (B and D). White dotted line

area between coast and sea delimits hard (Rock and *Posidonia* meadow) from soft bottom (Sand)

coastal systems, the circulation is highly variable inducing strong implications for larval dispersal. This high variability must be connected to biotic and abiotic factors and can yield variations of ichthyoplankton structures over small spatial and temporal scales. Changes of larval densities on a weekly basis were found off the Catalan coast, and wind fluctuations are also reported to influence larval densities in coastal areas at small temporal scales (Masó et al., 1998). The importance of these small scales corroborates the diffuse feature of mapped suitable habitat maps for larvae.

The structure of the bathymetry, substrate type, diversity of habitats per life stage and mechanisms conditioning the primary production of an area determine the location of spawning, whereas physical processes such as density front and associated currents or stratification of the water column affect distribution patterns of fish larvae (Sabates, 1990; Sabates & Olivar, 1996; Alemany et al., 2006) and have direct actions on passive transport and recruitment success.

All those parameters and processes are significant factors defining coastal suitable habitat. But, at this

stage, the spatial resolution of environmental variables needs to be refined for small area scales in order to better explain our coastal scenario and contribute usefully to a crucial aspect of marine conservation and fisheries management.

## Taxa suitable habitat

Seabreams are found in coastal waters worldwide and sustain important recreational and commercial fisheries (Fischer et al., 1987). Our results on adults show that their suitable habitats in spring are driven by PAR and Chl-a, and their suitable habitats in summer are oriented by POS and SAN. In spring, during the reproduction periods, suitable habitats are directly linked to the presence of food availability for success of recruitment of their progeny (Mariani, 2006), and in summer, suitable habitats are directly linked to the substrate where preys are more abundant (Deudero et al., 2008). Our results on larvae show that their spring suitable habitats are defined by SST and SAN, and their summer suitable habitats are defined by Chl-a and SAN. In the case of CBMP, suitable habitats are defined by a minimum value of
Table 6 Tre	ands and	1 Thresho	old Value (TV)	of variab	vles resultin	g from	GAM plot of mo	del for eacl	h taxa,	stage and area						
Taxa	Stage	Data type	Location	Season	Variables	Trend	TV	Variables	Trend	ΛL	Variables	Trend	TV	Variables	Trend	ΤV
Sparidae	Adult	P/A	MRCB+CBMP		PAR	I	50	SO4	I	20%	CHL-A	+	0.4 mg/ m <sup>3</sup>	SLA	Ι	0 cm
		IPUE	MRCB	SPR	PAR	I	40	DEP	H	30/45 m						
				SUM	POS	H	2/4%	CHL-A	+	$0.34 \text{ mg/m}^3$	SLA	+	3 cm	SAN	I	40%
			CBMP	SPR	CHL-A	+	0.6 mg/m <sup>3</sup>	SLA	I	-2 cm						
				SUM	SAN	+	30%	SST	I	19°C	CHL-A	+	0.4 mg/ m <sup>3</sup>	SLA	+	2 cm
	Larvae	P/A	MRCB+CBMP		SLA	H	-7/- 2 cm	ROC	I	2%	CHL-A	I	$0.3 \text{ mg/}{m^3}$			
		Density	MRCB	SPR	SST	+/∓	13/15/19°C	CHL-A	Ι	$0.48 \text{ mg/m}^3$	SAN	I	75%			
				SUM	CHL-A	+	0.18 mg/m <sup>3</sup>	SLA	+	1.5 cm	SAN	+	70%	SST	+	23°C
			CBMP	SPR	SAN	+	45%	PAR	I	57						
				SUM	SAN	+	45%									
Scorpaenidae	Adult	P/A	MRCB+CBMP		POS	+	20%	SAN	I	70%	SLA	+H	-2/ 4 cm	DEP	I	38 m
		IPUE	MRCB	SPR	SOG	+	12%	ROC	Ι	5%	DEP	Ι	40 m			
				SUM	POS	+	3.5%	ROC	+	5%						
			CBMP	SPR	SST	+	21°C	POS	+	40%	PAR	+	60			
				SUM	DEP	Ι	25 m	PAR	+	52	POS	+	45%			
	Larvae	P/A	MRCB+CBMP		CHL-A	+/-	$0.3/0.6 \text{ mg/m}^3$									
		Density	MRCB	SPR	CHL-A	+	0.55 mg/m <sup>3</sup>									
				SUM	CHL-A	Ι	0.18 mg/m <sup>3</sup>									
			CBMP	SPR	CHL-A	Ι	0.3	PAR	++	47/60						
				SUM	SLA	I	1.7 cm	POS	+	55%						

percentage of sand (45%) and can be explained by the configuration of bottoms substrate with, on the western side, the presence of anti-trawling artificial reefs on sand. This area offers also suitable habitats for these taxa on the eastern side that can influence fishing effort and catches distribution. In MRCB, suitable habitats are defined by SST, linked to the spawning period for sparids, and the Chl-a in summer is indirectly linked to the presence of food. In CBMP, on the eastern part of the MPA, a rocky reef zone with steep slopes characterised another favourable habitat for sparids, and on the west side, the implementation of the reserve of Couronne secured by anti-trawling artificial reefs also offer suitable habitats for sparids that can influence the distribution of catches. Vigliola et al. (1998) have shown that the settlement of sparids in our two study sites was highly variable in space and time, but presented some consistent patterns, probably related to hydroclimatic factors acting on several spatial and temporal scales. Through our results, evidencing a link between adults and larvae habitat remains difficult. Mobility of species, specific sexual comportment within taxa and seasonality of fishing activity hides any trend concerning coupling of both life stages. Sparids are usually described as mobile species (Harmelin, 1987). Moreover, these species are necto-benthic with important lateral and vertical movements with a spatial distribution highly dependent on the stage in life cycle (larvae, juveniles and reproductive adults) and habitat (Garcia-Rubies & Macpherson, 1995, Harmelin et al., 1995; Vigliola et al., 1998).

Scorpion fish are found in coastal waters worldwide and sustain important recreational and commercial fisheries (Fischer et al., 1987). Our results on adults show that their spring suitable habitats are driven by POS and SST, and their summer suitable habitats are oriented by POS and depth. In both seasons, scorpaenids are always linked to minimum percentage of *Posidonia* meadows in MRCB. *Posidonia* meadows, due to their shallow bathymetric range and high productivity and complex structure offering numerous hiding places for this cryptic species play the role of suitable habitat for adult stage and reproduction (Harmelin-vivien et al, 1989). Similar pattern can be observed in CBMP.

Our results on larvae of Scorpaenidae show that their spring suitable habitats are defined by Chl-a, and their summer suitable habitats are defined by Chl-a and SLA. In spring and summer, species of those families are directly linked to the presence of food or, in the case of CBMP, physical condition, induced by an upwelling phenomenon along the coast.

The fishing effort appeared widely distributed along the coast of CBMP and MRCB with 40–50 m depth lines marking the offshore limit of the fishing distribution. Such a distribution was directly linked to target species, and IPUE showed a tendency to decrease with increasing distance from coast. The main catches for this species were recorded very close to the coastal area, where fishing effort was also higher and particularly influenced in CBMP by the migration of *Sparus aurata* in spring and autumn along the shoreline.

A comparison of IPUE between locations showed adult values four times higher for sparids and between 50 and 150 times higher for scorpaenids in CBMP. For adults, these differences can be explained simply by the type of gear used for catching fish in each area. In CBMP, catches by Mullus and soup trammel nets (for Mullus surmuletus, Scorpaena porcus, Symphodus spp.) were more numerous and always closer to the reserve boundary. In MRCB, Scorpaena are more likely to be caught as by-catch species of the Palinurus sp trammel nets and not directly targeted in the Merlucius and Sparid gillnets used. Professional fishing activities and onboard sampling of catches gave a realistic picture of the influence of an MPA area on the fishing effort distribution, but these trends, due to protection effects, could not be clearly disentangled from other factors such as habitat heterogeneity and seasonality. In any case, numerous samples were needed to compensate for species heterogeneity in catches and to complete the experimental fishing design and other visual censuses (diving or video, Stobart et al., 2007) to reduce the effect of factors such as fishermen's habits or gear characteristics.

A comparison of density between locations showed sparids and scorpaenids larvae in similar proportions in both places in spring and 20 times higher in MRCB than in CBMP for both taxa. For larvae, the high variability observed in environmental factors and water circulation can explain the differences in density of larvae of both sites. The upwelling observed in the Cote Bleue coast induces replacement of near shore surface waters with eggs and larvae going directly offshore in a few hours. For this reason, mean concentrations of eggs and larvae observed are patchy with a high variability of densities.

#### Tools for fisheries

In summary, in applying this combined geostatistical/ GIS approach we found that suitable habitats for adult fish are mainly a result of a response to the substrate (*Posidonia* meadows and sand) and are mainly coastal suitable habitats, whereas larval suitable habitats are defined by environmental variables (Chl-a, SLA, SST), with more diffuse spatial patterns. Finally, we argue that our spatial approach used to estimate suitable habitats, combined with a temporal evolution, can provide insight into complex systems like coastal MPAs in the north-western Mediterranean and elsewhere.

Habitat modelling deals with complex species responses to interact between environmental and biological descriptors, and there is some caution to consider while producing spatial habitat suitability models as a simplified picture of habitat suitability and not to take into account many complex relationships and interactions both between species and between species and environmental variables. Direct survey of species distributions and density studies a small proportion of an area. Sampling stations should be spotted in space and time, defining each survey as a snapshot in relation between species and environment (Koubbi et al., 2006). However, in the absence of a more complete knowledge of the nature of these relationships and the spatial scales at which they occur, the habitat suitability modelling approach using GAM presents a relatively effective method for conducting an identification of likely distributions of important fishery habitats.

Although there is evidence that the habitat suitability models we produced provide predictive information on fish habitats and fish distribution for the taxa examined, the models and the hypotheses generated from the modelling process require further testing. Future applications of this approach could involve: (a) more substratum descriptors (e.g. complexity of substratum, distance to coast, benthos community); (b) more environmental descriptors (e.g. wind patterns or current speed and direction affecting horizontal transport and vertical mixing); and (c) the inclusion of the temporal evolution of these descriptors in order to asses the effects of the loss of specific spawning or nursing grounds on recruitment. Although present suitable habitat approaches do not allow for any of these in great detail, future work will also require an improved definition of taxa, and more spatially and seasonally extensive egg, larval, juvenile and reproductive adult surveys to validate such regional-scale models to provide a suitable habitat modelling predictive tool for fisheries management. The next step of this approach will be to detect species spawning, nursery and feeding aggregations, over-exploited areas and alternative fishing grounds.

Acknowledgements This work was funded by the European community (EnviEFH, Contract No: 022466; EMPAFISH; Contract No. 006539; BIOMEX, contract QRTL-2001-0891). We wish to thank the crew of the oceanographic ship Nereis II, fishermen from Cerbère-Banyuls and CBMP and all the volunteers who helped in field collection, sorting and identification. The authors thank F. Bachet from "Côte Bleue Marine Park", M. L. Licari from the "Marine Reserve of Cerbere Banyuls" and their respective teams. We also thank Suzanne Mills for language correction that improved readability.

#### References

- Akaike, H., 1973. Information theory and an extension of the maximum likelihood principle. In Petrov, B. N. & F. Csaki (eds), Proceedings of the 2nd International Symposium on Information Theory. Publishing House of the Hungarian Academy of Sciences, Budapest: 268–281.
- Akaike, H., 1974. A new look at the statistical identification model. IEEE Transactions on Automatic Control 19: 716–723.
- Alemany, F., S. Deudero, B. Morales-Nin, J. L. Lopez-Jurado, J. Jansa, M. Palmer & I. Palomera, 2006. Influence of physical environmental factors on the composition and horizontal distribution of summer larval fish assemblages off Mallorca island (Balearic archipelago, western Mediterranean). Journal of Plankton Research 28: 473–487.
- Bakun, A., 2006. Fronts and eddies as key structures in the habitat of marine fish larvae: opportunity, adaptive response and competitive advantage. Scientia Marina 70: 105–122.
- Bell, J. D., 1983. Effects of depth and marine reserve fishing restrictions on the structure of a rocky reef fish assemblage in the North-Western Mediterranean Sea. Journal of Applied Ecology 20: 357–369.
- Boudouresque, C. F., G. Bernard, P. Bonhomme, E. Charbonnel, G. Diviacco, A. Meinesz, G. Pergent, C. Pergent-Martini, S. Ruitton & L. Tunesi, 2006. Preservation et conservation des herbiers a Posidonia oceanica. RA-MOGE Publication: 1–202.
- Brown A. M., J. M. Bellido, V. D. Valavanis, A. Giraldez, 2006. Spatio-temporal shifts in the distribution of the Spanish Mediterranean pelagic community in relation to environmental influences. Proceedings of the ICES Annual Science Conference 2006, Sept. 19–23, 2006, Maastricht, The Netherlands. ICES CM 2006/O:13.
- Catalán, I. A., J. P. Rubín, G. Navarro & L. Prieto, 2006. Larval fish distribution in two different hydrographic

situations in the Gulf of Cádiz. Deep Sea Research Part II: Topical Studies in Oceanography 53: 1377–1390.

- Del Pilar Ruso, Y. & J. T. Bayle Sempere, 2006. Diel and vertical movements of preflexion fish larvae assemblages associated with *Posidonia oceanica* beds. Scientia Marina 70: 399–406.
- Deudero, S., G. Morey, A. Frau, J. Moranta & I. Isabel Moreno, 2008. Temporal trends of littoral fishes at deep *Posidonia oceanica* seagrass meadows in a temperate coastal zone. Journal of Marine Systems 70: 182–195.
- Eastwood, P. D., G. J. Meaden & A. Grioche, 2001. Modelling spatial variations in spawning habitat suitability for the sol *Solea solea* using regression quantiles and GIS procedures. Marine Ecological Progress Series 224: 251–266.
- European Commission, 2001. Green Paper: The Future of the Common Fisheries Policy. COM (2001): 135.
- Fischer, W., M. L. Bauchot & M. Schneider, 1987. Fiches FAO d'identification des espèces pour les besoins de la pêche. (Révision 1). Méditerranée et mer Noire. Zone de pêche 37(2): 761–1530.
- Fogarty, M. J., 1999. Essential habitat, marine reserves and fishery management. Trends in Ecology & Evolution 14: 133–134.
- Francour, P., 1997. Fish assemblages of *Posidonia oceanica* beds at Port-Cros (France, NW Mediterranean): Assessment of composition and long term fluctuations by visual census. Marine Ecology 18: 157–173.
- Francour, P., 2000. Evolution spatio-temporelle à long terme des peuplements de poissons des herbiers à *Posidonia* oceanica de la réserve naturelle de Scandola (Corse, Méditerranée nord-occidentale). Cybium 24: 85–95.
- Garcia-Charton, J. A. & A. Perez-Ruzafa, 1998. Correlation between habitat structure and a rocky reef fish assemblage in the southwest Mediterranean. Marine Ecology 19: 111–128.
- Garcia-Charton, J. A. & A. Perez-Ruzafa, 2001. Spatial pattern and the habitat structure of a Mediterranean rocky reef fish local assemblage. Marine Biology 138: 917–934.
- Garcia-Charton, J. A., A. Perez-Ruzafa, P. Saanchez-Jerez, J. T. Bayle-Sempere, O. Renones & D. Moreno, 2004. Multiscale spatial heterogeneity, habitat structure, and the effect of marine reserves on Western Mediterranean rocky reef fish assemblages. Marine Biology 144: 161–182.
- Garcia-Rubies, A. & E. Macpherson, 1995. Substrate use and temporal pattern of recruitment in juvenile fishes of the Mediterranean littoral. Marine Biology 124: 35–42.
- Guidetti, P., 2000. Differences among fish assemblages associated with nearshore *Posidonia oceanica* Seagrass beds, rocky–algal reefs and unvegetated sand habitats in the Adriatic Sea. Estuarine. Coastal and Shelf Science 50: 515–529.
- Guisan, A. & N. E. Zimmermann, 2000. Predictive habitat distribution models in ecology. Ecological Modelling 135: 147–186.
- Harmelin, J. G., 1987. Structure et variabilité de l'ichthyofaune d'une zone rocheuse protégée en Méditerranée (Parc National de Port - Cros, France). Marine Ecology 8: 263–284.
- Harmelin, J. G., F. Bachet & F. Garcia, 1995. Mediterranean Marine reserves: Fish indices as tests of protection efficiency. Marine Ecology 16: 233–250.
- Harmelin-Vivien, M. L., 1984. Ichtyofaune des Herbiers de Posidonies du Parc Naturel Regional de Corse. In

Boudouresque, C. F., A. Jeudy de Grissac & J. Olivier (eds), First International Workshop on *Posidonia oceanica* Beds. GIS Posidonie, Marseille: 291–301.

- Harmelin-Vivien, M. L., R. A. Kaim-Malka, M. Ledoyer & S. S. Jacob-Abraham, 1989. Food partitioning among Scorpaenid fishes in Mediterranean seagrass beds. Journal of Fish Biology 34: 715–734.
- Hastie, T. J. & R. J. Tibshirani, 1990. Generalized Additive Models. Chapman & Hall, London.
- Koubbi, P., C. Loots, G. Cotonnec, X. Harlay, A. Grioche, S. Vaz, C. Martin, M. Walkey & A. Carpentier, 2006. Spatial patterns and GIS habitat modelling of *Solea solea*, *Pleuronectes flesus* and *Limanda limanda* fish larvae in the eastern English Channel during the spring. Scientia Marina 70: 147–157.
- La Mesa, M., G. La Mesa & M. Micalizzi, 2005. Age and growth of Madeira scorpionfish, *Scorpaena maderensis* Valenciennes, 1833, in the central Mediterranean. Fisheries Research 74: 265–272.
- Le Pape, O., F. Chauvet, S. Mahevas, P. Lazure, D. Guerault & Y. Desaunay, 2003. Quantitative description of habitat suitability for the juvenile common sole (*Solea solea*, L.) and contribution of different habitats to the adult population in the Bay of Biscay (France). Journal of Sea Research 50: 139–149.
- Le Pape, O., L. Baulier, A. Cloarec, J. Martin, F. Le Loc'h & Y. Desaunay, 2007. Habitat suitability for juvenile common sole (*Solea solea*, L.) in the Bay of Biscay (France): A quantitative description using indicators based on epibenthic fauna. Journal of Sea Research 57: 126–136.
- Lloret, J. & S. Planes, 2003. Condition, feeding and reproductive success of white seabream (*Diplodus sargus*) as indicators of habitat quality and the effect of protection in the northwestern Mediterranean. Marine Ecology Progress Series 248: 197–208.
- Macpherson, E., A. Gordoa & A. García-Rubies, 2002. Biomass size spectra in littoral fishes in protected and unprotected areas in the NW Mediterranean. Estuarine Coastal and Shelf Science 55: 777–788.
- Masó, M., A. Sabatés & M. P. Olivar, 1998. Short-term physical and biological variability in the shelf-slope region of the NW Mediterranean during the spring transition period. Continental Shelf Research 18: 661–675.
- Mariani, S., 2006. Life-history- and ecosystem-driven variation in composition and residence pattern of seabream species (Perciformes: Sparidae) in two Mediterranean coastal lagoons. Marine Pollution Bulletin 53: 120–127.
- Maynou, F., 1998. The application of geostatistics in mapping and assessment of demersal resources. *Nephrops norvegicus* (L.) in the northwestern Mediterranean: A case study. Scienta Marina 62: 117–133.
- NMFS, 1996. Magnuson-Stevens Fishery Conservation and Management Act: As amended through October 11, 1996. U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, NOAA Technical Memorandum NMFS-F/SPO-23: 121.
- Olivar, M. P. & A. Sabates, 1997. Vertical distribution of fish larvae in the NW Mediterranean Sea in spring. Marine Biology 129: 289–300.
- Olivar, M. P., I. A. Catalán, M. Emelianov & M. L. Fernández de Puelles, 2003. Early stages of *Sardina pilchardus* and

environmental anomalies in the northwestern Mediterranean. Estuarine Coastal and Shelf Science 54: 609-619.

- Pajuelo, J. G. & J. M. Lorenzo, 1998. Population biology of the common pandora *Pagellus erythrinus* (Pisces: Sparidae) off the Canary Islands. Fisheries Research 36: 75–86.
- Parsons, T. R. & P. J. Harrison, 2000. Introduction. In Harrison, P. J. & T. R. Parsons (eds), Fisheries Oceanography. An Integrative Approach to Fisheries Ecology and Management. Oxford, Blackwell Science: 347.
- Petitgas, P., 1996. Geostatistics and their applications to fisheries survey data. In Moksness, E. & B. A. Megrey (eds), Computers in Fisheries Research. Chapman & Hall, London: 113–141.
- Petrakis, G. & K. I. Stergiou, 1995. Weight–length relationships for 33 fish species in Greek waters. Fisheries Research 21: 465–469.
- Planes, S., E. Macpherson, F. Biagi, A. Garcia-Rubies, J. Harmelin, M. Harmelin-Vivien, J. Y. Jouvenel, L. Tunesi, L. Vigliola & R. Galzin, 1999. Spatio-temporal variability in growth of juvenile sparid fishes from the Mediterranean littoral zone. Journal of the Marine Biological Association of the United Kingdom 79: 137–143.
- R Development Core Team, 2007. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org.
- Rufino, M. M., F. Maynou, P. Abello & F. Sarda, 2006. Spatial and environmental factors affecting the distribution of the main decapod crustacean prey species in the NW Mediterranean. Hydrobiologia 555: 129–141.
- Sabates, A., 1990. Distribution pattern of larval fish populations in the Northwestern Mediterranean. Marine Ecology Progress series 59: 75–82.
- Sabates, A. & P. Olivar, 1996. Variation of larval fish distributions associated with variability in the location of a shelf-slope front. Marine Ecology Progress series 135: 11–20.
- Sabatés, A., M. P. Olivar, J. Salat, I. Palomera & F. Alemany, 2007. Physical and biological processes controlling the distribution of fish larvae in the NW Mediterranean. Progress in Oceanography 74: 355–376.
- Santos, R. S., S. Hawkins, L. R. Monteiro, M. Alves & E. J. Isidro, 1995. Case studies and reviews. Marine research, resources and conservation in the Azores. Aquatic Conservation: Marine Freshwater Ecosystem 5: 311–354.
- Santos, M. N., M. B. Gaspar, P. Vasconcelos & C. C. Monteiro, 2002. Weight-length relationships for 50 selected fish species of the Algarve coast (southern Portugal). Fisheries Research 59: 289–295.
- Stelzenmüller, V., F. Maynou, S. Ehrich & G. P. Zauke, 2004. Spatial analysis of twaite shad, *Alosa fallax* (Lacepède, 1803), in the Southern North Sea: Application of nonlinear geostatistics as a tool to search for special areas of

conservation. International Review of Hydrobiology 89: 337–351.

- Stelzenmüller, V., S. Ehrich & G. P. Zauke, 2005. Effects of survey scale and water depth on the assessment of spatial distribution patterns of selected fish in the northern North Sea showing different levels of aggregation. Marine Biology Research 1: 375–387.
- Stelzenmüller, V., S. Ehrich & G. P. Zauke, 2006. Analysis of meso scaled spatial distribution of the dab (*Limanda limanda*) in the German Bight: Does the type of fishing gear employed matter? Fisheries Science 72: 95–104.
- Stelzenmüller, V., F. Maynou & P. Martin, 2007. Spatial assessment of benefits of a coastal Mediterranean Marine Protected Area. Biological Conservation 136: 571–583.
- Stergiou, K. I. & K. Erzini, 2002. Comparative fixed gear studies in the Cyclades (Aegean Sea): Size selectivity of small-hook longlines and monofilament gill nets. Fisheries Research 58: 25–40.
- Stobart, B., J. A. García-Charton, C. Espejo, E. Rochel, R. Goñi, O. Reñones, A. Herrero, R. Crec'hriou, S. Polti, C. Marcos, S. Planes & A. Pérez-Ruzafa, 2007. A baited underwater video technique to assess shallow-water Mediterranean fish assemblages: Methodological evaluation. Journal of Experimental Marine Biology and Ecology 345: 158–174.
- Stoner, A. W., J. P. Manderson & J. P. Pessutti, 2001. Spatially explicit analysis of estuarine habitat for juvenile winter flounder: Combining generalized additive models and geographic information systems. Marine Ecological Progress Series 213: 253–271.
- Stoner, A. W., M. L. Spencer & C. H. Ryer, 2007. Flatfishhabitat associations in Alaska nursery grounds: Use of continuous video records for multi-scale spatial analysis. Journal of Sea Research 57: 137–150.
- Tremblay, M. & M. Sinclair, 1984. Timing of spawning of Atlantic herring (*Clupea harengus harengus*) populations and the match-mismatch theory. Canadian Journal of Fisheries and Aquatic Sciences 41: 1055–1065.
- Valavanis, V. D., S. Georgakarakos, A. Kapantagakis, A. Palialexis & I. Katara, 2004. A GIS environmental modelling approach to essential fish habitat designation. Ecological Modelling 178: 417–427.
- Vanderklift, M. A. & C. A. Jacoby, 2003. Patterns in fish assemblages 25 years after major seagrass loss. Marine Ecology Progress Series 247: 225–235.
- Vigliola, L., M. L. Harmelin-Vivien, F. Biagi, R. Galzin, A. García-Rubies, J. G. Harmelin, J. Y. Jouvenel, L. Le Direach-Bousier, E. Macpherson & L. Tunesi, 1998. Spatial and temporal patterns of settlement among sparid fishes of the genus *Diplodus* in the northwestern Mediterranean. Marine Ecology Progress Series 168: 45–56.

FISH HABITAT MAPPING

# Mapping abundance distribution of small pelagic species applying hydroacoustics and Co-Kriging techniques

Stratis Georgakarakos · Dimitra Kitsiou

© Springer Science+Business Media B.V. 2008

Abstract Hydroacoustic technology provides ground tools for the estimation of abundance and spatial distribution of pelagic species. The final products of such surveys, the interpolated choropleth maps, are based on a Geostatistical analysis of the acoustic measurements to minimise, as much as possible, the interpolation error, and to quantify uncertainty. The current study is based on fisheries acoustic measurements and satellite images covering the sea area of Thermaikos Gulf over the years 1996, 1997 and 1998. Spatial interpolations describing the abundance and distribution of small pelagic species in the research area, as well as sea surface temperature (SST), Chlorophyll-a content (SSC) and average depth, were produced, based on Ordinary and Universal Kriging and Co-Kriging Geostatistical methods. The results of the Geostatistical analysis showed that the Co-Kriging spatial interpolation method produced the best results regarding fish

Guest editor: V. D. Valavanis Essential Fish Habitat Mapping in the Mediterranean

S. Georgakarakos (⊠) Sonar Laboratory, Department of Marine Sciences, University of the Aegean, University Hill, 81100 Mytilini, Lesvos, Greece e-mail: stratisg@aegean.gr

D. Kitsiou

GIS Laboratory, Department of Marine Sciences, University of the Aegean, University Hill, 81100 Mytilini, Lesvos, Greece abundance when SST and average depth variables were included in the model. The latter indicates that there is an existing spatial cross-correlation between fish abundance and the environmental variables. Consequently, the potential reduction of the overall error in the estimation process, as presented in this study, is very significant, particularly with regard to error reduction in stock assessment and management.

**Keywords** Fisheries acoustics · GIS · Co-Kriging · Small pelagic species

# Introduction

Traditionally, ecologists correlate the spatial heterogeneity of fish abundance to certain physicochemical and biological parameters, which define the ecological background of the specific organisms (Hensen, 1911; Lasker, 1978; Laevastu & Hayes, 1981). These factors can influence fish activities, such as feeding, predator avoidance, migration, reproduction and habitat selection, and are therefore accountable for the spatial characteristics of their biomass distribution (Koutsikopoulos & Lacroix, 1992; Simard et al., 1992; Horne et al., 1999). However, this more or less deterministic interpretation of the effect of environmental variables is not always and entirely evident (Fréon et al., 2005), and it is supposed that the generated forces interact in such a non-linear or chaotic way that the resulting spatial fish biomass structure, on most observation scales, is stochastic (Sharp & McLain, 1993; Webster & Oliver, 2001).

How difficult is the identification or the quantitative evaluation of such interactions? There are different approaches for analysis and modelling of the relationships between environmental factors, including bottom quality and geographic peculiarity on the one side and spatial heterogeneity in biomass on the other. Most approaches emphasise the spatial autocorrelation (Maravelias et al., 1996; Paramo & Roa, 2003; Giannoulaki et al., 2005) or the multivariate character (Sullivan, 1991; Stefánsson, 1996; Swartzman et al., 1994; Maravelias, 1999) of the data at different scale levels. Since pelagic fish biomass forms, in small scale, "schooling" and "clustering" aggregation patterns (Azzali et al., 1985; Fréon & Misund, 1999), the spatial structure has also been analysed in certain studies as a spatial point process (MacLennan & MacKenzie 1988; Petitgas et al., 2001).

Classical estimation methods assume stationarity in space and time, independence among the data and identical distribution of the parameters (Rossi et al., 1992). All these conditions are very rarely met in the aquatic environment, where the spatial structure is unstable through time, data are spatially autocorrelated and the number of samples is low compared with the high variability of the structure. Unfortunately the spatial information, which is critical for evaluating trends in biomass or correlations between the latter and the relevant environmental parameters, is neglected by the most commonly used statistical methods.

Specifically for pelagic fish, hydroacoustic measurements of fish density combined with Geostatistical analysis has been recognised as the best method for modelling the spatial distribution of species biomass or the joint spatial dependence between biomass and environmental parameters (Armstrong et al., 1989; Petitgas, 1993; Simard et al., 2002). Recently, Geostatistical analysis has been applied, showing a significant effect of certain topographic characteristics on the spatial organisation of the overall smallpelagic-fish assemblage (Giannoulaki et al., 2006).

In the present study, pelagic fish density, recorded by acoustics in four different stock assessment surveys, was geostatistically analysed in order to produce choropleth maps through Kriging. The spatial characteristics of both fish density and environmental parameters acquired by in situ or satellite techniques were investigated by means of Variograms and Cross-variograms, examining possible spatial relationships among the variables. These multivariate observations were interpolated in a manner similar to Ordinary and Universal Kriging techniques, by applying Ordinary and Universal Co-Kriging. The latter is a special case of the first, introduced by Matheron (1971), where the trend is modelled as a function of coordinates (Deutsch & Journel, 1998). Finally, the developed spatial models were tested by applying the "leave-one-out cross validation" procedure (Isaaks & Srivastava, 1989), evaluating if the incorporation of the environmental variables will improve the prediction at new spatial locations, where no acoustic data are available. Furthermore, the leave-one-out cross validation residuals were used to provide statistics concerning modelling assumptions and whether standard errors estimated by the models are accurate (Isaaks & Srivastava, 1989).

# Methodology

# Data collection

Acoustic survey data were collected on four surveys (10–12 October 1996, 13–15 October 1996, 21–25 May 1997 and 27 April–1 May 1998) during standard fish biomass assessment programmes in the Thermaikos Gulf in the NW part of the Aegean Sea. Measurements were carried out along predetermined sampling transects, to the south until the 100 m isobath, near Cape Kassandra, in an area of about 1,600 sq.n.mi. (Tsimenides et al., 1992).

The area backscattering coefficient Sa  $[m^2 n.mi^{-2}]$ was estimated every n.mi using a SIMRAD BI500/ EK500 echosounder (Knudsen, 1990). The system operated a 38 kHz transducer, calibrated with standard spheres (Foote, 1987), insonifying with 1 ms width pulses. The research vessel was sailing at 8 knots, and time, position and integrator values were recorded in the BI500/UNIX file system. Echograms were scrutinised to remove echo traces in the water column that were not pelagic fish. Catch data from biological sampling using a standard pelagic trawl and concurrent commercial catch data indicated that the majority of the insonified species in the study area were Sardina pilchardus, Engraulis encrasicolus and Trachurus spp. Other species represented less than 8% of the catches.

Temperature vertical profiles were recorded on a regular grid along survey transects by means of a calibrated Seabird S19 CTD. Surface temperature measurements were used in order to replace missing SST values, in satellite imageries, frequently observed in overcast or coastal areas. Satellite images, provided by the German Aerospace Agency's (DLR) and the Distributed Active Archive Center (NASA), were transformed into Sea Surface Temperature (SST) in Celsius and Sea Surface Chlorophyll-a concentration (SSC) using GIS tools (Valavanis et al., 2004). Salinity data have not been used, since the analysis is restricted to the two provided satellite imageries and the acoustically measured bottom depth.

# Data analysis

The presented results are based on Geostatistical analysis applying ESRI's ArcGIS Geostatistical Analyst Software (GAS), which provides an extensive set of tools for performing different Kriging and Co-Kriging methods. Also other software packages (GSLIB/Fortran, WinGSLIB and GSTAT/R) were used for comparison and evaluation purposes. In certain cases the results were slightly different, indicating small variations in the implementation of the Geostatistical algorithms.

# Selection of the geostatistical approach

There are different groups of Geostatistical techniques where auxiliary information is used to improve spatial prediction:

- Co-Kriging (CK), if the number of auxiliary variables is low and they are not available at all grid-nodes
- Kriging with External Drift (KED), if the auxiliary information is available at all grid-nodes and correlated with the target variable (Kriging with a trend model, Deutsch & Journel, 1998; Kriging with external drift, Wackernagel, 1995). Universal Kriging (UK) can be interpreted as a special case of KED where the drift is modelled as a function of only the coordinates.
- Kriging after De-trending (KAD), if drift and residuals can also be fitted separately and then summed (Goovaerts, 1997). This technique is also known as Regression Kriging (RK) and can

be combined with stratification and GAMs (McBratney et al., 2000).

UK, KED and KAD are, in fact, equivalent methods providing, under the same assumptions, the same predictions. The advantage of KED is that the equations are solved at once, while the advantage of KAD is that there is no danger of instability as with the KED system (Goovaerts, 1997).

KED techniques are not recommended for use directly on interpolated (bottom depth) data or on imputed missing values (satellite data), since the uncertainty of the predicted covariate is not taken into account and therefore the prediction variances are underestimated. Additional limitations concerning the application of the KED technique (for instance, linearity between dependent and auxiliary variables, smoothness of the external variables) are described by Goovaerts (1997) and Royle & Berliner (1999).

In our case, it is desirable to describe the spatial relationship between bottom depth, temperature, chlorophyll-a and pelagic biomass based upon the available measurements on all the variables of interest. For univariate analysis the Universal Kriging technique was chosen, since bottom depth is clearly correlated with the coordinates and partially interrelated with the rest of the covariates. The multiple surfaces described by such multivariate observations will then be interpolated in a manner similar to Universal Kriging, by applying the extended CK technique.

#### Stationarity test

The basic biological or environmental factors, which are involved in ecological processes, change with time and introduce non-stationary conditions into the system. Some important statistics especially correlations are reasonable under the condition of stationarity in the process. If that condition is not fulfilled, the correlation is random and any biological interpretation of it is erroneous (Bendat & Piersol, 1971). The process which generates the data is said to be second-order stationary (strict sense) if the distribution function and the joint distribution function are invariant under an arbitrary time shift. It is stationary in the wide sense if the mean and the autocorrelation are invariant (Papoulis, 1965). In Geostatistical terminology, it is required that the spatial Covariance structure is essentially identical throughout the spatial

domain of interest (Journel & Huijbregts, 1978). The ARC-GIS definition requires that the mean of all locations of interest be equal and that the Covariance between any two locations depends only on the distance and direction between them and not specifically on the actual location. When it is suspected that this is not the case, more complicated models may be required. Stationarity in the present work was achieved by data transformation (logarithmic), modelling the trend and using Universal Kriging, as well as by dividing the data set into subsets.

#### Empirical variograms and cross-variograms

This analysis typically aims at generating an empirical variogram and then fitting a parametric model that adequately captures the structure of the empirical variogram. Data were partitioned according to the distance between distinct pairs of observation locations, so that the bins are as small as possible to retain spatial resolution, and yet large enough that the empirical variogram estimate is stable (Cressie, 1993).

The semivariance or simply variogram ( $\gamma$ ) is estimated by the formula:

$$\gamma(h) = \frac{1}{2} \sum_{i=1}^{n} [Z(X_i) - Z(X_i + h)]^2$$

where  $X_i$  and  $X_i + h$  are two locations in space at a certain distance, which belongs to a binwidth class of lag h, over all directions or specific to a given direction inside the studied area.  $Z(X_i)$  and  $Z(X_i + h)$  are the magnitudes of the variable at the two locations and *n* is the number of data pairs in each lag class. The greater the number of data points, the greater the statistical reliability in each binwidth class.

The three key parameters in the variogram, Nugget, Range and Sill, were estimated applying the spherical model (Cressie, 1993).

- The nugget parameter represents the variation at very short distances (the variation due to measurement errors or the replication variance) (Rossi et al., 1992). It is the point at which the variogram model appears to intercept the y-axis.
- The range parameter represents the maximum spatial distance, where data are effectively spatially correlated or autocorrelated.
- The sill parameter describes the maximum variance of the variogram minus the nugget effect. In

some publications the maximum variance, including the nugget, is referred as the total sill.

Correspondingly, a cross-variogram model describes the co-variation (or correlation relationship) between each pair of variables (Journel & Huijbregts, 1978; Cressie, 1993; Goovaerts, 1997). The Crossvariogram ( $\gamma_{1.2}$ ) for two variables  $Z_1$  and  $Z_2$  is estimated by the formula:

$$\begin{split} \gamma_{1,2}(h) &= \frac{1}{2N} \sum_{i=1}^{N} \Big\{ [Z_1(x) - Z_1(x+h)] \\ &+ [Z_2(x) - Z_2(x+h)] \Big\}. \end{split}$$

Kriging

Ordinary and Universal Kriging, which are used in the present study, are gradual, local, and may not be exact, perfectly reproducing the measured data. Kriging selects weights so that the estimates are unbiased and the estimation variance is minimised. Identifying the best variogram may involve running and evaluating a large number of models, a procedure supported by the ArcGIS Geostatistical software.

Let Z represent the fish density in the x, y coordinate system, for which distances are linear (expressed in n.mi). Ordinary Kriging provides a statistical model for the process Z(x, y), at all points in space, (x, y), as follows:

Z(x, y) = u + e(x, y)

where u and e(x, y) are the overall, large-scale mean of the process across the spatial domain and the small-scale random fluctuation of the process accordingly. Unlike Universal Kriging, Ordinary Kriging places very little emphasis on the first mean component, focusing instead on modelling the structure of the small-scale random fluctuation component. Universal Kriging is an extension of Ordinary Kriging accommodating a spatially varying trend. It can be used both to produce local estimates in the presence of trend and to estimate the underlying trend itself. By incorporating the spatial varying trend, the previous equation is modified as:

$$Z(x, y) = u(x, y) + e(x, y)$$

where the mean term is described by the model u(x, y).

#### Co-Kriging

The multiple surfaces described by such multivariate observations can then be interpolated in a manner similar to the Kriging techniques as above. However, Co-Kriging requires much more estimations, including estimating the autocorrelation for each variable as well as all cross-correlations. If the main variable of interest is Z, both autocorrelation for Z and crosscorrelations between Z and all other variable types are used to make better predictions. The functions used to model those variograms and cross-variograms must be chosen so that the variance of any possible linear combination of these variables is always positive. The linear model of co-regionalisation, described in detail by Panatier (1996), is the most commonly used method for choosing such a set of functions so that the predictor of a given covariate at a given location X is a linear combination of all covariates of interest. Finally, it should be noted that often one of the auto- or cross-models may not fit its sample variogram very well compared to the others. In this case, the overall fit should be judged accordingly since each individual model is a small part of the total model (Isaaks & Srivastava, 1989).

The resulting Co-Kriging equations are slightly more complicated than those of Ordinary Kriging, but are still relatively straightforward, based on the Cross-variogram model (Journel & Huijbregts, 1978; Cressie, 1993; Goovaerts, 1997).

#### Specific performance measures

Finally, the developed models were evaluated by analysing the leave-one-out cross validation residuals and their statistics are compared and tested concerning modelling assumptions and whether standard errors estimated by the model are accurate (Isaaks & Srivastava, 1989).

The Leave-one-out cross validation residuals are generated using the following procedure:

- Create an empirical variogram using all of the N available observations.
- Estimate the theoretical variogram from the empirical variogram.
- For each observation Z(s<sub>i</sub>), i = 1,..., N in the data set,
- Remove the observation from the data set.

- Predict the Kriged value  $\hat{Z}(s_i)$  at the location of the removed observation using the remaining (N-1) observations.
- Calculate the difference between the predicted value and the true value, and divide this difference by the Kriging Standard Error (Bradley and Haslett, 1992).

$$SR_i = \frac{Z(s_i) - \overset{\wedge}{Z}(s_i)}{KSE}$$

 Record the value SR as the standardised residual at the location of the removed observation.

Once the residual at each location has been calculated as described, their distribution is tested for normality, validating if the Kriging model assumptions were correct, and if other modelling techniques should be considered.

The comparison among the different developed models was carried out based on the calculation of the root-mean-squared prediction error (RMS), the average standard error (ASE) and the coefficient of determination ( $\mathbb{R}^2$ ). In case the average standard error is close to the root-mean-squared prediction error, the variability in prediction is correctly assessed. If the average standard error is greater than the root-mean-squared predictions is overestimated; on the other hand, if the average standard error is less than the root-mean-squared prediction error, it is underestimated.

# Results

#### Exploratory data analysis

Since the data were autocorrelated multivariate measurements, the level of spatial influence may vary with distance and other factors making the autocorrelation function non-linear. In general, the closer the neighbours are, the greater the level of correlation, which distorts statistical tests of significance in analyses such as correlation, regression, or analysis of variance (Cliff & Ord, 1981). Therefore, the following multivariate regression analysis was of an introductory character to the Geostatistical approach and did not aspire to provide statistical models describing the relationships among the variables under study.

Simple and stepwise multiple linear regression analyses were used to investigate possible relationships

between the dependent variable LnSa (logarithmic transformed area backscattering coefficient), which represents an acoustically estimated fish density index and hypothesised covariates: spatial coordinates, time, bottom depth, SST and SSC, if the latter was available. The significance of the regression models was tested by ANOVA (probability of F to enter  $\leq 0.05$ ). The stepwise multiple regression analysis exhibited in general low proportion of variation explained by the model  $(R^2)$  on all significantly different from  $0 R^2$ values (Table 1). The most significant models that were developed were based on the acoustic surveys 1996 A, 1996 AB (pooled both data sets) and 1998. The acoustic estimated fish density (LnSa) was related to the following potential predictors: day-night time cycle, bottom depth, the spatial coordinates (Lon, Lat), SST and SSC (available only in 1998 survey).

Furthermore, residuals were calculated, based on non-linear modelling of acoustic fish density (LnSa) versus day-night time, fitted by least squares regression, by a sine signal (Zar, 1974). The linear regression models constructed using the derived residuals versus Latitude or bottom depth were significant (Table 1). As it is expected from the geography of the surveyed area, linear regression models confirmed a statistically significant (P < 0.1) and relative higher relationship ( $R^2 = 0.64$ ) between bottom depth and spatial coordinates. These results are justified in the following Geostatistical analysis, the development of Universal Kriging models, testing if there is a geographical trend in the LnSa surface that partly explains data variation.

# Environmental covariates

The horizontal spatial distribution of sea temperature showed a significantly different pattern between the two survey seasons (Fig. 1A: October 1996 and April/May 1997 and 1998). Lower temperatures were observed during the May and especially the April survey, where large surfaces in southern areas were in general cooler than the rest of the picture. In addition, cold spots appeared, associated with upwelling phenomena in the north-eastern part (Fig. 1, May-1997) or riverine outflow in the south-western part (Fig. 1, April-1998). The four SST images, corrected for missing values, were used in the Co-Kriging interpolation as covariates.

The bathymetry was modelled applying Universal Kriging on all bottom depth acoustic measurements, pooled all survey data (Fig. 1B). The bottom depth, as it is shown in the interpolated map, increased in south easterly direction until the 200 m isobath.

Since satellite imagery providing chlorophyll-a concentration was only available after 1997, the Co-Kriging estimation using chlorophyll data was restricted to the 1998 acoustic survey (Fig. 1C).

# Kriging and Co-Kriging interpolations

Outputs from the cross-variogram modelling, Kriging and Co-Kriging spatial interpolations for the four surveys (1996a, 1996b, 1997 and 1998) are shown in Figs. 2–5, respectively. Each figure illustrates the cross-variogram models used in the Co-Kriging interpolation (a) and the interpolated acoustic fish density (LnSa) using Kriging (b) and Co-Kriging (c) techniques. Cross-validation statistics between predicted and observed acoustic fish density (LnSa), applying the leave-one-out cross validation method, are shown in Table 2. In each survey, statistics with significant covariate main effects and interactions are included, sorted by increasing coefficient of determination ( $R^2$ ).

The four interpolated maps (Fig 2B, 3B, 4B and 5B) did not show, between seasons, any marked

Table 1 Simple or stepwise multiple regression analysis

Survey	Dependent variable	Separated/No of data	Independent variables	Model R <sup>2</sup>	F	Sig.
1996 A	LnSa	All, 260	DN, SST, Lat, Depth, Lon	0.265	18.27	0.00
1996 A	Res(LnSa $\sim$ time)	All, 260	Lat	0.382	159.80	0.00
1996 A	Res(LnSa $\sim$ time)	All, 260	Depth	0.213	70.07	0.00
1996 AB	LnSa	Night, 244	Lat, Lon, Depth, SST	0.292	24.74	0.00
1998	LnSa	441	DN, Lon, Lat, Chl, Lat, SST	0.243	27.95	0.00

Independent variable: LnSa or residuals from modelling LnSa with time as independent variable;  $R^2$ : Coefficient of determination in the leave-one-out cross validation prediction; F = ANOVA F-test, Sig = significance of the model, P < 0.01





Fig. 1 (A) Sea surface temperature for the four sampling surveys in Thermaikos Gulf, and (B) Bathymetry and (C) Spatial distribution of chlorophyll-a concentrations

differences in their fish distribution. In contrast, within seasons, some biomass movements were reflected on the maps, concurrent to temperature changes. Considering the short time lag between the two October surveys (1–2 days), the dynamic of the spatial distribution is very high.

Only bathymetry, SST and their interactions provided a significant effect on predicting LnSa measurements applying the leave-one-out cross validation test. Chlorophyll-a data did not improve the modelling approach. The omnidirectional variogram and cross-variogram models exhibited autocorrelation



Fig. 2 Sampling survey N96A: (A) Cross-Variogram (omnidirectional and exhaustive) of the Acoustic Estimated Fish Density (LnSa) using Co-Kriging (SST and depth), (B)

ranges of 5.7–25 km and 6 to 16 km, respectively (Table 2). Concerning the nugget effects of the cross-variograms, the October values (Figs. 2 and 3) were slighter than those of spring (Figs. 4 and 5).

# Discussion

Oceanographic features such as temperature fronts, eddies, rings and upwelling areas have been related to

Acoustic Estimated Fish Density (LnSa) using Kriging and (C) using Co-Kriging (SST and depth)

fish biomass concentrations—at least at certain spatial scales and magnitudes (Laurs et al., 1984; Fiedler & Bernard, 1987; Chen et al., 2005)—and satellite ocean colour and sea surface temperature images have been used commercially for this purpose. In general, SST and chlorophyll-a spatial patterns are very similar, since very often, warm, nutrient-depleted water has low chlorophyll-a content and cold, nutrient-rich water has high chlorophyll-a levels.



Fig. 3 Sampling survey N96B: (A) Cross-Variogram (omnidirectional and exhaustive) of the Acoustic Estimated Fish Density (LnSa) using Co-Kriging (SST and depth), (B)

The relationship between sea surface satellite imagery and species spatial distribution depends, among other things, upon the number of linkages between phytoplankton and the given species trophic level. Some species, such as anchovy and sardine, which are closer to phytoplankton at some time periods of their life cycle, may exhibit a stronger linkage (Ware & Thomson, 2005) than other species which are at a higher trophic level.

Acoustic Estimated Fish Density (LnSa) using Kriging and  $({\bf C})$  using Co-Kriging (SST and depth)

However, this more or less expected spatiotemporal relationship between environment and fish density is not always and clearly evident (Fréon et al., 2005). For instance, the biomass structure in areas developing lower magnitudes of the oceanographic features with a smaller spatiotemporal scale may be affected in a stochastic and less predictable way (Sharp & McLain, 1993; Webster & Oliver, 2001).



Fig. 4 Sampling survey N97: (A) Cross-Variogram (omnidirectional and exhaustive) of the Acoustic Estimated Fish Density (LnSa) using Co-Kriging (SST), (B) Acoustic Estimated Fish Density (LnSa) using Kriging and (C) using Co-Kriging (SST)

The Thermaikos Gulf, the study area in the present paper, is a relatively small region (30 nm wide  $\times$ 100 nm long), developing a mesoscale environmental dynamic. Its mean depth varies from 40 m in the northern inner continental shelf (Thermaikos Bay) until the south tip of the Kassandra Peninsula, facing the open NW Aegean Sea, at the 200 m isobath. Freshwater from four rivers (Aliakmon, Pinios, Loudias and Axios) runs in the western coast of the Thermaikos Gulf resulting in low salinity and high turbidity in the sea water. About 40% of the total water volume of the Gulf has its origin from the rivers (Poulos et al., 2000). Another source of cold and lowsaline waters is provided by the Black Sea inflow and other coast rivers emptying the northern Aegean Sea. This nutrient input can reach the Thermaikos Gulf, as it is clearly seen in surface chlorophyll-a satellite imagery (Agostini & Bakun, 2002).



Fig. 5 Sampling survey N98: (A) Cross-Variogram (omnidirectional and exhaustive) of the Acoustic Estimated Fish Density (LnSa) using Co-Kriging (depth and SST), (B)

The properties of the water masses within the Gulf vary seasonally. The water column is homogenised during winter and stratified between spring and autumn (Tragou et al., 2005). According to Zervakis et al. (2005) the vertical water structure in the Gulf, during September and October, is characterised by a two-layer system, with the less saline water mass occupying the upper layer.

The SST images during the first trip in October (Fig. 1, N96 A) showed two surface regions: a large

Acoustic Estimated Fish Density (LnSa) using Kriging and (C) using Co-Kriging (depth and SST)

area of a relatively warm water (WW) mass (>20.0°) dominating in the Gulf, and some middle temperature water (MW) masses,  $(16.0^{\circ}-20.5^{\circ})$  in the northwestern coast, originating from riverine discharges, flowing southwards (Kontoyiannis et al., 2003). The second trip of October (Fig. 1, N96 B) was undertaken after a rapid weather change in the surveyed area, dominated by a strong northern wind which lowered the SST values over all of the Gulf and especially in its south-eastern part. It is proposed that during northerly

Model		Range (Km)	RMS	ASE	$R^2$
1996a	LnSa	12.5	0.791	0.897	0.378
	LnSa & Depth	8.0	0.699	0.759	0.514
	LnSa & Depth & SST	12.0	0.684	0.696	0.534
1996b	LnSa	16.0	0.265	0.271	0.892
	LnSa & Depth & SST	16.0	0.265	0.260	0.982
1997	LnSa	25.0	0.853	0.918	0.265
	LnSa & SST	6.0	0.834	0.909	0.299
1998	LnSa	5.7	1.077	1.273	0.288
	LnSa & Depth	6.3	1.070	1.363	0.297
	LnSa & Depth & SST	6.8	1.062	1.350	0.307

 
 Table 2 Cross-validation statistics between predicted and observed acoustic fish density (LnSa), applying the leave-oneout cross validation method

First model represents the Kriging results, followed by the Co-Kriging with related covariates

winds a 2-gyre system is established in the area (Poulos et al., 2000). Zervakis et al. (2005) studied in detail the gyre structure of the Gulf in two hydrographic cruises during September and October. During September, a strong cyclonic gyre was presented in the southern part of the Gulf, whilst north of the gyre the circulation was anticyclonic. During October, the Gulf developed a slightly more complicated system; its central part was divided into two-gyre systems: a cyclonic in the west and an anticyclonic in the east.

The surface temperature pattern was different in May 1997 and April 1998. In May 1997, the rivers contributed warm waters forming a strong surface front, which is confirmed by hydrographic surveys carried out during the same period (Kontoyiannis et al., 2003). The MW surface mass  $(16.0^{\circ}-20.0^{\circ})$  dominated most of the Gulf area, whilst along the north-eastern coasts cold waters (CW,  $13.0^{\circ}-16.0^{\circ}$ ) appeared, associated with the upwelling phenomena (Fig. 1, N97). In April 1998, the surface temperature was very low over the entire Gulf and especially in its south-western part, where the riverine outflow remained cooler compared to the rest of the sea waters (Fig. 1, N98).

Due to the riverine outflow and the Black Sea waters, the Thermaikos Gulf is more productive than the oligotrophic Aegean Sea, representing a rich fishing area both for trawlers and purse seiners (Stergiou et al., 1997). Although the species composition inside the Gulf may reveal seasonal variations,

we decided to analyse the pelagic acoustic data as a whole, in order to avoid the introduction of species identification errors, by manually scrutinising the echograms or applying more sophisticated techniques (Haralabous and Georgakarakos, 1996). Since sardine appears to be by far the most abundant species in the area, possible drawbacks from pooling all species together are minimised.

The coastal morphology of the Gulf as well as the NW-SE bottom depth gradient dominated in the multiple regression analysis, especially after removing the time effect (Table 1). Consequently, a Universal Kriging interpolation was used, modelling fish density (LnSa) versus the spatial coordinates. The residuals of this model still included autocorrelation, which was exploited in the spatial multivariate analysis and the Co-Kriging interpolation (Table 2).

In the interpolated October choropleth maps (Figs. 2, 1996a; Fig. 3, 1996b), most of the fish abundance was observed near the shallow northern part of the Gulf, on both coastal sides, occupying warmer (WW) and middle warmer (MW) water temperatures. In contrast, during May 1997 and April 1998, the biomass was found further south in deeper areas where lower temperatures dominated (Figs. 4 and 5).

As mentioned above, the water mass is stratified between spring and autumn and consequentially the SST imagery reflects the upper sea layer condition. However, in most of the cases, the introduction of the SST covariate using Co-Kriging algorithms improved the coefficient of determination ( $R^2$ ) in the crossvalidation procedure (Table 2).

Bottom depth was the most important covariate and explained a portion of the cross-validation variance-additionally to the Kriging interpolationcontributing a minimum of 0.9% (1998) until a maximum of 13.6% (1996A). Bottom depth was also positively correlated with the LnSa-residuals of the time dependent model explaining 21.3% of the variability (Table 1). The encountered positive correlation between area backscattering coefficient Sa and depth can be explained by the fact that the acoustic beam volume increases with depth. However, this correlation strength varies due to the vertical heterogeneity of the pelagic biomass in the water column. Furthermore, bottom depth is partially interrelated with other environmental variables (SST, SSC) and fish density.

Co-Kriging with acoustic and SST data improved the prediction performance by 3.4% (1997), whilst expanding the bottom depth Co-Kriging by adding SST data increased the explained variance by 2.0% (1996A) and 1.0% (1998).

The observed small portions of the covariate variance are in accordance with the encountered spatial low auto- and cross-correlations (Figs. 2-5) and the expected intrinsic stochastic processes (Sharp & McLain, 1993; Webster & Oliver, 2001). Similar studies investigating the relationship between environmental factors and small pelagic fish abundance provide controversial or less evident results (Fréon et al., 2005). Positive responses are published for spawning anchovy in relation to certain environmental parameters (Castillo et al., 1996; Koutsikopoulos & Le Cann, 1996). However, the explained part of the observed sardine variance usually is small (Kerstan, 1993). GAMs applied on 11 years data from the South African sardine fishery using SST as a covariate explained only 0.5%-1.5% of the variance of the catch (Agenbag et al., 2003).

Despite the difficulty of scientifically proving relationships between environmental variables and fish density, satellite SST data are commonly used by pelagic fishing fleets searching for the best fishing areas (Santos, 2000). This is probably evidence of the importance of the spatiotemporal scale used (fishing fleets are able to access high resolution satellite images in short times) and the often greater strength of the phenomena (fronts and fish abundance) in the areas the satellite data is supplied.

The presented results show that despite the smaller spatiotemporal scale, Co-Kriging techniques can provide a useful tool for investigating possible environmental effects in the spatial distribution of small pelagic species. From the practical point of view, the resulted improvement in the accuracy, applying Co-Kriging algorithms, reduces the uncertainty in biomass estimation, which always is an important goal in stock assessment. Both the dynamic parameter (SST) and the static (bottom depth) parameter used in the analysis are the most important covariates for reducing estimation uncertainty. Bottom depth routinely is automatically measured during insonification. Therefore, bottom depth is perhaps the most useful auxiliary variable, which is also considered as a known and time invariant covariate in the surveyed area. Moreover, the SST and SSC covariates are commonly remotely assessed via satellite, requiring off-line processing.

From the aforementioned hydrographic studies, it is obvious that salinity gradient is important for understanding water stratification and potentially existed biomass distribution patterns. Certainly, increasing the number in the auxiliary variables, an improvement of the Co-Kriging efficiency could be expected. However, this paper is restricted to the methodological advantages of the simultaneous application of more than one Co-Kriging variables.

Concerning the spatial analysis presented in this paper, the incorporation simultaneously of more than one spatial covariate in the Co-Kriging technique improved the performance of the models, as it is depicted in Table 2. More advanced techniques have been proposed recently (Holland et al., 2003), modelling non-stationarity and heterogeneous covariance structures. It is suggested that these approaches, including hierarchical Bayesian techniques or Artificial Neural Networks (Georgakarakos et al., 2006), are very promising and require further research.

Acknowledgements In this work, the acoustic data collection and processing were supported by the Commission of the European Union (CLUSTER/FAIR, 1997). We would also like to thank V. Trygonis and D. Markopoulou and N. Fletcher for the initial analysis of the data.

#### References

- Agenbag, J. J., A. J. Richardson, H. Demarcq, P. Fréon, S. Weeks & F. A. Shillington, 2003. Relating local abundance of South African pelagic fish species to environmental variables using generalized additive and linear models. Progress in Oceanography 59: 275–300.
- Agostini, V. N. & A. Bakun, 2002. "Ocean trials" in the Mediterranean Sea: physical mechanisms potentially structuring reproductive habitat suitability (with example application to European anchovy, *Engraulis encrasicolus*). Fisheries Oceanography 11: 129–142.
- Armstrong, M., D. Renard & P. Berthou, 1989. Applying geostatistics to the estimation of a population of bivalves. ICES/CM/1989/K:37.
- Azzali, M., G. Buracchi, S. Conti, S. Gambetti & M. Luna, 1985. Relationship between the forms of pelagic fish distribution and nycthemeral periods. A tentative model of behaviour. Oebalia 11: 471–488.
- Bendat, J. S. & A. G. Piersol, 1971. Random data: analysis and measurement procedures. Wiley-Interscience, New York.
- Bradley, R. & J. Haslett, 1992. High-interaction diagnostics for geostatistical models of spatially referenced data. The Statistician 41: 371–380.

- Castillo, J., M. A. Barbieri & A. Gonzalez, 1996. Relationships between sea surface temperature, salinity, and pelagic fish distribution off northern Chile. ICES Journal of Marine Science 53: 139–146.
- Chen, I. C., P. F. Lee & W. N. Tzeng, 2005. Distribution of albacore (*Thunnus alalunga*) in the Indian Ocean and its relation to environmental factors. Fisheries Oceanography 14: 71–80.
- Cliff, A. D. & J. K. Ord, 1981. Spatial Processes: Models and Applications. Pion, London.
- Cressie, N. A. C., 1993. Statistics for Spatial Data. John Wiley & Sons, New York, New York.
- Deutsch, C. V. & A. G. Journel, 1998. GSLIB: Geostatistical Software Library and User's Guide. Oxford University Press, New York, New York.
- Fiedler, P. C. & H. J. Bernard, 1987. Tuna aggregation and feeding near fronts observed in satellite imagery. Continental Shelf Research 7: 871–881.
- Foote, K. G., 1987. Fish target strengths for use in echo integrator surveys. Journal of the Acoustical Society of America 82: 981–987.
- Fréon, P. & O. A. Misund, 1999. Dynamics of Pelagic Fish Distribution and Behaviour: Effects on Fisheries and Stock Assessment. Fishing News Books, Oxford.
- Fréon, P., P. Cury, L. Shannon & C. Roy, 2005. Sustainable exploitation of small pelagic fish stocks challenged by environmental and ecosystem changes: a review. Bulletin of Marine Science 76: 385–462.
- Georgakarakos, S., D. Koutsoubas & V. Valavanis, 2006. Time series analysis and forecasting techniques applied on loliginid and ommastrephid landings in Greek waters. Fisheries Research 78: 55–71.
- Giannoulaki, M., A. Machias, C. Koutsikopoulos & S. Somarakis, 2006. The effect of coastal topography on the spatial structure of anchovy and sardine. ICES Journal of Marine Science 63: 650–662.
- Giannoulaki, M., A. Machias, S. Somarakis & N. Tsimenides, 2005. The spatial distribution of anchovy and sardine in the northern Aegean Sea in relation to hydrographic regimes. Belgian Journal of Zoology 135: 151–156.
- Goovaerts, P., 1997. Geostatistics for Natural Resources Evaluation. Oxford University Press, New York.
- Haralabous, J. & S. Georgakarakos, 1996. Artificial Neural Networks as a tool for species identification of fish schools. ICES Journal of Marine Science 53: 173–180.
- Hensen, V., 1911. Das Leben im Ozean nach Zahlungen seiner Bewohner. Übersicht und Resultaten der quantitativen Untersuchungen. Ergebn. Plankton Expdn. der Humboldt Stiftung V.
- Holland, D., W. M. Cox, R. Scheffe, A. Cimorelli, D. Nychka & P. Hopke, 2003. Spatial Prediction of Air Quality Data. Environmental Manager: 31–35.
- Horne, J. K., P. E. Smith & D. C. Schneider, 1999. Comparative examination of scale-explicit biological and physical processes: recruitment of Pacific hake. Canadian Journal of Fisheries and Aquatic Sciences 56: 1–10.
- Isaaks, E. H. & R. M. Srivastava, 1989. Applied Geostatistics. Oxford University Press, New York.
- Journel, A. G. & C. J. Huijbregts, 1978. Mining Geostatistics. Academic Press, London.

- Kerstan, S., 1993. Relationships between pilchard distribution and environmental factors. Marine science for a sustainable future. In Proceedings of the 8th South African Marine Science Symposium, Langebaan.
- Kontoyiannis, H., V. H. Kourafalou & V. Papadopoulos, 2003. The seasonal characteristics of the hydrology and circulation in the Northwest Aegean Sea (Eastern Mediterranean): observations and modelling. Journal of Geophysical Research-Oceans 108: 3302.
- Knudsen, H. P., 1990. The Bergen echo integrator: an introduction. Journal du Conseil Internation pour l'Exploration de la Mer 47: 167–174.
- Koutsikopoulos, C. & N. Lacroix, 1992. Distribution, abundance of sole (*Solea solea* L.) eggs, larvae in the Bay of Biscay between 1986 and 1989. Netherlands Journal of Sea Research 29: 81–91.
- Koutsikopoulos, C. & B. Le Cann, 1996. Physical processes and hydrological structures related to the Bay of Biscay anchovy. Scientia Marina 60: 9–19.
- Laevastu, T. & M. L. Hayes, 1981. Fisheries Oceanography and Ecology. Fishing News Books, Oxford.
- Lasker, R., 1978. The relation between oceanographic conditions and larval anchovy food in the California Current: identification of factors contributing to recruitment failure. Rapport Réunion du Conseil International pour l' Exploration de la Mer 173: 212–230.
- Laurs, R. M., P. C. Fiedler & D. R. Montgomery, 1984. Albacore tuna catch distributions relative to environmental features observed from satellites. Deep-Sea Research 31: 1085–1099.
- MacLennan, D. N. & I. G. MacKenzie, 1988. Precision of acoustic fish stock estimates. Canadian Journal of Fisheries and Aquatic Sciences 45: 605–616.
- Maravelias, C. D., 1999. Habitat selection and clustering of a pelagic fish: effects of topography and bathymetry on species dynamics. Canadian Journal of Fisheries and Aquatic Sciences 56: 437–450.
- Maravelias, C. D., D. G. Reid, E. J. Simmonds & J. Haralabous, 1996. Spatial Analysis and Mapping of Acoustic Survey Data in the presence of High Local Variability: Geostatistical Application to North Sea Herring (*Clupea harengus*). Canadian Journal of Fisheries and Aquatic Sciences 53: 1497–1505.
- Matheron, G., 1971. The theory of regionalized variables and its applications. Ecole Nationale Supérieure des Mines de Paris, Fontainebleau.
- McBratney, A. B., I. O. A. Odeh, T. F. A. Bishop, M. S. Dunbar & T. M. Shatar, 2000. An overview of pedometric techniques for use in soil survey. Geoderma 97: 293–327.
- Panatier, Y., 1996. Statistics and Computing. VARIOWIN Software for Spatial Data Analysis in 2D. Springer-Verlag, New York.
- Papoulis, A., 1965. Probability Random Variables and Stochastic Processes. MacGraw Hill, Kogakusha, Tokyo.
- Paramo, J. & R. Roa, 2003. Acoustic-geostatistical assessment and habitat-abundance relations of small pelagic fish from the Colombian Caribbean. Fisheries Research 60: 309–319.
- Petitgas, P., 1993. Geostatistics for fish stock assessments: A review and an acoustic application. ICES Journal of Marine Science 50: 285–298.

- Petitgas, P., D. Reid, P. Carrera, M. Iglesias, S. Georgakarakos, B. Liorzou & J. Masse, 2001. On the relation between schools, clusters of schools, and abundance in pelagic-fish stocks. ICES Journal of Marine Science 58: 1150–1160.
- Poulos, S. E., G. T. Chronis, M. B. Collins & V. Lykousis, 2000. Thermaikos Gulf Coastal System, NW Aegean Sea: an overview of water/sediment fluxes in relation to airland-ocean interactions and human activities. Journal of Marine Systems 25: 47–76.
- Rossi, R. E., D. J. Mula, A. G. Journel & E. H. Franz, 1992. Geostatistical tools for modeling and interpreting ecological spatial dependence. Ecological Monographs 2: 277–314.
- Royle, J. A. & L. M. Berliner, 1999. A Hierarchical Approach to Multivariate Spatial Modeling and Prediction. Journal of Agricultural, Biological and Environmental Statistics 4: 29–56.
- Santos, A. M. P., 2000. Fisheries oceanography using satellite and airborne remote sensing methods: a review. Fisheries Research 49: 1–20.
- Sharp, G. D. & D. R. McLain, 1993. Fisheries, El Ninosouthern oscillation and upper-ocean temperature records: an Eastern Pacific example. Oceanography 6: 13–22.
- Simard, Y., D. Lavoie & F. J. Saucier, 2002. Channel head dynamics: Capelin (*Mallotus villosus*) aggregation in the tidally-driven upwelling system of the Saguenay-St. Lawrence Marine Park's whale feeding ground. Canadian Journal of Fisheries and Aquatic Sciences 59: 197–210.
- Simard, Y., P. Legendre, G. Lavoie & D. Marcotte, 1992. Mapping, estimating biomass, and optimizing sampling programs for spatially autocorrelated data: case study of the northern shrimp (*Pandalus borealis*). Canadian Journal of Fisheries and Aquatic Sciences 49: 32–45.
- Stefánsson, G., 1996. Analysis of ground fish survey abundance data: combining the GLM and delta approaches. ICES Journal of Marine Science 53: 577–826.
- Stergiou, K. I., E. D. Christou, D. Georgopoulos, A. Zenetos & E. Souvermezoglou, 1997. The Hellenic Seas: physics,

chemistry, biology and fisheries. Oceanology and Marine Biology: An Annual Review 35: 415–538.

- Sullivan, P. J., 1991. Stock abundance estimation using depthdependent trends and spatially correlated variation. Canadian Journal of Fisheries and Aquatic Sciences 48: 1691–1703.
- Swartzman, G. L., W. Stuetzle, K. Kulman & M. Powojowski, 1994. Relating the distribution of pollock schools in the Bering Sea to environmental factors. ICES Journal of Marine Science 51: 481–492.
- Tragou, E., V. Zervakis, E. Papageorgiou, S. Stavrakakis & V. Lykousis, 2005. Monitoring the physical forcing of resuspension events in the Thermaikos Gulf - NW Aegean during 2001–2003. Continental Shelf Research 25: 2315–2331.
- Tsimenides, N., G. Bazigos, S. Georgakarakos, A. Kapantagakis, 1992. Distribution of acoustic pelagic fish populations in the northern Aegean Sea. In Proceedings of the 1st World Fisheries Congress, Athens, 5: 33–42.
- Valavanis, V. D., S. Georgakarakos, A. Kapantagakis, A. Palialexis & I. Katara, 2004. A GIS environmental modelling approach to essential fish habitat designation. Ecological Modelling 178: 417–427.
- Wackernagel, H., 1995. Multivariate Geostatistics. Springer-Verlag, Berlin, Germany.
- Ware, D. M. & R. E. Thomson, 2005. Bottom-Up Ecosystem Trophic Dynamics Determine Fish Production in the Northeast Pacific. Science 308: 1280–1285.
- Webster, R. & M. A. Oliver, 2001. Geostatistics for Environmental Scientists. Wiley, Chichester.
- Zar, J. H., 1974. Biostatistical Analysis. Prentice-Hall International, London.
- Zervakis, V., A. P. Karageorgis, H. Kontoyiannis, V. Papadopoulos & V. Lykousis, 2005. Hydrology, circulation and distribution of particulate matter in Thermaikos Gulf (NW Aegean Sea), during September 2001-October 2001 and February 2002. Continental Shelf Research 25: 2332– 2349.

# FISH HABITAT MAPPING

# Identifying essential fish habitat for small pelagic species in Spanish Mediterranean waters

Jose M. Bellido · Alex M. Brown · Vasilis D. Valavanis · Ana Giráldez · Graham J. Pierce · Magdalena Iglesias · Andreas Palialexis

© Springer Science+Business Media B.V. 2008

**Abstract** Populations of small pelagic fish support important fisheries in Spanish Mediterranean waters, particularly sardine (*Sardina pilchardus*) and anchovy (*Engraulis encrasicolus*), and are distributed along the

Guest editor: V. D. Valavanis Essential Fish Habitat Mapping in the Mediterranean

J. M. Bellido (⊠) Centro Oceanográfico de Murcia, Instituto Español de Oceanografía, C/Varadero 1, Apdo 22, San Pedro del Pinatar, 30740 Murcia, Spain e-mail: josem.bellido@mu.ieo.es

A. M. Brown · G. J. Pierce School of Biological Sciences (Zoology), University of Aberdeen, Tillydrone Avenue, Aberdeen AB24 2TX, UK

V. D. Valavanis · A. Palialexis Marine GIS Laboratory, Institute of Marine Biological Resources, Hellenic Centre for Marine Research, Thalassocosmos, 71003 Heraklion, Crete, Greece

#### A. Giráldez

Centro Oceanográfico de Málaga, Instituto Español de Oceanografía, Puerto Pesquero, Apdo. 29640, Fuengirola, Malaga, Spain

#### G. J. Pierce

Centro Oceanográfico de Vigo, Instituto Español de Oceanografía, P.O. Box 1552, 36200 Vigo, Spain

#### M. Iglesias

Centro Oceanográfico de Baleares, Instituto Español de Oceanografía, Muelle de Poniente, Apdo. 291, 07015 Palma de Mallorca, Spain entire length of the Spanish continental shelf. Using annual acoustic survey data for the years 2003–2005, a GIS-based environmental modelling approach was used to investigate the distribution and abundance of small pelagic fish in relation to environmental variables. Multivariate analysis was applied to provide a preliminary picture of relationships between fish and environmental conditions, followed by application of Generalised Additive Models (GAMs). GAMs showed the presence/absence of fish to be related to bathymetry, sea surface chlorophyll-a concentration and sea surface temperature (SST). The strength and significance of these relationships varied spatially and temporally. High resolution Essential Fish Habitat (EFH) maps were generated for sardine and anchovy, based on the predicted probability of presence of each species. Substantial inter-annual variability in the distribution and quality of EFH was observed, particularly for anchovy. Identification of EFH is of great importance to assess and manage sardine and anchovy resources as it provides a natural link between population dynamics features and geographical scenarios.

# Introduction

Small pelagic fish are predominantly confined to coastal regions, with the largest populations occurring

in regions of upwelling. The spatial heterogeneity of the physical characteristics of the coastal pelagic environment, and the high mobility of small pelagic fish, generally leads to their distribution being concentrated within areas which they find most favourable (Massé et al., 1996; Fréon et al., 2005). To a certain extent, fish show the ability to alter their behaviour in response to environmental variation (Agenbag et al., 2003). However, all populations and species have an affinity for environmental conditions most favourable to their survival, growth and reproduction (review in Blaxter & Hunter, 1982).

Environmental variability can result in shifts in fish distributions over relatively short time-scales, with considerable fishery implications (Fréon et al., 2005). Rapid horizontal and vertical migrations can be induced, altering the distribution of fish and therefore their availability to fishing. While such shifts in distribution are often relatively local and temporary, they have been observed to persist for several months and over large areas, greatly influencing the exploitation of populations (Schwartzlose et al., 1999; Binet et al., 2001; Boyer et al., 2001; Bertrand et al., 2004).

An association between greater presence and/or abundance of fish, more mixed waters and thermal fronts has been observed for a number of species, including herring (Clupea harengus) in the northern North Sea (Maravelias & Reid, 1995); anchovy (Engraulis ringens) and sardine (Sardinops sagax) off the coast of Chile (Castillo et al., 1996); and sardine (Sardina pilchardus) and anchovy (Engraulis encrasicolus) in the northern Aegean Sea (Giannoulaki et al., 2005). However, such associations are commonly weak, and more direct relationships may be found between plankton abundance and fish distribution. Associations between high concentrations of plankton and fish have been observed for C. harengus in the northern North Sea (Maravelias, 1999) and anchovy (Engraulis mordax) in the eastern Pacific (Robinson, 2004).

The identification of Essential Fish Habitat (EFH) may be regarded as an application of studying fish– environment relationships. The term EFH has been defined by the EU Scientific, Technical and Economic Committee for Fisheries (STECF) in the Mediterranean as "a habitat identified as essential to the ecological and biological requirements for critical life history stages of exploited fish species, and which may require special protection to improve stock status and long term sustainability" (STECF, 2006).

A wide range of techniques is now available to model habitat requirements and these have been extensively reviewed (e.g. Guisan & Zimmermann, 2000; see also Redfern et al., 2006 for a particular review on marine species). Studies of habitat requirements of exploited marine fish have been driven both by the need to support management actions (e.g. to identify candidate Marine Protected Areas) and the increasing availability and accessibility of suitable tools. These include readily available remotely sensed data on a variety of surface oceanographic parameters, Geographic Information Systems (GIS) and powerful statistical modelling tools such as generalised additive models (GAM), which allow modelling of non-linear relationships, and generalised additive mixed models (GAMM), the latter allowing explicit consideration of spatial autocorrelation, particularly through the development of the "R" programming language (see Pierce et al., 2001, 2002; Valavanis et al., 2008, 2004; Zuur et al., 2007).

Valavanis et al. (2004) adopted a GIS-environmental modelling approach to identify EFH for short-finned squid (*Illex coindetti*) in the eastern Mediterranean Sea. Koubbi et al. (2006) reported an application on habitat modelling for flatfish larvae in the eastern English Channel. Both approaches aimed to model and predict fish distribution by using environmental relationships. An alternative approach was taken by Friedlander et al. (2007) and Le Pape et al. (2007), who examined the community assemblage and interactions between species and substrate in order to identify EFH.

Identifying EFH for highly mobile adult small pelagic fish presents different challenges to those associated with modelling habitat requirements of less mobile demersal species, which may for example be associated with particular seabed substrates. The environmental conditions which have been shown to influence the distribution of pelagic species are intrinsically spatially and temporally variable, therefore the corresponding EFH will show similar variability in predicted distribution.

This study aims to use a GIS and statistical modelling-based approach to investigate relationships between small pelagic fish and environmental conditions in Spanish Mediterranean waters. Small pelagic fish, in common with other short-lived species such as squid, are liable to show high variability in abundance year to year. This year to year fluctuation reflects variable recruitment strength and is thought to be strongly related to oceanographic conditions (temperature, salinity), e.g. due to their effect on juvenile growth and survival, as well as static ecogeographic variables such as bathymetry. Generalised Additive Models were applied to test the hypotheses suggested by initial data exploration using multivariate methods and GIS.

A further aim is to extend this approach to identify EFH and its temporal variability in sardine and anchovy. GAM predictions were used to reveal areas of high probability of presence and thus to identify EFH for both species.

#### Materials and methods

# Species and study area

A variety of species of small pelagic fish are present in Spanish Mediterranean waters. Sardine (*Sardina pilchardus*), anchovy (*Engraulis encrasicolus*), Mediterranean horse mackerel (*Trachurus mediterraneus*), Atlantic horse mackerel (*Trachurus trachurus*), round sardinella (*Sardinella aurita*), bogue (*Boops boops*), chub mackerel (*Scomber japonicus*) and Atlantic mackerel (*Scomber scombrus*) are all encountered on the continental shelf (Giráldez & Abad, 2000). Although all of these species are caught by commercial fisheries, sardine and anchovy have traditionally been the most economically important (Pertierra & Lleonart, 1996), and have therefore been the main focus of scientific studies.

The study area comprises the entire Mediterranean coast of Spain (Fig. 1). A boundary is defined to encompass the continental shelf environment (from coastline to 200 m isobath) and a small area immediately offshore of this. The study area was considered both as a whole and as the following 3 separate zones:

#### Zone 1: Southern Gulf of Lyon and Catalan coast

The Gulf of Lyon is a well documented region of high productivity, characterised by a combination of a fairly wide continental shelf, considerable river run-off from the Rhône and a high degree of windinduced mixing and upwelling from strong, predominantly north-westerly winds (Estrada, 1996; Salat, 1996; Agostini & Bakun, 2002). This is an important spawning area for anchovy and sardine (García & Palomera, 1996; Olivar et al., 2001). The Catalan

**Fig. 1** Area of study, including the acoustic transects locations for zone 1 (north), zone 2 (center) and zone 3 (south). Black line is 200 m isobath



coast is characterised by a relatively narrow shelf and deep slope canyons. Catalan coastal waters are influenced by the transport of nutrients from the north, with additional fertilization caused by local vertical mixing and intrusions of slope waters onto the shelf through submarine canyons (Salat et al., 2002).

# Zone 2: Gulfs of Valencia and Alicante

In the Gulf of Valencia, the coastal waters over the wide Iberian shelf are influenced by local meteorological events and freshwater input from the River Ebro (Salat, 1996). Meteorological events include strong north-westerly winds, causing intense water mixing around the Ebro delta (Estrada, 1996; Salat, 1996). The Iberian shelf provides important spawning grounds for anchovy and sardine (García & Palomer-a, 1996; Olivar et al., 2001).

# Zone 3: Gulf of Vera and northern Alboran Sea

The input of Atlantic surface water through the Strait of Gibraltar dominates the hydrographic characteristics of the northern Alboran Sea. A 'jet' of Atlantic water causes turbulent mixing in the Strait, and creates two anticyclonic gyres with associated upwelling along the Spanish coast of the Alboran Sea (Tintorè et al., 1991; Vargas-Yañez et al., 2002). This area has been described as favourable for reproduction and growth of coastal pelagic fishes (Bakun, 1998).

# GIS development

Fish data were obtained from the annual acoustic survey ECOMED, carried out by the Instituto Español de Oceanografía (IEO) during November–December. This coincides with the recruitment of anchovy to the fishery, and the earliest signs of spawning activity in sardine (Palomera, 1992; Pertierra & Lleonart, 1996; Olivar et al., 2001). A systematic design covering 128 transects perpendicular to the coastline provides 1290, 1292 and 1268 records for 2003, 2004 and 2005 respectively, with almost exact spatial overlap between years. Transects cover the continental shelf approximately between the 30 m and 200 m isobaths. Local fish abundance is quantified at each sampling point using the Nautical

Area Scattering Coefficient (NASC, m<sup>2</sup> of cumulative backscattering cross-section per nmi<sup>2</sup>). Routine experimental fishing determined the species composition of the NASC.

Monthly average environmental data were collated from internet-based sources and then processed into files suitable for use in a GIS (Table 1). GIS point layers of fish survey records were combined with environmental grids of 1 square nautical mile (nm<sup>2</sup>) to extract the environmental values associated with each location of the fish survey record. Care was taken to ensure that the temporal resolution of the environmental grid matched with that of the survey sampling time. Maps were produced to visualise the distribution of fish and, after fitting of models, the probabilistic predictions of EFH for sardine and anchovy throughout the study area.

# Multivariate analysis and GAM modelling for EFH identification

Multivariate analysis was applied in order to reveal plausible relationships between species and environmental variables. Correlation analysis and Redundancy Analysis (RDA) were applied to fishery and environmental data. RDA is a constrained ordination method which represents the relationships between two matrices: one dependent matrix of response variables (i.e. the species variables) and the other independent matrix of explanatory variables (i.e. the environmental variables). The ordination seeks the combination of explanatory variables that best explain the variation of the response variables and, using Monte Carlo permutation tests, determines the statistical significance of the effects of each of the suite of explanatory variables.

RDA graphic results are presented in the form of a correlation biplot, showing the response and explanatory variables on the same diagram. The length and angles in the RDA correlation biplot reflect correlations between response and environmental variables, and between response or environmental variables themselves. Since a limitation of this technique is that effects are assumed to be linear, most of the explanatory variables were log-transformed. The multivariate analysis results were also utilised as an exploratory analysis prior to GAM modelling. A high degree of co-linearity existed between several of the variables.

Table 1 Sources and descriptions c	of environ	mental data used in the GIS		
Variable	Units	Source	Sensor/Model	URL
Photosynthetically active radiation (PAR)	(E/m <sup>2</sup> / d)	Oceancolor WEB, GSFC/ NASA, USA	SeaWiFS	http://oceancolor.gsfc.nasa.gov
Sea level anomaly (ALT)	сш	Live Access Server	Merged (TOPEX/Poseidon, Jason-1, ERS-1/2, Envisat)	http://www.aviso.oceanobs.com/
Sea surface temperature (SST)	°C	DLR EOWEB, Germany	AVHRR SST	http://eoweb.dlr.de:8080/
Sea surface chlorophyll-a concentration (Chl-a)	(mg/ m <sup>3</sup> )	Oceancolor WEB, GSFC/ NASA, USA	SeaWiFS	http://oceancolor.gsfc.nasa.gov
Sea surface salinity (SSS)	nsd	IRI/LDEO, USA	CARTON-GIESE SODA and CMA BCC GODAS	http://ingrid.ldeo.columbia.edu/
Wind speed (WS)	(m/sec)	RS Systems, USA	QuikSCAT	http://www.ssmi.com/
Wind direction (WD)	(° from N)	RS Systems, USA	QuikSCAT	http://www.ssmi.com/
Bathymetry (depth)	н	NGDC, NOAA, USA	Geostat ERS-1 satellite & ship depth echosoundings	http://www.ngdc.noaa.gov/mgg/image/2minrelief.html

Finally SST, Chlorophyll-a concentration (Chl-a) and depth were selected for GAM models as they showed considerable variability throughout the study area and were believed to be easier to interpret biologically than some other variables available. The use of GAM allows for non-linear relationships between response and explanatory variables.

Binomial GAMs were developed for sardine and anchovy. Local occurrence (presence = 1and absence = 0) was modelled against environmental variables for all zones and all years combined. GAMs were also developed for individual zones. Step-wise selection and cross-validation were applied to select the best models (based on the lowest AIC). The constructed models, from all years and all zones combined, were then used to predict the probability of sardine and anchovy presence in each year at the resolution of the environmental grids, i.e. 1 nm<sup>2</sup>. The mean probability for each grid square over the period 2003-2005 was calculated and mapped to represent the average EFH distribution over the study period. The differences between this average EFH and probabilities for individual years were also calculated and mapped to show inter-annual variations in the distribution and quality of EFH, for instance  $\text{Dev}_{2003} = \text{EFH}-\text{Prob}_{2003}$ .

# Results

General patterns in the distribution of small pelagic fish

High concentrations of anchovy were found in zone 1, near the Spanish–French border in the southern Gulf of Lyon (Fig. 2). This pattern was consistent throughout the 3 years analysed. In 2003 anchovy was almost absent from the northern Catalan coast to Barcelona whilst it was present at a low level during 2004 and 2005. The most consistent high concentrations of fish were located in zone 2, particularly around the mouth of the river Ebro. These were also areas of high Chl-a (Fig. 2). Anchovy showed reduced abundance and occurrence further south as far as the Gulf of Alicante. In zone 3, anchovy was concentrated around Málaga during 2003 to 2005, being totally absent in the Gulf of Vera. The Málaga area was also characterised by high concentrations of Chl-a.

The patterns of distribution and abundance of sardine (Fig. 3) were rather similar to those of



Fig. 2 Chlorophyll-a distribution and anchovy abundance for 2003, 2004 and 2005 throughout the study area

anchovy, although sardine appeared to be more widespread and abundant. The pattern was quite consistent for all years, the River Ebro delta being the area with highest sardine concentration. Abundance and occurrence both declined towards the Gulf of Vera, where sardine was practically absent. The northern Alboran Sea showed intermediate levels of sardine abundance, although an important increase is apparent in 2005.

# Multivariate analysis

*P*-values from Monte Carlo tests show the significance of the RDA ordination method both for the first canonical axis and all canonical axes (Table 2). The first axis comprised up to 97.3% of the cumulative variance of species–environment relationships, reaching up the 100% in the third axis. The first axis accounted for a species–environment correlation of 0.275, whilst the second and third axes accounted for 0.174 and 0.157 respectively (Table 2).

Chl-a, longitude, latitude, depth, SSS and SST appeared to be the most important variables (Fig. 4). Chl-a showed a positive effect on anchovy and sardine occurrence. Depth and SST had an important negative effect on all species variables. Additionally SSS seems to have a notable negative effect. SSS may become more important in estuarine areas and river plumes, such as the River Ebro outflow. Latitude and longitude are considered secondary variables, as their effect can be hidden in other environmental variables. Other environmental variables such as altimetry, wind speed and wind direction seemed to be less important or at least not to have an apparent effect on the species variables.

# Generalised additive models

The model for presence/absence of anchovy, for all years and all zones combined, explained 27.3% of the deviance (Table 3). Separate models for each zone explained 26.5, 37.2 and 33.6% of the deviance for zones 1, 2 and 3, respectively. For sardine, the presence–absence model explained 30.7% of the deviance for all years and all zones combined. For separate-zone models the deviance explained was 23.9, 36.3 and 40.3% for zones 1, 2 and 3, respectively (Table 3). All models included effects of depth, SST and chlorophyll, except the model for anchovy in zone 3, which did not include SST. Some common trends in these results were apparent. With the exception of zone 1, models for individual zones

Fig. 3 Chlorophyll-a distribution and sardine abundance for 2003, 2004 and 2005 throughout the study area



Table 2 Species-environment RDA correlations and Monte Carlo tests of significance of canonical axes

	1st Axis	2nd Axis	3rd Axis
Eigenvalues	0.070	0.001	0.001
Species-environment correlations	0.275	0.174	0.157
Cumulative percentage variance of species data	7.0	7.2	7.2
Cumulative percentage variance of species-environment relation	97.3	99.2	100.0
	Sum of all Eigenvalues	1.000	
	Sum of all canonical Eig	genvalues 0.072	
Monte Carlo test of significance (999 permutations)		F-ratio	P-value
First canonical axis	Eigenvalue = 0.070	290.014	0.0010
All canonical axes	Trace = 0.072	29.871	0.0010

explained a greater proportion of the deviance than models for all zones combined.

Relationships between fish presence/absence and environmental variables were quite similar for both species (see Fig. 5 for anchovy and Fig. 6 for sardine). In all models, depth was highly significant and the most important variable. The relationship between fish presence/absence and depth was generally negative, with a strong negative effect at depths in excess of approximately 100 m (4.6 on natural log scale, Figs. 5a and 6a). Chl-a was generally the second most important explanatory variable and its effect was significant for all models. The relationship between fish presence/absence and Chl-a was generally weakly positive, with wide confidence limits at very high Chl-a due to limited data (Figs. 5b and 6b). SST was generally the least important explanatory variable. A slight peak of positive influence on anchovy presence was apparent between approximately 15.5 and 17.5°C (2.74 and 2.86 on natural log scale, see Fig. 5c). However it seems that SST has little effect on sardine presence (Fig. 6c).

#### Essential fish habitat mapping

The areas of higher probabilities for EFH of anchovy were located in the vicinity of the River Ebro Delta and the southern Gulf of Lyon (Fig. 7). Other coastal



Fig. 4 RDA correlation biplot. Species variables are PELAG: Small pelagics acoustic abundance; ANCH: Anchovy acoustic abundance; SARD: Sardine acoustic abundance. PA\_ANCH: Presence/Absence of Anchovy; PA\_SARD: Presence/Absence of Sardine; Environmental variables are LAT: Latitude; LON: Longitude; PAR: Photosynthetically Active Radiation (Natural Log); ALT: Altimetry (or Sea Level Anomaly); SST: Sea Surface Temperature (Natural Log); CHL: Sea surface Chlorophyll-a concentration (Natural Log); SSS: Sea Surface Salinity (Natural Log); WD: Wind Direction; WS: Wind Speed; DEP: Depth (or Bathymetry) (Natural Log); See Table 1 for Units

areas of high EFH were north of Valencia and some local areas of the northern Alboran Sea. Unsurprisingly, the areas of highest predictions were very similar to the areas of higher anchovy abundance identified in Fig. 2.

Year deviation is a measure of how far the average anchovy EFH deviates from the EFH of a particular year at every predicted point. The years with higher deviations were 2003 and 2004. Along the Catalan Coast and Ebro Delta, average EFH showed a positive deviation with respect to 2003 whilst EFH-2004 showed a negative trend, i.e. 2003 was a worse year than average EFH and 2004 was a better year than average EFH. Further south along the Gulf of Vera, EFH-2003 showed a negative trend and EFH-2004 showed slight positive deviations. It is important to note that for both the years the higher deviations were located around the middle shelf and generally around the areas of higher EFH probabilities, for example the northern Catalan coast and the River Ebro Delta. In contrast to 2003 and 2004, 2005 did not exhibit high deviations from the average anchovy EFH.

For sardine, high probabilities of presence are more extensive and of a greater magnitude than those of anchovy. The coastal area from Valencia to the northern Catalan coast showed an almost continuous high probability of sardine presence (Fig. 8). This was particularly true for the River Ebro Delta, Valencia and Barcelona area, and the southern Gulf of Lyon (Cape of Creus). Moving south from Valencia towards the Strait of Gibraltar there was an intermediate level of EFH, exhibiting a patchy distribution of some local areas with higher probability of presence.

For sardine, inter-annual deviation in EFH was quite similar to that of anchovy (see Figs. 8 vs. 7). The area of highest deviations was located in the northern Catalan coast; they are also located in the middle shelf, which is the area with more variability. Years 2003 and 2004 were the most different to the general EFH sardine pattern, following the same

Species	Zone	n	Variables (P-value)	Deviance explained (%)
Anchovy	All	3849	Depth (<0.01), Chl-a (<0.01), SST (<0.01)	27.3
	1	893	Depth (<0.01), SST (<0.01), Chl-a (<0.01)	26.5
	2	1973	Depth (<0.01), Chl-a (<0.01), SST (<0.01)	37.2
	3	983	Depth (<0.01), Chl-a (<0.01)	33.6
Sardine	All	3849	Depth (<0.01), Chl-a (<0.01), SST (<0.01)	30.7
	1	893	Depth (<0.01), SST (<0.01), Chl-a (<0.01)	23.9
	2	1973	Depth (<0.01), Chl-a (<0.01), SST (<0.01)	36.3
	3	83	Depth (<0.01), Chl-a (<0.01), SST (<0.01)	40.3

Table 3 Sardine and anchovy presence/absence GAM results, showing the best model for each zone using data from all years combined

Variables are ordered according to their importance in the model, based on results from classification trees. The order runs from left (most important) to right (least important)



Fig. 5 GAM plots for anchovy presence/absence (all years all zones combined) showing the effect of every environmental variable on fish presence. (a) (left): depth (natural log). (b) (centre): chl-a (natural log). (c) (right): SST (natural log)



Fig. 6 GAM plots for sardine presence/absence (all years all zones combined) showing the effect of every environmental variable on fish presence. (a) (left): depth (natural log). (b) (centre): chl-a (natural log). (c) (right): SST (natural log)

pattern as anchovy, i.e. a positive trend was apparent in EFH-2003 and a negative trend was apparent in EFH-2004. In contrast, 2005 seemed to be a year rather similar to the general EFH sardine pattern.

#### Discussion

Environmental influences on the distribution of small pelagic fish

While the studied fish were distributed throughout Spanish Mediterranean waters, several areas were identified where fish could be found in high concentrations. The southern Gulf of Lyon, the Catalan coast around Barcelona, the vicinity of the Ebro delta and some local areas of the western Alboran coast all showed high concentrations of fish. Previous studies have documented the productivity of these areas, where oceanographic processes such as mixing by river flow and upwelling cause the nutrient enrichment of surface waters (Estrada, 1996; Salat, 1996; Agostini & Bakun, 2002). Nutrient enrichment results in phytoplankton, and then zooplankton growth providing feeding grounds for fish.

The strong relationship between presence/absence of anchovy and sardine and depth showed a preference for depths shallower than 100 m. This is consistent with previous studies which have investigated the distribution of small pelagic fish in relation to depth (e.g. Giannoulaki et al., 2005). The distribution of Chl-a suggested higher levels of nutrient enrichment in shallower waters and close to the coastline. It is likely that fishes select these areas due to the higher concentrations of food associated with these productive waters. **Fig. 7** EFH maps showing the predicted probability of presence of anchovy and inter-annual deviation from the general EFH model





The results indicate that two main areas of fish distribution can be described, following a north– south axis. The first area extends from the Gulf of Lyon to the Cape of Palos, in the vicinity of Cartagena. This was an area of widespread occurrence and high abundance for the two studied species. Most of this area is characterized by a wide

continental shelf, with important inputs from fluvial currents, particularly from the river Rhône and the Ebro. This area is considered a separate Management Unit by the General Fisheries Commission for the Mediterranean (GFCM) and it is named as Geographical Sub-Area 06—Northern Spain (GSA-06). Then a transition zone is apparent after Cape of Palos,

Fig. 8 EFH maps showing the predicted probability of presence of sardine and inter-annual deviation from the general EFH model occupying the Gulf of Vera. This is a hydrodynamic border, usually named the Almeria-Oran front, where the Atlantic Jet bifurcates into two currents, the Algerian current to the east and the Septentrional current to the northeast. This Septentrional current completes a cyclonic gyre through the Ligurian Sea, Gulf of Lyon and Catalan Sea (Millot, 1999; Pinot et al., 2002).

West of the Gulf of Vera, the Northern Alboran Sea is characterised by a very narrow shelf, where submarine canyons create a dynamic topography which direct many fish assemblages and delineate fish habitats, particularly important at a local scale. This area is also considered a separate Management Unit by the GFCM, named as Geographical Sub-Area 01— Northern Alboran Sea (GSA-01). GSA-01 extends from the Strait of Gibraltar to the Cape of Palos.

Both multivariate analysis and GAMs show a significant positive relationship between the distribution and abundance of fish and Chl-a. Although significant, these relationships are relatively weak. This suggests that Chl-a and fish are not directly related, but that higher Chl-a is an indicator of conditions favouring fish. Chl-a is a measure of the standing stock of phytoplankton in surface waters, therefore higher concentrations are likely to be associated with productive feeding grounds for planktivorous fish such as small pelagics.

Relationships between fish and SST were typically weaker and less significant than those with Chl-a. SST is likely to be less direct in its relationship with fish than Chl-a. Cooler SST can be indicative of nutrient enrichment processes such as wind mixing, upwelling and river-run off, which are associated with favourable conditions for fish.

Using Chl-a and SST with a time lag of several weeks may produce stronger relationships with fish distribution and abundance. Thus enrichment events indicated by high Chl-a and low SST may be more associated with fish after sufficient time has passed for both zooplankton abundance to rise, and fish to locate the area.

#### Essential fish habitat mapping

EFH maps showed the predicted probability of anchovy and sardine presence. Predictions were made according to the environmental conditions at a specific time, based on modelled relationships between environmental conditions and fish presence over 3 years of survey data. In this study, EFH was not defined as habitat with a predicted probability of presence above a specific threshold value. Instead, all areas within the study area were treated as EFH, with comparisons based on the pattern of predictions. The pattern of predictions can be considered a measure of the quality of EFH. Higher predicted probability of occurrence clearly indicate better quality habitat, in terms of the environmental variables considered in the model on which the predictions are based. The EFH maps act as a tool for identifying areas where environmental conditions are favourable or less favourable for fish to occur.

Results showed the EFH of anchovy to be concentrated in specific areas of more favourable conditions, such as the Ebro Delta and southern Gulf of Lyon. However, EFH of sardine showed a more widespread distribution, occupying most of the Cataluña and Valencia coasts as well as some local areas of the northern Alboran Sea.

Quality of EFH showed large inter-annual variation, particularly in the southern Gulf of Lyon and the Catalan coast. The most notable difference was a sharp decline of predicted presence for sardine in the southern Gulf of Lyon in 2003. A similar, but less extreme, trend was observed for anchovy. The same area in 2004 showed high predicted presence for both species. Chl-a was very similar in both 2004 and 2005, but SST was much cooler in 2004 (by around 2°C). This suggests that cooler SSTs in the southern Gulf of Lyon present more favourable conditions for sardine and anchovy.

Large inter-annual variations in the characteristics of predictions reflect substantial temporal variation in the distribution of areas which can be considered EFH. This could have considerable implications for both the ecology and management of the populations.

A management implication of substantial interannual variations in EFH could be the influence of these variations on the catchability of fish. Changes in catchability (the ease with which fish can be caught) are likely to arise when environmental conditions cause an expansion, contraction or shift in distribution of fish (Fréon et al., 2005). EFH maps reflect such changes in fish distribution (albeit with some degree of uncertainty). For example, a reduction in the distribution and quality of EFH, such as was seen in 2003, may cause fish to concentrate in remaining areas of favourable habitat. This should increase the efficiency of fishing activities due to less time spent searching for fish. Alternatively, an increase in the distribution and quality of EFH, such as was seen in 2004, may cause fish to disperse over a larger area. This should reduce the efficiency of fishing activities due to greater time spent searching for fish. Large-scale shifts in the distribution of EFH might bring fish within range of different fishing fleets, with different exploitation capacities.

Monitoring the catchability of fish is particularly important in the Mediterranean Sea as the fishing industry is regulated by effort and gear restrictions, not quotas. Fishing is not required to cease once a certain weight of fish are landed. Therefore, an increase in the catchability of a stock will cause a persistent rise in fishing mortality. If patterns in catchability are not taken into consideration, increasing commercial landings may give the false impression that fish are becoming more abundant, when they are only becoming more available to fishing.

# Future work

Predictions for EFH mapping are only as accurate as the models they are based on. The use of different environmental variables at different temporal resolutions should be investigated, with a view to explaining a greater proportion of the deviance in fish distribution and abundance. Another logical step forward is to produce predictions of abundance in addition to presence. However, this task is reliant upon finding sufficiently strong relationships between environmental conditions and fish abundance.

Survey data of the quality used in this study are not readily available for many areas which support similar assemblages of fish. The spatial transferability of models developed in this study should be tested to see if models based on fish in Spanish Mediterranean waters can predict the distribution of fish in other areas. Temporal transferability can also be tested by using models based on data from 2003 to 2005 to predict fish distribution in other years.

#### Conclusions

Anchovy and sardine in Spanish Mediterranean waters are predominantly distributed in coastal areas,

with a strong preference for waters shallower than 100 m; the most persistent areas of occurrence and higher abundance are located along the northern Catalan Coast and around the Delta of the River Ebro.

Environment and topography plays an important role in directing local distribution and variability of these EFH. However, the underlying relationships between oceanographic conditions and fish require further investigation. Spatial transferability of this modelling should be tested to see if models based on fish in Spanish Mediterranean waters can predict EFH of anchovy and sardine in other areas.

Size and shape of EFH can also have important effects on the fishing pattern as catchability of fish could be affected by schools gathering or fish dispersion. This is particularly important in the Mediterranean Sea as its fishery management system is based on effort and gear restrictions, not quotas. It is highly recommended to monitor these plausible interactions between environment and fishery, particularly in relation to the recently worldwide agreed framework of an ecosystem-based approach for the management of fisheries.

Acknowledgements The authors are obliged to the ECOMED scientific and technical crew of the R/V Cornide de Saavedra. Thanks are also due to Colin MacLeod and Manuel Vargas for technical contributions and comments. Alex Brown was funded by a studentship from the UK Natural Environment Research Council (NERC). Andreas Palialexis was funded by the FP6 EnviEFH Project (No 022466). GJP would also like to acknowledge support from the ANIMATE project (MEXC-CT-2006-042337).

#### References

- Agenbag, J. J., A. J. Richardson, H. Demarcq, P. Fréon, S. Weeks & F. A. Shillington, 2003. Estimating environmental preferences of South African pelagic fish species using catch size and remote sensing data. Progress in Oceanography 59: 275–300.
- Agostini, V. N. & A. Bakun, 2002. 'Ocean triads' in the Mediterranean Sea: physical mechanisms potentially structuring reproductive habitat suitability (with example application to European anchovy, *Engraulis encrasicolus*). Fisheries Oceanography 11: 129–142.
- Bakun, A., 1998. Ocean triads and radical interdecadal stock variability: bane and boom for fishery management science. In Pitcher, T. J., P. J. B. Hart & D. Pauly (eds), Reinventing Fisheries Management. Chapman and Hall, London: 331–358.
- Bertrand, A., M. Segura, M. Gutiérrez & L. Vásquez, 2004. From small-scale habitat loopholes to decadal cycles: a

habitat-based hypothesis explaining fluctuation in pelagic fish populations off Peru. Fish and Fisheries 5: 296–316.

- Binet, D., B. Gobert & L. Maloueki, 2001. El Niño-like warm events in the Eastern Atlantic (6°N, 20°S) and fish availability from Congo to Angola (1964–1999). Aquatic Living Resources 14: 99–113.
- Blaxter, J. H. S. & J. R. Hunter, 1982. The biology of the Clupeoid fishes. Advances in Marine Biology 20: 1–223.
- Boyer, D. C., H. J. Boyer, I. Fossen & A. Kreiner, 2001. Changes in abundance of the northern Benguela sardine stock during the decade 1990–2000, with comments on the relative importance of fishing and the environment. South African Journal of Marine Science 23: 67–84.
- Castillo, J., M. A. Barbieri & A. González, 1996. Relationships between sea surface temperature, salinity, and pelagic fish distribution off northern Chile. ICES Journal of Marine Science 53: 139–146.
- Estrada, M., 1996. Primary production in the northwestern Mediterranean. Scientia Marina 60: 55–64.
- Fréon, P., P. Cury, L. Shannon & C. Roy, 2005. Sustainable exploitation of small pelagic fish stocks challenged by environmental and ecosystem changes: a review. Bulletin of Marine Science 76: 385–462.
- Friedlander, A. M., E. K. Brown & M. E. Monaco, 2007. Coupling ecology and GIS to evaluate efficacy of marine protected areas in Hawaii. Ecological Applications 17: 715–730.
- García, A. & I. Palomera, 1996. Anchovy early life history and its relation to its surrounding environment in the Western Mediterranean basin. Scientia Marina 60: 155–166.
- Giannoulaki, M., A. Machias, S. Somarakis & N. Tsimenides, 2005. The spatial distribution of anchovy and sardine in the northern Aegean Sea in relation to hydrographic regimes. Belgian Journal of Zoology 135: 151–156.
- Giráldez, A. & R. Abad, 2000. Serie histórica de capturas de los pequeños pelágicos en el Mediterráneo español (1945– 1997) y capturas y esfuerzos de la Región Surmediterránea. Datos y Resúmenes del Instituto Español de Oceanografía 13: 26.
- Guisan, A. & N. E. Zimmermann, 2000. Predictive habitat distribution models in ecology. Ecological Modelling 135: 147–186.
- Koubbi, P., C. Loots, G. Cotonnec, X. Harlay, A. Grioche, S. Vaz, C. Martin, M. Walkey & A. Carpentier, 2006. Spatial patterns and GIS habitat modelling of *Solea solea*, *Pleuronectes flesus* and *Limanda limanda* fish larvae in the eastern English Channel during the spring. Scientia Marina 70: 147–157.
- Le Pape, O., L. Baulier, A. Cloarec, J. Martin, F. Le Loc'h & Y. Desaunay, 2007. Habitat suitability for juvenile common sole (*Solea solea*, L.) in the Bay of Biscay (France): a quantitative description using indicators based on epibenthic fauna. Journal of Sea Research 57: 126–136.
- Maravelias, C. D., 1999. Habitat selection and clustering of a pelagic fish: effects of topography and bathymetry on species dynamics. Canadian Journal of Fisheries and Aquatic Sciences 56: 437–450.
- Maravelias, C. D. & D. G. Reid, 1995. Relationship between herring (*Clupea harengus*, L.) distribution and sea surface salinity and temperature in the northern North Sea. Scientia Marina 59: 427–438.

- Massé, J., C. Koutsikopoulos & W. Patty, 1996. The structure and spatial distribution of pelagic fish schools in multispecies clusters: an acoustic study. ICES Journal of Marine Science 53: 155–160.
- Millot, C., 1999. Circulation in the Western Mediterranean Sea. Journal of Marine Systems 20: 423–442.
- Olivar, M. P., J. Salat & I. Palomera, 2001. A comparative study of spatial distribution patterns of early stages of anchovy and pilchard in the NW Mediterranean Sea. Marine Ecology Progress Series 217: 111–120.
- Palomera, I., 1992. Spawning of anchovy *Engraulis encrasic*olus in the Northwestern Mediterranean relative to hydrographic features in the region. Marine Ecology Progress Series 79: 215–223.
- Pertierra, J. P. & J. Lleonart, 1996. NW Mediterranean anchovy fisheries. Scientia Marina 60: 257–267.
- Pierce, G. J., J. Wang, X. Zheng, J. M. Bellido, P. R. Boyle, J. P. Robin & V. Denis, 2001. The cephalopod fishery GIS for the northeast Atlantic: development and application. International Journal of Geographical Information Science 15: 763–784.
- Pierce, G. J., J. Wang & V. Valavanis, 2002. Application of GIS to cephalopod fisheries: workshop report. Bulletin of Marine Science 71: 35–46.
- Pinot, J. M., J. L. López-Jurado & M. Riera, 2002. The Canales experiment (1996–1998). Interannual, seasonal and mesoscale variability of the circulation in the Balearic Channels. Progress in Oceanography 55: 335–370.
- Redfern, J. V., M. C. Ferguson, E. A. Becker, K. D. Hyrenbach, C. Good, J. Barlow, K. Kaschner, M. F. Baumgartner, K. A. Forney, L. T. Ballance, P. Fauchald, P. Halpin, T. Hamazaki, A. J. Pershing, S. S. Qian, A. Read, S. B. Reilly, L. Torres & F. Werner, 2006. Techniques for cetacean-habitat modeling. Marine Ecology Progress Series 310: 271–295.
- Robinson, C. J., 2004. Responses of the northern anchovy to the dynamics of the pelagic environment: identification of fish behaviours that may leave the population under risk of overexploitation. Journal of Fish Biology 64: 1072–1087.
- Salat, J., 1996. Review of hydrographic environmental factors that may influence anchovy habitats in northwestern Mediterranean. Scientia Marina 60: 21–32.
- Salat, J., M. A. Garcia, A. Cruzado, A. Palanques, L. Arín, D. Gomis, J. Guillén, J. de León, J. Puigdefàbregas, J. Sospera & Z. R. Velásquez, 2002. Seasonal changes of water mass structure and shelf-slope exchanges at the Ebro Shelf (NW Mediterranean). Continental Shelf Research 22: 327–348.
- Schwartzlose, R. A., J. Alheit, A. Bakun, T. R. Baumgartner, R. Cloete, R. J. M. Crawford, W. J. Fletcher, Y. Green-Ruiz, E. Hagen, T. Kawasaki, D. Lluch-Belda, S. E. Lluch-Cota, A. D. MacCall, Y. Matsuura, M. O. Nevárez-Martínez, R. H. Parrish, C. Roy, R. Serra, K. V. Shust, M. N. Ward & J. Z. Zuzunaga, 1999. Worldwide large-scale fluctuations of sardine and anchovy populations. South African Journal of Marine Science 21: 289–347.
- STECF, 2006. Report of the Scientific, Technical and Economic Committee for Fisheries Opinion on 'Sensitive and Essential Fish Habitats in the Mediterranean Sea'. Brussels 3–7 April 2006, http://stecf.jrc.cec.eu.int/.

- Tintorè, J., D. Gomis, S. Alonso & G. Parilla, 1991. Mesoscale dynamics and vertical motion in the Alboran Sea. Journal of Physical Oceanography 21: 811–823.
- Valavanis, V. D., S. Georgakarakos, A. Kapantagakis, A. Palialexis & I. Katara, 2004. A GIS environmental modelling approach to essential fish habitat designation. Ecological Modelling 178: 417–427.
- Valavanis, V. D., G. J. Pierce, A. F. Zuur, A. Palialexis, A. Saveliev, I. Katara & J. Wang, 2008. Modelling of essential fish habitat based on remote sensing, spatial

analysis and GIS. Hydrobiologia. doi:10.1007/s10750-008-9493-y.

- Vargas-Yáñez, M., F. Plaza, J. García-Lafuente, T. Sarhan, J. M. Vargas & P. Vélez-Belchí, 2002. About the seasonal variability of the Alboran Sea circulation. Journal of Marine Systems 35: 229–248.
- Zuur, A. F., E. N. Ieno & G. M. Smith, 2007. Analysing Ecological Data. Springer Series, Statistics for Biology and Health, New York: 700.

# FISH HABITAT MAPPING

# European anchovy (*Engraulis encrasicolus*) landings and environmental conditions on the Catalan Coast (NW Mediterranean) during 2000–2005

Paloma Martín · Nixon Bahamon · Ana Sabatés · Francesc Maynou · Pilar Sánchez · Montserrat Demestre

© Springer Science+Business Media B.V. 2008

Abstract Generalized additive models are proposed for a better understanding of the underlying mechanisms for anchovy variations in abundance. Environmental variables derived from satellite imagery (surface chlorophyll, sea surface temperature and wind-mixing index), river discharge (Rhône River and Ebre River) and anchovy landings (landings per unit of effort) as proxy for abundance were used, and three fishing zones were defined along the Catalan Coast. A time shift among wind index mixing, sea surface temperature and chlorophyll was observed for these variables to be significantly correlated with anchovy. Results pointed out to processes that appear to greatly influence species abundance and affect different life stages of anchovy (conditions preceding reproduction, larvae growth and survival and recruits growth). A high proportion of anchovy LPUE variability could be explained by environmental variables. Thus, some univariate models explained deviance are more than 50%, even up to around 70% of anchovy variability. In several cases the deviance explained by a given variable was even higher at the longer time-lags.

P. Martín ( $\boxtimes$ ) · N. Bahamon · A. Sabatés ·

F. Maynou · P. Sánchez · M. Demestre

Among all univariate and bivariate models fitted, the model that best explained anchovy LPUE variability, 79% of total deviance, was a model proposed for the central zone, based on the additive effect of surface chlorophyll and Rhône River discharge, considering time lags of 15 and 18 months, respectively, for each variable.

Keywords Engraulis encrasicolus ·

NW Mediterranean  $\cdot$  Environmental conditions  $\cdot$  Anchovy landings  $\cdot$  GAM

# Introduction

The European anchovy (*Engraulis encrasicolus* L. 1758) is widely distributed in the whole Mediterranean Sea and constitutes one of the main fishing resources. In the western basin, anchovy landings show a decreasing trend since the early 1990s. This is not, though, a common trend for the anchovy landings around the Mediterranean (for example, anchovy landings in the Italian coast, the bulk of which is captured in the Adriatic Sea, started an increasing trend since early 1990s; FAO Fish Stat Dataset).

Life history traits of small pelagic fishes (high mobility, plankton based food chains and short life span) make them particularly sensitive to environmental forcing. Populations of small pelagic fishes,

Guest editor: V. D. Valavanis Essential Fish Habitat Mapping in the Mediterranean

Institut de Ciències del Mar, Consejo Superior de Investigaciones Científicas, P. Marítim de la Barceloneta 37-49, 08003 Barcelona, Spain e-mail: paloma@icm.csic.es

such as sardine and anchovy, show evidence of important natural fluctuations in their abundance (Lluch-Belda et al., 1989). These fluctuations seem to be related, among other factors, to climate variability (e.g. Beamish, 1995; Bakun, 1996; Alheit & Hagen, 1997; Sabatés et al., 2006). The timing of seasonal spawning peak and the location of the anchovy spawning grounds are generally associated with months/areas of high productivity, and specifically with conditions favouring adult feeding (Somarakis et al., 2004). Although overfishing has played a role in many of the major declines of small pelagic stocks, environmental variability is also thought to be a key contributor to this extreme population variability (e.g. Bakun, 1996; Cury et al., 2000; Boyer et al., 2001). Research effort has been oriented to demonstrate the importance of environmental factors on recruitment variability (e.g. Bakun & Parrish, 1991; Borja et al., 1996; Cole & McGlade, 1998; Alheit & Hagen, 1997; Bakun & Broad, 2003).

Previous studies conducted in the Mediterranean have focussed on anchovy biology and yield variability, and their link with environmental conditions, which may affect different life stages. Thus, habitat conditions have been related with anchovy growth, reproduction, abundance, recruitment and landings (see, among others, Lloret et al., 2001, 2004; Basilone et al., 2004, 2006; Patti et al., 2004; García Lafuente et al., 2005; Santojanni et al., 2006).

The main spawning areas of anchovy in the northwestern Mediterranean are located in the vicinity of the mouths of the two largest rivers in the region, the Rhône and the Ebre (Palomera & Sabatés, 1990; Palomera, 1992; García & Palomera, 1996). Larvae have been found strongly associated with the presence of less saline water (Palomera, 1992; Sabatés et al., 2001; Coombs et al., 2003). Anchovy displays different spawning duration, which can be related to differential latitudinal sea surface temperature (Sabatés et al., 2007a; Zarrad et al., 2006). Along the Catalan coast, spawning starts earlier in the southern part, where lasts for several months from April to October (peak in May-June), gradually spreading northwards (peak June–July) (Palomera, 1992). Trophic studies of adult anchovy and larvae have shown that this species feeds on small zooplankton. The main prey of adults are copepods, and to a lesser extent, molluscs, cladocerans, other crustaceans and appendicularians (Tudela & Palomera, 1995, 1997; Plounevez & Champalbert, 2000), while stomach contents of larvae consist mostly of copepod eggs, nauplii and copepodites (Tudela et al., 2002).

In 2005, anchovy annual landings in the Catalan Coast were around 3,800 ton and the purse seining fleet consisted of 112 vessels (DGPAM fishing statistics and fleet census, the General Direction of Fishing and Maritime Affairs of the Catalan Government). The number of vessels operating in summer during the anchovy season can be higher, given that the fleet from southern ports beyond the study area moves northwards as the anchovy season advances, operating also into the Gulf of Lions.

Anchovy landings, as in other Mediterranean areas, depend on recruitment success and fish growth (Pertierra & Lleonart, 1996; Patti et al., 2004; Santojanni et al., 2006). Therefore, changes in environmental conditions at different life stages are likely to be reflected in the short term in the landings.

The present study addressed the definition of the conditions characterizing the anchovy essential fish habitat (EFH) in the Catalan coast, using environmental variables derived from satellite imagery, river discharge data, and landings (landings per unit of effort) as proxy for abundance. The aim is to elucidate to what extent anchovy landings variation can be explained by environmental conditions.

#### Materials and methods

#### Study area

The Catalan coast is located in the NW Mediterranean Sea, south of the Gulf of Lions (Fig. 1). The northern sector, which is more directly influenced by strong northerly winds, is generally colder than the central and southern parts and a surface thermal front roughly coincides with the limit of frequent northerly winds (López García et al., 1994). The Catalan coast is characterized by a continental shelf, which is, in general, quite narrow. It widens clearly in the southernmost part, in the vicinity of the Ebre River Delta, and in the north between the main submarine canyons, south of the Gulf of Lions. Input of continental water plays an important role in this region. The southern shelf receives a significant river outflow from the Ebre River, while the northern areas are affected by the outflow of the Rhône River, the


**Fig. 1** Study areas showing the three defined zones along the Catalan Coast, North (N), Centre (C) and South (S). The dots indicate the fishing ports located in each zone

largest river in the Western Mediterranean basin, which outflows into the Gulf of Lions.

Considering the physical features along the Catalan coast and the daily displacements of the purseseining fleet, three zones, limited by the 200 m depth isobath, are defined in the study area (North, Centre and South). This is due to the fact that, although the landings data are obtained daily by port, fleets travel to fishing grounds which are shared by different ports, thus the geographical origin of the landings cannot be ascertained with precision.

#### Data

We have considered the following as the main environmental variables determining anchovy abundance: chlorophyll (as an indicator of primary production, given that anchovy is a plankton feeder species); sea surface temperature (temperature is known to determine the species distribution, trigger maturation and enhance growth of larvae); wind (wind is known to play a major role in the processes of water mixing and local fertilization); and Rhône and Ebre Rivers flow rates (as anchovy is known to be associated with river plume during spawning and waters rich in nutrients and low salinities).

Data on mean monthly values of surface chlorophyll-a (CHL; mg m<sup>-3</sup>), sea surface temperature (SST; °C), and wind speed (m s<sup>-1</sup>), in each of the three zones considered were extracted from the environmental database developed in the frame of the EnviEFH project, through an ad hoc protocol designed in ArcGIS 9.2 environment. The cube of the wind speed (WI) was used as an index of windinduced turbulent mixing that is independent of the wind direction, and has been used in a number of ecological studies (Ueyama & Monger, 2005; Lloret et al., 2004). Average monthly flow rates (m<sup>3</sup> s<sup>-1</sup>) at the mouth of Rhône River (RR) and Ebre River (ER), 2000–2005, were obtained from Compagnie Nationale du Rhône—Station Beaucaire and Confederación Hidrográfica del Ebre—Station Tortosa.

Daily anchovy landings, per vessel and port, along the Catalan Coast, during 2000-2005 (75181 records on anchovy daily landings in total), were obtained from the DGPAM fishery statistics. During this period fishing effort has not displayed any marked inter-annual variations (around  $12500 \pm 1500$  fishing days per year with records of anchovy landings; DGPAM fishing statistics). As anchovy is caught during spring/summer, when most of the individuals are 1-year old (Pertierra & Lleonart, 1996), landings of anchovy can be considered as a proxy for annual recruitment strength. Anchovy is a high valued species, and discards are considered to be negligible, hence landing per unit of effort (LPUE; kg per day and vessel) is assumed to be a proxy of the species abundance. Data on daily landings from ports included in each zone were merged and monthly LPUE were estimated by zone.

#### Statistical analyses

The decomposition of the monthly anchovy LPUE time series by zone is based on loess smoothing (Cleveland et al., 1990), allowing the identification of the seasonal pattern and trend during 2000–2005.

For each zone, time-lagged cross-correlations were performed between anchovy LPUE and CHL, SST and WI; RR was cross-correlated with anchovy LPUE from north and central zones; and ER was cross-correlated with anchovy LPUE from the southern zone. The partial correlation coefficient was estimated by fitting autoregressive models of successively higher orders up to 24-month lag. The lags showing the highest significant correlations between LPUE and individual variables were chosen for further hypothesis validation using generalized additive models (GAMs). The influence of the environmental variables on the anchovy LPUE was modelled using a log-Gaussian link function in generalized additive models (Hastie & Tibshirani, 1990). GAMs extend the generalized linear model (GLM) by replacing the linear predictors by the sum of non-parametric smoothing spline functions of the covariates (environmental variables) plus a conventional parametric component of the linear predictor. The non-parametric curves are estimated iteratively, cycling through the predictors until the optimal multivariate fit is reached using back-fitting algorithms. The GAMs used in the analysis has the form:

$$y = \beta_0 + \sum_{j=1}^p f_j(X_j) + \varepsilon$$

where  $\beta_0$  is the intercept; the covariates  $(X_j)$  can be just one variable (univariate model) or a number of them (p) (multivariate model) and the function  $f_j$  is the cubic spline (specific for each covariate) representing the nonparametric term of the equation. The cubic spline function makes the difference with the linear models;  $\varepsilon$  is the error term. The link function is the log of the response variable. The candidate predictors are the environmental variables: mean monthly values of CHL, SST and WI, as well as Rhône River discharges for models in the north and central zones, and Ebre River discharges for models in the south zone.

In order to ensure that the overall level of smoothing is optimal, and to guard against trapping by local minima, a highly efficient global minimization with respect to an overall smoothing parameter is made at each iteration, based on mgcv algorithm (Wood, 2000).

Model predictors were tested for statistical significance ( $P \le 0.05$ ). The model deviance explained by individual predictors (e.g. time-lagged CHL) was compared against the deviance of models with combined predictors (e.g. time-lagged CHL + time-lagged SST). Step-wise selection was applied to select the best models. The best model combination was that representing the largest (total) amount of deviance, having all terms in the equation below a significant level ( $P \le 0.05$ ) of deviance reduction. The total deviance compares the fit of the saturated model to the null model, thus, expresses the total variability around a fitted line which can be

decomposed to explained and unexplained (error) variability. Other criteria (used in package mgcv in R, www.R-project.org) were also taken into account to select the best model: the smaller the gradients at convergence, the better; model residual closer to normal distribution the better; and definite positive Hessian that if not positive then some of covariates could be highly collinear or show very high variance.

# Results

Environmental conditions along the Catalan Coast

Figure 2 shows the data used in the analyses, by variable, quarter and zone. Chlorophyll peaked in winter, and a secondary peak was also observed in autumn. The southern zone appeared to be the most productive, although highest values were attained in the central zone in March 2005. Sea surface temperature exhibited a clear seasonal pattern, with peaks in summer. Latitudinal differences were also observed: while in the colder months (winter) SST was similar in the three zones considered, in summer maximum values were lower in the northern zone and highest in the south. Wind-mixing index was clearly highest in the northern zone, with peaks in winter and autumn (secondary); the central and south zones exhibited the same pattern and values. As for Rhône and Ebre River's monthly flow, the reservoirs constructed in the river basins have modified their natural pattern, diminishing seasonal variations. Rhône River discharge is much larger than that of Ebre, and peaks were observed in autumn and winter, but also in spring, whereas Ebre flow peaks were observed mainly in winter.

Anchovy LPUE seasonal pattern

Overall landings during 2000–2005 were higher in the northern zone. The decomposition of anchovy LPUE data series allowed the identification of the seasonal pattern, which differed among zones (Fig. 3). Thus, highest LPUE during the year was reached first in the southern zone (peak in May– June), gradually expanding northwards (peak in July in central zone and in June–September in north zone). Moreover, it was in the southern zone that the anchovy LPUE seasonal pattern was more distinct **Fig. 2** Monthly means of surface chlorophyll concentration, sea surface temperature, wind-mixing index, and Rhône and Ebre Rivers discharge, by quarter and zone, during 2000–2005



(lowest remainder of the decomposition of LPUE data series). Trends of LPUE during 2000–2005 in the central and south zones were similar, with maximum values attained in summer 2002. The north zone showed high landings over the whole period, especially between 2001 and 2003.

#### Time-lagged cross-correlations

Time-lagged cross-correlations between anchovy LPUE and environmental variables provided a first approach to potential optimal conditions for anchovy abundance. A seasonal pattern prevailed for most



Fig. 3 Decomposition of the monthly anchovy landings time series (2000–2005), in zones North, Centre and South: data, seasonal pattern, trend and remainder

paired cross-correlations (Table 1, results related with Tables 2 and 3). Maximum positive and negative correlations generally alternated every 6 months. Furthermore, the correlations in the months preceding and following the month with highest correlation (the time-lags mentioned below) were also significant, thereby pointing not only to a given month, but to a 2-3-months period when the correlation between anchovy and a given variable was significant. CHL in the northern zone showed the highest positive correlations with time lags of 5 and 18 months, and negative correlations with 0 and 12 months lag. In the central and southern zones, the pattern was similar, the highest positive correlations were estimated at 3 and 15-months lag, whereas the highest negative correlations were observed at 8-9 months lag. SST showed the highest correlations in northern zone at 0, 5, 12 and 18 months-lag; 3, 10 and 15 months lag in central zone; and 4, 10 and 16 months in southern zone. As for WI, the time lag for the variable to be significantly correlated with anchovy was longer than in the case of CHL, and of the same sign. In the north, Rhône River discharges showed the highest (positive) correlation at 18-month lag; the same correlation pattern was observed in the central zone. In the south, the Ebre River discharges showed the highest (positive) correlation with anchovy at 14-month lag.

Modelling approach using GAMs

The different time response of anchovy LPUE to the environmental conditions by zone was validated by fitting univariate and multivariate GAMs (Tables 2 and 3). The time lags of the environmental variables showing the highest correlations with anchovy LPUE were used to GAM development.

In the univariate models, i.e. anchovy LPUE fitted against single environmental variables, the deviance explained by the models was generally higher in the south zone than in the central and north zones indicating a stronger association of the environmental conditions and anchovy landings (Table 2). The models with non-lagged environmental conditions explained very low deviance of the anchovy LPUE series, and in some cases the environmental variable was not significant (not shown here).

Some univariate models explained a large amount of the model deviance (more than 50%, even up to around 70%). In several cases the deviance explained by a given variable was even higher at the longer

<b>Table</b> Centra	<b>1</b> Lagg (2) and	ed cross- l South (	correlati 3), as de	ions bet	ween me Fig. 1	onthly aı	nchovy I	PUE an	id chlorc	phyll (C	(HL), se	a surface	e temper	ature (S	ST), and	l wind-r	aixing iı	ndex (W	/I), in zo	nes Nor	th (1),
	Lag (n	nonths)																			
	-20	-19	-18	-17	-16	-15	-14	-13	-12	-11	-10	6-	-8	L	9	-5	-4	-3	-2	-1	0
CHL1	0.22	0.36	0.44	0.37	0.26	-0.01	-0.20	-0.37	-0.40	-0.37	-0.35	-0.22	-0.03	0.25	0.44	0.51	0.47	0.24	-0.07	-0.33	-0.43
CHIL2	-0.23	-0.12	0.04	0.17	0.32	0.34	0.26	0.04	-0.15	-0.27	-0.35	-0.36	-0.37	-0.22	-0.02	0.19	0.42	0.54	0.43	0.16	-0.15
CHIL3	-0.21	-0.04	0.17	0.39	0.57	0.62	0.45	0.17	-0.16	-0.40	-0.57	-0.57	-0.46	-0.23	0.04	0.27	0.44	0.47	0.33	0.04	-0.25
SST1	-0.15	-0.36	-0.48	-0.48	-0.33	-0.08	0.16	0.33	0.42	0.43	0.37	0.21	-0.04	-0.31	-0.51	-0.56	-0.44	-0.18	0.11	0.36	0.52
SST2	0.28	0.08	-0.13	-0.32	-0.46	-0.48	-0.39	-0.14	0.17	0.45	0.56	0.49	0.29	0.06	-0.18	-0.39	-0.56	-0.57	-0.44	-0.14	0.20
SST3	0.28	0.01	-0.23	-0.42	-0.52	-0.51	-0.38	-0.12	0.23	0.54	0.69	0.59	0.32	-0.03	-0.34	-0.55	-0.64	-0.59	-0.41	-0.10	0.28
W11	0.27	0.29	0.23	0.17	0.03	-0.16	-0.32	-0.44	-0.31	-0.10	0.11	0.22	0.29	0.33	0.21	0.17	-0.02	-0.10	-0.32	-0.46	-0.40
W12	0.11	0.22	0.28	0.34	0.27	0.14	-0.07	-0.22	-0.30	-0.38	-0.29	-0.13	0.19	0.40	0.43	0.29	0.19	0.06	-0.07	-0.27	-0.39
WI3	0.20	0.38	0.40	0.33	0.18	0.02	-0.11	-0.23	-0.31	-0.37	-0.33	-0.18	0.16	0.45	0.62	0.49	0.24	0.00	-0.22	-0.34	-0.40
<b>RR1</b>	0.20	0.33	0.38	0.36	0.25	0.08	-0.15	-0.23	-0.24	-0.19	-0.16	-0.14	0.00	0.10	0.22	0.26	0.24	0.13	-0.11	-0.26	-0.21
RR2	0.16	0.41	0.52	0.47	0.44	0.40	0.25	0.05	-0.16	-0.29	-0.38	-0.28	-0.16	0.00	0.07	0.14	0.17	0.22	0.17	0.07	-0.11
ER3	-0.23	-0.11	0.10	0.26	0.45	0.52	0.54	0.38	0.11	-0.21	-0.43	-0.53	-0.47	-0.31	-0.07	0.15	0.26	0.25	0.13	-0.02	-0.21
d.f.	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	99	67	68	69	70
In addi	tion Rh	ône Rive	r discha	roe (RR	) was cr	4100-330.	elated w	ith anch	Id I wwe	IF in zoi	nec Nort	h (1) and	d Centra	1 (7) an	d Fhre F	iver dis	charge (	FR ) wa	J-SSUJJ S	orrelate	4 with



Zone	Envi	Environmental variable												
	CHL	r		SST			WI			Rive	r discharg	je –		
	Time	e Lag	Model deviance	Time	Lag	Model deviance	Time	e Lag	Model deviance	Time	e Lag	Model deviance		
North	5	(+)	37.8	5	(-)	36.9	7	(+)	17.6	5	(+)	16.9 <sup>RR</sup>		
	12	(-)	21.4	12	(+)	23.9	13	(-)	29.3					
	18	(+)	40.5	18	(-)	41.1	19	(+)	25.4	18	(+)	22.9 <sup>RR</sup>		
Central	3	(+)	44.9	3	(-)	34.8	6	(+)	19.0					
	8	(-)	15.2	10	(+)	44.1	11	(-)	35.6					
	15	(+)	20.6	15	(-)	34.6	18	(+)	41.3	18	(+)	51.4 <sup>RR</sup>		
South	3	(+)	22.5	4	(-)	56.9	6	(+)	42.7	4	(+)	15.3 <sup>ER</sup>		
	9	(-)	58.0	10	(+)	69.7	11	(-)	49.2					
	15	(+)	48.3	16	(-)	56.7	18	(+)	64.2	14	(+)	18.9 <sup>ER</sup>		

 Table 2
 Model deviance (%) of monthly anchovy LPUE explained by univariate GAMs

The time lags (month) for the environmental variables are those showing the highest significant *P*-values in the cross-correlation analysis. The sign of the correlation (+ and -) between the environmental variable and anchovy LPUE is indicated

CHL = Chlorophyll (mg/m<sup>3</sup>); SST = Sea Surface Temperature (°C); WI = Cubed wind speed (m<sup>3</sup>/s<sup>3</sup>); RR = Rhône River discharge (m<sup>3</sup>/s); ER = Ebre River discharge (m<sup>3</sup>/s)

time-lags. It is remarkable that the Rhône River discharge explained 51% (18 months lag) of the total deviance of the model in the central zone. The models proposed for the southern zone, with CHL, SST and WI as predictor variables, at time-lags of 15, 16 and 18 months, respectively, were selected to illustrate our results on univariate GAMs (Figs. 4 and 5). When the response was positive, anchovy LPUE showed a linear relationship with CHL (positive) and SST (negative). In the case of WI, though, the situation was different: linear relationship could be assumed within a certain WI range (aprox. 250–400), beyond which higher WI did not result in increasing LPUE. The model based on WI was the best among these three, explaining better the evolution of anchovy LPUE, including both the maximum LPUE observed in summer 2002 and the secondary LPUE peak in autumn 2002 (64.2% model deviance). The model based on CHL explained well the LPUE peaks, but failed to reproduce 2003 (56.7% model deviance), while the model based in SST explained the seasonality, but showed a lack of fit for LPUE in 2002.

Multivariate GAMs suggested that the maximum number of significant covariates to explain the anchovy LPUE was two. The bivariate models presented here are those combining chlorophyll with another environmental variable (SST, WI and river discharge). Some bivariate models slightly improved the univariate model fitting (Table 3). It is worth mentioning the model proposed for the central zone, where the predictions based on the additive effect of CHL and Rhône River discharge, lagged 15 and 18 months, respectively, explained 79.2% of LPUE deviance (Figs. 6 and 7). GAMs suggested a major role of river discharge as environmental variable explaining anchovy LPUE variance.

Potential optimal environmental ranges defining anchovy EFH

Results evidenced the different timing of the response of anchovy LPUE to environmental conditions and thus, models were proposed for each zone separately. The significant time-lags in northern zone appeared to be longer as compared to those identified in the central and southern zones (Tables 2 and 3). These different time-lags are in fact pointing to the same time of the year. Thus, for example, when considering the time of the year with higher LPUE as starting point to go backwards, 5 months-lag in the northern zone, and 3-months lag in the central and south zones, would point to environmental conditions in winter the same year. Likewise, time lags of 18 months (north zone) and 15 months (central and south zones) would be related with winter the preceding year, and time-

Table 3 Model deviance (%) of monthly anchovy LPUE explained by bivariate GAMs

Zone	Time	Lag	Model covariates	Total deviance	Time	lag	Model covariates	Total deviance	Time	lag	Model covariates	Total deviance
North	(+)	5	CHL	38.1	(-)	12	CHL*		(+)	18	CHL*	44.0
	(-)	5	SST*		(+)	12	SST*		(-)	18	SST	
	(+)	5	CHL*	38.3	(-)	12	CHL*	34.4	(+)	18	CHL	42.1
	(+)	7	WI		(-)	13	WI		(+)	19	WI*	
										18	CHL	43.9
										18	RR	
Central	(+)	3	CHL	45.0	(-)	8	CHL*	45.9	(+)	15	CHL*	37.5
	(-)	3	SST*		(+)	10	SST		(-)	15	SST	
	(+)	3	CHL	58.3	(-)	8	CHL*	39.8	(+)	15	CHL	40.5
	(+)	6	WI		(-)	11	WI		(+)	18	WI	
										15	CHL	79.2
										18	RR	
South	(+)	3	CHL*	58.4	(-)	9	CHL	72.4	(+)	15	CHL	70.2
	(-)	4	SST		(+)	10	SST		(-)	16	SST	
	(+)	3	CHL	43.8	(-)	9	CHL	60.3	(+)	15	CHL	59.0
	(+)	6	WI		(-)	11	WI*		(+)	18	WI	
										15	CHL	48.4
										15	ER	

The time lags (month) for the environmental variables are those showing the highest significant *P*-values in the cross-correlation analysis. The sign of the correlation (+ and -) between the environmental variable and anchovy LPUE is indicated

 $CHL = Chlorophyll (mg/m^3); SST = Sea Surface Temperature (^{C}); WI = Cubed wind speed (m^3/s^3); RR = Rhône River discharge (m^3/s); ER = Ebre River discharge (m^3/s)$ 

\*Non-significant model covariates (P > 0.05)

lags of 10 months in central and south zones and 12 months in the northern zone point to summer the previous year. Our results indicated that high CHL and low SST in winter, preceded by high WI, are conditions favouring anchovy abundance, as well as high river discharge and extended summer conditions. The potential optimal environmental ranges defining anchovy essential fish habitat in the Catalan coast (those matching anchovy LPUE values above the average from best-fitting univariate GAMs) were practically coincidental with the observed monthly values during the season concerned (Table 2 and Figs. 2, 4 and 6). Thus, for example, SST optimal environmental ranges as deduced from best-fitting univariate GAMs were the following, for southern zone: winter-early spring, 12.5-17°C, and summer, 20.5-29.3°C. These ranges reflect the seasonal pattern shown in the time-lagged cross-correlations, maximum positive and negative correlations alternating every 6 months.

#### Discussion

Anchovy LPUE seasonality

During the time period considered in this study, 2000–2005, anchovy landings displayed certain stability and fishing effort remained at similar level, which facilitates the detection of landings seasonality and the effect of environmental variables on anchovy abundance.

Anchovy LPUE along the year showed a seasonal pattern, characteristic of the species in the Mediterranean. The anchovy fishing season can last for several months (late spring–autumn), but the bulk of the landings concentrate in a shorter period, which can be of only 1–2 months, in spring–summer; landings in winter are lowest. Since anchovy spawns and is caught during spring/summer, when most of the individuals are 1-year old (Pertierra & Lleonart, 1996), the peak of landings corresponds to anchovy



**Fig. 4** Univariate GAMs proposed for the southern zone. Effect of surface chlorophyll, sea surface temperature, and wind-mixing index on anchovy LPUE, considering time lags of 15, 16 and 18 months respectively, for each variable (95% confidence intervals shown)

recruitment to the fishery. Landings peak occurs first in the southern zone, later shifting northwards. This pattern would be related with the species reproductive cycle in relation with the sea temperature evolution. Thus, spawning starts in the southern zone, where surface temperature increases earlier than in the north, and extends progressively northwards (Palomera, 1992; Sabatés et al., 2007a). Anchovy reproduction in the Gulf of Lions has been reported to take place in summer (SAC-GFCM, 2007).

Anchovy LPUE and winter conditions in the previous and same years

Our results suggest that windy and colder winters which increase primary production by the end of winter and beginning of spring, before anchovy spawning, would result in higher anchovy landings the following year. The observed shift among WI, SST and CHL for their corresponding time-lags to be significantly cross-correlated with anchovy (WI significant time-lags were advanced with regard to those of SST and CHL) suggests that these variables would be involved in different phases of a same process. From our results, the relationship between anchovy LPUE and WI was positive at 18-19 months-lag (winter preceding spawning the year before the observed landings peak); was negative with SST at 16–18 months-lag; and positive with CHL within 15– 18 months-lag (Table 2). Thus, periods with strong winds which favour vertical mixing, correspond with a certain time shift to low temperature and increased primary production. In the western Mediterranean, Estrada (1985) reported that cold years tended to be more productive, partly because winter mixing may reach greater depth, and in part because the formation of deep water (enrichment mechanism of superficial waters) in the Gulf of Lions may occur over a larger area. This enhanced production during cold winters and spring also gives rise to an increase in zooplankton production (Fernández de Puelles et al., 2007). Positive correlations between reproductive investment and prior phytoplankton and zooplankton abundance (food concentration) have been reported in clupeoid species in different geographic areas (e.g. Hay & Brett, 1988; Luo & Musick, 1991; Regner, 1996; Lapolla, 2001; Peebles, 2002). It has been argued that the high productivity may afford adequate



Fig. 5 Univariate GAMs proposed for the southern zone. Model predictions and observed monthly anchovy LPUE, based on surface chlorophyll, sea surface temperature, and

wind-mixing index, considering time lags of 15, 16 and 18 months, respectively, for each variable

adult feeding (Blaxter & Hunter, 1982), thereby increasing spawning intensity and affording a suitable habitat for larval development and survival (Castro & Cowen, 1991; Peebles et al., 1996). Within the Mediterranean, Somarakis (2005), in his study conducted in the northern Aegean Sea, emphasized the importance of adult prey availability in determining anchovy egg production. In the Adriatic Sea, Basilone et al. (2006) reported that inter-annual variations of gonadosomatic index of anchovy were mainly governed by changes in the amount of chlorophyll in the period preceding spawning, suggesting that the intensity and seasonality of spawning were governed by oceanographic processes in the months prior to spawning. These processes would be probably associated with prey availability, increase in anchovy energy reserves and gonadal development.

Anchovy abundance and production in the Catalan Coast depends on recruits' growth, as these are the main component of the landings. It has been reported



Fig. 7 Bivariate GAM proposed for the central zone. Model predictions and observed monthly anchovy LPUE, based on the additive effect of surface chlorophyll and Rhône River discharge, considering time lags of 15 and 18 months respectively, for each variable

that sea surface estimates of chlorophyll concentrations are good indicators of food availability for anchovy (Basilone et al., 2004). These authors, in line with our results, showed in their studies conducted in the Strait of Sicily a good correspondence between anchovy growth and chlorophyll concentration.

Anchovy LPUE and summer conditions in the previous year

The observed relationships of sea surface temperature, wind mixing index and chlorophyll, with anchovy LPUE at time lags pointing to conditions by the end of summer were of opposite sign to those linked to winter conditions (positive for SST and negative for WI and CHL). In summer, when larvae are in the plankton, high temperature and low wind intensity, which favours the stability of the water column, would allow maintaining larval food patches, associated during the summer period with the deep chlorophyll maximum, located at depths of 40–80 m (Sabatés et al., 2007a). This would favour larvae survival, in line with the water column stability hypothesis proposed by Lasker (1981). Similar to our results, Basilone et al. (2006) indicated that anchovy in the Strait of Sicily have evolved to spawn when seasonal wind speeds are lowest. Temperature would also enhance faster larval growth rate (Palomera et al., 2007), the period when larvae are more vulnerable to mortality by predation being reduced (Bailey & Houde, 1989). In any case, this positive relationship with SST by the end of summer might point to a longer spawning period. Thus, the deviance explained by the univariate models (Table 2, SST) was much higher in the southern zone, and decreased in central and north zones, especially in this last one. This variability would be in line with the observations by Palomera (1992), indicating a longer reproduction period for anchovy in the southern Catalan Coast than in the north.

The above discussed summer conditions, low WI and high SST, are related with low CHL, and, hence, a negative relationship between CHL and anchovy,

lacking any significance regarding the species biology, was observed. In fact, in summer chlorophyll at surface is barely detectable, which is a feature of the oligotrophic character of the study area temperate latitude (Estrada, 1985).

Anchovy LPUE and river discharge

This study has shown a positive relationship between anchovy and river discharge for central and north zones with Rhône River, and for the southern zone with Ebre River.

The relationship between river runoff and small pelagic fish production is well established for a number of species in different estuarine areas of the world, e.g. the Mississippi (Grimes, 2001), Black Sea (Daskalov, 1999), and Mediterranean (Lloret et al., 2001, 2004; Santojanni et al., 2006). Waters under the influence of continental run-off are more productive and have higher nutrient, and phytoplankton and zooplankton concentrations than adjacent oceanic waters (Cruzado & Velásquez, 1990; Razouls & Kouwenberg, 1993). Santojanni et al. (2006) indicated that seasonal peaks of phytoplankton production in the northern Adriatic tend to coincide with maximum Po River flow rates in autumn. These authors also found a link between anchovy recruitment and Po River discharge the preceding year. Since anchovy larvae feed mainly on juvenile copepod stages (Tudela et al., 2002) and in the initial developmental stages may also feed on phytoplankton (Lasker, 1975), conditions in the waters under the influence of river discharge would be favourable to anchovy larval development.

Results in the southern zone agree with those by Lloret et al. (2004). These authors pointed out the importance of Ebre River discharges for anchovy production and hypothesized that river runoff influences spawning and the survival rate of the anchovy early stages and, hence, recruitment. Likewise, Lloret et al. (2001) also found anchovy catch and catch per unit of effort in the Gulf of Lions to be significantly correlated with Rhône River flow during the reproductive season, at a time-lag of 13 months. In our study, though, anchovy LPUE in zone north was best explained considering a time-lag of 18 months. An explanation for this difference in the significant timelags could be that Lloret et al. (2001) considered the river discharge only during the reproduction period. Nevertheless, the relationship between anchovy and river discharge was much more evident in the case of Rhône River flow and the central Catalan Coast (Table 2). This relationship, related with the Rhône River run-off with a 18-months time-lag, corresponds to the winter-spring discharge the preceding year, before the species reproduction in the Gulf of Lions. Thus, higher Rhône discharge in the Gulf of Lions would result in higher landings in fishing grounds located southwards Gulf of Lions. Although this relationship might seem surprising, it has to be taken into account that the Gulf of Lions is one of the main anchovy spawning areas in the NW Mediterranean (García & Palomera, 1996), and, moreover, environmental conditions increasing primary production, as river discharge, would favour adult feeding thereby increasing spawning intensity (Blaxter & Hunter, 1982; Castro & Cowen, 1991; Peebles et al., 1996). Furthermore, recent studies have demonstrated that larvae from the spawning grounds of the Gulf of Lions were transported towards the Catalan coast by the shelf-slope current along the continental slope towards nursery areas (Sabatés et al., 2001; 2007b). Sabatés et al. (2007b) pointed out that the dependence of anchovy population of the Catalan coast on this transport mechanism still has to be determined. Our results suggest that this dependence might be strong and further studies are required to understand the underlying mechanisms driving this relationship.

#### Conclusions

A high proportion of anchovy LPUE variability could be explained by environmental variables. Results in the three fishing zones in the Catalan Coast pointed to the same processes having a great influence on anchovy abundance, which would affect different life stages of anchovy. These are the following: environmental conditions in winter (period preceding reproduction) and by the end of summer the previous year (larvae growth and survival), and winter conditions some months before the landings peak the same year (recruits growth).

A close link between Rhône River discharge in the Gulf of Lions and anchovy landings in the central fishing zone of the Catalan Coast has been highlighted, thereby supporting previous findings on anchovy larvae advection from the Gulf of Lions. Acknowledgements We acknowledge the DGPAM, the General Direction of Fishing and Maritime Affairs of the Catalan Government, for providing the data on the anchovy fishery. This study was funded by the EC EnviEFH project (SSP8 Contract Number 022466).

## References

- Alheit, J. & E. Hagen, 1997. Long-term climate forcing of European herring and sardine populations. Fisheries Oceanography 6: 130–139.
- Bailey, K. M. & E. D. Houde, 1989. Predation on early developmental stages of marine fishes and the recruitment problem. Advances in Marine Biology 25: 1–83.
- Bakun, A., 1996. Patterns in the ocean—Ocean processes and marine population dynamics. California Sea Grant College System, NOAA.
- Bakun, A. & K. Broad, 2003. Environmental loopholes and fish population dynamics: comparative pattern recognition with particular focus on El Niño effects in the Pacific. Fisheries Oceanography 12: 458–473.
- Bakun, A. & R. H. Parrish, 1991. Comparative studies of coastal pelagic fish reproductive habitats: the anchovy (*Engraulis anchoita*) of the southwestern Atlantic. ICES Journal of Marine Science 48: 343–361.
- Basilone, G., C. Guisande, B. Patti, S. Mazzola, A. Cuttitta, A. Bonnano & A. Kallianotis, 2004. Linking habitat conditions and growth in the European anchovy (*Engraulis encrasicolus*). Fisheries Research 68: 9–190.
- Basilone, G., C. Guisande, B. Patti, S. Mazzola, A. Cuttitta, A. Bonnano, A. R. Vergara & I. Maneiro, 2006. Effect of habitat conditions on reproduction of the European anchovy (*Engraulis encrasicolus*) in the Strait of Sicily. Fisheries Oceanography 15: 271–280.
- Beamish, R. J., 1995. Climate change and northern fish populations. Canadian Special Publications in Fisheries and Aquatic Sciences 121: 739.
- Blaxter, J. H. S. & J. R. Hunter, 1982. The biology of clupeoid fishes. Advances in Marine Biology 20: 1–223.
- Borja, A., A. Uriarte, V. Valencia, L. Motos & A. Uriarte, 1996. Relationships between anchovy (*Engraulis encra-sicolus* L.) recruitment and the environment in the Bay of Biscay. Scientia Marina 60: 179–192.
- Boyer, D. C., H. J. Boyer, I. Fossen & A. Kreiner, 2001. Changes in abundance of the northern Benguela sardine stock during the decade 1990–2000, with comments on the relative importance of fishing and the environment. South African Journal of Marine Science 23: 67–84.
- Castro, L. R. & R. K. Cowen, 1991. Environmental factors affecting the early life history of bay anchovy Anchoa mitchilli in Great South Bay, New York. Marine Ecology Progress Series 76: 235–247.
- Cleveland, R. B., W. S. Cleveland, J. E. McRae & I. Terpenning, 1990. STL: a seasonal-trend decomposition procedure based on Loess. Journal of Official Statistics 6: 3–73.
- Cole, J. & J. McGlade, 1998. Clupeoid population variability, the environment and satellite imagery in coastal upwelling systems. Reviews in Fish Biology and Fisheries 8: 445–471.

- Coombs, S. H., O. Giovanardi, N. Halliday, G. Franceschini, D. V. P. Conway, L. Manzueto, C. D. Barrett & I. R. B. McFadzen, 2003. Wind mixing, food availability and mortality of anchovy larvae *Engraulis encrasicolus* in the northern Adriatic Sea. Marine Ecology Progress Series 248: 221–235.
- Cruzado, A. & Z. R. Velásquez, 1990. Nutrients and phytoplankton in the Gulf of Lions, northwestern Mediterranean. Continental and Shelf Research 10: 931–942.
- Cury, P., A. Bakun, R. J. M. Crawford, A. Jarre, R. Quiñones, L. Shannon & H. Verheye, 2000. Small pelagics in upwelling systems: patterns of interaction and structural changes in "wasp-waist" ecosystems. ICES Journal of Marine Science 57: 603–618.
- Daskalov, G., 1999. Relating fish recruitment to stock biomass and physical environment in the Black Sea using generalized additive models. Fisheries Research 41: 1–23.
- Estrada, M., 1985. Deep phytoplankton and chlorophyll maxima in the Western Mediterranean. In Moraitou-Apostolopoulou, M. & V. Kiortis (eds), Mediterranean Marine Ecosystems. Plenum Press, New York: 247–276.
- FAO Fish Stat Dataset, http://www.fao.org/fishery/statistics/ global-capture-production.
- Fernández de Puelles, M. L., F. Alemany & J. Jansá, 2007. Zooplankton time-series in the Balearic Sea (Western Mediterranean): variability during the decade 1994–2003. Progress in Oceanography 74: 329–354.
- García, A. & I. Palomera, 1996. Anchovy early life history and its relation to its surrounding environment in the Western Mediterranean Basin. Scientia Marina 60: 155–166.
- García Lafuente, J., J. M. Vargas, F. Criado, A. García, J. Delgado & S. Mazzola, 2005. Assessing the variability of hydrographic processes influencing the life cycle of the Sicilian Channel anchovy, *Engraulis encrasicolus*, by satellite imagery. Fisheries Oceanography 14: 32–46.
- Grimes, C. B., 2001. Fishery production and the Mississippi river discharge. Fisheries 26: 17–26.
- Hastie, T. J. & R. J. Tibshirani, 1990. Generalized Additive Models. Chapman & Hall, New York.
- Hay, D. E. & J. R. Brett, 1988. Maturation and fecundity of Pacific herring (*Clupea harengus pallasi*). Canadian Journal of Fisheries and Aquatic Sciences 45: 399–406.
- Lapolla, A. E., 2001. Bay anchovy Anchoa mitchilli in Narragansett Bay, Rhode Island. II. Spawning season, hatchdate distribution and young-of-the-year growth. Marine Ecology Progress Series 217: 103–109.
- Lasker, R., 1975. Field criteria for survival of anchovy larvae: the relation between inshore chlorophyll maximum layers and successful first feeding. U.S. Fisheries Bulletin 73: 453–462.
- Lasker, R., 1981. The role of a stable ocean in larval fish survival and subsequent recruitment. In Lasker, R. (ed.), Marine fish larvae: morphology, ecology, and relation to fisheries. Washington Sea Grant Program. University of Washington Press, Seattle: 80–87.
- Lloret, J., J. Lleonart, I. Solé & J. M. Fromentin, 2001. Fluctuations of landings and environmental conditions in the north-western Mediterranean Sea. Fisheries Oceanography 10: 33–50.
- Lloret, J., I. Palomera, J. Salat & I. Solé, 2004. Impact of freshwater input and wind on landings of anchovy

(*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*) in shelf waters surrounding the Ebre River Delta (northwestern Mediterranean). Fisheries Oceanography 13: 102–110.

- Lluch-Belda, D., R. M. J. Crawford, T. Kawasaki, A. D. MacCall, R. H. Parrish, R. A. Schwartzlose & P. E. Smith, 1989. World-wide fluctuations of sardine and anchovy stocks: the regime problem. South African Journal of marine Science 8: 195–205.
- López-García, M. J., C. Millot, J. Font & E. García-Ladona, 1994. Surface circulation variability in the Balearic Basin. Journal of Geophysical Research 99: 3285–3296.
- Luo, J. & J. A. Musick, 1991. Reproductive biology of the bay anchovy in Chesapeake Bay. Transactions of the American Fisheries Society 120: 701–710.
- Palomera, I., 1992. Spawning of anchovy *Engraulis encrasic*olus in the North Western Mediterranean relative to hydrographic features in the region. Marine Ecology Progress Series 79: 215–223.
- Palomera, I., M. P. Olivar, J. Salat, A. Sabatés, M. Coll, A. García & B. Morales-Nin, 2007. Small pelagic fish in the NW Mediterranean Sea: an ecological review. Progress in Oceanography 73: 377–396.
- Palomera, I. & A. Sabatés, 1990. Co-occurrence of *Engraulis* encrasicolus and *Sardinella aurita* eggs and larvae in the western Mediterranean. Scientia Marina 54: 51–67.
- Patti, B., A. Bonnano, G. Basilone, S. Goncharov, S. Mazzola, G. Buscaino, A. Cuttitta, J. García Lafuente, A. García, V. Palumbo & G. Cosimi, 2004. Inter-annual fluctuations in acoustic biomass and in landings of small pelagic fish populations in relation to hydrology in the Strait of Sicily. Chemistry and Ecology 20: 365–375.
- Peebles, E. B., 2002. Temporal resolution of biological and physical influences on bay anchovy *Anchoa mitchilli* egg abundance near a river-plume frontal zone. Marine Ecology Progress Series 237: 257–269.
- Peebles, E., B. Hall & J. R. Tolley, 1996. Egg production by the bay anchovy *Anchoa mitchilli* in relation to adult and larval prey fields. Marine Ecology Progress Series 131: 61–73.
- Pertierra, J. P. & J. Lleonart, 1996. NW Mediterranean anchovy fisheries. Scientia Marina 60: 257–267.
- Plounevez, S. & G. Champalbert, 2000. Diet, feeding behaviour and trophic activity of the anchovy (*Engraulis encrasicolus* L.) in the Gulf of Lions (Mediterranean Sea). Oceanografica Acta 23: 175–192.
- Razouls, C. & J. H. M. Kouwenberg, 1993. Spatial distribution and seasonal variation of mesozooplankton biomass in the Gulf of Lions (northwestern Mediterranean). Oceanologica Acta 16: 393–401.
- Regner, J. H., 1996. Effects of environmental changes on early stages and reproduction of anchovy in the Adriatic Sea. Scientia Marina 60: 167–177.
- Sabatés, A., P. Martín, J. Lloret & V. Raya, 2006. Sea warming and fish distribution: the case of the small pelagic fish

Sardinella aurita in the western Mediterranean. Global Change Biology 12: 2209–2219.

- Sabatés, A., M. P. Olivar, J. Salat, I. Palomera & F. Alemany, 2007a. Physical and biological processes controlling the distribution of fish larvae in the NW Mediterranean. Progress in Oceanography 74: 355–376.
- Sabatés, A., J. Salat & M. P. Olivar, 2001. Advection of continental water as export mechanism for anchovy, *Engraulis encrasicolus*, larvae. Scientia Marina 65: 77–88.
- Sabatés, A., J. Salat, I. Palomera, M. Emelianov, M. L. Fernández de Puelles & M. P. Olivar, 2007b. Advection of anchovy larvae along the Catalan continental slope (NW Mediterranean). Fisheries Oceanography 16: 130–141.
- SAC-GFCM, 2007. Subcommittee of Stock Assessment-General Fisheries Commission for the Mediterranean Assessment Forms. Doc7anchovyGSA07, available at: http://www.icm.csic.es/rec/projectes/scsa/.
- Santojanni, A., E. Arneri, V. Bernardini, N. Cingolani, M. Di Marco & A. Russo, 2006. Effects of environmental variables on recruitment of anchovy in the Adriatic Sea. Climate Research 31: 181–193.
- Somarakis, S., 2005. Marked interannual differences in reproductive parameters and daily egg production of anchovy in the northern Aegean Sea. Belgian Journal of Zoology 135: 247–252.
- Somarakis, S., I. Palomera, A. García, L. Quintanilla, C. Koutsikopoulos, A. Uriarte & L. Motos, 2004. Daily egg production of anchovy in European waters. ICES Journal of Marine Science 61: 944–958.
- Tudela, S. & I. Palomera, 1995. Diel feeding intensity and daily ration in the anchovy *Engraulis encrasicolus* in the Northwest Mediterranean sea during the spawning period. Marine Ecology Progress Series 129: 55–61.
- Tudela, S. & I. Palomera, 1997. Trophic ecology of European anchovy *Engraulis encrasicolus* in the Catalan Sea (Northwest Mediterranean). Marine Ecology Progress Series 160: 121–134.
- Tudela, S., I. Palomera & G. Quílez, 2002. Feeding of anchovy *Engraulis encrasiclolus* larvae in the northwest Mediterranean. Journal of the Marine Biological Association of the United Kingdom 82: 349–350.
- Ueyama, R. & B. C. Monger, 2005. Wind-induced modulation of seasonal phytoplankton blooms in the North Atlantic derived from satellite observations. Limnology and Oceanography 50: 1820–1829.
- Wood, S. N., 2000. Modelling and smoothing parameter estimation with multiple quadratic penalties. Journal of the Royal Statistical Society 62: 413–428.
- Zarrad, R., H. Missaoui, F. Alemany, R. M. Salah, A. García, M. Ridha, J. Othman & E. A. Amor, 2006. Spawning areas and larval distributions of anchovy Engraulis encrasicolus in relation to environmental conditions in the Gulf of Tunis (Central Mediterranean Sea). Scientia Marina 70S2: 137–146.

# FISH HABITAT MAPPING

# Modeling and predicting potential spawning habitat of anchovy (*Engraulis encrasicolus*) and round sardinella (*Sardinella aurita*) based on satellite environmental information

Eudoxia Schismenou · Marianna Giannoulaki · Vasilis D. Valavanis · Stylianos Somarakis

© Springer Science+Business Media B.V. 2008

**Abstract** Anchovy and round sardinella are two important small pelagic species in the Mediterranean that spawn during the summer period. This is a first attempt to model and predict the two species' potential spawning habitats in this area. Generalized additive models (GAMs) were constructed based on satellite environmental variables and presence/absence egg data, available from ichthyoplankton surveys conducted in the North Aegean Sea during early summer (June 2003–2006). These models were subsequently used to predict the probability of anchovy and round sardinella spawning in the Greek Seas as well as the entire Mediterranean and Black Sea during the same month of the year. The interaction of bottom depth and chlorophyll explained most of the deviance in the

Guest editor: V. D. Valavanis Essential Fish Habitat Mapping in the Mediterranean

E. Schismenou · S. Somarakis (⊠) Department of Biology, University of Crete, Vassilika Vouton, P.O. Box 2208, 71409 Heraklion Crete, Greece e-mail: somarak@her.hcmr.gr

E. Schismenou · M. Giannoulaki · S. Somarakis Institute of Marine Biological Resources, Hellenic Centre for Marine Research, Thalassocosmos, 71003 Heraklion Crete, Greece

V. D. Valavanis

Marine GIS Laboratory, Institute of Marine Biological Resources, Hellenic Centre for Marine Research, Thalassocosmos, 71003 Heraklion Crete, Greece presence/absence GAMs of both species, indicating spawning over continental shelf areas with increased surface chlorophyll values. Round sardinella spawned closer to coast than anchovy. Predicted potential spawning areas for anchovy and round sardinella in unsampled areas of the Greek Seas and the entire Mediterranean and Black Sea were in good agreement with existing information on the distribution and extent of the spawning grounds, especially for anchovy. Modeling the species' reproductive activity in relation to easily accessible environmental information and applying the models in a predictive way could be an initial, low-cost step to designate potential spawning fish habitats.

**Keywords** Anchovy · Sardinella · Potential spawning habitat · GAMs · Satellite data

# Introduction

European anchovy (*Engraulis encrasicolus*) and round sardinella (*Sardinella aurita*) are two of the most important (together with sardine, *Sardina pilchardus*, and sprat, *Sprattus sprattus*) small pelagic species in the Mediterranean in terms of commercial interest (Lleonart & Maynou, 2003). Anchovy is abundant in the northern Mediterranean basins, whereas round sardinella is most important in the southern part of this Sea (Pawson & Giama, 1985; Wassef et al., 1985; Stergiou et al., 1997; Lleonart & Maynou, 2003; Palomera et al., 2007).

Both species spawn during the summer period (Pawson & Giama, 1985; Wassef et al., 1985; Palomera & Sabates, 1990; Giraldez & Abad, 1995; Garcia & Palomera, 1996; Lisovenko & Andrianov, 1996; Somarakis et al., 2004; Gaamour et al., 2005; Tsikliras & Antonopoulou, 2006; Palomera et al., 2007). Eggs and larvae can be found in the plankton from spring to autumn (Palomera & Sabates, 1990; Sabates, 1990; Garcia & Palomera, 1996; Regner, 1996). Anchovy mainly spawns over continental shelf areas characterized by waters of low salinity and high primary and secondary production (Garcia & Palomera, 1996; Regner, 1996; Kideys et al., 1999; Somarakis et al., 2004; Somarakis et al., 2007; Palomera et al., 2007). Its spawning is usually associated with hydrographic structures (e.g., jets, gyres, eddies) that favor the advection of eggs and larvae within appropriate habitats (Salat, 1996; Agostini & Bakun, 2002; Garcia Lafuente et al., 2002; Cuttitta et al., 2003; Sabates et al., 2007; Somarakis & Nikolioudakis, 2007). The spawning of round sardinella is strongly associated with warm surface temperatures (Palomera & Sabates, 1990; Sabates et al., 2006; Tsikliras & Antonopoulou, 2006; Palomera et al., 2007) probably due to the species subtropical origin. However, in recent years, a number of studies have reported the occurrence and/or spawning of round sardinella in northern parts of the Mediterranean Sea (northern Aegean: Tsikliras & Antonopoulou, 2006; northern Adriatic: Dulcic & Grbec, 2000; Sinovcic et al., 2004; Gulf of Lions: Francour et al., 1994).

In recent years, predictive habitat distribution models have been gaining high popularity in ecology. This is mainly due to the introduction of new powerful statistical techniques and GIS (Geographic Information System) tools (Guisan & Zimmermann, 2000). Satellite environmental data have become largely available through international databases and provide promptly accessible and low-cost environmental variables to be used in habitat modeling.

In this paper, an attempt is made to model and predict the potential spawning habitat of anchovy and round sardinella in the Greek Seas, the entire Mediterranean basin, and the Black Sea. The term "potential spawning habitat," (PSH) has been recently defined by Planque et al. (2007). It is used to describe the areas where the environmental conditions are suitable for spawning, i.e., the broad geographical area that could support the spawning activity of a species, defined by environmental conditions and the preferred ranges for spawning. The PSH can change spatially and temporally according to changes in climate and the environment and includes the actual 'realized spawning habitat', i.e., the area where "spawning actually occurs" (Planque et al., 2007).

To predict the PSH for anchovy and round sardinella, we modeled presence/absence egg data from DEPM (Daily Egg Production Method) surveys in the North Aegean Sea (June 2003–2006, Somarakis et al., 2007) and satellite environmental data using Generalized Additive Models (GAMs). Spawning probability was subsequently predicted for nonsampled areas (including other areas of the Greek Seas and the entire Mediterranean and Black Seas) and compared with published information on the distribution and characteristics of spawning grounds of the two species.

# Materials and methods

The egg data were used to fit the GAM models derived from four DEPM surveys for estimation of the spawning stock biomass of the North Aegean anchovy stock (Somarakis et al., 2007). The ichthyoplankton surveys were carried out during June of the years 2003-2006. The sampling scheme was based on transects spaced approximately ten nautical miles apart and stations located at five-nautical-mile intervals on each transect (Fig. 1). The sampling protocol was the same during all DEPM surveys. Standard vertical plankton tows were made at each station using a WP2 sampler (mouth opening: 0.255 m<sup>2</sup>, mesh-size: 0.200 mm). Plankton samples were preserved in 10% buffered formalin. In the laboratory ichthyoplankton was sorted from the plankton samples and anchovy and round sardinella eggs and larvae were counted. The presence/absence data were used in the GAM models.

The environmental data analyzed here originated from satellite monitoring of the area. Sea surface temperature distribution (SST in °C) was downloaded from the German Aerospace Agency's (DLR) satellite data archive and sea surface chlorophyll



concentration (CHLO in mg/m<sup>3</sup>) was provided through NASA's Distributed Active Archive Center. Sea surface salinity (SSS) was downloaded from the Mediterranean Oceanic Database as a decadal climatological product (Brasseur et al., 1996). Bathymetry was calculated through processing (kriging) of a point dataset derived from a blending of depth soundings collected from ships with detailed gravity anomaly information obtained from the Geosat and ERS-1 satellite altimetry missions (Smith and Sandwell, 1997). Sea level anomaly (SLA in cm) was provided from the AVISO website using their Live Access Server. Photosynthetically active radiation (PAR in  $Ein/m^2/day$ ) is defined as the quantum energy flux from the sun in the spectral range 400-700 nm and it is available through Oceancolor web, NASA's online Distributed Active Archive Center. The mean monthly values of satellite imagery were estimated for all these variables (Valavanis et al., 2004).

Anchovy and round sardinella egg presence/ absence data and satellite environmental data were used to fit a GAM model in order to define the set of parameters that describe the PSH of the two species. For the selection of the GAMs smoothing predictors we applied the methodology proposed by Wood and Augustin (2002), using the "mgcv" library in the R statistical software (R Development Core Team, 2004). GAMs produced smoothed fits for each environmental predictor. The individual models could not be tested for significance based on the *P*values from the "mgcv" library output, since it was not possible to define the true number of degrees of freedom. The true number of degrees of freedom is probably much smaller than the one used to calculate the P-value because of strong spatial autocorrelation in the data (Planque et al., 2007). Thus, each fit was analyzed on the level of deviance explained (0-100%; the higher the better), the Akaike Information Criterion (AIC; the lower the better) and the confidence region for the smooth (which should not include zero throughout the range of the predictor). The degree of smoothing was selected based on the observed data and the Generalized Cross Validation method suggested by Wood (2006) and available in the "mgcv" library. According to the above criteria, the environmental predictors were ranked and the best model for anchovy and round sardinella was selected based on a stepwise forward selection method. The presence/absence of anchovy and round sardinella eggs were used as a response variable (y). The predictor variables (x) that we examined were the decadic logarithm of the bottom depth (DEP), the decadic logarithm of the chlorophyll (CHL), the SST, the SLA, and the PAR. The parameters bottom depth and chlorophyll were transformed in order to stabilize the variance (Venables & Dichmont, 2004). To ensure a good prediction of anchovy and round sardinella PSH, applicable over larger areas, data collected from a wide range of environmental conditions should be applied to fit the model (Planque et al., 2007). Thus, we used pooled data from all four years (2003–2006). The total number of positive (egg presence) stations for anchovy and round sardinella was 335 and 216, respectively. The data were modeled using a binomial error distribution and a logit link. All first-order interactions of the parameters included in the final model were tested.

To evaluate the predictive performance of the final models we used the Receiver Operating Characteristic (ROC)-plots (Fieldings & Bell, 1997; Guisan & Zimmerman, 2000) and the area under the Receiver Operating Characteristic curve (AUC) for each examined year. AUC measures the ability of a model to discriminate between those sites where a species is present and those where it is absent and has been broadly used in the species' distribution modeling literature (Hanley & McNeil, 1982). AUC values range from 0 to 1, with 1 standing for perfect discrimination, 0.5 for predictive discrimination that is no better than a random guess, and values <0.5indicate performance worse than random (Boyce et al., 2002; Elith et al., 2006). For the estimation of ROC and AUC the presence/absence library of the R statistical software was applied.

Finally, the GAM models were used to predict areas that could serve as PSHs of anchovy and round

sardinella in larger grids: the Greek Seas and the Mediterranean Sea with the adjacent Black Sea at a GIS resolution of 4 and 8 km, respectively. The 4-km GIS resolution was the best resolution available for chlorophyll (which had the less dense grid of all parameters), while the 8-km GIS resolution was chosen to reduce the volume of the dataset to a size that could be processed. These prediction grids included mean monthly satellite data of the environmental parameters that were selected in the final models concerning June 2003, 2004, 2005, and 2006. It must be pointed out here that predicted PSHs included those located in areas with environmental parameters of the range encountered during the Aegean Sea research surveys (i.e., the ranges of parameters used to develop the GAMs). For mapping we used the Surfer v8.0 of the Golden Software Inc. software.

# Results

The distribution and abundance of anchovy and round sardinella eggs are presented in Figs. 2 and 3,



Fig. 2 Distribution and abundance of anchovy eggs (eggs  $m^{-2}$ ) in June 2003–2006. The symbol (x) denotes negative station



Fig. 3 Distribution and abundance of round sardinella eggs (eggs  $m^{-2}$ ) in June 2003–2006. The symbol (x) denotes negative station

respectively. Anchovy eggs were occurring frequently and with higher abundance in the Thracian Sea, the Strymonikos Gulf, and the Thermaikos Gulf, except in 2004 and 2005 when spawning was less intense in the latter two gulfs. On the other hand, round sardinella eggs were consistently present and more abundant in the Strymonikos Gulf and the inner part of the Thermaikos Gulf.

The final model selected for anchovy eggs' presence/absence data (total deviance explained: about 41%) included SST as a main effect and the interaction of depth (DEP) and chlorophyll (CHL) (Table 1). All parameters in the final model were statistically significant.

In Fig. 4, results of the final GAM model are presented as plots of the best-fitting smooths for the effect of the environmental variables on anchovy egg presence. The 95% confidence intervals are also plotted around the best-fitting smooths for the main effect. The interactive effect is shown as perspective plot without error bounds. The relative importance of each environmental variable of the model is presented in x- and y-axes. In the z-axis, the interactive effect of both variables is presented (Fig. 4b). The rug under

the single variable effects plot indicates the density of points for different variable values (Fig. 4a). The effect of each variable is the conditional effect, i.e., the effect that this variable has, given that the other variables are included in the model. For anchovy, the SST plot indicated increasing probability of spawning with increasing temperature (Fig. 4a). The interaction plot of DEP and CHL indicated increasing probability of spawning with increasing values of CHL and intermediate available values of DEP (Fig. 4b).

The final model for round sardinella included Sea Level Anomaly (SLA) and the interaction of DEP and CHL (Table 1) and explained a low percentage of the deviance (about 20%). All parameters in the final model were statistically significant. In Fig. 5, results of the final GAM model are also presented as plots of the best-fitting smooths for the effect of the environmental variables on sardinella egg presence. For round sardinella, the SLA plot revealed increasing probability of spawning for values between -8 and -4 cm (Fig. 5a). The interaction plot of DEP and CHL indicated increasing probability of finding sardinella eggs with increasing values of CHL and in smaller depths (Fig. 5b).

	Parameter	Res. Df	Residual deviance	Deviance explained (%)	AIC	P-value
Anchovy	Null model	549	760.42			
	s(SST)	541.91	725.624.58450.3440.80	741.81	0.026	
	s(SST) + s(DEP : CHL)	536.71	450.34	40.80	476.92	$\ll 0.000$
Round sardinella	Null model	531	626.52			
	s(SLA)	522.94	589.29	5.94	607.42	0.002
	s(SLA) + s(DEP : CHL)	509.10	500.41	20.10	546.21	$\ll 0.000$

Table 1 Analysis of deviance for GAM covariates and their interactions of the final model fitted for anchovy and round sardinella

Level of significance was set to 0.05. The (:) sign denotes interaction. Res. d.f. = residual degrees of freedom.; AIC = Akaike Information Criterion value



Fig. 4 Plots of the smoothing response of the Generalized Additive Model for anchovy spawning against (a) SST and (b) the interaction of DEP and CHL. Black thick line indicates the

Model validation indicated good discrimination ability for both models as in most cases the estimated values of AUC exceeded 0.80 (Elith et al., 2006). More specifically, AUC values ranged between 0.87 and 0.91 for anchovy and between 0.81 and 0.87 for round sardinella, with the exception of 2003 when the AUC value for sardinella was lower (0.65).

The models for the two species were applied in a predictive way for the Greek Seas as well as for the entire Mediterranean and adjacent Black Sea. The resultant maps are presented in Figs. 6–9. For anchovy, the model indicated that the northern Aegean Sea is the major potential spawning ground (Fig. 6), while in the Mediterranean Sea, potential sites of increased spawning probability were mainly predicted in the Alboran Sea, the Gulf of Lions and



value of the GAM smoothing response and dotted lines represent the 95% confidence intervals

the Catalan coast, the eastern part of the Adriatic Sea, the Gulf of Gabes, the northern Aegean Sea, and the entire Black Sea (Fig. 8). For round sardinella, the model also indicated the northern Aegean Sea as the major potential spawning ground (Fig. 7). In the Mediterranean Sea, round sardinella potential spawning grounds were consistently predicted in the Gulf of Lions, the Gulf of Gabes, the northern and eastern Adriatic, the northern Aegean, and the coastal waters of Egypt (Fig. 9).

# Discussion

The application of the northern Aegean Sea GAM models to larger areas of similar environmental ranges

**Fig. 5** Plots of the smoothing response of the Generalized Additive Model for round sardinella spawning against (**a**) SLA and (**b**) the interaction of DEP and CHL. Black thick line in order to predict PSHs of anchovy and round sardinella seemed to depict reasonably well the two species' spawning grounds as known from past studies and publications. More specifically, in the Greek Seas the main spawning areas for anchovy were predicted in the North Aegean Sea (Fig. 6), which is in agreement with the observed distribution patterns of eggs (Fig. 2) and data from previous surveys (Somarakis et al., 2004; Somarakis, 2005; Somarakis et al., 2006). The North Aegean Sea is largely influenced by the Black Sea Water and river runoffs exhibiting characteristics

Sea Water and river runoffs exhibiting characteristics that are favorable for anchovy spawning (Agostini & Bakun, 2002; Somarakis et al., 2002a; Isari et al., 2006; Somarakis & Nikolioudakis, 2007). Other smaller spawning grounds were also predicted by the model in the central Ionian and Aegean Seas, which match well survey results of July 1998 and June 1999 in this area (Somarakis et al., 2002b; Somarakis et al., 2006). Certain recurring spots have also been identified in coastal areas of Asia Minor, along the Turkish coasts (e.g., Izmir Bay), which have been reported as anchovy fishing areas (Turan et al., 2004).

The main spawning areas of round sardinella in the Greek Seas were also predicted to be located in the North Aegean Sea (Fig. 7), as observed in the June 2003–2006 surveys (Fig. 3) and published elsewhere (Somarakis et al., 2002a; Tsikliras & Antonopoulou, 2006). Potential spawning sites were also identified in specific coastal sites of central Greece and Turkey.

indicates the value of the GAMs smoothing response and dotted lines represent the 95% confidence intervals

The anchovy model predictions for the entire Mediterranean and Black Sea indicated areas that corresponded well to already known spawning grounds (Fig. 8). Namely, the model indicated that the Black Sea is a major anchovy spawning ground. Indeed, anchovy is the most abundant species in the Black Sea and spawns all over the basin (Niermann et al., 1994; Kideys et al., 1999).

In the Adriatic Sea, anchovy was predicted to spawn with a high probability in the northern and the western part of the basin (Fig. 8). This Sea is characterized by major river outflows and increased primary production, especially in its shallow northern part, and anchovies are known to spawn mainly along the western part of the basin (Regner, 1996). This is in good agreement with the predictions of our GAM model.

In the western Mediterranean, potential anchovy spawning grounds were found in the Gulf of Lions and the Catalan Sea, the Alboran Sea, and, to a lesser extent, along the Italian coasts of the Ligurian and Tyrrhenian Seas. Indeed, these are the main anchovy spawning areas in the western Mediterranean as indicated in all published reviews (Garcia & Palomera, 1996; Palomera et al., 2007).

Anchovy spawning was further predicted along the south Sicilian coasts, the Gulf of Gabes, the coasts of Egypt and the northeastern corner of the Levantine Basin (Iskenderum Bay). Although the Sicilian channel is known to be inhabited by a small, highly



(a)

Effect on round sardinella spawning

5

0

5

N

ŝ

4

-12

-10

-8

-6

SLA

0

.2



Fig. 6 Map of areas representing anchovy potential spawning habitat in Greek waters based on the GAM model from the North Aegean Sea. Gray color: >25%; black color: >50% probability of spawning

fluctuating anchovy stock (Cuttitta et al., 2003; Somarakis et al. 2004), very few are known about anchovy spawning in the remaining areas (e.g., Zarrad et al., 2006). However, anchovy constitutes a significant proportion of the pelagic fish catch in Tunis (Gaamour et al., 2005), Egypt (Wassef et al., 1985) and the Iskenderum Bay (Turan et al., 2004).

Except the Greek Seas, potential spawning grounds for round sardinella in the eastern Mediterranean (Fig. 9) were mainly predicted along the coasts of Egypt where round sardinella is the most important of the exploited species (Wassef et al., 1985). The prediction of potential spawning for sardinella in the Black Sea for June 2003 is not supported by existing knowledge, although there are records of round sardinella presence in the area (Bauchot, 1987).

In the central Mediterranean, round sardinella potential grounds were consistently predicted in the Adriatic Sea and the Gulf of Gabes. Although relevant information is scant, there are several reports of spawning of this species in the Adriatic (Gamulin & Hure, 1983; Sinovcic et al., 2004) and its abundance has been increasing during recent years (Dulcic & Grbec, 2000). In the Tunisian waters there are also several reports for round sardinella reproductive activity and spawning (Gaamour et al., 2005; Zarrad et al., 2007). The round sardinella is an important



Fig. 7 Map of areas representing round sardinella potential spawning habitat in Greek waters based on the GAM model from the North Aegean Sea. Gray color: >25%; black color: >50% probability of spawning

catch of the Tunisian pelagic fishery (Gaamour et al., 2005).

In the western Mediterranean, potential spawning sites for round sardinella were mainly predicted in the Gulf of Lions and the Catalan coasts in accordance with known spawning grounds (Palomera & Sabates, 1990; Sabates et al., 2006; Palomera et al., 2007).

In this study, egg presence data of anchovy and round sardinella were modeled with satellite environmental data. The data do not represent the actual environmental conditions that the populations experience in the water column. They rather reflect the sea surface conditions. However, the predictions for anchovy and round sardinella potential spawning areas corresponded well with our knowledge of the distribution and extent of the spawning grounds. Especially for anchovy, the model was quite effective explaining almost 41% of the deviance and predicted well the main spawning grounds of the species in the Mediterranean Sea (northern Aegean, western Adriatic, Gulf of Lions and Catalan coast, Alboran Sea). The deviance explained by the sardinella model was low (about 20%) and this could be partially attributed to the limited number of positive stations used to estimate the general additive model.

Further development of such models with larger datasets covering numerous spawning sites in

**Fig. 8** Mediterranean Sea. Map of areas representing anchovy potential spawning habitat based on the GAM model from the North Aegean Sea. Gray color: >25%; black color: >50% probability of spawning



different seasons and years (i.e., taking into account a wider range of environmental conditions) would be expected to significantly increase the effectiveness of the method and the predicting capacities of spawning habitats (Twatwa et al., 2005). Predicting PSHs using parameters that represent layers of the water column

other than the surface would evidently improve our understanding of species spawning habitats. For example, Planque et al. (2007) found that anchovy potential spawning in the Bay of Biscay was primarily related to bottom temperature followed by surface temperature and the mixed-layer depth. Fig. 9 Mediterranean Sea. Map of areas representing round sardinella potential spawning habitat based on the GAM model from the North Aegean Sea. Gray color: >25%; black color: >50% probability of spawning



Our models for both anchovy and round sardinella incorporated the interaction term of depth and chlorophyll. This term explained the larger part of deviance, especially in the anchovy model. Both species seem to have a preference for relatively high values of chlorophyll, i.e., high primary productivity. However, they are both coastal species seeking for particular depth ranges. This can explain the significance of the depth-chlorophyll interaction, i.e., the two species spawn in the more productive areas within their preferred depth ranges over the continental shelf.

The observed patterns of egg distribution and predicted spawning habitats indicate that there might be significant overlap between the spawning areas of the two species in both the Greek Seas and the Mediterranean basin. Spawning habitats are mainly located over continental shelf waters (<200 m); however, the spawning areas of round sardinella seem to be located more closely to the coast compared to those of anchovy, which is evident in this study if we consider the >50% probability of spawning (Figs. 6-9). Consequently, although the spawning periods of the two species largely coincide, a degree of spatial segregation seems to exist. These observations are consistent with published studies from the NW Mediterranean (Palomera & Sabates, 1990; Palomera et al., 2007).

In the anchovy model, there was a linear positive relationship with temperature. The association of anchovy eggs and larvae with areas of higher surface temperature has recently been demonstrated in Somarakis & Nikolioudakis (2007). In the northern Aegean Sea, such areas are mainly those characterized by anticyclonic circulation, which are rich in zooplankton and likely to constitute important areas for the retention of ichthyoplankton (Somarakis & Nikolioudakis, 2007).

The GAM model for round sardinella did not include the SST but this may again be attributed to poor model definition due to the limited positive egg data available for this species. Temperature is well known to play a major role in controlling the distribution and spawning of round sardinella in the Mediterranean Sea (Sabates et al., 2006). In recent years, there have been an increasing number of studies reporting the incidence of the warm-water round sardinella in northern areas of the Mediterranean basin. This has been attributed to climate change and sea warming (Francour et al. 1994; Dulcic & Gbrec, 2000; Sabates et al. 2006; Tsikliras & Antonopoulou, 2006). An increase of the species' population sizes in the northern Mediterranean could result in the expansion of its spawning grounds. Based on the potential spawning grounds maps produced in this study such an expansion is likely to cause major spatial overlap, increasing interspecific competition of the two species.

Finally, in the round sardinella model, the SLA was included as a main effect. The three peaks of SLA seemed to correspond to different ranges of the

parameter prevailing in different years. However, it is hard to evaluate at this stage the full ecological significance of this parameter.

Information on and prediction of potential spawning as well as habitats of other important life history phases (e.g., nursery habitats) could be of use in fisheries management for the design of appropriate actions to protect the exploited stocks. For example, the implementation of measures such as closed areas and seasons requires good knowledge of the spatial/ temporal distribution of sensitive habitats based on the collection and synthesis of fisheries-independent information on species requirements. Modeling the species' biological activities (e.g., spawning) in relation to easily accessible environmental information and applying the models in a predictive way could be an initial, low-cost step to designate potential habitats.

Acknowledgments The present study was partly supported by the DEPM and acoustic cruises of the National Program for Fisheries Data collection (2002–2006). The authors would like to thank the captain and the crew of R/V 'PHILIA' as well as Mr. A. Siapatis and Mrs. C. Stamataki for their help in sample collection and analysis.

# References

- Agostini, V. N. & A. Bakun, 2002. "Ocean triads" in the Mediterranean Sea: physical mechanisms potentially structuring reproductive habitat sustainability (with example application to European anchovy, *Engraulis encrasicolus*). Fisheries Oceanography 11: 129–142.
- Bauchot, M. L., 1987. Poissons osseux. In Fisher, W., M. Schneider & M. L. Bauchot (eds), Fishes FAO d'identification des especes pour les besoins de la peche: Mediterranee et mer Noire, Zone de peche 37, Vertebres: 861–1422.
- Boyce, M. S., P. R. Vernier, S. E. Nielsen & F. K. A. Schmiegelow, 2002. Evaluating resource selection functions. Ecological Modelling 157: 281–300.
- Brasseur, P., J. M. Brankart, R. Schoenauen & J. M. Beckers, 1996. Seasonal temperature and salinity fields in the Mediterranean Sea: climatological analyses of an historical data set. Deep-Sea Research 43: 159–192.
- Cuttitta, A., V. Carini, B. Patti, A. Bonanno, G. Basilone, S. Mazzola, J. Garcia Lafuente, A. Garcia, G. Buscaino, L. Aguzzi, L. Rollandi, G. Morizzo & C. Cavalcante, 2003. Anchovy egg and larval distribution in relation to biological and physical oceanography in the Strait of Sicily. Hydrobiologia 503: 117–120.
- Dulcic, J. & B. Grbec, 2000. Climate change and Adriatic ichthyofauna. Fisheries Oceanography 9: 187–191.
- Elith, J., C. H. Graham, R. P. Anderson, M. Dudık, S. Ferrier, A. Guisan, R. J. Hijmans, F. Huettmann, J. R. Leathwick,

A. Lehmann, J. Li, L. G. Lohmann, B. A. Loiselle, G. Manion, C. Moritz, M. Nakamura, Y. Nakazawa, J. McC,
A. T. Overton, S. J. Peterson, K. S. Phillips, R. Richardson, R. E. Scachetti-Pereira, J. Schapire, S. Soberon, M. S. Williams, N. E. Wisz & Zimmermann, 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography 29: 129–151.

- Fieldings, A. H. & J. F. Bell, 1997. A review of methods for the assessment of prediction errors in conservation presence: absence models. Environmental Conservation 24: 38–49.
- Francour, P., C. F. Boudouresque, J. G. Harmelin, M. L. Harmelin-Vivien & J. P. Quignard, 1994. Are the Mediterranean waters becoming warmer? Information from biological indicators. Marine Pollution Bulletin 28: 523–526.
- Gaamour, A., L. Ben-Abdallah, S. Khemiri & S. Mili, 2005. Etudes de la biologie et de l'exploitation des petits pélagiques en Tunisie. MedSudMed Technical Documents 5.
- Gamulin, T. & J. Hure, 1983. The spawning and spawning areas of pelagic fishes (Sardina plichardus, Engraulis encrasicolus, Scomber scombrus, Sardinella aurita and Sprattus sprattus sprattus) in the Adriatic Sea. Acta Adriatica 24: 97–131.
- Garcia, A. & I. Palomera, 1996. Anchovy early life history and its relation to its surrounding environment in the Western Mediterranean basin. Scientia Marina 60: 155–166.
- Garcia Lafuente, J., A. Garcia, S. Mazzola, L. Quintanilla, J. Delgado, A. Cuttita & B. Patti, 2002. Hydrographic phenomena influencing early life stages of the Sicilian Channel anchovy. Fisheries Oceanography 11: 31–44.
- Giraldez, A. & R. Abad, 1995. Aspects on the reproductive biology of the Western Mediterranean anchovy from the coasts of Malaga (Alboran Sea). Scientia Marina 59: 15–23.
- Guisan, A. & N. E. Zimmermann, 2000. Predictive habitat distribution models in ecology. Ecological Modelling 135: 147–186.
- Hanley, J. A. & B. J. McNeil, 1982. The meaning and use of the area under a Receiver Operating Characteristic (ROC) curve. Radiology 143: 29–36.
- Isari, S., A. Ramfos, S. Somarakis, C. Koutsikopoulos, A. Kallianiotis & N. Fragopoulu, 2006. Mesozooplankton distribution in relation to hydrology of the Northeastern Aegean Sea, Eastern Mediterranean. Journal of Plankton Research 28: 241–255.
- Kideys, A. E., A. D. Gordina, F. Bingel & U. Niermann, 1999. The effect of environmental conditions on the distribution of eggs and larvae of anchovy (*Engraulis Encrasicolus* L.) in the Black Sea. ICES Journal of Marine Science 56: 58–64.
- Lisovenko, L. A. & D. P. Andrianov, 1996. Reproductive biology of anchovy (*Engraulis encrasicolus ponticus* Alexandrov 1927) in the Black Sea. Scientia Marina 60: 209–218.
- Lleonart, J. & F. Maynou, 2003. Fish stock assessments in the Mediterranean: state of the art. Scientia Marina 67: 37–49.
- Niermann, U., E. Bingel, A. Gorban, A. D. Gordina, A. C. Gucu, A. E. Kideys, A. Konsulov, G. Radu, A. A. Subbotin & V. E. Zaika, 1994. Distribution of anchovy eggs and larvae (*Engraulis encrasicolus* Cuv.) in the Black Sea in 1991– 1992. ICES Journal of Marine Science 51: 395–406.
- Palomera, I. & A. Sabates, 1990. Co-occurrence of *Engraulis encrasicolus* and *Sardinella aurita* eggs and larvae in the northwestern Mediterranean. Scientia Marina 54: 61–67.

- Palomera, I., M. P. Olivar, J. Salat, A. Sabates, M. Coll, A. Garcia & B. Morales-Nin, 2007. Small pelagic in the NW Mediterranean Sea: An ecological review. Progress in Oceanography 74: 377–396.
- Pawson, M. G. & M. S. Giama, 1985. A biological sampling problem illustrated by the population structure and growth patterns of *Sardinella aurita* at Tripoli, Libya. Environmental Biology of Fishes 12: 143–154.
- Planque, B., E. Bellier & P. Lazure, 2007. Modelling potential spawning habitat of sardine (*Sardina pilchardus*) and anchovy (*Engraulis encrasicolus*) in the Bay of Biscay. Fisheries Oceanography 16: 16–30.
- R Development Core Team, 2004. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.Rproject.org.
- Regner, S., 1996. Effects of environmental changes on early stages and reproduction of anchovy in the Adriatic Sea. Scientia Marina 60: 167–177.
- Sabates, A., 1990. Distribution pattern of larval fish populations in the Northwestern Mediterranean. Marine Ecology Progress Series 59: 75–82.
- Sabates, A., P. Martin, J. Lloret & V. Raya, 2006. Sea warming and fish distribution: the case of the small pelagic fish *Sardinella aurita*, in the western Mediterranean. Global Change Biology 12: 2209–2219.
- Sabates, A., M. P. Olivar, J. Salat, I. Palomera & F. Alemany, 2007. Physical and biological processes controlling the distribution of fish larvae in the NW Mediterranean. Progress in Oceanography 74: 355–376.
- Salat, J., 1996. Review of hydrographic environmental factors that may influence anchovy habitats in northwestern Mediterranean. Scientia Marina 60: 21–32.
- Sinovcic, G., M. Franicevic & V. Cikes-Kec, 2004. Unusual occurrence and some aspects of biology of juvenile gilt sardine (*Sardinella aurita* Valenciennes, 1847) in the Zrmanja River estuary (eastern Adriatic). Journal of Applied Ichthyology 20: 53–57.
- Smith, W. H. F. & D. T. Sandwell, 1997. Global sea floor topography from satellite altimetry and ship depth soundings. Science 277: 1956–1962.
- Somarakis, S., 2005. Marked interannual differences in reproductive parameters and daily egg production of anchovy in the northern Aegean Sea. Belgian Journal of Zoology 134: 123–132.
- Somarakis, S., P. Drakopoulos & V. Filippou, 2002a. Distribution and abundance of larval fish in the northern Aegean Sea -eastern Mediterranean- in relation to early summer oceanographic conditions. Journal of Plankton Research 24: 339–357.
- Somarakis, S., C. Koutsikopoulos, A. Machias & N. Tsimenides, 2002b. Applying the daily egg production method (DEPM) to small stocks in highly heterogenous seas. Fisheries Research 55: 193–204.
- Somarakis, S., A. Machias, M. Giannoulaki, E. Schismenou, K. Tsagarakis, A. Siapatis, C. Stamataki, M. Torre, A. Anastasopoulou, V. Vassilopoulou, A. Kalianiotis & C. Papaconstantinou, 2007. Ichthyoplanktonic and acoustic biomass estimates of anchovy in the Aegean Sea (June 2003, 2004, 2005 and 2006). General Fisheries Commission for the Mediterranean, Scientific Advisory

Committee, Sub-Committee for Stock Assessment, Working Group on Small Pelagic Species, Athens: 29.

- Somarakis, S. & N. Nikolioudakis, 2007. Oceanographic habitat, growth and mortality of larval anchovy (*Engraulis encrasicolus*) in the northern Aegean Sea (eastern Mediterranean). Marine Biology 152: 1143–1158.
- Somarakis, S., I. Palomera, A. Garcia, L. Quantanilla, C. Koutsikopoulos & L. Motos, 2004. Daily egg production of anchovy in European waters. ICES Journal of Marine Science 61: 944–958.
- Somarakis, S., D. E. Tsianis, A. Machias & K. I. Stergiou, 2006. An overview of biological data related to anchovy and sardine stocks in Greek waters. In Palomares, M. L. D., K. I. Stergiou & D. Pauly (eds), Fishes in Databases and Ecosystems. Fisheries Centre Research Reports 14. Fisheries Centre, University of British Columbia: 56–64.
- Stergiou, K. I., E. D. Christou, D. Georgopoulos, A. Zenetos & C. Souvermezoglou, 1997. The Hellenic Seas: Physics, chemistry, biology and fisheries. Oceanography and Marine Biology 35: 415–538.
- Tsikliras, A. C. & E. Antonopoulou, 2006. Reproductive biology of round sardinella (*Sardinella aurita*) in the north-eastern Mediterranean. Scientia Marina 70: 281–290.
- Turan, K., D. Erguden, M. Gurlek, N. Basusta & F. Turan, 2004. Morphometric structuring of the Anchovy (*Eng-raulis encrasicolus* L.) in the Black, Aegean and Northeastern Mediterranean Seas. Turkish Journal of Veterinary and Animal Sciences 28: 865–871.
- Twatwa, N. M., C. D. van der Lingen, L. Drapeau, C. L. Moloney & J. G. Field, 2005. Characterising and

comparing the spawning habitats of anchovy *Engraulis encrasicolus* and sardine *Sardinops sagax* in the southern Benguella upwelling ecosystem. African Journal of Marine Science 27: 487–499.

- Valavanis, V. D., S. Georgakarakos, A. Kapantagakis, A. Palialexis & I. Katara, 2004. A GIS environmental modeling approach to Essential Fish Habitat Designation. Ecological Modeling 178: 417–427.
- Venables, W. N. & C. M. Dichmont, 2004. GLMs, GAMs and GLMMs: an overview of theory for applications in fisheries research. Fisheries Research 70: 319–337.
- Wassef, E., A. Ezzat, T. Hashem & S. Faltas, 1985. Sardine fishery by purse-seine on the Egyptian Mediterranean coast. Marine Ecology Progress Series 26: 11–18.
- Wood, S. N., 2006. Generalized Additive Models. An Introduction with R. Chapman & Hall/CRC, Boca Raton.
- Wood, S. N. & N. H. Augustin, 2002. GAMs with integrated model selection using penalized regression splines and applications to environmental modelling. Ecological Modelling 157: 157–177.
- Zarrad, R., H. Missaoui, F. Alemany, R. M. Salah, A. Garcia, M. Ridhah, J. Othman & E. Amor, 2006. Spawning areas and larval distributions of anchovy *Engraulis encrasicolus* in relation to environmental conditions in the Gulf of Tunis (Central Mediterranean Sea). Scientia Marina 70: 137–146.
- Zarrad, R., H. Missaoui, M. S. Romdhane, O. Jarboui & R. M'Rabet, 2007. Sardinella aurita egg and larval distributions and sea temperature in the Tunis Gulf. Rapporte de la Communaute Internationale de la Mer Mediterranee 38: 640.

# FISH HABITAT MAPPING

# Habitat discrimination of juvenile sardines in the Aegean Sea using remotely sensed environmental data

Konstantinos Tsagarakis · Athanassios Machias · Stylianos Somarakis · Marianna Giannoulaki · Andreas Palialexis · Vasilis D. Valavanis

© Springer Science+Business Media B.V. 2008

**Abstract** Despite the importance of the recruitment process for small pelagic fish and the high economic importance of European sardine (*Sardina pilchardus*, Walbaum 1792) in the Mediterranean Sea, knowledge on the distribution and environmental characteristics of its nursery grounds is very limited. In the present study, we used pelagic trawl data collected during 1995–2006 to explore the spatial distribution of sardine juveniles in the Aegean Sea in early summer. Based on sardine abundance per length

K. Tsagarakis · S. Somarakis · M. Giannoulaki · A. Palialexis

Institute of Marine Biological Resources, Hellenic Centre for Marine Research, Thalassocosmos, 71003 Heraklion Crete, Greece

K. Tsagarakis · A. Palialexis Department of Biology, University of Crete, Vassilika Vouton, P.O. Box 2208, 71409 Heraklion Crete, Greece

A. Machias (🖂)

Institute of Marine Biological Resources, Hellenic Centre for Marine Research, Aghios Kosmas, 16777 Helliniko, Greece e-mail: amachias@ath.hcmr.gr

c-man: amacmas@atn.nem

V. D. Valavanis

Marine GIS Laboratory, Institute of Marine Biological Resources, Hellenic Centre for Marine Research, Thalassocosmos, 71003 Heraklion Crete, Greece class, a cluster analysis was initially used to define hauls dominated by juveniles. In a subsequent step, Discriminant Function Analysis (DFA) was applied to discriminate stations with high relative abundance of juveniles using satellite environmental data and bottom depth. The parameters contributing mostly to the discrimination of juvenile grounds were sea level anomaly, photosynthetically active radiation, sea surface temperature, chlorophyll- $\alpha$  and bottom depth. The classification functions of DFA were finally used to post classify unsampled areas in the Greek Seas and the Mediterranean Sea in order to map grounds that meet characteristic environmental conditions for young sardine. Such areas were mostly located inshore, in semi-closed productive areas and often in proximity to river mouths, a pattern that is generally supported by existing information.

**Keywords** Small pelagic fish · Sardine's juveniles · Nursery grounds · Remote sensing · Aegean Sea · Eastern Mediterranean

# Introduction

Knowledge on the distribution of the different life stages of a species is fundamental in ecology and conservation planning (Freon & Misund, 1999; Reynolds et al., 2001). Especially when it comes to decision making, as in the case of fisheries

Guest editor: V. D. Valavanis Essential Fish Habitat Mapping in the Mediterranean

management, this knowledge almost constitutes a requirement. For several fish species, especially small pelagic, different patterns in the spatial distribution of juvenile and adult fish have been observed. Regarding the European sardine (Sardina pilchardus, Walbaum 1792), Porteiro et al. (1986) described a gradient in species distribution off Galicia, which was related to age classes. In the Gulf of Lions (Western Mediterranean—France), sardine juveniles are mostly located close to the coast (Bigot, 2007) while in the Tramontana region (Western Mediterranean-Spain) sardine juveniles are mainly located near the Ebro river delta (Giráldez et al., 2005). This differentiation in the spatial distribution of juveniles and adults is probably related to biological requirements, environmental conditions, hydrographic characteristics and biotic factors and may reflect the fish response to the gradient rather than to the absolute value of a parameter (Freon & Misund, 1999).

Sardine constitutes almost 20% of Mediterranean (Lleonard & Maynou, 2003) and 12% of the Greek annual landings (Stergiou et al., 1997). Despite its high economic importance and demand for effective management, the knowledge on basic aspects of juvenile sardine ecology, distribution and the environmental characteristics of nursery grounds is limited (Palomera et al., 2007). The growing availability and reliability of environmental information through remote sensing techniques during the recent years may serve as a tool to overcome these gaps of knowledge (Turner et al., 2003). This environmental information has the advantage that it can be obtained easily and almost in real time allowing its application in habitat modelling and the development of largescale descriptive and predictive models for various time periods that field sampling is not necessarily available (Turner et al., 2003; Elith et al., 2006).

In the present work, we identify the grounds of sardine juveniles during June. Identification is based on the discrimination of environmental characteristics (i.e. satellite environmental data as well as bathymetry data) of certain areas in Aegean Sea (Eastern Mediterranean—Greece), which presented high relative abundance of sardine juveniles in experimental trawling. Results are applied to predict and map the areas characterized by environmental conditions that could serve as nursery grounds for sardine juveniles in Greek Seas and the entire Mediterranean Sea.

#### Materials and methods

#### Study area

The northern Aegean Sea is one of the most important fishing grounds for small pelagic fish (mainly anchovy and sardine) in Greek waters (Stergiou et al., 1997; Somarakis et al., 2006). Aegean Sea is generally characterized by a complex hydrography and diverse topographic characteristics (Lykousis et al., 2002; Somarakis et al., 2002). Surface water layers are influenced by nutrient rich, low saline, Black Sea Water inputs while water column is influenced by oligotrophic Levantine Intermediate Waters (Stergiou et al., 1997; Siokou-Frangou et al., 2002). The coastal zone of the Aegean Sea is influenced by river flows, enhancing the productivity of the area locally (Karageorgis et al., 2001; Isari et al., 2006). Certain gyre-eddy formations and thermal fronts increase the complexity of the water characteristics (Nittis & Perivoliotis, 2002; Somarakis et al., 2002; Zervakis & Georgopoulos, 2002). Moreover, the region is characterized by peculiar topography, with variable sized open areas (e.g. Thracian Sea) connected with semi-enclosed gulfs (e.g. North Evoikos, Strymonikos and Thermaikos gulfs) affecting the ecological features of the marine ecosystem and the spatial distribution of small pelagic fish (Giannoulaki et al., 2003, 2006).

#### Data collection

Data were collected on board R/V Philia in Aegean Sea (Greece) (Fig. 1) during six research surveys (1998-99 and 2003-06). All surveys were held during June of each year, which coincides with the recruitment period for sardine in the Greek Seas (Somarakis et al., 2006; Machias et al., 2007). Fish specimens were collected with experimental fishing in the framework of acoustic surveys. Hauls were mainly held on locations with high fish concentrations and were well distributed along the surveyed areas (Fig. 1). A pelagic trawl with 10 m opening and 8 mm codend mesh size was used. Trawl duration ranged between 37 and 151 min. For each haul, a representative sample of at least 150 specimens was used to measure the total length to the closest mm, and the length frequency distribution (numbers/hour weighted by the total catch of the haul) per 5 mm **Fig. 1** Aegean (study area) and Ionian Seas. Major areas used in this work are indicated in the map. Cross symbols indicate the positions of the hauls held between 1998 and 2006



length classes was estimated. In total, data from 63 hauls with sardine catches were used.

## Data analysis

In a first step of the analysis, we explored whether there were hauls dominated by juveniles or all hauls presented similar compositions. We therefore examined the similarity of the hauls based on the abundance per length class in each haul. The hauls were grouped by applying multivariate techniques using as variables the weighted abundance (fourth root transformation of numbers/hour) at each length class recorded in the haul. For this purpose, we applied cluster analysis using a Bray–Curtis similarity matrix (Field et al., 1982). The analysis was carried out using the Primer v.5 software (Clarke & Warwick, 1994).

Cluster grouping was subsequently examined in relation to the relative abundance of juveniles, i.e. fish smaller than 115 mm length, which approximates the length at first maturity for sardine in the Aegean Sea (Somarakis et al., 2006). Hauls with 100%, >75%, >50% and >25% contribution of juveniles to the total sardine catch were considered.

The second analytical step included the application of a stepwise backward Discriminant Function Analysis (DFA) in order to examine whether the dominance of juveniles could be explained in terms of certain environmental characteristics. We used relative abundance of juveniles (as described above) as classification factor and environmental satellite data and mean bottom depth at the haul route as explanatory variables. Bottom depth (D in m) was calculated through processing (kriging) of a point dataset derived from a blending of depth soundings collected from ships with detailed gravity anomaly information obtained from the Geosat and ERS-1 satellite altimetry missions (Smith & Sandwell, 1997). Concerning environmental data, we used mean weekly values of sea surface temperature (SST in °C) available through the German Aerospace Agency's (DLR) satellite data archive (EOWEB), chlorophyll- $\alpha$  (CHLA in mg/m<sup>3</sup>) and photosynthetic active radiation (PAR in Ein/m<sup>2</sup>/day) downloaded through Oceancolor Web (NASA's online Distributed Active Archive Center), sea level anomaly (SLA in cm) available through AVISO website using their Live Access Server, and mean monthly values of sea surface salinity (SSS in ppt) estimated from CMA BCC GODAS model, (Liu et al., 2005) available through the International Research Institute for Climate and Society (IRI-University of Columbia) online data distribution archive. The location (coordinates) of each haul was used to assign environmental variables using GIS techniques (for details see Valavanis et al., 2004). Through this procedure, we estimated the environmental parameters as well as the classification functions that discriminate areas where juveniles tend to

concentrate. Cross-validation based on the leave-oneout method was used to evaluate the performance of the Discriminant function (McLachlan, 1992). Discriminant analysis was performed using the S-PLUS 2000 (MathSoft Inc, 1999) statistical software.

In the last analytical step, we used environmental satellite and bottom depth data to post classify areas based on the estimated classification functions of DFA. In this way, we mapped the regions, which were characterized by those environmental conditions that can likely support increased presence of juvenile sardine. Mapping was applied at 1.3 km (Aegean and Ionian Seas) and 4 km resolution (Mediterranean Sea) for June 2004–2006. The Surfer v8.0 software (Golden Software, 2002) was used for mapping.

#### Results

Seven hauls included 100% juveniles while 19, 23 and 32 hauls contained more than 75%, 50% and 25% juveniles, respectively. Hauls with juveniles were generally grouped together by the cluster analysis (Fig. 2), except those hauls containing 100% juveniles, which were very few in number. Best match with cluster grouping was observed for hauls containing 75% and 50% juveniles (Fig. 2B, C).

The results of the DFA (including classification function coefficients and cross-validation results) are shown in Table 1. The analysis for hauls with 100% juveniles is not shown due to low number of hauls as well as non significant results derived from discrimination. The high percentages of correct assignments (>77% and >66% for cross-validated values) denoted satisfactory results (Table 1), but the percentage of correctly classified cases was higher for the hauls containing more than 50% juveniles. The parameters mostly contributing to the aforementioned discrimination were D, SST, CHLA, PAR and SLA (Table 1).

Following the examination of cluster and DFA results, the classification factor ">50% juveniles" and the corresponding Discriminant Function were chosen as the most appropriate factors for mapping potential 'juvenile areas'. Maps indicate the spots that were post-classified as juvenile areas in the Greek Seas according to the included environmental parameters (Fig 3). Indicated areas, although exhibiting spatial variability across years, are mostly confined to the coastal waters



Fig. 2 Cluster analysis results. Black dots indicate hauls with relative abundance of juveniles (A) 100% (B) at least 75%, (C) at least 50% and (D) at least 25%

Table 1 DFA results. SLA: sea level anomaly, PAR: photosynthetic active radiation, SST: sea surface temperature, CHLA: chlorophyll-a, SSS: sea surface salinity. D: depth. Classification Function Coefficients for juvenile (A) and non juvenile (B) areas are shown. Cross validated assignments were based on-leave-one-out cross-validation

Factor	Wilks' $\lambda$	<i>P</i> -	Variables	Classification function co	pefficients	Correct	Cross
		value		A	В	assignments (%)	Validated assignments (%)
Over 75%	0.74	0.007	SLA	10.589	10.161	77.78	77.78
juveniles			PAR	11.294	11.380		
			SST	0.324	0.509		
			CHLA	63.368	62.726		
			SSS	376.580	375.964		
			D	-0.834	-0.815		
				Constant = -7534.360	Constant = -7521.920		
Over 50%	0.74	0.004	SLA	-1.583	-1.941	84.13	73.02
juveniles			PAR	6.515	6.723		
			SST	3.828	3.961		
			CHLA	74.159	75.418		
			D	0.245	0.265		
				Constant = -252.983	Constant = -270.723		
Over 25% juveniles	0.66	0.000	SLA	-0.925	-1.416	79.37	66.67
			PAR	6.013	6.042		
			SST	3.474	3.422		
			CHLA	72.984	77.160		
			D	0.208	0.237		
				Constant = -236.38	Constant = -242.01		

of Thracian Sea and Thermaikos Gulf, the northern part of North Evoikos Gulf, in almost the entire South Evoikos Gulf as well as in certain parts of the Saronikos, Corinthiakos and Patraikos gulfs.

Extrapolated mapping for the Western Mediterranean predicted areas located in the Adriatic Sea, the Sicily Channel, the Tyrrhenian Sea (northwestern Italy), and the Gulf of Lions, Catalan and Alboran seas (Fig. 4). In Eastern Mediterranean maps (Fig. 5), indicated areas in Turkish coastal waters of the Aegean Sea, along the Egyptian coastline (mainly off the Nile River Delta), coastal waters of Tunisia (Gulf of Gabes) and Libya.

# Discussion

We propose a simple methodology for the discrimination of regions that could support the occurrence of sardine juveniles. The methodology allows (i) flexibility in setting the criteria to define the nursery grounds (because it is based on the relative abundance of juveniles), (ii) the selection of the most significant environmental parameters for the discrimination of the nursery areas and (iii) the mapping of regions that feature the predicted characteristics Furthermore, the main advantage of the proposed method is that it permits a definition and mapping of potential nursery grounds with relatively few data.

During early summer the population of sardine in the Greek Seas is characterized by high abundance of juveniles (Machias et al., 2007). Cluster analysis revealed the grouping of hauls with increased presence of sardine juveniles suggesting that, in the Aegean Sea, there are spatial differences in the relative abundance of juveniles and adults, which is very important for the management of the stocks. Furthermore, given that the horizontal distributions of juvenile and adult fish overlap at varying degrees, a criterion such as 50% or 75% of juveniles in the catch seems to be a reasonable cutoff point for the definition of nursery grounds.



**Fig. 3** Geographic distribution of regions post-classified as "juvenile" areas, by applying the DFA for a grid of spots within the Greek Seas, for June 2004–2006

22°

24°

26

28°

DFA indicated that areas with juveniles were adequately discriminated based on the values of certain satellite environmental parameters and bottom depth (SST, PAR, SLA, CHLA and D), probably reflecting differences in habitat preferences of juveniles. The use of satellite data has the advantage that it can be easily obtained for various years and areas,

35

2006

20°



**Fig. 4** Geographic distribution of regions post-classified as "juvenile" areas, by applying the DFA for a grid of spots within the Western Mediterranean Sea, for June 2004–2006

while they are available almost in real time. Although satellite data do not describe the actual conditions at sea, they seem to provide a general good description of the areas that sardine juveniles are concentrated during early summer.

Mapping for the Greek Seas, based on the classification functions estimated by DFA, indicated that juveniles are concentrated inshore, in semiclosed productive areas and often in proximity to river estuaries (Fig. 3). Despite the fact that our



**Fig. 5** Geographic distribution of regions post-classified as "juvenile" areas, by applying the DFA for a grid of spots within the Eastern Mediterranean Sea, for June 2004–2006

knowledge on the distribution of juveniles in Greek Seas is limited, certain areas known to serve as nursery grounds were post-classified as "Juvenile" areas, confirming the reliability of results. These areas include the coastal waters of the northern part of Corinthiakos and Patraikos gulfs (Anonymous, 2001), characterized by local, seasonal upwelling events and/or river outflow.

Results also agree with findings from other regions of the Mediterranean Sea. In the Gulf of Lions, nursery areas of sardine are known to be located in lagoons and close to the coast (Bigot, 2007) while in Tramontana region, the most important concentration area for juvenile sardines is located near the mouth of the Ebro River (Giráldez et al., 2005). Moreover, nursery grounds have also been reported in the North Alboran Sea (Alemany et al., 2006). Extended parts of these regions were consistently classified as sardine nursery grounds (Figs. 4, 5).

The size of the nursery areas as indicated by our mapping (Figs. 3–5), seems to present inter-annual variability depending on the environmental conditions. These fluctuations may also be related to the successful recruitment of sardine. The broad nursery areas of 2004 (Figs. 3–5) may be an explanation for the increase of Greek sardine landings (from 9,217 mt to 11,258 mt; Greek National Statistical Service) and Mediterranean sardine landings (from 181,738 mt to 203,541 mt; FAO) in 2005. The approach we follow here could be useful in justifying similar trends.

The absence of field data concerning the spatial distribution of sardine juveniles did not allow a quantitative evaluation of our predictions. The reliability of such maps should be checked by collecting appropriate field data. However, considering the lack of information regarding the spatial distribution of small pelagic juveniles, the proposed method might be particularly useful in mapping juvenile habitat across years and areas and may turn out helpful when addressing management issues and especially for precautionary measures (e.g. MPAs definition). In addition, the method could be a practical tool for sampling design through selection of survey areas for the study of juvenile fish. The use of data from additional years, seasons and areas will improve the identification of such areas while a regular field monitoring may track variations of juvenile fish habitat preferences due to large scale atmospheric, oceanic and climate change.

Acknowledgements The present work was based on data collected during surveys for the "Greek National Fisheries Data Collection Program" (Hellenic Ministry of Rural Development and Food) and was co-funded by the Commission of the European Communities through the projects "Environmental Approach to Essential Fish Habitat Designation" (FP6-22466) and "SARDONE: Improving Assessment and Management of Small Pelagic Species in the Mediterranean" (FP6-44294). We would like to thank the captain and the crew of R/V Philia for their invaluable help.

#### References

- Alemany, F., I. Alvarez, A. Garcia, D. Cortes, T. Ramirez, J. Quintanilla, F. Álvarez & J. M. Rodriguez, 2006. Postflexion larvae and juvenile daily growth patterns of the Alborán Sea sardine (*Sardina pilchardus* Walb.): influence of wind. Scientia Marina 70: 93–104.
- Anonymous, 2001. Evaluation of the Southern Greek Sardine Stocks, Final Report: 51.
- Bigot, J. L., 2007. Stock Assessment form regarding *Sardina pilchardus* in the Gulf of Lions, GSA07. GFCM SCSA, Working Group on the Small Pelagic.
- Clarke, K. R. & R. M. Warwick, 1994. Change in Marine Communities: An Approach to Statistical Analysis and Interpretation. Plymouth, UK.
- Elith, J., C. H. Graham, R. P. Anderson, M. Dudik, S. Ferrier, A. Guisan, R. J. Hijmans, F. Huettmann, J. R. Leathwick, A. Lehmann, J. Li, L. G. Lohmann, B. A. Loiselle, G. Manion, C. Moritz, M. Nakamura, Y. Nakazawa, J. M. Overton, A. T. Peterson, S. J. Phillips, K. S. Richardson, R. Scachetti-Pereira, R. E. Schapire, J. Soberon, S. Williams, M. S. Wisz & N. E. Zimmermann, 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography 29: 129–151.
- Field, J. C., K. R. Clarke & R. M. Warwick, 1982. A practical strategy for analysing multispecies distribution patterns. Marine Ecology Progress Series 8: 37–52.
- Freon, P. & O. E. Misund, 1999. Dynamics of Pelagic Fish Distribution and Behaviour: Effects on Fisheries and Stock Assessment. Oxford: 360.
- Giannoulaki, M., A. Machias, C. Koutsikopoulos, J. Haralabous, S. Somarakis & N. Tsimenides, 2003. Effect of coastal topography on the spatial structure of the populations of small pelagic fish. Marine Ecology Progress Series 265: 243–253.
- Giannoulaki, M., A. Machias, C. Koutsikopoulos & S. Somarakis, 2006. The effect of coastal topography on the spatial structure of anchovy and sardine. ICES Journal of Marine Science 63: 650–662.
- Giráldez, A., P. Torres, L. Quintanilla & J. Baro, 2005. Anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*) Stock Assessment in the GFCM Geographical Sub-Area 01 (Northern Alboran Sea) and 06 (Northern Spain). GFCM/ SAC Working Group on Small Pelagic, Rome.
- Golden Software, 2002. Surfer 8. Golden Software Inc., Golden, CO 80401 USA.
- Isari, S., A. Ramfos, S. Somarakis, C. Koutsikopoulos, A. Kallianiotis & N. Fragopoulou, 2006. Mesozooplankton distribution in relation to hydrology of the Northeastern Aegean Sea, Eastern Mediterranean. Journal of Plankton Research 28: 241–255.
- Karageorgis, A. P., C. L. Anagnostou, E. Kaberi & T. Kanellopoulos, 2001. Particulate matter distribution over the north Aegean Sea. North Aegean System Functioning and Inter-Regional Pollution, Interreg Meeting, Kavala, Greece: 37.
- Liu, Y., R. Zhang, Y. Yin & T. Niu, 2005. The application of ARGO data to the global ocean data assimilation operational system of NCC. Acta Meteorological Sinica 19: 355–365.

- Lleonard, J. & F. Maynou, 2003. Fish stock assessments in the Mediterranean: state of the art. Scientia Marina 67: 37–49.
- Lykousis, V., G. Chronis, A. Tselepides, N. B. Price, A. Theocharis, I. Siokou-Frangou, F. Van Wambeke, R. Danovaro, S. Stavrakakis, G. Duineveld, D. Gergopoulos, L. Ignatiades, A. Souvermezoglou & F. Voutsinou-Taliadouri, 2002. Major outputs of the recent multidisciplinary biogeochemical researches undertaken in the Aegean Sea. Journal of Marine Systems 33(34): 313–334.
- Machias, A., M. Giannoulaki, S. Somarakis, E. Schismenou, K. Tsagarakis, A. Siapatis, C. Stamataki, V. Vasilopoulou, A. Kallianiotis & C. Papaconstantinou, 2007. Acoustic biomass estimates of sardine in the Aegean Sea (June 2003, 2004, 2005 and 2006). WD to the GFCM SCSA, Working Group on the Small Pelagic. Athens.
- MathSoft Inc., 1999. S-PLUS 2000. Data Analysis Products Division. MathSoft Inc., Seattle, WA.
- McLachlan, G. J., 1992. Discriminant Analysis and Statistical Pattern Recognition. John Wiley & Sons, New York.
- Nittis, K. & L. Perivoliotis, 2002. Circulation and hydrological characteristics of the North Aegean Sea: a contribution from real-time buoy measurements. Mediterranean Marine Science 3: 21–31.
- Palomera, I., M. P. Olivar, J. Salat, A. Sabates, M. Coll, A. Garcia & B. Morales-Nin, 2007. Small pelagic fish in the NW Mediterranean Sea: An ecological review. Progress in Oceanography 74: 377–396.
- Porteiro, C., F. Alvarez & J. A. Pereiro, 1986. Sardine (Sardina pilchardus, Walb.) stock differential distribution by age class in ICES Divisions VIIIc and IXa. ICES CM H28: 19.
- Reynolds, J. D., G. M. Mace, K. H. Redford & J. G. Robinson, 2001. Conservation of Exploited Species. Cambridge University Press: 544.
- Siokou-Frangou, I., M. Bianchi, U. Christaki, E. D. Christou, A. Giannakourou, O. Gotsis, L. Ignatiades, K. Pagou, P. Pitta, S. Psarra, E. Souvermezoglou, F. Van Wambeke & V. Zervakis, 2002. Carbon flow in the planktonic food web along a gradient of oligotrophy in the Aegean Sea (Mediterranean Sea). Journal of Marine Systems 33(34): 335–353.
- Smith, W. H. F. & D. T. Sandwell, 1997. Global sea floor topography from satellite altimetry and ship depth soundings. Science 277: 1956–1962.
- Somarakis, S., P. Drakopoulos & V. Filippou, 2002. Distribution and abundance of larval fish in the northern Aegean Sea—eastern Mediterranean—in relation to early summer oceanographic conditions. Journal of Plankton Research 24: 339–358.
- Somarakis, S., D. E. Tsianis, A. Machias & K. I. Stergiou, 2006. An overview of biological data related to anchovy and sardine stocks in Greek waters. In Palomares, M. L. D., K. I. Stergiou & D. Pauly (eds), Fishes in Databases and Ecosystems, Fisheries Centre Research Reports. Fisheries Centre, University of British Columbia: 56–64.
- Stergiou, K. I., E. D. Christou, D. Georgopoulos, A. Zenetos & C. Souvermesoglou, 1997. Hellenic Seas: physics, chemistry, biology and fisheries. Oceanography and Marine Biology: An Annual Review 35: 415–538.
- Turner, W., S. Spector, N. Gardiner, M. Fladeland, E. Sterling & M. Steininger, 2003. Remote sensing for biodiversity

science and conservation. Trends in Ecology and Evolution 18: 306–314.

- Valavanis, V. D., S. Georgakarakos, A. Kapantagakis, A. Palialexis & I. Katara, 2004. A GIS environmental modelling approach to essential fish habitat designation. Ecological Modelling 178: 417–427.
- Zervakis, V. & D. Georgopoulos, 2002. Hydrology and circulation in the North Aegean (eastern Mediterranean) throughout 1997 and 1998. Mediterranean Marine Science 3: 5–19.
# FISH HABITAT MAPPING

# Modelling the presence of anchovy *Engraulis encrasicolus* in the Aegean Sea during early summer, based on satellite environmental data

Marianna Giannoulaki · Vasilis D. Valavanis · Andreas Palialexis · Konstantinos Tsagarakis · Athanassios Machias · Stylianos Somarakis · Costas Papaconstantinou

© Springer Science+Business Media B.V. 2008

**Abstract** Acoustic and satellite environmental data as well as bathymetry data were used to model the presence of anchovy, *Engraulis encrasicolus* during early summer in the northern Aegean Sea (Eastern Mediterranean). Generalized Additive Models (GAMs) were used for modelling and subsequently applied in a predictive mode to identify those areas in the Greek Seas and the entire Mediterranean basin that could support species' presence. Model results were evaluated with the estimation of Receiver Operating Characteristic (ROC)-plots as well as

M. Giannoulaki (🖂) · K. Tsagarakis · S. Somarakis Institute of Marine Biological Resources, Hellenic Centre for Marine Research, Thalassocosmos, 71003 Heraklion Crete, Greece e-mail: marianna@her.hcmr.gr

V. D. Valavanis · A. Palialexis Marine GIS Laboratory, Institute of Marine Biological Resources, Hellenic Centre for Marine Research, Thalassocosmos, 71003 Heraklion Crete, Greece

A. Palialexis ⋅ K. Tsagarakis Department of Biology, University of Crete, Vassilika Vouton, P.O. Box 2208, 71409, Heraklion Crete, Greece

A. Machias · C. Papaconstantinou

Institute of Marine Biological Resources, Hellenic Centre for Marine Research, Aghios Kosmas, 16777 Helliniko, Greece qualitatively, based on (a) acoustic data from concurrent studies in certain areas of the northern Aegean Sea that were not included in the estimation of the GAM model and (b) historical acoustic data from the central Aegean and Ionian Seas. Mapping the estimated environmental conditions in the Mediterranean basin indicated areas that generally agree with the known distribution grounds of anchovy, such as the straits of Sicily and coastal waters of Tunisia, areas in the Tyrrhenian Sea, the Adriatic Sea, the Gulf of Lions and the Catalan Sea.

**Keywords** European anchovy · Habitat modelling · Potential habitat · Generalized Additive Models · Satellite environmental data · Aegean Sea

# Introduction

European anchovy (*Engraulis encrasicolus*) along with sardine (*Sardina pilchardus*) are the two most important small-sized pelagic species in the Mediterranean (Lleonart & Maynou, 2003), representing almost 40% of the total annual landings. Regarding Greece, the two species comprise 18–25% of the total Greek landings and 60–70% of the total purse seine landings (Stergiou et al., 1997). Small pelagics like anchovy, present high fluctuations regarding their abundance and their distribution, largely depending on environmental conditions (Freon & Misund, 1999).

Guest editor: V. D. Valavanis Essential Fish Habitat Mapping in the Mediterranean

The study of those environmental parameters that affect the spatial distribution of economically important stocks like anchovy, has gained particular attention lately due to the concern regarding the effect of climate change on fisheries resources (Cury et al., 2003). Habitat modelling of a species in relation to environmental parameters has expanded considerably in the last decade (Guisan & Zimmermann, 2000; Riou et al., 2001; Francis et al., 2005; Planque et al., 2007). It is increasingly becoming an effective tool for understanding the processes that affect the interannual variability in species distribution and provide essential information for ecological studies and management purposes. Defining the potential habitat of a species practically means determining the combination of those environmental factors that constitute suitable conditions for its survival (Guisan & Zimmermann, 2000; Planque et al., 2007).

Satellite environmental data are flexible allowing predictions in various years and regions and could be used as proxies to infer spatial variations of environmental factors and assess possible ecological relationships. In addition new powerful statistical techniques and Geographical Information Systems (GIS) tools have evoked during the last decade and are being widely adapted in the development of predictive habitat distribution models in ecology (Guisan & Zimmermann, 2000; Riou et al., 2001; Francis et al., 2005).

Habitat modelling can provide the basis for designing and executing intensive surveys in certain areas. Furthermore, sustainable management requires the knowledge of species habitat as well as how habitat area changes depending on environmental parameters. Thus, the development of large-scale descriptive and predictive models of fish presence and abundance is fundamental for effective management activities, such as placement of Marine Protected Area networks (Conover et al., 2000), spatial zoning of different permitted fishing activities (Rice & Cooper, 2003) and regulative use of the coastal environment (Coleman et al., 2004; Francis et al., 2005).

In the present study, the relationship of the adult anchovy, *Engraulis encrasicolus* presence during early summer was modelled with satellite environmental data and bathymetry data as proxies to infer spatial variations of environmental factors, in order to identify those areas in the Greek Seas and the Mediterranean basin that could serve as potential habitat for the species. Analysis was based on data obtained from acoustic surveys undertaken in the northern Aegean Sea during a 3-year period and statistical models (i.e. Generalized Additive Models) were used to model the relationship between anchovy presence/absence and environmental data.

# Materials and methods

#### The study area

The northern Aegean Sea is characterized by high hydrological complexity mostly related to the Black Sea waters (BSW) that enter the Aegean Sea through the Dardanelles strait as a surface current (Zervakis & Georgopoulos, 2002). The area is characterized by the presence of two anticyclonic systems: one in the Samothraki plateau (the Samothraki gyre) and another one in the Strymonikos Gulf (Somarakis et al., 2002; Fig. 1B). These gyres are an almost permanent feature in the area during early summer and are coupled with a cyclonic system located south of the island of Thasos. The overall circulation is mainly determined by the presence of the Limnos-Imvros stream (LIS), which carries waters of Black Sea origin onto the Samothraki plateau (Somarakis et al., 2002, Fig. 1B). The outflow of BSW (salinity < 30) enhances local productivity and its advection in the Aegean Sea induces high hydrological and biological complexity (Isari et al., 2006, 2007; Somarakis & Nikolioudakis, 2007). This is further enhanced by the presence of a series of large rivers that end in semi-closed gulfs, such as Thermaikos and Strymonikos Gulfs (Stergiou et al., 1997; Isari et al., 2006).

#### Sampling

Acoustic data were collected on board the R/V Philia during June 2004, 2005 and 2006, in the framework of assessing anchovy stock biomass during the peak of the spawning season in northern Aegean Sea. Acoustic surveys were carried out along predetermined parallel transects in Thracian Sea and Thermaikos gulf, whereas, zigzagged transects were sampled in Strymonikos, North Evoikos and South Fig. 1 (A) Map of the study area showing acoustic transects in June 2004, 2005 and 2006. (B) Map of the study area showing water circulation. Arrows indicate the presence of fronts and gyres (redrawn from Somarakis et al., 2002). LIS: Limnos-Imvos Steam, SG: Samothraki Gyre. Positions of the main rivers in the area are also shown. Toponyms mentioned in the text are also indicated. - Acoustic

transect



24°

Evoikos gulfs (Fig. 1A), by means of a Biosonic Split Beam DT-X echosounder at 38 kHz. The system was regularly calibrated using the standard sphere method (Foote, 1987). The distance between transects was 10 nautical miles (nm). The speed of the vessel was 8 nautical miles (nm) per hour. Anchovy echoes discrimination was based on the characteristic echogram shape of the schools and the catch composition of pelagic trawling held in the surveyed area (MacLennan & Simmonds, 1992). A pelagic trawl

38 22º

23°

with a vertical opening of 10 m and an 8 mm codend was used to identify echo traces. Catch composition of a total of 109 hauls revealed that the main species in the study area were Engraulis encrasicolus, Sardina pilchardus, Sardinella aurita and Trachurus spp. The size of the Elementary Distance Sampling Unit (EDSU) was one nautical mile. The EDSU is the length of the cruise track along which the acoustic measurements are integrated to give one sample (MacLennan & Simmonds, 1992). Acoustic data

25°

26°

	1			
Parameter	Sensor/Model	Range/Mean	Resolution	Source
Sea surface chlorophyll- <i>a</i> (CHLO)	MODISA	0.07–24.62/0.32 mg/m <sup>3</sup>	4 km	oceancolor.gsfc.nasa.gov
Sea surface temperature (SST)	AVHRR	18.5–28.9/22.9 °C	1.1 km	eoweb.dlr.de:8080
Photosynthetically active radiation (PAR)	SeaWiFS	20.3–64.7/57.8 Einstein/m <sup>2</sup> /day	9 km	oceancolor.gsfc.nasa.gov
Sea level anomaly (SLA)	Merged Jason-1, Envisat, ERS-2, GFO, T/P	-12.3 to 0.7/-5.3 cm	0.25°	www.jason.oceanobs.com
Sea surface salinity (SSS)	CARTON-GIESE SODA and CMA BCC GODAS	38.3–38.9/38.6 psu	0.5°	iridl.ldeo.columbia.edu

Table 1 Environmental satellite parameters and their characteristics

analysis was performed using the Sonardata Echoview software v3.30.

models

Furthermore, acoustic data from past surveys that were held in central Aegean and Ionian Seas (July 1998; June 1999) with a Dual Beam Biosonic echosounder at 120 kHz and the same acoustic methodology (acoustic sampling is described in detail in Giannoulaki et al., 2006), were used for model evaluation purposes.

# Environmental data

The area is well monitored in terms of monthly satellite imagery (summarized in Table 1). Specifically, the sea surface temperature distribution (SST in °C), the sea surface chlorophyll concentration (CHLO in mg/m<sup>3</sup>), the Photosynthetically Active Radiation (PAR in Ein/m<sup>2</sup>/day), the sea surface salinity distribution (SSS in psu BCC GODAS model, Liu et al., 2005) and the sea level anomaly (SLA in cm) were downloaded from respective databases (see Table 1) and used. SLA describes ocean processes, such as gyres, meanders and eddies (Larnicol et al., 2002; Pujol & Larnicol, 2005), which enhance productivity and often function as physical barriers differentiating the distribution of species or species life stages. These aforementioned parameters might be important either as a direct influence on the distribution of anchovy or as a proxy for other factors (Bellido et al., 2001), for example PAR which is defined as the quantum energy flux from the sun in the spectral range 400-700 nm at the surface, representing the amount of solar radiation useable for plants to photosynthesize (Frouin et al., 2003), might be indicative of the extent of the euphotic zone, with its lower limit defined as the depth to which PAR values are reduced to 0.1% of the surface measurements (Hader et al., 1994). Bathymetry was also calculated through processing (kriging) of a point dataset derived from a blending of depth soundings collected from ships with detailed gravity anomaly information obtained from the Geosat and ERS-1 satellite altimetry missions (Smith & Sandwell, 1997). All monthly averaged satellite images were processed as regular grids under a Geographic Information Systems (GIS) environment using ArcInfo GRID software (ESRI, 1994). The mean environmental monthly values for June 2004, 2005 and 2006 were estimated for all surveyed points of acoustic data based on the available spatial resolution of satellite data (Valavanis et al., 2004).

# Model estimation

Generalized Additive Models (GAMs) were used in order to define the set of the environmental parameters that describe areas of anchovy presence in Northern Aegean Sea. A GAM (Hastie & Tibshirani, 1990) is a generalized linear model with a linear predictor involving a sum of smooth functions of covariates (Wood, 2006). The main advantage of GAMs over traditional regression methods is their capability to model non-linearities using non-parametric smoothers (Hastie & Tibshirani, 1990; Wood, 2006).

The selection of the GAMs smoothing predictors followed the method proposed by Wood & Augustin (2002), using the 'mgcv' library in the R statistical software (R Development Core Team, 2005). The output of the GAMs is smoothed fits for each environmental variable. The individual models cannot be tested for significance using the *P*-values provided by 'mgcv' library since the true number of degrees of freedom is unknown. However, each fit was analysed with regards to the level of deviance explained (0-100%; the higher the better), the Unbiased Risk estimator (UBRE, the lower the better), the Akaike's Information Criterion (AIC, the lower the better) and the confidence region for the smooth (which should not include zero throughout the range of the predictor). The degree of smoothing was also chosen based on the observed data and the Generalized Cross Validation method suggested by Woods (2006) and incorporated in the MGCV library. Because collinearity in the independent variables is a crucial problem in GAMs application, associated with stepwise model selection (Guisan et al., 2002, Wood, 2006), the best model was chosen based on a stepwise forward selection method that reduces the collinearity problem starting from a simple initial model with few explanatory variables (Sacau et al., 2005; Zuur personal communication). Specifically, models were compared using the estimated AIC, UBRE and deviance, the environmental variables were ranked and selection of the final model was based on the minimization of the above criteria.

As response variable (y), we used the presence/ absence of anchovy. As independent variables we used: the cubic root of the bottom depth (to achieve a uniform distribution of bottom depth), the natural logarithm of CHLO (to achieve a uniform distribution of CHLO), the SST, the SSS, the SLA and the PAR. Bottom depth and CHLO presented high variability in their original values, thus transformation was necessary in order to achieve uniform distribution for GAM application (Hastie & Tibshirani, 1990). The appropriate type of transformation was based on the inspection of Quantile-Quantile plots (QQ-plots) to check if variables under certain transformations follow the normal distribution.

For the construction of such a model data collected over a wide range of environmental conditions should be collated. Therefore, pooled data from all three examined years deriving from both Thracian Sea and Thermaikos Gulf (two areas that vary highly in respect to environmental conditions and water circulation) were used, in order to obtain more possible observed conditions and ensure potentiality (ICES, 2005).

The binomial error distribution with the logit link function was used. Also the natural cubic spline

smoother that applies splines with knots at each distinct value of the variable, (Hastie & Tibshirani, 1990) and minimizes the *penalised residual sum of squares* (Wood, 2006) was used for the independent variables smoothing and fitting GAM. Following the selection of the main effects of the model, all first order interactions of the parameters included in the final model were tested (Wood, 2006). Validation graphs (e.g. residual plot vs. fitted values, QQ-plot and residual plot against the original explanatory variables) were plotted in order to detect model misspecification.

# Model validation

Furthermore, a GAM model was applied for the estimation of the probability of anchovy presence to each point of the area used for modelling, based on the available mean monthly values of satellite data (i.e. of the parameters incorporated in the final model). Therefore a specific set of satellite conditions was attributed to a specific probability of finding anchovy present. In a next step, the GAM model was applied in a predictive mode using as prediction grid the mean monthly satellite values measured for the Greek Seas as well as the entire Mediterranean basin, at a GIS resolution of 4 km in June 2004, 2005 and 2006. The areas with a specific set of satellite conditions corresponding to different probabilities of anchovy presence were plotted.

The predictive accuracy of the final model was tested and evaluated with the estimation of Receiver Operating Characteristic (ROC)-plots (Fieldings & Bell, 1997; Guisan & Zimmermann, 2000) and the estimation of the area under the Receiver Operating Characteristic curve (AUC) for (a) the Thracian Sea and Thermaikos gulf for each examined year, (b) North Evoikos and South Evoikos gulfs, areas that were surveyed concurrently in June 2004, 2005 and 2006 but they were not included in the estimation of the GAM model and (c) for past acoustic data from central Aegean and Ionian Sea in July 1998 and June 1999. AUC has been used extensively in the species' distribution modelling literature, measuring the ability of a model to discriminate between those sites where a species is present, versus those where it is absent (Hanley & McNeil, 1982). It provides an indication of the usefulness of the models for indicating areas in terms of their relative importance as habitat for the particular species. The values of AUC ranges from 0 to 1, where a score of 1 indicates perfect discrimination, a score of 0.5 implies predictive ability that is no better than a random guess, and values <0.5 indicate performance worse than random (Boyce et al., 2002; Elith et al., 2006). ROC and AUC estimation was made with the presence/absence library of the R statistical software. Model results were also evaluated qualitative by comparing the obtained maps with the anchovy's known distribution (a) from the concurrent acoustic surveys in North Evoikos and South Evoikos Gulf and (b) from acoustic data obtained at central Aegean and Ionian Seas in July 1998 and June 1999. The Surfer v8.0 of the Golden Software Inc. software was used for mapping.

#### Results

Anchovy distribution in northern Aegean Sea

The distribution of anchovy in northern Aegean Sea is shown in Fig. 2. Although its abundance and distribution shows a large degree of interannual variability, the highest abundances were observed in the northern part of Thermaikos gulf, the coastal waters of Thracian Sea and the inner part of Strymonikos gulf where large rivers outflow (Figs. 1B, 2). For example, the spatial distribution of anchovy in Thermaikos gulf in June 2005 and 2006 was patchy compared to June 2004, where anchovy was distributed over most of the shelf (Fig. 2). A more consistent pattern was observed in North Evoikos gulf during all years, where the main concentrations were generally confined in the northwest part and in the south most part of the gulf.

# Model estimation

The final selected GAM model based on satellite data included as main effects: PAR, Depth as well as the interactive effect of SST and SLA, and it is described in Table 2. All variables selected in the final model were statistically significant. Inspection of the validation graphs (not shown) indicated a distinct pattern regarding the plot of residuals versus fitted values which is because of the presence–absence nature of the data and does not indicate a lack of fit. The plots of residuals of the model against the original explanatory variables did not show any apparent trend.



Fig. 2 Distribution maps of anchovy according to the ln of NASC (Nautical Area Scattering Coefficient in  $m^2/nm^2$ ) for June 2004, 2005 and 2006, respectively. Kriging was used as the interpolation method (spacing 1 nm, spherical variogram model and anisotropy)

Parameter	Res. Df	Residual deviance	Deviance explained (%)	AIC	P-value
Null model	2126	2321.669		2323.669	
s(Depth)	2120.93	1652.656	28.8	1664.796	<<0.000
s(Depth) + s(PAR)	2119.27	1616.155	30.4	1631.605	<< 0.000
s(Depth) + s(PAR) + s(SST:SLA)	2103.74	1495.933	35.56	1542.452	<< 0.000
Total variation % explained			35.56		

Table 2 Analysis of deviance for GAM covariates and their interactions of the final model fitted

Level of significance was set at 0.05. The ":" sign denotes interaction. Res. d.f = residual d.f.; Res. Deviance = residual deviance; AIC = Akaike Information Criterion value; *P*-value (chi-square) = significance values

The results of the final GAM model are shown as plots of the best-fitting smooths for the effect of the environmental parameters on anchovy presence (Fig. 3). The 95% confidence intervals were also plotted around the best-fitting smooths for the main effects. Interaction effects are shown as a perspective plot (Fig. 3) without error bounds. The y-axis reflects the relative importance of each parameter of the model, and for the interaction effects, this is presented on the z-axis. The rug under the single variable effects plots indicates the density of points for different variable values (Fig. 3). It should be noted that the effect of each variable is the conditional effect, i.e. the effect that this variable has, given that the other variables are included in the model. Plots indicated a higher probability of finding anchovy present in shallow waters (less than 140 m depth) and PAR values less than 56  $\text{Ein/m}^2$ /day. The interaction plot between SST and SLA also indicated higher probability of finding anchovy present in the lower available values of SST (<22°C) when co-existing with the lower available values of SLA (less than -6 cm) (Figs. 3, 5).

# Model validation

The estimated values of AUC for each ROC plot for each year incorporated in the model indicated good

Effect on anchovy presence Effect on anchovy presence 0 Ģ 3 -10 2 6 8 10 DEPTH SST Effect on anchovy presence 1.5 1.0 50 0.0 -0.5 -1.0 PAR

**Fig. 3** Coefficients of the Generalized Additive Models (GAMs) for anchovy against Bottom depth and PAR. The interaction plot of SST and SLA is also shown. Black thick lines indicate the value of GAMs coefficient, dotted lines represent the confidence intervals at P = 0.05

Year	Area	Ν	AUC	Sensitivity = Specificity threshold
2004	Thracian Sea & Thermaikos Gulf	697	0.87	0.27
2005	Thracian Sea & Thermaikos Gulf	698	0.86	0.28
2006	Thracian Sea & Thermaikos Gulf	729	0.88	0.34
2004	North & South Evoikos Gulf	203	0.82	0.43
2005	North & South Evoikos Gulf	195	0.67	0.37
2006	North & South Evoikos Gulf	189	0.68	0.42
1998	Central Aegean & Ionian Sea	675	0.58	0.20
1999	Central Aegean & Ionian Sea	725	0.70	0.23

 Table 3 Estimated area under the ROC curve (AUC) for anchovy per area and year

N: number of observations. Sensitivity equal specificity threshold is also shown. Sensitivity is defined as the probability that a model yields a positive prediction where species actually occurs (i.e. 1), whereas, specificity is the probability that the species is absent (i.e. 0). The threshold that sensitivity equals specificity, coincides with the optimum probability threshold for model performance

prediction ability of the model for the surveyed area according to Elith et al. (2006), since it exceeded 0.85 in all cases (Table 3). Regarding the prediction ability of the model for North Evoikos and South Evoikos Gulf, the central Aegean and Ionian Seas in 1998 and 1999, the estimated AUC values varied from 0.58 to 0.82. The lowest values were observed when both the area and the period highly diverged from the ones used for modelling for (i.e. central Aegean and Ionian Seas in July 1998). However, the comparison of maps for the entire Greek seas revealed a general good agreement between the predicted areas based on the measured satellite conditions (i.e. areas with a specific set of satellite parameters associated to specific probability of anchovy presence, e.g. 50%) and the observed distribution of anchovy (Machias et al., 2000; Figs. 2, 4, 6). Areas have been indicated in the most productive waters of the northwest part of Saronikos gulf which is under strong urban influence, in Patraikos gulf and in the inner part of the Ionian Sea between the islands and the mainland. These areas generally agree with the species actual distribution during early summer (Figs. 4, 6).

Furthermore, similar maps were also obtained for the entire Mediterranean Sea to indicate areas, where the specific set of satellite conditions associated with specific probability values, e.g. 50% of finding anchovy present, is met (Figs. 7, 8). In the western Mediterranean Sea areas, such as the Adriatic Sea, the Straits of Sicily, the Catalan Sea, the Gulf of Lions and the gulf of Gabes, where the presence of anchovy distribution grounds is known, have been indicated. In the Eastern Mediterranean Sea, areas have been indicated in the Turkish coastal waters of Aegean Sea, the Mersin gulf and the Nile Delta area. However, in these areas the distribution of anchovy is generally unknown.

## Discussion

Satellite data although they do not describe the actual conditions at sea, they seem to provide a generally good description of the areas that anchovy distributes during early summer. Specifically, results indicated a higher probability of finding anchovy present at <140 m depth and at PAR values less than 56 Ein/m<sup>2</sup>/day, which are both indicative of the shallow coastal waters of the studied area. In addition, the higher probability of finding anchovy present in areas characterized by the interaction of SST (values between 20 and 22°C) and the lower available values of SLA implies the association of anchovy with an anticyclonic system in the Samothraki plateau (i.e. the Samothraki gyre; Figs. 1B, 5). This is a downwelling water formation that is related to the inflow of BSW from the Dardanelles and is a permanent feature in northern Aegean Sea during early summer (Zervakis & Georgopoulos, 2002; Somarakis et al., 2002; Somarakis & Nikolioudakis, 2007). Anchovy association with anticyclonic systems during early summer in the studied area has also been shown, based on field measurements of environmental data (Giannoulaki et al., 2005). Early summer is the peak of the spawning season for anchovy in northern Aegean Sea (Stergiou et al., 1997; Somarakis, 2005), therefore a large



◄ Fig. 4 Map of the probability for anchovy potential presence in the Greek region, based on GAM model from Aegean Sea. GIS resolution used for prediction was 4 km of mean monthly satellite values from June 2004, 2005 and 2006

fraction of adult anchovy population is associated with spawning grounds. Anchovy spawning grounds are known to be highly dependent on surface water dynamics in areas like the Catalan sea, the Gulf of Lions and the Straits of Sicily (Giráldez & Abad, 1995; García Lafuente et al., 2002; Cuttita et al., 2003; Sabates et al., 2007; Palomera et al., 2007).

Furthermore, the coastal waters of Thracian Sea, Strymonikos gulf and Thermaikos gulf, areas indicated by the model results, are under the influence of rivers runoff (Fig. 1). European anchovy spawning areas and juvenile grounds are also related to the influence of river outflow as shown in the Bay of Biscay, the Adriatic Sea, the Bay of Tunis (Motos et al., 1996; Agostini &Bakun, 2002; Zarrad et al., 2006), in the Catalan Sea and the Gulf of Lions (Palomera et al., 2007; Sabates et al., 2007). However, SSS did not enter the final model most likely because the given range of values of SSS at the best available resolution is very small and insufficient to capture and describe the river influence (Table 1).

The evaluation of the model outcome using acoustic observations of anchovy in the Thracian Sea and Thermaikos gulf (areas used for modelling), the North and South Evoikos gulfs (data from concurrent surveys in 2004, 2005 and 2006) and in central Aegean and Ionian Seas (July 1998 and June 1999) offered satisfactory results (i.e. estimated AUC values and map comparisons). Results were less satisfactory in the case of the central Aegean and Ionian Seas in July 1998, but the range of available values for the satellite parameters was highly divergent from the ones used for modelling because of the different survey period. However, in this case predicted areas also coincide with the most productive waters that are influenced either by urban runoffs like the northwest part of Saronikos gulf or by freshwater runoffs like Patraikos gulf and the inner part of the Ionian Sea. These results generally agree with the species' actual distribution during early summer and indicate that the model could generally describe it quite well (Figs. 4, 6).

Maps for the entire Mediterranean Sea (Figs. 7, 8) indicated areas with a certain set of environmental conditions as estimated by the model. These areas are





discussed in respect to known anchovy distribution grounds based on literature (areas summarized in Table 4). Specifically, in the eastern part, areas have been indicated in the Turkish waters of the Aegean Sea such as the Saros bay and the gulf of Izmir, the gulf of Mersin in the Levantine Sea, the coastal Syrian and Lebanese waters and the coastal waters of the Nile Delta region (Fig. 7). Anchovy presence in the Turkish coastal waters is known (Aka et al., 2004; Turan et al., 2004) and there is an established purse seine fishery in the region (Lleonart & Maynou, 2003), however, species spatial distribution is largely unknown. An established fishery for anchovy has also been reported in the Lebanese coastal waters (Bariche et al., 2006, 2007) but concerning the Nile Delta area there is no published information.

The related information is generally very scarce regarding the northern African waters. However regarding the Gulf of Tunis published work based on acoustic and egg surveys (Ben Abdallah & Gaamour, 2005; Zarrad et al., 2006) refers that the higher anchovy abundances are mostly located in the south part of the gulf, such as the inshore waters of the gulf of Gabes and the gulf of Sousse, areas that coincide with the locations characterized of high probability of finding anchovy present (>0.5) based on model results.

In the western Mediterranean basin the indicated areas generally agree with the major grounds of **Fig. 6** Distribution maps of anchovy according to the ln of NASC (Nautical Area Scattering Coefficient in  $m^2/nm^2$ ) for June 1998 and 1999, respectively. Kriging was used as the interpolation method (spacing 1 nm, spherical variogram model and anisotropy)



anchovy's known distribution (Table 4) like the straits of Sicily, the Adriatic Sea, the gulf of Lions and the Catalan Sea (Abad et al., 1998; Guennegan et al., 2000; Patti et al., 2000; Alemany et al., 2002; Giraldez & Alemany, 2002; Cuttitta et al., 2003; Patti et al., 2004, 2005; Bonanno et al., 2005; Palomera et al., 2007; Giraldez et al., 2007). In the Adriatic, results from acoustic and trawl surveys (Cingolani et al., 1996; Azzali et al., 2005; Leonori et al., 2007a, b) have shown that anchovy's shows a patchy spatial distribution that covers the coastal waters of the northern part in association with the Po delta (Leonori et al., 2007a), the southwest part of the Adriatic (Leonori et al., 2007b) and to a lesser extent the Croatian coastal waters in the east part (Ticina et al., 2005), higher anchovy densities were generally observed within the bathymetric range of 60-200 m (Azzali et al., 2005; Leonori et al., 2007a, b). Anchovy distribution in the Straits of Sicily and the Catalan Sea has been associated with surface waters dynamics (Cuttitta et al., 2003; Palomera et al., 2007) and the presence of river outflow (García Lafuente et al., 2002; Palomera et al., 2007; Giraldez et al., 2007).

The aim of this article was to (a) construction of a general model that describes these areas that could potentially but not necessarily, support anchovy presence and (b) examine if this could be applicable over larger areas. The use of data from additional areas as well as pooled data from several years could better define the set of the environmental parameters that characterize the areas of anchovy's distribution and improve the application of the model over a wider range of areas. This kind of a general model



**Fig. 7** Eastern Mediterranean Sea: Map of the probability for anchovy potential presence based on GAM model from Aegean Sea. GIS resolution used for prediction was 4 km of mean monthly satellite values from June 2004, 2005 and 2006

presents special interest from a managerial perspective. Small pelagics like anchovy are highly exploited species, characterized by large fluctuations in abundance and spatial distribution that are largely



Fig. 8 Western Mediterranean Sea: Map of the probability for anchovy potential presence based on GAM model on records from Aegean Sea. GIS resolution used for prediction was 4 km of mean monthly satellite values from June 2004, 2005 and 2006

depending on environmental parameters. Regions assigned as potential habitat for such species could be used to define suitable areas for scientific purposes like ecological studies, e.g. estimation of spawning or

Table 4 Areas in the Me	editerranean Sea with	1 known anchovy distribution	grounds	
	Region	Area	Type of data	Source
Eastern Mediterranean	Aegean Sea	Greek coastal waters	Acoustic surveys data	Present paper; Machias et al. (2000)
	Ionian Sea	Greek coastal waters	Acoustic surveys data	Machias et al. (2000)
	Aegean Sea	Turkish coastal waters	Landings data	Turan et al. (2004); Aka et al. (2004)
	Levantine	Lebanese coastal waters	Landings data	Bariche et al. (2006, 2007)
	Gulf of Tunis	Inshore waters of the Gulf of Gabes and the Gulf of Sousse	Acoustic & Egg Surveys data	Ben Abdallah & Gaamour (2005); Zarrad et al. (2006)
Western Mediterranean	Straits of Sicily		Acoustic surveys, ichthyoplankton surveys	Patti et al. (2000); García Lafuente et al. (2002); Cuttitta et al. (2003); Patti et al. (2004, 2005); Bonanno et al. (2005)
	Adriatic Sea	Italian part	Landings data, Acoustic Surveys data	Cingolani et al. (1996); Azzali et al. (2005); Leonori et al. (2007a, b)
		Croatian part	Acoustic Surveys data	Ticina et al. (2005)
	Gulf of Lions	Gulf of Lions	Acoustic surveys	Abad et al., 1998; Guennegan et al. (2000); Alemany et al. (2002); Palomera et al. 2007;
	Catalan Sea	Catalan Sea; Ebro shelf	Acoustic surveys, ichthyoplankton surveys	Abad et al. (1998); Giraldez & Alemany (2002); Giraldez et al. (2007); Palomera et al. (2007)

dietrib 4 ith br Ú 4:10 N.C. ţ . Ż

nursery grounds. Furthermore, regions assigned as potential habitat could be used in adapting management decisions such as spatial zoning, defining and delimiting Marine Protected Areas (MPAs). Improvement of such a model with data from other areas, along with the availability of satellite data from international databases, can allow the historical or real time estimation of anchovy potential distribution grounds, the estimation of spatialized indicators (Freon et al., 2005; Babcock et al., 2005) and the implementation of a precautionary ecosystem approach to fisheries management (i.e. the estimation of spatial interactions between small pelagics, top predators and fisheries).

Acknowledgements The study was partially financed by the Greek National Fisheries Data Collection Program and the Commission of the European Union ("Environmental Approach to Essential Fish Habitat Designation" (FP6-22466). We also thank the captain and the crew of RV "Philia" for their assistance during the surveys and A. Zuur for his help and statistical advice regarding data analysis.

#### References

- Abad, R., M. Miquel, M. Iglesias & F. Alvarez, 1998. Acoustic estimation of abundance and distribution of anchovy in the NW Mediterranean. Scientia Marina 62: 37–43.
- Agostini, V. N. & A. Bakun, 2002. 'Ocean triads' in the Mediterranean Sea: physical mechanisms potentially structuring reproductive habitat suitability (with example application to European anchovy, *Engraulis encrasicolus*). Fisheries Oceanography 11: 129–142.
- Aka, Z., H. Torcu Koc & C. Turan, 2004. A study of the growth of anchovy *Engraulis encrasicolus* Linaeus (1758) in Turkish Seas. Pakistan Journal of Biological Sciences 7: 1121–1126.
- Alemany, F., J. L. Bigot, A. Giraldez, Y. Guenegan, B. Liorzou, J. Miguel & I. Palomera, 2002. Preliminary results on anchovy shared stock in the Gulf of Lions. WD to the GFCM SCSA, Working Group on the Small Pelagic, Rome 20–22 March 2002.
- Azzali, M., A. De Felice, T. Karis, M. Luna, V. Ticina & M. Franicevic, 2005. Pilot joint echo-survey in the northern part of the Adriatic Sea on small pelagic fish and itsimplications on the historical surveys. WD to the GFCM SCSA, Working Group on the Small Pelagic, Rome 26–30 September 2005.
- Babcock, E. A., E. K. Pikitch, M. K. McAllister, P. Apostolaki & C. Santora, 2005. A perspective on the use of spatialized indicators for ecosystem-based fishery management through spatial zoning. ICES Journal of Marine Science 62: 469–476.

- Hydrobiologia (2008) 612:225-240
- Bariche, M., N. Alwan & M. El-Fadel, 2006. Structure and biological characteristics of purse seine landings off the Lebanese coast (eastern Mediterranean). Fisheries Research 82: 246–252.
- Bariche, M., R. Sadek, M. S. Al-Zein & M. El-Fadel, 2007. Diversity of juvenile fish assemblages in the pelagic waters of Lebanon (eastern Mediterranean). Hydrobiologia 580: 109–115.
- Bellido, J. M., G. Pierce & J. Wang, 2001. Modelling intraannual variation in abundance of squid *Loligo forbesi* in Scottish waters using generalised additive models. Fisheries Research 52: 23–39.
- Ben Abdallah, L. & A. Gaamour, 2005. Répartition géographique et estimation de la biomasse des petits pélagiques des côtes tunisiennes. MedSudMed Technical Documents 5: 28–38.
- Bonanno, A., B. Patti, S. Goncharov, G. Basilone, A. Cuttitta, G. Buscaino, J. García Lafuente, A. García, V. Palumbo, M. Cancemi & S. Mazzola, 2005. Fluctuation of sardine and anchovy abundance in the Strait of Sicily investigated by acoustic surveys. MedSudMed Technical Documents 5: 39–47.
- Boyce, M. S., P. R. Vernier, S. E. Nielsen & F. K. A. Schmiegelow, 2002. Evaluating resource selection functions. Ecological Modelling 157: 281–300.
- Cingolani, N., G. Gianneti & E. Arneri, 1996. Anchovy fisheries in the Adriatic Sea. Scientia Marina 60: 269–277.
- Coleman, F. C., W. F. Figueira, J. S. Ueland & L. B. Crowder, 2004. The Impact of United States recreational fisheries on marine fish populations. Science 305: 1958–1960.
- Conover, D., J. Travis & F. C. Coleman, 2000. Essential fish habitat and marine reserves: an introduction to the Second Monte Symposium in Fisheries Ecology. Bulletin of Marine Science 66: 527–534.
- Cury, P., L. Shannon & Y.-J. Shin, 2003. The functioning of marine ecosystems: a fisheries perspective. In Sinclair, M. & G. Valdimarsson (eds), Responsible Fisheries in the Marine Ecosystem. CABI Publishing, FAO, Rome: 103–124.
- Cuttitta, A., V. Carini, B. Patti, A. Bonanno, G. Basilone, S. Mazzola, J. Garcia Lafuente, A. Garcia, G. Buscaino, L. Aguzzi, L. Rollandi, G. Morizzo & C. Cavalcante, 2003. Anchovy egg and larval distribution in relation to biological and physical oceanography in the Strait of Sicily. Hydrobiologia 503: 117–120.
- Elith, J., C. H. Graham, R. P. Anderson, M. Dudık, S. Ferrier, A. Guisan, R. J. Hijmans, F. Huettmann, J. R. Leathwick, A. Lehmann, J. Li, L. G. Lohmann, B. A. Loiselle, G. Manion, C. Moritz, M. Nakamura, Y. Nakazawa, J. Mc C. Overton, A. T. Peterson, S. J. Phillips, K. S. Richardson, R. Scachetti-Pereira, R. E. Schapire, J. Soberon, S. Williams, M. S. Wisz & N. E. Zimmermann, 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography 29: 129–151.
- ESRI, 1994. ARC Macro Language. Environmental Systems Research Institute Inc, Redlands, CA, USA: 3–37.
- Fieldings, A. H. & J. F. Bell, 1997. A review of methods for the assessment of prediction errors in conservation presence: absence models. Environmental Conservation 24: 38–49.

- Foote, K. G., 1987. Fish target strengths for use in echo integrator surveys. Journal of the Acoustical Society of America 82: 981–987.
- Francis, M. P., M. A. Morrison, J. Leathwick, C. Walsh & C. Middleton, 2005. Predictive models of small fish presence and abundance in northern New Zealand harbours. Estuarine. Coastal and Shelf Science 64: 419–435.
- Freon, P., L. Drapeau, J. H. M. David, A. Fernandez Moreno, R. W. Leslie, W. H. Oosthuizen, L. J. Shannon & C. D. van der Lingen, 2005. Spatialized ecosystem indicators in the southern Benguela. ICES Journal of Marine Science 62: 459–468.
- Freon, P. & O. A. Misund, 1999. Dynamics of Pelagic Fish Distribution and Behaviour: Effects on Fisheries and Stock Assessment. Fishing New Books, Oxford.
- Frouin, R., B. A. Franz & P. J. Werdell, 2003. The SeaWiFS PAR Product. In Hooker, S. B. & E. R. Firestone (eds), Algorithm Updates for the Fourth SeaWiFS Data Reprocessing, NASA/TM 2003–206892, 22: 46–50.
- García Lafuente, J., A. García, S. Mazzola, L. Quintanilla, A. Delgado, A. Cuttitta & B. Patti, 2002. Hydrographic phenomena influencing early life stages of the Sicilian Channel anchovy. Fisheries Oceanography 11: 31–44.
- Giannoulaki, M., A. Machias, S. Somarakis & N. Tsimenides, 2005. The spatial distribution of anchovy and sardine in the northern Aegean Sea in relation to hydrographic regimes. Belgian Journal of Zoology 135: 151–156.
- Giannoulaki, M., A. Machias, C. Koutsikopoulos & S. Somarakis, 2006. The effect of coastal topography on the spatial structure of anchovy and sardine. ICES Journal of Marine Science 63: 650–662.
- Giráldez, A. & R. Abad, 1995. Aspects on the reproductive biology of the western Mediterranean anchovy from the coast of Málaga (Alboran Sea). Scientia Marina 59: 15–23.
- Giraldez, A. & F. Alemany, 2002. Echo-survey estimations of anchovy, sardine, gilt sardine, bogue and horse mackerel populations in the NW Mediterranean Sea (from Creus Cape to La Nao Cape). Working Paper, Working Group on the Small Pelagic.
- Giraldez, A., M. Iglesias, J. Miquel, N. Diaz & P. Torres, 2007. Anchovy (*Engraulis encrasicolus*) Stock Assessment by Acoustic Methods in the GFCM Geographical Sub-Area 06, Northern Spain. WD to the GFCM SCSA, Working Group on the Small Pelagic, Athens 13–14 September 2007.
- Guennegan, Y., B. Liorzou & J. L. Bigot, 2000. Exploitation des petites pelagique dans le Golf du Lion et suivi de l'evolution des stocks par echo-integration de 1999 a 2000. Paper Presented at WG of Small Pelagics. Fuengirola (Spain) 1–3 March 2000: 27.
- Guisan, A., T. C. Edwards Jr & T. Hastie, 2002. Generalized linear and generalized additive models in studies of species distributions: setting the scene. Ecological Modelling 157: 89–100.
- Guisan, A. & N. E. Zimmermann, 2000. Predictive habitat distribution models in ecology. Ecological Modelling 135: 147–186.
- Hader, D. P., R. C. Worrest, H. D. Kumar & R. C. Smith, 1994.
   Effects of Increased Solar Ultraviolet Radiation on Aquatic Ecosystems. United Nations Environment

Programme Environmental Effects of Ozone Depletion, 1994 Assessment. http://sedac.ciesin.org/ozone/UNEP/ UNEP94toc.html

- Hanley, J. A. & B. J. McNeil, 1982. The meaning and use of the area under a Receiver Operating Characteristic (ROC) curve. Radiology 143: 29–36.
- Hastie, T. & R. Tibshirani, 1990. Generalized Additive Models. London, Chapman and Hall.
- ICES, 2005. Report on the study group on regional scale ecology of small pelagic fish (SGRESP). ICES CM/2005 G:06.
- Isari, S., S. Psarra, P. Pitta, P. Mara, M. O. Tomprou, A. Ramfos, S. Somarakis, A. Tselepides, C. Koutsikopoulos & N. Fragopoulu, 2007. Differential patterns of mesozooplankters' distribution in relation to physical and biological variables of the Northeastern Aegean Sea (eastern Mediterranean). Marine Biology 151: 1035–1050.
- Isari, S., A. Ramfos, S. Somarakis, C. Koutsikopoulos, A. Kallianiotis & N. Fragopoulou, 2006. Mesozooplankton distribution in relation to hydrology of the Northeastern Aegean Sea, Eastern Mediterranean. Journal of Plankton Research 28: 241–255.
- Larnicol, G., N. Ayoub & P. Y. Le Traon, 2002. Major changes in Mediterranean Sea level variability from 7 years of TOPEX/Poseidon and ERS–1/2 data. Journal of Marine Systems 33: 63–89.
- Leonori, I., M. Azzali & A. De Felice, 2007a. Assessment of small pelagic fish by acoustic methods in south western Adriatic Sea. WD to the GFCM SCSA, Working Group on the Small Pelagic, Athens 13–14 September 2007.
- Leonori, I., M. Azzali & A. De Felice, 2007b. Assessment of small pelagic fish by acoustic methods in north western Adriatic Sea. WD to the GFCM SCSA, Working Group on the Small Pelagic, Athens 13–14 September 2007.
- Liu, Y., R. Zhang, Y. Yin & T. Niu, 2005. The application of ARGO data to the global ocean data assimilation operational system of NCC. Acta Meteorological Sinica 19: 355–365.
- Lleonart, J. & F. Maynou, 2003. Fish stock assessment in the Mediterranean: state of the art. Scientia Marina 67: 37–49.
- MacLennan, D. N. & E. J. Simmonds, 1992. Fisheries Acoustics. Chapman and Hall, London.
- Machias, A., S. Somarakis, C. Koutsikopoulos, A. Magoulas & N. Tsimenides, 2000. Evaluation of the southern Greek anchovy stocks. Project Final Report (EU contract No 97/ 0048).
- Motos, L., A. Uriarte & V. Valência, 1996. The spawning environment of the Bay Biscay anchovy (*Engraulis en*crasicolus L.). Scientia Marina 60: 117–140.
- Palomera, I., M. P. Olivar, J. Salat, A. Sabates, M. Coll, A. Garcia & B. Morales-Nin, 2007. Small pelagic in the NW Mediterranean Sea: An ecological review. Progress in Oceanography 74: 377–396.
- Patti, B., A. Bonnano, G. Basilone, S. Gonchanrov, S. Mazzola, G. Buscaino, A. Cuttitta, J. Garcia Lafuente, A. Garcia, V. Paumbo & G. Cosimi, 2004. Interannual fluctuations in acoustic biomass estimates and in landings of small pelagic fish populations in relation to hydrology in the Strait of Sicily. Chemistry and Ecology 20: 365–375.
- Patti, B., A. Cuttitta, A. Bonanno, G. Basilone, G. Buscaino, C. Patti, J. García Lafuente, A. García & S. Mazzola, 2005.

Coupling between the hydrographic circulation in the Strait of Sicily and the reproductive strategy of the European anchovy *Engraulis encrasicolus*: effects on distribution of spawning grounds. MedSudMed Technical Document 5: 19–27.

- Patti, B., S. Mazzola, L. Calise, A. Bonnano, G. Buscaino & G. Gosimi, 2000. Echosurveys estimates and distribution of small pelagic fish concentrations in the Strait of Sicily during June 1998. Paper Presented at WG of Small Pelagics. Fuengirola, Spain: 11.
- Planque, B., E. Bellier & P. Lazure, 2007. Modelling potential spawning habitat of sardine (*Sardina pilchardus*) and anchovy (*Engraulis encrasicolus*) in the Bay of Biscay. Fisheries Oceanography 16: 16–30.
- Pujol, M. I. & G. Larnicol, 2005. Mediterranean Sea eddy kinetic energy variability from 11 years of altimetric data. Journal of Marine Systems 58: 121–142.
- R Development Core Team, 2005. R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing. http://www.Rproject.org
- Rice, J. & A. Cooper, 2003. Management of flatfish fisheries and what factors matter? Journal of Sea Research 50: 227–243.
- Riou, P., O. Le Pape & S. I. Rogers, 2001. Relative contributions of different sole and plaice nurseries to the adult population in the Eastern Channel: application of a combined method using generalized linear models and a geographic information system. Aquatic Living Resources 14: 125–135.
- Sabates, A., M. P. Olivar, J. Salat, I. Palomera & F. Alemany, 2007. Physical and biological processes controlling the distribution of fish larvae in the NW Mediterranean. Progress in Oceanography 74: 355–376.
- Sacau, M., G. J. Pierce, J. Wang, A. I. Arkhipkin, J. Portela, P. Brickle, M. B. Santos, A. F. Zuur & X. Cardoso, 2005. The spatio-temporal pattern of Argentine shortfin squid *Illex argentinus* abundance in the southwest Atlantic. Aquatic Living Resources 18: 361–372.
- Smith, W. H. F. & D. T. Sandwell, 1997. Global sea floor topography from satellite altimetry and ship depth soundings. Science 277: 1956–1962.
- Somarakis, S., 2005. Marked interannual differences in reproductive parameters and daily egg production of

anchovy in the northern Aegean Sea. Belgian Journal of Zoology 135: 247–252.

- Somarakis, S., P. Drakopoulos & V. Filippou, 2002. Distribution and abundance of larval fishes in the northern Aegean Sea -Eastern Mediterranean- in relation to early summer oceanographic conditions. Journal of Plankton Research 24: 339–357.
- Somarakis, S. & N. Nikolioudakis, 2007. Oceanographic habitat, growth and mortality of larval anchovy (*Engraulis encrasicolus*) in the northern Aegean Sea (eastern Mediterranean). Marine Biology 152: 1143–1158.
- Stergiou, K. I., E. D. Christou, D. Georgopoulos, A. Zenetos & C. Souvermezoglou, 1997. The Hellenic Seas: Physics, chemistry, biology and fisheries. Oceanography and Marine Biology: An Annual Review 35: 415–538.
- Ticina, V., I. Katavic, V. Dadic, L. Crubisic, M. Franicevic & V. E. Ticina, 2005. Acoustic estimates of small pelagic fish stocks in the eastern part of the Adriatic Sea: September 2004. WD to the GFCM SCSA, Working Group on the Small Pelagic, Rome 26–30 September 2005.
- Turan, C., D. Ergüden, M. Gürlek, N. Başusta & F. Turan, 2004. Morphometric structuring of the anchovy (*Eng-raulis encrasicolus* L.) in the black, Aegean and Northeastern Mediterranean seas. Turkish Journal of Veterinary and Animal Sciences 28: 865–871.
- Valavanis, V. D., S. Georgakarakos, A. Kapantagakis, A. Palialexis & I. Katara, 2004. A GIS environmental modeling approach to Essential Fish Habitat designation. Ecological Modelling 178: 417–427.
- Wood, S. N., 2006. Generalized Additive Models. An Introduction with R. Chapman & Hall, London.
- Wood, S. N. & N. H. Augustin, 2002. GAMs with integrated model selection using penalized regression splines and applications to environmental modelling. Ecological Modelling 157: 157–177.
- Zarrad, R., H. Missaoui, F. Alemany, R. M. Salah, A. Garcia, M. R. Ridha, J. Othman & El. A. Amor, 2006. Spawning areas and larval distributions of anchovy *Engraulis encrasicolus* in relation to environmental conditions in the Gulf of Tunis (Central Mediterranean Sea). Scientia Marina 70: 137–146.
- Zervakis, V. & D. Georgopoulos, 2002. Hydrology and circulation in the Northern Aegean Sea throughout 1997 and 1998. Mediterranean Marine Science 3: 5–19.

## FISH HABITAT MAPPING

# Distribution of swordfish in the eastern Mediterranean, in relation to environmental factors and the species biology

George Tserpes · Panagiota Peristeraki · Vasilis D. Valavanis

© Springer Science+Business Media B.V. 2008

Abstract Swordfish catch per unit effort (CPUE) data from the Greek commercial fisheries operating in the eastern Mediterranean have been modeled on a seasonal basis as functions of environmental spatial, and temporal variables, including Sea Surface Temperature (SST), Chlorophyll-a (Chl-a), Mean Sea Level Anomaly (MSLA), Latitude, Longitude and Year. All variables were highly significant but most of the CPUE variation was explained by the spatial factors. Model predictions were used to generate swordfish density distributions maps, which revealed that swordfish migrates toward the eastern Levantine for spawning and suggested the existence of a major spawning ground in a region between the islands of Cyprus and Rhodes surrounded by persistent eddies and the Rhodes gyre. During periods other than the time of spawning migration, swordfish distribution is

Guest editor: V. D. Valavanis Essential Fish Habitat Mapping in the Mediterranean

G. Tserpes (⊠) · P. Peristeraki Institute of Marine Biological Resources, Hellenic Centre for Marine Research, Thalassocosmos, 71003 Heraklion, Crete, Greece e-mail: gtserpes@her.hcmr.gr

V. D. Valavanis

Marine GIS Laboratory, Institute of Marine Biological Resources, Hellenic Centre for Marine Research, Thalassocosmos, 71003 Heraklion, Crete, Greece much broader with relatively higher concentrations occurring in areas with important prey potential.

**Keywords** Swordfish · Mediterranean · Environmental parameters · Migration · Reproduction · Distribution

# Introduction

The swordfish, *Xiphias gladius* (Linnaeus, 1758), is a commercially important highly migratory fish, globally distributed between the latitudes 45° N and 45° S (Palko et al., 1981). Mediterranean swordfish populations constitute a unique stock having different growth and maturity characteristics from the adjacent Atlantic ones (Cavallaro et al., 1991; Ehrhardt, 1992; Kotoulas et al., 1995, 2003; Tserpes & Tsimenides, 1995).

The swordfish fisheries in the Mediterranean are characterized by relatively high catch levels and the annual reported catches (on average 14,500 t from 1984 to 2002) are similar to those observed for larger marine areas, such as the North Atlantic (Anonymous, 2003).

The Greek swordfish fishery started developing in the early 1980s and Greek fleets currently exploit a large part of the E. Mediterranean basin extending their activities from the east Ionian to the Levantine Seas (Tserpes et al., 2003a, b). Fishing is carried out by means of two different drifting longline types: the traditional and the so-called American, owing its name to its similarity to the longline used by the USA fishery in the Atlantic. Detailed descriptions of the Greek swordfish fishery have been presented elsewhere (Tserpes et al., 2003a, b; Tserpes & Peristeraki, 2004). Recent ICCAT catch records indicate that Greece together with Italy, Spain and Morroco are the most important swordfish producers in the Mediterranean (Anonymous, 2006).

Although certain aspects of the biology and fisheries of the Mediterranean swordfish, such as age, growth, maturity and fishing tactics, have been examined (e.g., Cavallaro et al., 1991; Orsi-Relini et al., 1995; Tserpes & Tsimenides, 1995; De La Serna et al., 1996; Tserpes et al., 2001a, b, 2003a, b, 2006; Stergiou et al., 2003; Tserpes & Peristeraki, 2007), studies on the distribution of the fish in relation to biological and environmental parameters are limited and very little information has been provided on the species migration pattern (Tserpes et al., 2001b; Damalas et al., 2007; Peristeraki et al., 2007).

In the present work, we attempted to model seasonal spatial trends in swordfish abundance in the eastern Mediterranean as functions of environmental spatial and temporal variables. Those variables were: Sea Surface Temperature (SST), Chlorophyll-a (Chl-a), Mean Sea Level Anomaly (MSLA), Latitude, Longitude and Year. As swordfish has a near-surface distribution, at least during the night (Carey & Robison, 1981), we expected that SST will be important either as a direct influence on distribution or as a proxy for other factors (e.g., prey abundance). Chl-a level provides information on the primary production of an area, while MSLA is an indicator of possible oceanographic activities such as gyres and eddies. There may be spatial trends in abundance due to other reasons (e.g., topography of the area) than oceanographic parameters. Consequently, we included longitude and latitude as possible predictors. Finally, year was included as a predictor variable to account for abundance trends due to annual recruitment variations.

Abundance variations were modeled by means of Generalized Additive models (GAM) techniques (Hastie, 1990) commonly used for examining fisheries data in relation to environmental and spatiotemporal variables (e.g., Bigelow et al., 1999; Daskalov, 1999; Walsh & Kleiber, 2001; Maravelias & Papaconstantinou, 2003). Apart from exploratory purposes, GAM analysis was utilized in a predictive way, as the model estimates were used to construct density distribution maps of the swordfish in the studied area.

### Materials and methods

#### CPUE and oceanographic data

A series of catch and effort data from the main Greek longline fleets exploiting the eastern Mediterranean basin have been gathered, past projects which sought to monitor the Greek large pelagic fisheries and since 2002, through the National Fisheries Data Collection Program established in accordance with 1639/2001 EU Regulation. Data were obtained from trained technicians located at the main landing ports or through onboard observations. Further details on the sampling scheme that has been followed are provided in Tserpes et al. (2003a).

In the present study, we used only datasets available on a trip basis and for which the fishing location could be identified on a fairly accurate basis, i.e., within a circle of 50 Km diameter, taking into account the length of the longline and its drifting potential. Catch per unit effort (CPUE) that was calculated from the available catch-effort data and expressed in terms of kg/1,000 hooks, was assumed to represent the local abundance index. As already mentioned, the Greek fishermen use two types of longlines that differ in catchability. For the needs of the current analysis, the CPUE series from the different gear-types were harmonized through the application of a multiplication factor previously identified from a large dataset (Tserpes & Peristeraki, 2004). Considering that gears have not changed in the last years, it was assumed that the already estimated catchability differences remain constant throughout the examined years.

The analyzed CPUE records were collected from 1998 to 2006. Based on the species biology and the fisheries characteristics, data were divided into three sets, representing different fishing periods: (a) the peak of the spawning period, i.e., June and July (Tserpes et al., 2001b), (b) two months before and after the spawning peak, when the fleets migrate toward and off the spawning grounds following the migration patterns of the fish, and (c) the rest months, representing the fish presence in the winter feeding grounds (Stergiou et al., 2003).

The oceanographic data used to characterize fish habitats included satellite-derived estimates of monthly averages of SST, Chl-a and MSLA for the corresponding fishing locations. AVHRR-SST (Advanced Very High Resolution Radiometer-Sea Surface Temperature) data were downloaded through DLR's (Deutsches Zentrum fur Luftund Raumfahrt) EOWEB Server (http://eoweb. dlr.de:8080/) as monthly averaged image products and were processed as ArcGIS grids.

### Data analysis

The effects of environmental conditions, and fishing location on CPUE in the three aforementioned fishing periods were examined by means of Generalized Additive models (GAMs). GAMs, which are able to deal with nonlinear relationships between a dependent variable and multiple predictors in the same model, are nonparametric generalizations of multiple linear regression that are less restrictive in assumptions about the underlying distribution of data (Hastie & Tibshirani 1990). In GAMs, a pre-defined link function is related to predictor variables by scatterplot smoothers in lieu of least-squares fits.

In the present case, our nonlinear components were fitted with a locally weighted regression scatterplot smoother (*loess* smoother, Cleveland & Devlin, 1988) by means of the S-PLUS software package, in the way described by Venables & Ripley (1997). The span of the smoother, which determines the fraction of data used for smoothing at each point, was set at 0.2. Preliminary trials showed that this was the most suitable choice, as smaller span sizes were resulting in unrealistically bumpy and complex responses.

Based on the diagnostic residual plots of preliminary runs, we assumed a Poisson distribution accompanied by its canonical log-link function. Apart from the environmental parameters and the fishing location, the year parameter was also modeled as a categorical variable. Hence, six variables were included in the analysis: Year, Latitude (Lat), Longitude (Lon), SST, Chlorophyll (Chl-a) and MSLA. The GAM model was of the form:

$$CPUE = a + Year + lo_1(Lat) + lo_2(Lon) + lo_3(SST) + lo_4(Chl-a) + lo_5(MSLA) + e,$$

where a is a constant,  $lo_i$  is the *loess* smoother function of the corresponding independent variable and e is a random error term.

Variable selection proceeded by a stepwise forward entry and the Akaike Information Criterion (AIC) was used to detect the relative importance of each variable in explaining variations and determine the order of those that should be included in the final model. The AIC statistic accounts simultaneously for the degrees of freedom used and the goodness of fit, whereas a smaller AIC statistic corresponds to a better model in the sense of smaller residual deviance penalized by the number of parameters that are estimated in fitting the model. At each stage of the forward entry, the AIC was computed for every candidate predictor not yet entered. The variable resulting in the highest AIC decrease was entered into the model. Forward entry continued until additional variables no longer yielded reductions in the AIC statistic. Significant levels for the added predictors were estimated by means of the Chi-square test and the level of significance was set at 95%.

The predicted CPUE values from the GAM analysis were used to construct density distribution maps of the swordfish in the examined area. Maps were generated using the SURFER software (Golden Software, 2002) and interpolation was made by means of the "natural neighbor" griding method, which is considered to produce good contours for irregularly spaced data (Sibson, 1981). The method does not generate data in areas without data and contouring is based on an algorithm that creates different size polygons from the existing dataset. For this reason, the produced contours may not match exactly the sampled area.

#### Results

A total of 1,647 longline sets broadly distributed from  $20-35^{\circ}$  E to  $34-39^{\circ}$  N were analyzed (Fig. 1). Data covered 10,056 fishing days of 63 commercial boats. The three stepwise GAMs explained 46–59% of the total variation (Table 1) and all variables were highly significant (P < 0.0001). Spatial covariates (longitude, latitude) and the "year" accounted for a large part of the variance (40–48%), while MSLA had a relatively high explanatory power (16.30%) during the feeding period. Latitude provided the largest reduction in residual deviance in the migration and feeding periods, while longitude was the most important variable in terms of explanatory power during the peak spawning.

The effect (loess plot) of the spatial and environmental predictors that explained at least 2% of the total variation on CPUE is shown on the y-axis for





 
 Table 1
 Analysis of deviance for the GAM models fitted to the swordfish CPUE data by fishing period

Explanatory variable	Residual d.f.	Residual deviance	Cumulative variance explained in CPUE
Spawning			
Mean	480.00	82635.42	
Longitude	468.84	64217.27	22.29
Year	460.83	53404.53	35.37
Latitude	450.48	50273.84	39.16
MSLA	440.18	47665.50	42.32
SST	429.57	45872.56	44.49
Chl-a	418.06	44406.80	46.26
Migration			
Mean	826.00	165225.00	
Latitude	816.00	109900.10	33.48
Longitude	805.73	93979.90	43.12
Year	797.68	84744.10	48.71
SST	787.83	79358.20	51.97
Chl-a	777.36	77679.50	52.99
MSLA	767.25	76284.20	53.83
Winter feeding			
Mean	338.00	154697.50	
Latitude	327.38	114474.70	26.00
MSLA	316.47	89255.90	42.30
Year	309.38	75132.70	51.43
Longitude	298.70	67414.50	56.42
SST	287.41	64710.40	58.17
Chl-a	275.76	63024.60	59.26

different values of the predictor (*x*-axis) (Figs. 2–4). The zero line indicates mean CPUE estimated by the model, while the *y*-axis is a relative scale where the effect of different values of the predictors on the response variable is shown. Hence, negative values on the *y*-axis indicate that at the corresponding levels of the predictor (*x*-axis), the model estimates CPUE that is lower than the mean, while the opposite holds for positive values on the *y*-axis.

During the peak spawning period, catch rates showed their maximum between longitudes ca. 30 and  $32^{\circ}$  E and latitudes ca.  $35-36^{\circ}$  N. Concerning SST, the maximum catch rate was around  $22.5^{\circ}$ C. MSLAs had a positive effect on catch rates only in a narrow range of values (2–3) although variations were rather small for values higher than -4(Fig. 2).

During the migration (transitional) period the loess plot of latitude exhibited a negative effect on catch rates from ca.  $35^{\circ}$  N northward. The effect was stronger beyond  $39^{\circ}$  N. Considering longitude, its effect was positive from ca.  $27^{\circ}$  E eastward. The most prominent feature of the loess plot of SST was its sharp decline after ca.  $26^{\circ}$ C (Fig. 3).

In the winter feeding period, there was a positive relationship between latitude and catch rate from  $36^{\circ}$  N up to ca.  $39^{\circ}$  N. Beyond  $39^{\circ}$  N, catch rates seem to decline. Catch rates were higher at the MSLA range of -2 to 2. In general, catch rate was increasing as the negative MSLA values were

**Fig. 2** GAM derived effects on swordfish CPUE during the peak spawning period. Each plot represents the contribution of the corresponding variable to the fitted predictor. The fitted values are adjusted to average zero and the broken lines indicate two standard errors. The relative density of data points is shown by the "rug" on the *x*-axis





approaching zero. Longitude was positively related with catch rate from ca. 24° E eastward (Fig. 4).

The density distribution maps indicated that during the peak spawning period the highest swordfish biomass density is expected in the eastern Levantine basin in the region around  $30^{\circ}$  E and  $35.5^{\circ}$  N. In general, higher densities are expected from ca.  $28^{\circ}$  E eastward to  $36^{\circ}$  N southward. With some local exceptions, densities in the region north of  $36^{\circ}$  N are considerably lower (Fig. 5).

In the migration period, densities are also higher in the south-eastern region from ca.  $30^{\circ}$  E eastward to  $36^{\circ}$  N southward but maximum density is expected further east than during the peak spawning. Relatively lower but homogeneous density is observed in the rest area (Fig. 6). **Fig. 4** GAM derived effects on swordfish CPUE during the winter feeding period. Each plot represents the contribution of the corresponding variable to the fitted predictor. The fitted values are adjusted to average zero and the broken lines indicate two standard errors. The relative density of data points is shown by the "rug" on the *x*-axis

Effect on CPUE

Effect on CPUE

42

40

38

36

34

32

30

20

22

24

26

28

30

Longitude (East)

32

Latitude (North)

c

7



Hydrobiologia (2008) 612:241-250

The most prominent feature of the winter feeding period is the relatively high fish density north of  $36^{\circ}$  N. On the contrary, density is very low in the region which is south of ca.  $36^{\circ}$  N and west of ca.  $27^{\circ}$  E (Fig. 7).

### Discussion

Our results indicated that in all seasons, the spatial and temporal variables played an important role in explaining swordfish abundance variations. Past authors who have studied the effects of spatial and environmental variables on swordfish abundance in various areas have also reported that spatial variables are of greater importance in explaining abundance variations (Bigelow et al., 1999; Damalas et al., 2007).

34

36

38

200

100

In general, in agreement with previous findings (Damalas et al., 2007), swordfish abundance was found to be higher in the eastern Levantine. In the present case, however, the use of the GAM predictions for constructing density maps enabled us to detect seasonal differences in the spatial distribution pattern. Such differences seem to be related, at least partly, to the species biological cycle.

**Fig. 6** Map of swordfish distribution during the migration period, based on the GAM predictions. Abundance is expressed in terms of kg/1,000 hooks. Observations are depicted on the small map on the upper right corner; the diameter of the circles is proportional to the CPUE value



Fig. 7 Map of swordfish distribution during the winter feeding period based on the GAM predictions. Abundance is expressed in terms of kg/1,000 hooks. Observations are depicted on the small map on the upper right corner; the diameter of the circles is proportional to the CPUE value

The high swordfish density during the peak of spawning season between the islands of Cyprus and Rhodes provides indirect evidence for the presence of a major spawning ground in that region. This hypothesis is supported by the fact that the highest abundance rates are expected for SST ca. 22.5°C, which is within a preferred narrow temperature range during spawning (Palko et al., 1981). Results of a regional plankton survey, carried out in the Levantine Sea in July 2000 seem to support this hypothesis as it was found a small number of fertilized swordfish eggs in the samples (Tserpes et al., 2001a, b).

The available information on the reproductive activity of the Mediterranean swordfish is rather limited. Spawning occurs in the summer months and since the beginning of the twentieth century it is known the presence of a spawning ground in the Straits of Sicily (Palko et al., 1981; Cavallaro et al., 1991). Rey (1988), based on the capture of few young specimens along the Spanish Mediterranean coast, has also speculated the presence of a spawning ground in the area. Large-scale ichtyoplankton surveys for large pelagic species are lacking in the eastern Mediterranean and the fact that large pelagic larvae are able to avoid the typical plankton samplers (Doherty, 1987) makes difficult the identification of spawning grounds through general plankton surveys.

Mejuto et al. (1995, 1998) who revised literature information on spatiotemporal variation of swordfish sex ratio in commercial catches from the Atlantic and the Indian oceans suggested that a male biased sex ratio, in certain size ranges, is typical for several spawning areas. Tserpes et al. (2001a, b) have also reported a similar male biased sex ratio, regarding individuals of lower jaw fork length greater than 120 cm, in commercial catches of the eastern Levantine basin during the spawning period and suggested the possible existence of a major spawning ground in the broader area. The current approach has provided more specific information on the location of the spawning ground which seems to be located near the Anaximander seamounts, at an area between the Anaximander eddy, the Antalya eddy and the Rhodes Gyre, which is one of the most distinct features of the Levantine basin (Ozsoy et al., 1993; Zervakis et al., 2005). According to Bakun (2006), zones situated near eddies outer edges often produce outbursts in biological productivity and in some cases support spawning of highly migrating fishes.

Although, the effect of environmental variables was always significant, their explanatory power was relatively lower, with the exception of MSLA during the winter feeding period, when it explained about 16% of the total variance. Further examination of the MSLA values in the studied area revealed that the MSLA range which corresponds to high swordfish density values in the feeding period is found in areas surrounding eddies. These zones are often characterized by high productivity (Bakun, 2006) and it is likely that high concentrations of swordfish prey occur in such areas, supporting the hypothesis that swordfish abundance variations are closely related to prey availability during the winter feeding period. It is notable that in the above period, swordfish appear in relatively high densities in the northern part of the Aegean Sea (north of  $36^{\circ}$  N), where their presence is infrequent in the rest of the year.

Our analysis suggest that swordfish in the eastern Mediterranean migrates toward the eastern Levantine for spawning, concentrating in specific areas during the peak of the spawning season. During the migration period (i.e., the months before and after the reproduction peak) high abundance indices are observed only in the wider area of the proposed spawning ground providing further support on the hypothesis of existence of a major spawning ground in the Levantine basin. In the rest of the year, swordfish spatial distribution is much broader with relatively higher concentrations occurring in areas with important prey potential.

As fisheries management in the Mediterranean is mainly realized through technical measures and effort control regimes, distribution studies can provide useful background information regarding the potential establishment of fisheries limitations on certain essential habitats. The present study has provided information on swordfish distribution in a region of high fishing activity. Such information could be utilized for the rational management of the resource. In particular, this study may become of major importance if recent inferences based on genetics findings (Kotoulas, Hellenic Centre for Marine Research, personal communication) that swordfish in the eastern Mediterranean form a unique substock are corroborated.

Acknowledgments We wish to thank Drs. John Neilson (St. Andrews Biological Station, Canada) and Jaime Mejuto (IEO, Spain) for providing helpful comments that greatly improved the manuscript.

# References

- Anonymous, 2003. Mediterranean Swordfish. In International Commission for the Conservation of Atlantic Tunas (ICCAT), Report of the Standing Committee on Research and Statistics (SCRS) for biennial period 2002–03, Part I (2002), Vol. 2: 125–129, Madrid, Spain.
- Anonymous, 2006. Mediterranean Swordfish. International Commission for the Conservation of Atlantic Tunas (ICCAT). Report of the Standing Committee on Research and Statistics (SCRS) for biennial period 2004–2005, Part II-3: 33–45.
- Bakun, A., 2006. Fronts and eddies as key structures in the habitat of marine fish larvae: opportunity, adaptive response and competitive advantage. Scientia Marina 70: 105–122.
- Bigelow, K. A., C. H. Boggs & X. He, 1999. Environmental effects on swordfish and blue shark catch rates in the US North Pacific longline fishery. Fisheries Oceanography 8: 178–198.
- Carey, F. G. & B. H. Robison, 1981. Daily patterns in the activities of swordfish, *Xiphias gladius*, observed by acoustic telemetry. Fishery Bulletin U.S. 79: 277–292.
- Cavallaro, G., A. Potoschi & A. Cefali, 1991. Fertility gonadsomatic index and catches of eggs and larvae of *Xiphias* gladius L. 1758 in the southern Tyrrhenian Sea. International

Commission for the Conservation of Atlantic Tunas. Collective Volume of Scientific Papers 35: 502–507.

- Cleveland, W. S. & S. J. Devlin, 1988. Locally-weighted regression: an approach to regression analysis by local fitting. Journal of American Statistical Association 83: 596–610.
- Damalas, D., P. Megalofonou & M. Apostolopoulou, 2007. Environmental, spatial, temporal and operational effects on swordfish (*Xiphias gladius*) catch rates of eastern Mediterranean Sea longline fisheries. Fisheries Research 84: 233–246.
- Daskalov, G., 1999. Relating fish recruitment to stock biomass and physical environment in the Black Sea using generalised additive models. Fisheries Research 41: 1–23.
- De La Serna, J. M., J. M. Ortiz de Urbina & D. Macias, 1996. Observations on sex-ratio, maturity and fecundity by length-class for swordfish (*Xiphias gladius*) captured with surface longline in the western Mediterranean. International Commission for the Conservation of Atlantic Tunas. Collective Volume of Scientific Papers 45: 117–122.
- Doherty, P. J., 1987. Light-traps: selective but useful devices for quantifying the distributions and a abundance of larval fishes. Bulletin of Marine Science 41: 423–431.
- Ehrhardt, N. M., 1992. Age and growth of swordfish, *Xiphias gladius*, in the northwestern Atlantic. Bulletin of Marine Science 50: 292–301.
- Golden Software, 2002. SURFER, Version 8. Golden Software Inc., Golden, Colorado.
- Hastie, T. J. & R. J. Tibshirani, 1990. Generalized Additive Models. Chapman and Hall, London: 335.
- Kotoulas, G., A. Magoulas, N. Tsimenides & E. Zouros, 1995. Marked mitochondrial DNA differences between Mediterranean and Atlantic populations of the swordfish, *Xiphias gladius*. Molecular Ecology 4: 473–481.
- Kotoulas, G., J. Mejuto, G. Tserpes, B. Garcia-Cortes, P. Peristeraki, J. M. De la Serna & A. Magoulas, 2003. DNA microsatellite markers in service of swordfish stock structure analysis in the Atlantic and Mediterranean. International Commission for the Conservation of Atlantic Tunas. Collective Volume of Scientific Papers 55: 1632–1639.
- Maravelias C. D., & C. Papaconstantinou, 2003. Size-related habitat use, aggregation patterns and abundance of anglerfish (*Lophius budegassa*) in the Mediterranean Sea determined by generalized additive modeling. Journal Marine Biological Association U.K. 83: 1171–1178.
- Mejuto, J., J. M. De la Serna & B. Garcia, 1995. An overview of the sex-ratio at size of the swordfish (*Xiphias gladius* L.) around the world: similarity between different strata. International Commission for the Conservation of Atlantic Tunas. Collective Volume of Scientific Papers 44: 197–205.
- Mejuto, J., J. M. De la Serna & B. Garcia, 1998. Some considerations on the spatial and temporal variability in the sex-ratio at size of the swordfish (*Xiphias gladius* L.). International Commission for the Conservation of Atlantic Tunas. Collective Volume of Scientific Papers 48: 205–215.
- Orsi-Relini, L., F. Garibaldi, C. Cima & G. Palandri, 1995. Feeding of the swordfish, the bluefin tuna and other pelagic nekton in the western Ligurian Sea. International Commission for the Conservation of Atlantic Tunas. Collective Volume of Scientific Papers 44: 283–286.

- Ozsoy, E., A. Hecht, U. Unluata, S. Brenner, H. I. Sur, J. Bishop, M. A. Latif & T. O. Rozentraub, 1993. A synthesis of the Levantine Basin circulation and hydrography, 1985–1990. Deep-Sea Research II 40: 1075–1119.
- Palko, R. J., G. L. Beardsley, & W. J. Richards, 1981. Synopsis of the biology of the swordfish *Xiphias gladius* L. National Oceanic and Atmospheric Administration. Technical Report National Marine Fisheries Service, Circular: 441.
- Peristeraki, P., G. Lazarakis, K. Skarvelis, N. Kypraios & G. Tserpes, 2007. Temporal growth differences of swordfish recruits in the eastern Mediterranean. International Commission for the Conservation of Atlantic Tunas. Collective Volume of Scientific Papers 60: 2063–2068.
- Rey, J. C., 1988. Comentarios sobre las areas de reproduccion del pez espada (*Xiphias gladius*) en el Atlantico y Mediterraneo. International Commission for the Conservation of Atlantic Tunas. Collective Volume of Scientific Papers 27: 180–192.
- Sibson, R., 1981. A brief description of natural neighbor interpolation. In Barnett, V. (ed.), Interpreting Multivariate Data. John Wiley & Sons, New York: 21–36.
- Stergiou, K. I., G. Tserpes & P. Peristeraki, 2003. Modelling and forecasting monthly swordfish catches in the Eastern Mediterranean. Sciencia Marina 67: 283–290.
- Tserpes, G., C. Darby, A. Di Natale, P. Peristeraki & A. Mangano, 2003a. Assessment of the Mediterranean swordfish stock based on Greek and Italian fisheries data. International Commission for the Conservation of Atlantic Tunas. Collective Volume of Scientific Papers 55: 94–106.
- Tserpes, G., D. K. Moutopoulos, P. Peristeraki, G. Katselis & C. Koutsikopoulos, 2006. Study of swordfish fishing dynamics in the eastern Mediterranean by means of machine-learning approaches. Fisheries Research 78: 196–202.
- Tserpes, G. & P. Peristeraki, 2004. Catchability differences among the longlines used in the Greek swordfish fishery. International Commission for the Conservation of Atlantic Tunas. Collective Volume of Scientific Papers 56: 860–863.
- Tserpes, G. & P. Peristeraki, 2007. Effects of a seasonal closure of the Mediterranean swordfish fisheries on the stock production levels. International Commission for the Conservation of Atlantic Tunas. Collective Volume of Scientific Papers 60: 2059–2062.
- Tserpes, G., P. Peristeraki & A. Di Natale, 2001a. Size distribution of swordfish landings in the central and eastern Mediterranean. International Commission for the Conservation of Atlantic Tunas. Collective Volume of Scientific Papers 52: 733–739.
- Tserpes, G., P. Peristeraki & A. Di Natale, 2003b. Swordfish abundance trends in the Mediterranean. In Mediterranean Biological Time Series, Commission Internationale pour l'Exploration Scientifique de la mer Mediterranee (CIESM) Workshop Monographs 22: 101–108.
- Tserpes, G., P. Peristeraki & S. Somarakis, 2001b. On the reproduction of swordfish (*Xiphias gladius* L.) in the Eastern Mediterranean. International Commission for the Conservation of Atlantic Tunas. Collective Volume of Scientific Papers 52: 740–744.
- Tserpes, G. & N. Tsimenides, 1995. Determination of age, growth of swordfish, *Xiphias gladius* L., 1758, in the

eastern Mediterranean using anal-fin spines. Fishery Bulletin 93: 594-602.

- Venables, W. N. & B. D Ripley, 1997. Modern Applied Statistics with S-PLUS, Second Edition. Springer.
- Walsh, A., & P. Kleiber, 2001. Generalized additive model and regression tree analyses of blue shark (*Prionace glauca*) catch rates by the Hawaii-based commercial longline fishery. Fisheries Research 53: 115–131.
- Zervakis, V., A. Theocharis & D. Georgopoulos, 2005. Circulation and hydrography of the open seas. In: Papathanassiou, E. & A. Zenetos (eds), State of the Hellenic Marine Environment. Hellenic Center for Marine Research Publication: 104–111.

# FISH HABITAT MAPPING

# **Results of a short study of interactions of cetaceans and longline fisheries in Atlantic waters: environmental correlates of catches and depredation events**

Gema Hernandez-Milian · Sabine Goetz · Catuxa Varela-Dopico · José Rodriguez-Gutierrez · Jorge Romón-Olea · José R. Fuertes-Gamundi · Edelmiro Ulloa-Alonso · Nick J. C. Tregenza · Andy Smerdon · Monserrat G. Otero · Vicente Tato · Jianjun Wang · M. Begoña Santos · Alfredo López · Rebeca Lago · Julio M. Portela · Graham J. Pierce

© Springer Science+Business Media B.V. 2008

**Abstract** In the Atlantic, economic losses have been reported from shark, swordfish and tuna longline fisheries due to depredation by cetaceans. We examined interactions of odontocete cetaceans with commercial longliners operating in waters off Brazil and the Azores archipelago during 2006–2007, analysing relationships between catches, depredation on hooked fish, cetacean sightings, acoustic records of cetacean presence and environmental variables. Data were provided by skippers of six vessels and by on-

Guest editor: V. D. Valavanis Essential Fish Habitat Mapping in the Mediterranean

G. Hernandez-Milian  $(\boxtimes) \cdot J$ . Wang  $\cdot$  G. J. Pierce University of Aberdeen, Tillidrone Avenue, Aberdeen AB24 2TZ, UK e-mail: g.hernandez-m@abdn.ac.uk

S. Goetz · M. B. Santos · J. M. Portela · G. J. Pierce Instituto Español de Oceanografía, Centro Oceanográfico de Vigo, Cabo Estai, Canido, 36200 Vigo, Spain

#### C. Varela-Dopico

Estación de Biología Mariña da Graña, University of Santiago de Compostela, Casa do Hórreo e Casa da Estrela, Rúa da Ribeira 1-4, A Graña, 15590 Ferrol, Spain

C. Varela-Dopico · J. Rodriguez-Gutierrez ·

J. Romón-Olea · J. R. Fuertes-Gamundi ·

Cooperativa de Armadores de Pesca del Puerto de Vigo, Sociedad Coop. Ltda., Puerto Pesquero, Edif. Cooperativa de Armadores, Apdo. 1078, 36202 Vigo, Spain board observers for two vessels. The percentage of longline sets depredated by cetaceans was low (ranging from 1% to 9% of total sets per ship) but the proportion of fish damaged was high (up to 100%) when depredation occurred. Catches were related to the phase of the moon, cloud cover, sea surface temperature and water depth whereas cetacean sightings were primarily related to catches. In particular there was a positive association between *Delphinus delphis* sightings and catches of swordfish, and between *Stenella frontalis* sightings and mako catches. Acoustic detection was low when depredation by false killer whales occurred although high

N. J. C. Tregenza Chelonia Limited, Beach Cottage, 5 Beach Terrace, Long Rock, Cornwall TR20 8JE, UK

A. Smerdon Aquatec Group Ltd., High Street, Hartley Wintney, Hampshire RG27 8NY, UK

M. G. Otero · V. Tato MG Otero Consultores SL, Porto Pesqueiro, Nvo Tinglado Xeral Empaque Of. 8, PO Box 1132, 36202 Vigo, Spain

A. López · R. Lago CEMMA, Apdo. 15, 36380 Gondomar, Pontevedra, Spain

E. Ulloa-Alonso

rates of clicks were detected when delphinids were sighted and false killer whales were by-caught. This may indicate that false killer whales are not echolocating when feeding on fish hooked on a longline.

**Keywords** Cetaceans · False killer whale · Longline fishery · Depredation · Hydrophones · Behaviour · Habitat modelling

# Introduction

Pelagic longline fisheries in the Atlantic usually operate in offshore waters, mainly targeting tuna, swordfish, billfishes (Istiophoridae) and sharks (Brothers et al., 1999a). In contrast to the Pacific, catches of these species have not increased over the last decade (ICCAT, 2007). The most important Atlantic fishing grounds for longliners are located in the South Central tropical area and NW-W Azores waters (Lewison et al., 2004). The Spanish tuna and swordfish longline fishery is one of the most important in the Atlantic (ICCAT, 2007), a significant source of income for the Spanish fishing sector (Garza Gil et al., 2003). The lines used are approximately 50 miles long and typically carry 1200–1250 hooks.

Toothed whales (Odontoceti) are attracted to longlines because they provide an easily accessible source of food and the fish caught on them are often large. Cetaceans cause significant economic losses due to damage and removal of bait and hooked fish in a range of longline fisheries around the world (Northridge, 1984; Dahlheim, 1988; Ashford et al., 1996; Capdeville, 1997; Dalla Rosa & Secchi, 2002, 2007; Donoghue et al., 2002; Gilman et al., 2006; Zollett & Read, 2006; Ramos-Cartelle & Mejuto, 2007). Odontocetes are believed to develop familiarity with the sounds produced by longliners (such as the sound of the engine, the gear haulers and the electric equipment) and are frequently observed to follow vessels for days in order to take advantage of the catches (Gilman et al., 2006; Ramos-Cartelle & Mejuto 2007). Depredation rates tend to be higher for longer soak times (Gilman et al., 2007a, b).

In tropical and subtropical Atlantic waters, the killer whale (Orcinus orca, Linnaeus 1758) and the

false killer whale (Pseudorca crassidens, Owen 1846) are known to interact with the pelagic longline fishery for tuna and swordfish (Dalla Rosa & Secchi, 2002, 2007; Dalla Rosa et al., 2006; Ramos-Cartelle & Mejuto, 2007). Killer whales and false killer whales are distributed in all oceans, the former best known from cooler waters and the latter preferring tropical, subtropical and warm temperate waters. Killer whales are found from the surf zone to 800 km from the coast, with large concentrations over the continental shelf, whereas false killer whales inhabit deep offshore waters. Both species mainly feed on fish, cephalopods and other marine mammals (Jefferson et al., 1993; Stacey et al., 1994; Carwadine, 1995). Environmental and oceanographic features, such as water temperature, bathymetry, oceanic fronts, lunar cycle, and spatiotemporal factors are believed to play an important role in the distribution of the cetaceans and their prey (e.g. Damalas et al., 2007; Romo et al., 2007; De Stephanis et al., 2008).

Marine mammal presence in offshore waters is usually determined by means of sightings recorded from vessels. However, use of passive acoustic methods, e.g. deployment of T-PODs (www. chelonia.com), can increase the detection rate, especially when visibility is low or the animals spend little time on the surface, and the range of detection may be wider than if only visual observation is used (Carstensen et al. 2006; Leeney & Tregenza 2006; Philpott et al., 2007).

The present short study aimed to describe the interactions of cetaceans, in particular killer and false killer whales, with longline fisheries for swordfish and tuna in two regions of the Atlantic (Brazil and Azores), determining the relationships between catches, cetacean presence, the incidence of depredation and environmental variables. Specifically: (1) Are the fish caught in particular places and is the size of catch related to environmental conditions? (2) Is cetacean presence and/or the occurrence of depredation related to particular environmental conditions? (3) Is depredation associated with the presence of particular cetaceans species and is it related to the amount of fish caught? Finally, since turtle bycatches were frequent we also investigated possible relationships between turtle by-catch, fish catch and environmental conditions.

#### Materials and methods

#### Sampling effort and study area

Data were gathered from eight Spanish commercial pelagic surface longline vessels, operating in Atlantic waters (1) off Brazil and extending into mid-Atlantic waters and (2) to the west of the Azores archipelago, between June 2006 and June 2007 (Fig. 1, Table 1). The two vessels with observers were fishing off Brazil (V7) and west of the Azores (V8), respectively.

The oceanography of the study area off Brazil is dominated by the South Equatorial Current, which has an offshoot along Brazil's North Coast (the North Brazil Current) and to the South (the Brazil Current). Offshore, in the waters of the Brazil Current, important fishery resources include Thunnus albacares in the southern region and T. alalunga in the northern region (Zavala-Camin & Antero da Silva, 1991), which are caught around seamounts and banks. The Brazil Current is a weak western boundary current carrying warm subtropical water with a temperature range of 18-28°C, which runs south along the coast of Brazil from about 9° S to about 38° S and is generally confined to the upper 600 m of the water column (Memery et al., 2000; Zavilov et al., 1999).



Fig. 1 Fishing areas of vessels V1–V8 in the Atlantic Ocean. Squares indicate where fishing operations took place

The second study area is to the west of the Azores archipelago, a group of nine volcanic islands situated on the Mid-Atlantic ridge, in an area dominated oceanographically by the Gulf Stream. The richness of fishing resources in the Azores originates from the complex relations between intermediate depth hydro-thermal fields and seamount ecosystems. Tuna and swordfish are the most important target groups in the vicinity of the islands, although sharks—mainly blue shark (*Prionace glauca*) and shortfin mako (*Isurus oxyrinchus*)—can outnumber swordfish 10:1 in long-line catches (Morato et al., 2001).

#### Sampling methods

Skippers of six vessels (V1–V6) recorded data on catches of fish, cetacean sightings and depredation on catches. In addition, two vessels (V7 operating off North East Brazil between January and March 2007 and V8 operating South West of the Azores between April and June 2007) each carried a scientific observer on board, who registered data on fishing activity, cetacean sightings, acoustic detection of cetaceans, depredation on catches, and environmental data (Table 1).

Data on fishing activity included the time and location of each set, the number of hooks on the line, total catch (number and biomass of fish, by species) and any by-catch of marine mammals or sea turtles. The fish caught were identified as follows: swordfish (*Xiphias gladius*), shortfin mako (*Isurus oxyrinchus*), blue shark (*Prionace glauca*), tuna (*Thunnus spp.*, mainly *T. alalunga*, *T. albacore*, and *T. Obesus*), marlin (Istiophoridae), dolphinfish (*Coryphaena hippurus*), barracuda (*Sphyraena spp.*) or garfish (Belonidae).

The number and species of fishes damaged by predators was logged and, based on the nature of the damage, the depredation was identified as due to cetaceans, sharks or other species, such as sea turtles. Fish damaged by cetaceans can be distinguished from shark-damaged fish since sharks typically bite the fish in half leaving clean borders or multiple smaller bites, whereas cetaceans such as killer whales and false killer whales tear the body of the fish, leaving bites with ragged borders and often just the head or the lips and upper jaw of the fish on the hook (Secchi & Vaske, 1998; Donoghue et al., 2002; Gilman et al., 2006; Varela-Dopico, pers. obs.). Fishermen report **Table 1** Fishing effort and depredation rates of eight Spanish commercial longline vessels operating in Atlantic waters (June 2006–July 2007): Vessel number (V1–V8), total no. of monitored sets per vessel, total no. of hooks deployed per vessel during monitored trips, average no. of hooks per set, average amount of catch per set (kg), percentage and number of sets with cetacean depredation, Spearman correlation

coefficients (r) and associated probability (P) for the relationship between average weight of catches/set and total catch lost per vessel due to cetacean depredation (V1–V6: Both fish damaged and bait/fish removed from the hooks were considered; V7–V8: Only damaged fish was considered), and percentage and number of sets with sea turtle/marine mammal by-catch

Vessel	ssel Sets Hooks Hooks/set Average catch/se		Average catch/set	Sets with		Correlation		% of Catch lost	Sets with by-catch			
					cetac depre	cean edation	between and depreda	n catch ation		Sea turtle	s	Marine mammals
					%	No.	r	Р		%	No.	No.
V1	76	102,600	1,350	1198.9	5.3	4	-0.07	0.547	1.6	10.5	8	0
V2	45	43,200	960	1574.7	8.9	4	-0.47	0.001	8.6	4.4	2	0
V3	126	163,800	1,300	886.1	5.6	7	-0.24	0.022	3.7	0	0	0
V4	137	185,358	1,353	1177.7	4.4	6	0.08	0.482	3.0	5.1	7	0
V5	94	116,100	1,235	1268.4	1.1	1	-0.01	0.934	0.2	10.6	10	0
V6	71	98,500	1,387	1715.6	4.3	3	-0.22	0.071	0.6	12.7	9	0
V7	30	37,673	1,256	2064.0	3.3	1	0.22	0.238	0.6	33.3	10	0
V8	56	62,198	1,111	1335.8	3.6	2	0.09	0.518	0.9	12.5	7	1
Total	635	809,429	1,275			28					53	1

**Table 2** Number and percentage of sets monitored using different numbers of hydrophones (T-PODs), for vessels V7 (Brazil) andV8 (Azores)

Vessel	sel 3 T-PODs		2 T-POI	Ds	1 T-POI	1 T-POD		No T-PODs	
	Sets	%	Sets	%	Sets	%	Sets	%	
V7	8	26.7	16	53.3	3	10.0	3	10.0	30
V8	55	98.2	0	0	0	0	1	1.8	56
Total	63		16		3		4		86

that cetaceans may occasionally also remove the fish entirely from the lines. Sea turtles leave several small bites on the fish, mainly eating the commercial parts (Varela-Dopico, pers. obs.).

Environmental data recorded on board by observers comprised sea state on the Douglas scale (Sea), cloud cover on a scale from 0 to 8 (Cd), moon phase (M1: new moon, M2: waxing moon, M3: full moon, M4: waning moon), sea surface temperature (SST) and water depth (Depth). In addition, bathymetry and coast line data for all trips were obtained from the GEBCO Atlas 2003, and a map was generated using ESRI Arc/View 3.3 (Fig. 1).

Sightings of cetaceans were recorded throughout fishing operations by the two observers, whereas sightings on the remaining six vessels were opportunistic. Geographic position, number of animals and species were recorded when they were sighted. The following categories were used: sperm whale (*Phys-eter macrocephalus*), killer whale (*Orcinus orca*), false killer whale (*Pseudorca crassidens*), common dolphin (*Delphinus delphis*), Atlantic spotted dolphin (*Stenella frontalis*), unidentified Odontoceti and Mysticeti.

Between one and three T-PODs (Table 2) were deployed along the line during most sets by vessels V7 and V8, in approximately 5 m water depth, one at each end and one in the middle. In order to prevent possible losses, they were attached to a buoy. The T-PODs used (version 5, www.chelonia.co.uk) detect clicks and click trains of specific cetacean species. They consist of a hydrophone, an analogue processor, a system to log echolocation clicks, and software that is able to filter cetacean clicks within a specific bandwidth. The T-PODs were programmed to detect false killer whales using parameters values calculated

Table 3 Number of clicks detected by the hydrophones for vessels V7 (Brazil) and V8 (Azores)

				•	• •								
Vessel	CetHi		CetLo		Doubtful		Very dou	btful	Positives		Negatives	5	Total
_	Clicks	%	Clicks	%	Clicks	%	Clicks	%	Clicks	%	Clicks	%	
V7	17,186	21.3	21,253	27.0	21,782	27.0	20,400	25.3	68,268	84.7	12,352	15.3	80,621
V8	50,439	11.9	71,193	16.8	188,374	44.5	113,358	26.8	121,370	28.7	301,994	71.3	423,364
Total	67,625		92,446		210,156		133,758		189,638		314,346		503,985

CetHi, clicks with high probability of coming from a cetacean; CetLo, clicks with lower probability of coming from a cetacean; Doubtful, clicks which are often from cetaceans, but are sometimes unreliable; Very doubtful, click sequences which are more likely to arise from other sources; Positives, sum of CetHi + CetLo; Negatives, sum of doubtful and very doubtful; Total, Total number of clicks detected by the T-PODs regardless of source

for free-ranging false killer whales by Madsen et al., (2004) (filter A = 41 kHz, filter B = 16 kHz, bandwidth = 4-6, sensitivity = various, minimum click duration = 40  $\mu$ s). They registered the number of clicks and classified the clicks according to the probability of coming from a false killer whale as high, low, doubtful or very doubtful (Table 3). P. crassidens produces echolocation sounds of 30-70 kHz (Madsen et al., 2004). However, this overlaps with the frequency range for other delphinid species, e.g. Delphinus delphis echolocation pulse frequency is between 20 and 100 kHz (Wood & Evans, 1980) and Stenella spp. emit clicks between 30 and 85 kHz (Lammers et al., 2003) or show bimodal click spectra with peaks at 40-60 kHz and 120-140 kHz (Schotten et al., 2003). Therefore the degree of species-specificity of the detections depends on the species present in the study area and in the present case was low due to the presence of both Delphinus and Stenella.

Data from the T-PODs were downloaded and stored on a laptop after hauling each line. Due to technical problems not all T-PODs worked all the time during the survey in Brazilian waters. In the Azores, T-PODs were used during all but one set. For each T-POD and each set, we extracted the number of clicks that were considered likely to come from delphinids ("positives", the sum of "CetHi" and "CetLo" categories, also known as "CetAll", see www.chelonia.co.uk) and the number of other clicks ("negatives"). Two additional indicators of cetacean activity were calculated (after Tougaard et al., 2004; Skov et al., 2002; Leeney & Tregenza, 2006): average click rate (the number of positive clicks divided by the total recording time) and click intensity (the mean number of positive clicks during minutes with clicks). Both indicators were calculated by T-POD and set.

#### Data analysis

Variables used for data analysis comprised descriptors of catch composition, occurrence and amount of depredation on catches, cetacean sightings, acoustic detections of cetaceans, and environmental data (see Table 4). Possible relationships between variables were initially explored using Spearman rank correlations, treating data from each set as a sample and analysing data from each vessel separately.

To provide a more detailed insight into relationships between response and explanatory variables, redundancy analysis (RDA) and generalised additive models were used with data from vessels 7 and 8 (recorded by observers). Data for Brazil and the Azores were analysed separately. For both surveys, (a) catches (numbers) of swordfish, tuna, shortfin mako and blue shark and (b) acoustic data on cetacean presence (click rate and click intensity) could be used as response variables for the RDA. For the Azores survey, there was sufficient data to also treat (c) cetacean sightings (numbers seen for Delphinus delphis, Stenella frontalis, Orcinus orca, Pseudorca crassidens, Physeter macrocephalus, Mysticetes and unidentified Odontocetes) and (d) incidence of depredation (numbers of damaged fish for swordfish, shortfin mako and escolar) as response variables. Thus, six RDA analyses were carried out in total (Table 5). In each case, all remaining variables were treated as explanatory variables. When using acoustic or depredation variables as response variables, cetacean sightings were converted to presence-absence data for use as explanatory variables, since we

#### Table 4 List of variables

Variables		Abbreviation	Descriptor
Fishery data	Catches of:		No. of fish caught or biomass
	Swordfish (X. gladius)	XGL	of fish caught (kg)
	Shortfin mako (I. oxyrinchus)	IOX	
	Blue shark (P. glauca)	PGL	
	Tuna (Thunnus spp.)	THU	
	Marlin (Istiophoridae)	IST	
	Dolphinfish (C. hippurus)	CHI	
	Barracuda (Sphyraena spp.)	SPH	
	Sharks (sum of all shark species)	Shark	
	Dimension of longline	Hook	No. of hooks
	Turtle by-catch	Turt	No. of animals by-caught
Acoustic data	Likely false killer whale clicks	Pos	No. of clicks
	Unlikely false killer whale clicks	Neg	
	Average click rate	Rate	No. of clicks/recording time
	Intensity of clicks	Ints	No. of clicks/minutes with clicks
Cetacean sightings	Sperm whale (P. macrocephalus)	PMA	No. of animals seen or
	Killer whale (O. orca)	OOR	presence of animals
	False killer whale (P. crassidens)	PCR	
	Common dolphin (D. delphis)	DDE	
Fishery data S S Fishery data S S S S S S S S S S S S S S S S S S S	Atlantic spotted dolphin (S. frontalis)	SFR	
	Unidentified Odontoceti	ODO	
	Mysticeti	MIS	
Depredation	Swordfish (X. gladius)	XGLd	No. of fish damaged or presence
	Shortfin mako (I. oxyrinchus)	IOXd	of damage
	Escolar (L. flavobrunneum)	LFLd	
	Depredation (sum of all species)	dprd	
Environmental data	Sea state	Sea	Douglas scale: from 0 to 9
	Cloud cover	Cd	Scale: from 0 to 8
	Moon phase	М	M1: New moon
			M2: Waxing moon
			M3: Full moon
			M4: Waning moon
	Sea surface temperature	SST	in °C
Acoustic data Cetacean sightings Depredation	Water depth	Depth	in m

considered the visually confirmed presence or absence of cetaceans to be more important than the precise number present. RDA output indicates the proportion of variation in the response variables explained by the explanatory variables. The statistical significance of the effects of explanatory variables was obtained using a Monte Carlo permutation test with n = 4,999permutations. The relationships between the response and explanatory variables were also displayed as point-vector biplots (see Zuur et al., 2007). When RDA detected significant relationships between response and explanatory variables, these were further investigated using Generalised Additive Models (GAMs) and Generalised Linear Models (GLMs) for individual response variables within each of the four groups (catch, acoustic detections, sightings, and depredation), thereby allowing non-linearity in the relationships to be taken into account. Response variables could generally be assumed to follow binomial (presence–absence data) or Poisson **Table 5** Numerical output of the Redundancy analysis (RDA) for vessels V7 (Brazil) and V8 (Azores) indicating individual eigenvalues of the first and second axis ( $\lambda_1$ ,  $\lambda_2$ ), sum of all canonical eigenvalues (Sum), and results of *F* tests (*F* and

associated probability, P) for the significance of effects of individual explanatory variables (only explanatory variables with significant effects are shown)

Vessel	Response variables	$\lambda_1$	$\lambda_2$	Sum	Explanatory variables	F	Р
V7	Fish catches	17.91	12.21	0.46	Turt	2.92	0.010
					M4	2.40	0.032
	Acoustic data	33.62	0.68	0.34	M2	4.94	0.027
V8	Fish catches	24.59	13.69	0.47	M3	5.99	0.000
					Depth	3.14	0.017
					SST	3.00	0.019
					M4	0.04	0.037
Acoustic data	Acoustic data	46.68	0.54	0.47	DDE	8.27	0.004
					SFR	5.37	0.016
	Sightings	14.38	8.44	0.40	XGL	2.94	0.012
					M3	2.08	0.032
					Rate	2.10	0.034
					dprd	4.45	0.039
					IOX	2.70	0.045
	Depredation	30.42	6.95	0.44	PCR	21.72	0.001

When one set of variables (see Table 4) was used as response variables, all variables from the other four sets were potentially available as "explanatory" variables

(count data) distributions, with an addition parameter for dispersion included in the model if overdispersion was detected, and using appropriate link functions. The exceptions were click intensity, which was logtransformed to achieve an approximately Gaussian distribution, and average click rate, which had an approximately Gaussian distribution. For the Brazil data set both average click rate and click intensity were consistently low so the number of positive clicks was used as the response variable in GAMs. Cetacean sightings and depredation data were converted to presence-absence for use in GAMs and GLMs. Cloud cover (on a scale of 0-8) was treated as a continuous variable. For all continuous explanatory variables, degrees of freedom were constrained to be less than 5 to avoid overfitting.

The fitted GAMs had the general form:

$$y_i = \alpha + f_1(x_{i1}) + \ldots + f_m(x_{im}) + \beta_n x_{in} + \ldots + \beta_p x_{ip} + \varepsilon_i \quad \varepsilon_i \sim N(0, \sigma^2)$$

where  $y_i$  is the response variable,  $f_j$ () are the smoothing functions,  $\beta_q$  are coefficients for parametric terms (e.g. dummy variables generated from categorical variables) and  $\varepsilon$  a random error parameter (Zuur et al., 2007). Models were fitted using a

combination of forwards and backwards selection until all remaining terms were significant or none remained. Where none of the explanatory variables remaining was a continuous variable or could be treated as such, model fitting continued using generalised linear modelling (GLM). Plots of residuals were examined to confirm goodness of fit. RDA, GAMs and GLMs were performed using Brodgar 2.5.2 (www.brodgar.com). More information about these techniques can be found in Zuur et al. (2007).

Since turtle by-catch occurred quite frequently we also examined possible causal factors (environmental conditions and catch). Kruskal-Wallis tests were used to compare fish catches and environmental conditions during sets with and without turtle by-catch.

#### Results

Overall fishing effort, catches, by-catch and losses due to depredation

The fishing effort of the eight longline vessels monitored was located in the South Equatorial Current (V1–V7) and the Gulf Stream (V8) (Fig. 1). Between July 2006 and June 2007 the vessels performed 635 sets, deploying an average number of 1,275 hooks per set and catching a total of 1185.5 tons of marketable fish. Depredation by cetaceans occurred during between 1% and 9% of sets per vessel, with overall estimated losses (per vessel) between 0.2% and 8.6% of the total catch (V1–V6: Both fish damaged and bait/fish removed from the hooks were considered; V7–V8: Only damaged fish was considered) (Table 1).

By-catch of turtles was reported for all vessels, except for V3, occurring on an average in 11.2% of all sets. The number of turtles by-caught ranged between 1 and 5 animals per set. Leatherback turtle *Dermochelys coriacea* (39% of turtle individuals bycaught) and green turtle *Chelonia mydas* (31%) were the most frequently caught species, followed by loggerhead turtle *Caretta caretta* (19%) and Olive Ridley turtle *Lepidochelys olivacea* (11%). Most turtles were caught alive and released. Marine mammal by-catch was registered only once: during one set off the Azores, two false killer whales were caught on the longline (Table 1).

#### Catches and depredation on non-observer vessels

For the non-observer trips (V1–V6), skippers recorded that all catch damaged was due to cetacean depredation, based on the type of bite marks seen. The average percentage of sets depredated was low (4.6%) but when depredation occurred, between 2% and 100% of the catch was lost, with over 25% of the catch lost on two-thirds of these occasions. For two of the six vessels, the occurrence of depredation was significantly negatively correlated with catch (V2: r = -0.47, P = 0.001; V3: r = -0.24, P = 0.022) (Table 1), suggesting that depredation may significantly reduce catches.

Catches, by-catches and depredation on vessels with observers

The total catch of the two vessels with observers on board (V7 and V8) was 136.7 tonnes (3,645 individuals) of fish, of which 87% (by number) were marketable. The main species caught off Brazil (V7) by number were tuna (54.5%), swordfish (29.4%) and marlin (7.5%). Off the Azores (V8), the principal species caught by number were sharks (73.6%, blue sharks and shortfin mako sharks) and swordfish

(24.6%). Depredation of catches occurred during 19 out of 86 sets: nine times off Brazil and ten times off the Azores. However, based on visual inspection of the damaged fish, this was attributed to cetaceans, presumed to be false killer whales, on only three occasions, once off Brazil (3.3% of sets) and twice off the Azores (3.6% of sets) (Table 1). This compares to twelve instances of depredation by sharks and four that were attributed to turtles. The overall proportion of catches (by number) damaged by cetaceans across all sets was only 0.2% and 0.9% of total catch, respectively. The fish damaged by cetaceans were swordfish (85.7% by number) and shortfin mako (14.3% by number).

RDA results indicated that catches of the principal target species off Brazil were significantly related to turtle by-catch and moon phase (waning moon) (Table 5, Fig. 2). GLM results indicated weakly significant relationships between swordfish catches and both cloud cover and the interaction between moon phase and cloud cover. In the case of tuna catches the only effect that was marginally significant



Fig. 2 RDA biplot for catch data from vessel V7 (Brazil). Response variables (represented by thin lines): Catches of swordfish (XGL), tuna (THU), barracuda (SPH), dolphinfish (CHI), marlin (IST), garfish (AGU) and sharks (Shark). Explanatory variables (represented by thick lines if continuous and by squares if nominal): see Table 4 for abbreviations. The plot shown was based on re-running the RDA having removed the least important (non-significant) explanatory variables, to achieve greater visual clarity

Response variables	Explanatory variables	Туре	t	F	Р	Sign	edf	%dev	AIC
XGL								29.2	211.6
	Moon	Ν			All >0.05				
	Cd	L	2.22		0.0364	+			
	Cd-M3	Ν	-2.08		0.0492	_			
THU								45.2	302.6
	Moon	Ν			All >0.05				
	Cd	Ν	1.71		>0.05				
	M2-Cd	Ν	-2.12		0.0448	-			
Pos								51.9	838.2
	M1	Ν	-2.93		0.0084	-			
	M2	Ν	2.45		0.0237	+			
	Depth	S		3.49	0.0263		3.64		

The response variables were catches (number) of swordfish and tuna per set, and the number of likely delphinid echolocation clicks. In all cases, a quasi-Poisson distribution was assumed for the response variable. Results displayed are as follows: explanatory variables (and interactions) included in the final model, whether they were included as smoothers (S), linear terms (L) or nominal variables (N), their significance (based on F or t tests, with P-value), the direction (sign) of the effect (+ or -) and degrees of freedom for smoothers. Also given are the overall percentage of deviance explained (%dev) and AIC value for the model. Full moon (M4) was used as the reference value when evaluating effect of moon phase (since there was only one record with new moon). Explanatory variables used: Table 4

was the interaction term, with both main effects (cloud cover, moon phase) non-significant (Table 6). The co-plot (Fig. 3) illustrates the interaction between the effects of cloud cover and moon phase



Fig. 3 Co-plot for swordfish catches by vessel V7 (Brazil), illustrating the interactions between effects of moon phase and cloud cover

in relation to swordfish catches. Due to the small sample size, further investigation of these relationships is not possible.

Off the Azores, RDA showed catches of the three main fish species were related to moon phase, water depth and SST (Table 5, Fig. 4). GAMs showed that swordfish catches were related to water depth, moon phase, cloud cover and sightings of Stenella frontalis (Table 7). Catches peaked at a cloud cover value of 2 (Fig. 5a), showed a minimum value at around 3,000 m depth (increasing in shallower and deeper waters) (Fig. 5b) and decreased in the presence of Stenella. Given that spotted dolphins are unlikely to remove large fish from the lines, the interpretation of the latter relationship is unclear.

Mako catches off the Azores showed significant relationships with moon phase, SST, click rate and sightings of Delphinus delphis and Stenella frontalis (Table 7). Catches were lower at higher temperatures and lower at the highest values for click rate (Fig. 5c). Catches were strongly negatively associated with presence of common dolphins and positively associated with presence of spotted dolphins. Finally blue shark catches were related to moon phase, with higher catches around full moon (Table 7).



**Fig. 4** RDA biplot for catch data from vessel V8 (Azores). Response variables (represented by thin lines): catches of swordfish (XGL) tuna (THU), shortfin mako (IOX) and blue shark (PGL). Explanatory variables (represented by thick lines if continuous and by squares if nominal): see Table 4. The plot shown was based on re-running the RDA having removed the least important (non-significant) explanatory variables, to achieve greater visual clarity

In the Brazil survey, turtle by-catch occurred during 10 out of 30 sets and was not related to depth, SST, moon phase, sea state or catches of tuna or swordfish. Turtle by-catch was associated with higher catches of sharks (Kruskal-Wallis test, P = 0.002) and "other species" (P = 0.001). In the Azores survey, turtle by-catch occurred during seven of 56 sets, and was weakly positively associated with shortfin mako catches (P = 0.035).

#### Acoustic data collected during observer trips

T-PODs were deployed on 96.5% of lines. It was not always possible to set three T-PODs in each line, but 92% of the lines had two or three T-PODs that registered acoustic data (Table 2). Data were obtained covering approximately 96% of the time that the T-PODs were in the water, the remaining 4% being lost due to technical problems.

Off Brazil, hydrophones registered a low number of click trains, of which 84.7% were classified as "positive", i.e. likely to have been produced by delphinids. Off the Azores, the number of clicks registered was considerably higher but only 28.7% of clicks were "positive" (Table 3). During both surveys, when depredation by false killer whales occurred, click intensity was low (Fig. 6a, b). However, on one occasion five swordfish were removed and two false killer whales were by-caught during the same set (set 20) off the Azores, and click intensity registered by the T-POD closest to the by-caught animals was high.

Redundancy analysis for the acoustic data from Brazil showed that the number of likely delphinid clicks recorded was affected by moon phase (waxing moon) (Table 5, Fig. 7). GAM showed that the detection of likely delphinid clicks was highest over the deepest water and confirmed the effect of moon phase (Table 6; Fig. 5d). During this survey depredation by false killer whales was recorded for only one fish.

In the Azores survey, RDA analysis revealed that acoustic detections were related to sightings of small delphinids (*Delphinus delphis* and *Stenella frontalis*) (Table 5, Fig. 8). GLM results indicated that click intensity was weakly related to sightings of spotted dolphins and moon phase (waning moon) although unrelated to other environmental factors or to catches. Average click rate, however, was positively related to depth (Table 7).

#### Cetacean sightings recorded by observers

The number of cetacean sightings differed for the two study areas: off Brazil, only 12 false killer whales and one sperm whale were sighted. No further analysis of these data was carried out.

Off the Azores 613 individual cetaceans were sighted, of which 94% were Odontoceti species (*Stenella frontalis, Delphinus delphis, Pseudorca crassidens, Physeter macrocephalus* and *Orcinus orca* in descending order of occurrence). Peaks of clicks were detected by the T-PODs when sightings of dolphins, false killer whales and killer whales were reported. RDA analysis showed that cetacean sightings were related to catches of swordfish and shortfin mako, moon phase, click rate and occurrence of depredation (Table 5, Fig. 9).

Satisfactory models could be fitted only for the two most commonly sighted species (*Delphinus delphis* and *Stenella frontalis*). The presence of
Table 7 GAM and GLM results using data from vessel V8 (Azores)

Response variables	Explanatory variables	Туре	t or z	<i>F</i> or $\chi^2$	Р	Sign	edf	%dev	AIC
XGL								55.9	305.5
	M2	Ν	-2.83		0.0068	—			
	SFR	Ν	-2.92		0.0054	—			
	Cd	S		3.52	0.0138		2.9		
	Depth	S		5.96	0.0006		2.6		
IOX								70.8	276.7
	M2	Ν	2.90		0.0058	+			
	M3	Ν	2.74		0.0089	+			
	M4	Ν	-2.12		0.0393	-			
	SST	S		13.78	0.0006		1		
	Rate	S		4.57	0.0036		4		
	DDE	Ν	-4.63		0.0016	-			
	SFR	Ν	3.88		0.0020	+			
PGL								16.4	443.9
	M3		2.54		0.0141	+			
Ints								22.8	83.3
	M4	Ν	-2.29		0.0263	—			
	SFR	Ν	2.12		0.0390	+			
Rate								24.1	391.0
	Depth	S		16.82	0.0001		1		
DDE								38.7	52.2
	XGL	L	2.56		0.0105	+			
	IOX	L	-2.24		0.0252	-			
	Ints	L	1.97		0.0486	+			
SFR								45.7	54.2
	M2	Ν	-2.53		0.0114	—			
	M3	Ν	-2.68		0.0073	—			
	XGL	L	-2.69		0.0072	—			
	IOX	L	2.28		0.0225	+			
	Rate	L	3.02		0.0025	+			
dpdr								25.9	46.8
	Rate	L	2.053		0.0400	+			
	DDE	Ν	-2.13		0.0332	—			
	SFR	N	-2.60		0.0094	_			

The response variables were catches (number) of swordfish, shortfin mako and blue shark per set, intensity of clicks, average click rate, sightings of *Delphinus delphis* and *Stenella frontalis* and depredation. In all cases, a quasi-Poisson distribution was assumed for the response variable. Results displayed are as follows: explanatory variables (and interactions) included in the final model, whether they were included as smoothers (S), linear terms (L) or nominal variables (N), their significance (based on *F*,  $\chi^2$ , z or *t* tests, with *P*-value), the direction (sign) of the effect (+ or -) and degrees of freedom for smoothers. Also given are the overall percentage of deviance explained (%dev) and AIC value for the model. New moon (M1) was used as the reference value when evaluating effect of moon phase. Explanatory variables used: Table 4

*D. delphis* was related to higher catches of swordfish and lower catches of shortfin mako catches. The presence of *Stenella frontalis* was associated with higher mako catches and lower swordfish catches. Both species were more frequently sighted when detection of "positive" clicks was high. In addition, Fig. 5 GAM results: Azores (V8)—smoothing curves for partial effect of (a) cloud cover and (b) water depth on swordfish catches, and (c) click rate on mako catches. Brazil (V7)—smoothing curve for partial effect of (d) water depth on the number of likely delphinid clicks recorded. Dotted lines indicate 95% confidence bands



sightings of *Stenella frontalis* were lower during full and waxing moon (Table 7).

#### Depredation

Nine fish were depredated during the Brazil survey of which only one may have been depredated by false killer whales. Further statistical analysis was therefore not possible.

During the Azores survey, depredation affected three species (swordfish, shortfin mako and escolar), but false killer whales probably mainly removed swordfish. RDA suggested that depredation was related with sightings of false killer whales (Table 5, Fig. 10). The GLM, however, revealed that the occurrence of depredation increased when click rate was high and sightings of small delphinids (*D. delphis* and *S. frontalis*) were low (Table 7).

## Discussion

Our results suggest that catches of the main target species of the fishing vessels observed were affected

by environmental variables such as light conditions (cloud cover and moon phase), water temperature and water depth. Tuna, swordfish and sharks are all oceanic migratory species, which are mostly found in temperate surface waters where thermal fronts and upwelling processes occur (Collette & Nauen, 1983; Bigelow et al., 1999; Brill et al., 1999; Dagorn et al., 2000; De Stephanis et al., 2008). They show diel vertical movement patterns, feeding at the surface layer during the night (Nakamura, 1985; Bigelow et al., 1999; Domokos et al., 2007) and descending to deeper waters during the day. Therefore, longlines targeting these species are usually set in surface waters around sunset, soaking during the night, and hauled around sunrise.

Based on this small data set, moon phase appears to have an important effect on swordfish and shark catches. This was also found in other areas, e.g. the Pacific (Pallares & Garcia-Mamolar, 1985; Bigelow et al., 1999) and the Mediterranean (Damalas et al., 2007). Cloud cover also affects seabird by-catch on longlines. A higher intensity of moon and daylight (depending on moon phase and cloud cover) may improve the visibility of bait on the lines and **Fig. 6** Click intensity and occurrence of depredation for (**a**) vessel V7 (Brazil) and (**b**) vessel V8 (Azores), by set

Neg

Pos

0

-0.5

axis 2



**Fig. 7** RDA biplot for acoustic data from vessel V7 (Brazil). Response variables (represented by thin lines): likely delphinid clicks (Pos) and unlikely delphinid clicks (Neg). Explanatory variables (represented by thick lines if continuous and by squares if nominal): see Table 4. The plot shown was based on re-running the RDA having removed the least important (nonsignificant) explanatory variables, to achieve greater visual clarity

Fig. 8 RDA biplot for acoustic data from vessel V8 (Azores). Response variables (represented by thin lines): likely delphinid clicks (Pos) and unlikely delphinid clicks (Neg). Explanatory variables (represented by thick lines if continuous and by squares if nominal): see Table 4. The plot shown was based on re-running the RDA having removed the least important (nonsignificant) explanatory variables, to achieve greater visual clarity



**Fig. 9** RDA biplot for cetacean sightings data from vessel V8 (Azores). Response variables (represented by thin lines): Sightings of Mysticetes (MIS), *Delphinus delphis* (DDE), *Stenella frontalis* (SFR), *Pseudorca crassidens* (PCR) and *Orcinus orca* (OOR), *Physeter macrocephalus* (PMA) and not identified odontocetes (ODO). Explanatory variables (represented by thick lines if continuous and by squares if nominal): see Table 4. The plot shown was based on re-running the RDA having removed the least important (non-significant) explanatory variables, to achieve greater visual clarity

therefore attract more fish (and sea birds) to the fishing gear (Cherel et al., 1996; Brothers et al., 1999a, b).

Bigelow et al. (1999) found that swordfish CPUE in the northern Pacific Ocean was lowest over a range of 2,000–3,000 m bottom depth, and then increased in deeper water. Our results suggest that a similar relationship applies in Atlantic waters.

The by-catch rate of cetaceans during our study was very low and similar to rates reported by Dalla Rosa & Secchi (2002). Two false killer whales were by-caught during one set off the Azores. This is consistent with the observation by Perrin et al. (1994) that, although cetacean by-catch is a major issue in fishing gear such as gillnets and trawls, with longlines it occurs only occasionally.

The frequency of false killer whale sightings was very low, perhaps because they were primarily feeding underwater on fishes hooked on the line (between 15 and 100 m water depth) and were therefore not visible for observers. Other delphinids, however, were frequently sighted. *Delphinus delphis* 



**Fig. 10** RDA biplot for depredation data from vessel V8 (Azores). Response variables (represented by thin lines): Depredation on swordfish (XGLd), shortfin mako (IOXd) and Escolar (LFLd). Explanatory variables (represented by thick lines if continuous and by squares if nominal): see Table 4. The plot shown was based on re-running the RDA having removed the least important (non-significant) explanatory variables, to achieve greater visual clarity

sightings off the Azores were more frequent when catches of swordfish were high and mako catches were low, while for sightings of *Stenella frontalis* it was the other way around. This might indicate that both delphinid species share the same habitat, but feed on different prey. However, other studies suggest that the trophic ecology of *Delphinus delphis* and *Stenella frontalis* is quite similar (Aguiar dos Santos & Haimovici, 2001).

Although they are unlikely to prey directly on large swordfish and mako sharks, respectively, they may feed on the same fish and squid species that are taken by these species. The association between swordfish and dolphins may be similar to the strong tuna-dolphin (*D. delphis* and *Stenella* species) association found in other areas (e.g. Hall & Donovan, 2002; Reeves & Reijnders, 2002). This association was originally exploited by fishermen in the Eastern Tropical Pacific where yellowfin tuna swam underneath dolphins and were thus located.

T-PODs are useful to give insight into cetacean activity under water. However, analysis of acoustic data in relation to sightings data suggested that most of the recorded clicks came from small delphinids, which produce echolocation sounds in the same frequency range as those emitted by false killer whales. False killer whales, like other odontocete species, use biosonar to echolocate their prey. Fishes hooked on a surface longline are easy to prey on and the use of echolocation may not be necessary for feeding on them.

In our study, both observer and skipper data indicate that the frequency of depredation on pelagic longlines operating in Atlantic waters was low. Less than 1% of the overall catch per trip was lost during both trips when scientific observers were on board. However, if depredation occurred, the amount of catch lost per set reported by skippers exceeded 25% on most occasions and could reach up to 100%. Similar results were reported by Dalla Rosa & Secchi (2007), Kock et al. (2006), Poisson et al. (2007) and Ramos-Cartelle & Mejuto (2007). When depredation occurred, the economic loss could be as high as 40% of the value of the catches, including vessel operation costs and fishing time lost (ARVI, unpublished data). A possible reason for the low incidence of depredation is that skippers avoid fishing areas where cetacean presence is known to be high in order to reduce interactions (Dahlheim, 1988). However, fishermen think that these animals learn to follow the longline vessels (e.g. Poisson & Taquet, 2000; Donoghue et al., 2002). It should be noted that depredation rates may be underestimated because only damaged fish were counted when calculating depredation rates, while fish removed entirely from the hooks could not be quantified.

Our results suggest that false killer whale was the main marine mammal predator removing catch from the longlines, although few instances were recorded and depredation by sharks was four times as frequent as that attributed to marine mammals. Although the species most frequently sighted in our study were D. delphis and S. frontalis, dolphins were hardly ever observed when depredation occurred which indicates that they were most likely not feeding on the hooked fish. Therefore, the co-occurrence of depredation and cetacean clicks may have been coincidental. For two of the non-observer vessels, the amount of fish caught was significantly lower when depredation by false killer whales occurred. In addition, RDA suggested a relationship between the occurrence of depredation and sightings of *Pseudorca* for the observer vessels and the only by-catch of false killer whales coincided with the removal of five swordfish from the line during one set. Dalla Rosa & Secchi (2007) reported that depredation on longline fisheries targeting swordfish in Brazilian waters was primarily caused by killer whales, but occasionally by other cetaceans such as false killer whales. However, their research was carried out closer to the coast where killer whales are more abundant (Jefferson et al., 1993).

False killer whales mainly feed on fish and cephalopods (Koen-Alonso & Pedraza, 1999; Hernandez-Garcia, 2002; Ramos-Cartelle & Mejuto, 2007). Previous studies (Secchi & Vaske, 1998; Gilman et al., 2006; Zollett & Read, 2006) demonstrated that fish hooked on longlines was becoming a new resource, changing the feeding customs of the cetaceans. According to Ramos-Cartelle & Mejuto (2007), the cetaceans learnt to use the bait and catches retained on the fishing gear as an 'easy' prey to capture and thereby reduce the energy costs of feeding. They seem to be selective when taking fish from the lines (Kock et al., 2006). In our study, the main fish species consumed by cetaceans was swordfish. This was also found by Poisson & Taquet (2000) and Dalla Rosa & Secchi (2007). However, off Brazil tuna was the main fish captured and sharks were the main target species (followed by swordfish) off the Azores. Thus the consumption of swordfish might indicate a preference of the cetaceans for this species, as suggested by Dalla Rosa & Secchi (2007) and Poisson and Taquet (2000).

While observers reported depredation by sharks and other animals, skippers on the other six vessels reported depredation in general, with the assumption that false killer whales were responsible being based on sightings of this species alongside the boats. Donoghue et al., (2002) indicated that fish damaged by sharks may be inaccurately reported. Skippers may not distinguish between different types of bite marks.

Turtle by-catch was frequent, especially when a higher number of sharks were caught, and involved at least four different turtle species. Carranza et al. (2006) found that mako sharks preyed upon various species of sea turtles in the Equatorial Eastern Atlantic. This might also apply in our study area. Several instances of damage to hooked fish were attributed to turtles. Although in this study most turtles were apparently released alive, turtle by-catch remains a major issue in longline fisheries, one which can possibly be reduced by use of alternative hook designs and bait or by fishing deeper (e.g. Gilman et al. 2007a, b).

# Conclusions

In our study, catch rates were influenced by environmental parameters such as light conditions, SST and water depth, whereas cetacean presence was mainly related to the catch rates of particular fish species, possibly indicating trophic relationships between species. Acoustic recordings probably reflected the presence of delphinids in general rather than false killer whales in particular and it is possible that false killer whales preying on longlines do not need to use biosonar to locate their prey. The depredation rate and the overall amount of catch consumed during our survey were low, but when depredation occurred, the proportion of catch lost mostly exceeded 25%. Although the statistical analysis revealed some potentially interesting relationships between catches, cetacean presence, depredation and environmental variables, it is important to note that this was a smallscale study: we analysed data from 86 observed sets and more data are needed to further explore and quantify these relationships.

Acknowledgements We would like to thank the Spanish Secretaría General de Pesca Marítima for funding the present study 'Developing an Acoustic Prototype to Reduce Depredation by Marine Mammals on Swordfish Fisheries (Pingers)'. GHM, SG and GJP received additional support from the EU-funded projects Envi-EFH (SSA 022466), ECOSUMMER (MEST-CT-2005-020501) and ANIMATE (MEXC-CT-2006-042337), respectively. Furthermore, we would like to address our special thanks to all captains and fishermen for their cooperation and to the members of CEMMA (Coordinadora para los estudios de mamíferos marinos) who helped with the design of the cetacean surveys and the review of the results. We also like to thank Colin MacLeod and Alain Zuur for assisting with the statistical analysis and Gema Martinez for assisting with production of maps.

### References

Aguiar dos Santos, R. & M. Haimovici, 2001. Cephalopods in the diet of marine mammals stranded or incidentally caught along southeastern and southern Brazil (21–34°S). Fisheries Research 52: 99–112.

- Ashford, J. P., P. S. Rubilar & A. R. Martin, 1996. Interactions between cetaceans and longline fishery operations around South Georgia. Marine Mammal Science 12: 452–457.
- Bigelow, K. A., C. H. Boggs & X. He, 1999. Environmental effects on swordfish and blue shark catch rates in the US North Pacific longline fishery. Fisheries Oceanography 8: 178–198.
- Brill, R. W., B. A. Block, C. H. Boggs, K. A. Bigelow, E. V. Freund & D. J. Marcinek, 1999. Horizontal movements and depth distribution of large, adult yellowfin tuna (*Thunnus albacares*) near the Hawaiian Islands, recorded using ultrasonic telemetry: implications for the physiological ecology of pelagic fishes. Marine Biology 133: 395–408.
- Brothers, N. P., J. Cooper & S. Løkkeborg, 1999a. The incidental catch of seabirds by longline fisheries: worldwide review and technical guidelines for mitigation. FAO Fisheries Circular 937. FAO, Rome.
- Brothers, N. P., R. Gales & T. Reid, 1999b. The influence of environmental variables and mitigation measures on seabird catch rates in the Japanese tuna longline fishery within the Australian Fishing Zone, 1991–1995. Biological Conservation 88: 85–101.
- Capdeville, D., 1997. Interaction of marine mammals with the longline fishery around the Kerguelen Islands (Division 58.5.1) during the 1995/96 cruise. CCAMLR Science 4: 171–174.
- Carranza, A., A. Domingo & A. Estrades, 2006. Pelagic longlines: a threat to sea turtles in the Equatorial Eastern Atlantic. Biological Conservation 131: 52–57.
- Carstensen, J., O. D. Henriksen & J. Teilmann, 2006. Impacts of offshore wind farm construction on harbour porpoises: acoustic monitoring of echolocation activity using porpoise detectors (TPODs). Marine Ecology Progress Series 321: 295–308.
- Carwadine, M., 1995. Whales, Dolphins and Porpoises. Dorling Kindersley, London.
- Cherel, Y., H. Weimerskirch & G. Duhamel, 1996. Interactions between longline vessels and seabirds in Kerguelen waters and a method to reduce seabird mortality. Biological Conservation 75: 63–70.
- Collette, B. B. & C. E. Nauen, 1983. FAO species catalogue. Scombrids of the world. An annotated catalogue of tunas, mackerels, bonitos and related species known to date. FAO Fisheries Synopsis 125-2. FAO, Rome.
- Dagorn, L., P. Bach & E. Josse, 2000. Movement patterns of large bigeye tuna (*Thunnus obesus*) in the open ocean, determined using ultrasonic telemetry. Marine Biology 136: 361–371.
- Dahlheim, M. E., 1988. Killer Whale (Orcinus orca) Depredation on Longline Catches of Sablefish (Anoplopoma fimbria) in Alaskan Waters. Alaska Fisheries Science Centre, Seattle, Washington. NWAFC Report 88-14.
- Dalla Rosa, L. & E. R. Secchi, 2002. Comparative analysis of the interactions between killer whales/sharks and the tuna/ swordfish fishery in southern and southeastern Brazil. In Donoghue, M., R. R. Reeves & G. S. Stone (eds), Report of the Workshop on Interactions Between Cetaceans and Longline Fisheries. Apia, Samoa, 2002.
- Dalla Rosa, L. & E. R. Secchi, 2007. Killer whale (Orcinus orca) interactions with the tuna and swordfish longline fishery off

southern and south-eastern Brazil: a comparison with shark interactions. Journal of the Marine Biological Association of the United Kingdom 87: 135–140.

- Dalla Rosa, L., E. R. Secchi & D. Monteiro, 2006. Killer whale depredation on longline catches in Brazilian waters. Proceedings of the Workshop on Fisheries Depredation by Killer and Sperm Whales: Behavioural Insights, Behavioural Solutions, British Columbia, Canada, 2006.
- Damalas, D., P. Megalofonou & M. Apostolopoulou, 2007. Environmental, spatial, temporal and operational effects on swordfish (*Xiphias gladius*) catch rates of eastern Mediterranean Sea longline fisheries. Fisheries Research 84: 233–246.
- De Stephanis, R., T. Cornulier, P. Verborgh, J. Salazar-Sierra, N. Perez Gimeno & C. Guinet, 2008. Summer spatial distribution of cetaceans in the Strait of Gibraltar in relation to the oceanographic context. Marine Ecology Progress Series 353: 275–288.
- Domokos, R., M. P. Seki, J. J. Polovina & D. R. Hawn, 2007. Oceanographic investigation of the American Samoa Albacore (*Thunnus alalunga*) habitat and longline fishing grounds. Fisheries Oceanography 16: 555–572.
- Donoghue, M., R. R. Reeves & G. S. Stone, 2002. Report of the Workshop on Interactions Between Cetaceans and Longline Fisheries. New England Aquarium Press, Boston MA, USA.
- Garza Gil, M. D., M. M. Varela-Lafuente & C. Iglesias Malvido, 2003. Spain's North Atlantic swordfish fishery. Marine Policy 27: 31–37.
- Gilman, E., N. Brothers, G. McPherson & P. Dalzell, 2006. A review of cetacean interactions with longline gear. Journal of Cetacean Research and Management 8: 215–223.
- Gilman, E., S. Clarke, N. Brothers, J. Alfaro-Shigueto, J. Mandelman, J. Mangel, S. Petersen, S. Piovano, N. Thomson, P. Dalzell, M. Donoso, M. Goren & T. Werner, 2007a. Shark Depredation and Unwanted By-catch in Pelagic Longline Fisheries: Industry Practices and Attitudes, and Shark Avoidance Strategies. Western Pacific Regional Fishery Management Council, Honolulu, USA.
- Gilman, E., D. Kobayashi, T. Swenarton, N. Brothers, P. Dalzell & I. Kinan-Kelly, 2007b. Reducing sea turtle interactions in the Hawaii-based longline swordfish fishery. Biological Conservation 139: 19–28.
- Hall, M. A. & G. P. Donovan, 2002. Environmentalists, fishermen, cetaceans and fish: is there a balance and can science help to find it? In Evans, P. G. H. & J. A. Raga (eds), Marine Mammals: Biology and Conservation. Kluwer Academic Press, New York: 491–521.
- Hernandez-Garcia, V., 2002. Contents of the digestive tract of a false killer whale (*Pseudorca crassidens*) stranded in Gran Canaria (Canary Islands, central east Atlantic). Bulletin of Marine Science 71: 367–369.
- International Commission for the Conservation of Atlantic Tunas (ICCAT), 2007. Report for the Biennial Period, 2006–2007, Part 1–2. http://www.iccat.int.
- Jefferson, T., S. Leatherwood & M. Webber, 1993. FAO Species Identification. Marine Mammals of the World. FAO, Rome.
- Koen-Alonso, M. & S. N. Pedraza, 1999. Stomach contents of false killer whales (*Pseudorca crassidens*) stranded on the

coasts of the Strait of Magellan, Tierra del Fuego. Marine Mammal Science 15: 712–724.

- Kock, K. H., M. Purves & G. Duhamel, 2006. Interactions between cetaceans and fisheries in the Southern Ocean. Polar Biology 29: 379–388.
- Lammers, M. O., W. W. L. Au, R. Aubauer & P. E. Nachtigall, 2003. A comparative analysis of the pulsed emissions of free-ranging Hawaiian spinner dolphins (*Stenella longirostris*). In Thomas, J. E., C. F. Moss & M. Vater (eds), Echolocation in Bats and Dolphins. University of Chicago Press, Chicago.
- Leeney, R. H. & N. J. C. Tregenza, 2006. Proceedings of the Workshop on Static Acoustic Monitoring of Cetaceans, Gdynia, Poland, 2006. ECS Newsletter 46, Special Issue.
- Lewison, R. L., S. A. Freeman & L. B. Crowder, 2004. Quantifying the effects of fisheries on threatened species: the impact of pelagic longlines on loggerhead and leatherback sea turtles. Ecology Letters 7: 221–231.
- Madsen, P. T., I. Kerr & R. Payne, 2004. Echolocation clicks of two free-ranging, oceanic delphinids with different food preferences: false killer whales *Pseudorca crassidens* and Risso's dolphins *Grampus griseus*. Journal of Experimental Biology 207: 1811–1823.
- Memery, L., M. Arhan, X. A. Alvarez-Salgado, M. J. Messias, H. Mercier, C. G. Castro & A. F. Rios, 2000. The water masses along the western boundary of the south and equatorial Atlantic. Progress in Oceanography 47: 69–98.
- Morato, T., S. Guénette & T. Pitcher, 2001. Fisheries of the Azores, 1982–1999. In Zeller, D., R. Watson, T. Pitcher & D. Pauly (eds), Fisheries Impacts on North Atlantic Ecosystems: Catch, Effort and National/Regional Data Sets, Vol. 9. Fisheries Centre Research Reports, University of British Columbia, British Columbia: 214–220.
- Nakamura, I., 1985. FAO species catalogue. Billfishes of the World. An annotated and illustrated catalogue of marlins, sailfishes, spearfishes and swordfishes known to date. FAO Fisheries Synopsis 125-5. FAO, Rome.
- Northridge, S. P., 1984. World review of interactions between marine mammals and fisheries. FAO Fisheries Technical Paper 251. FAO, Rome.
- Pallares, P. & J. M. Garcia-Mamolar, 1985. Efectos de las fases de la luna sobre los rendimientos de la flota atuneratropical española. Collective Volume of Scientific Papers. International Commission for the Conservation of Atlantic Tunas (ICCAT) 23: 228–236.
- Perrin, W. F., G. P. Donovan & J. Barlow, 1994. Report of the International Whaling Commission. Gillnets and Cetaceans. International Whaling Commission, Special Issue 15, Cambridge, UK.
- Philpott, E., A. Englund, S. Ingram & E. Rogan, 2007. Using T-PODs to investigate the echolocation of coastal bottlenose dolphins. Journal of the Marine Biological Association of the UK 87: 11–17.
- Poisson, F. & M. Taquet, 2000. French Swordfish longline fishery in South-West Indian Ocean: preliminary results from the PPR Program. IOTC Proceedings, WPB00-06.
- Poisson, F., C. Marjolet, K. Mete & M. Vanpouille, 2007. Interactions of cetaceans and sharks with the Reunion Island swordfish longline fishery in the Indian Ocean between 1997 and 2000. Report of the IOTC Workshop

on the Depredation in the Tuna Longline Fisheries in the Indian Ocean, Victoria, Seychelles.

- Ramos-Cartelle, A. & J. Mejuto, 2007. Interaction of the false killer whale (*Pseudorca crassidens*) and depredation on the swordfish catches of the Spanish surface longline fleet in the Atlantic, Indian and Pacific Oceans. Report of the Standing Committee on Research and Statistics SCRS of the International Commission for the Conservation of Atlantic Tunas (ICCAT) 25 (ICCAT/SCRS/07/25).
- Reeves, R. R. & P. J. H. Reijnders, 2002. Conservation and management. In Hoelzel, A. R. (ed.), Marine Mammal Biology: An Evolutionary Approach. Blackwell Science, Oxford.
- Romo, A., C. Casanova, J. Sanz, A. Calle & J. L. Casanova, 2007. Relation between meteorological conditions and the catching of red tuna (*Thunnus thynnus*) from the measurements of the TOVS and AVHRR sensors of the NOAA satellites. International Journal of Remote Sensing 28: 2671–2681.
- Schotten, M., W. W. L. Au, M. O. Lammers & R. Aubauer, 2003. Echolocation recordings and localization of wild spinner dolphins (*Stenella longirostris*) and pantropical spotted dolphins (*S. attenuata*) using a four-hydrophone array. In Thomas, J. E., C. F. Moss & M. Vater (eds), Echolocation in Bats and Dolphins. University of Chicago Press, Chicago.
- Secchi, E. R. & T. Vaske Jr., 1998. Killer whale (Orcinus orca) sightings and depredation on tuna and swordfish longline catches in Southern Brazil. Aquatic Mammals 24: 117–122.

- Skov, H., J. Teilmann, O. D. Henriksen & J. Carstensen, 2002. Investigations of harbour porpoises at the planned site for wind turbines at Horns Reef. Status report: 1/1/2001–31/12/ 2001. Commissioned by Tech-wise A/S. Ornis Consult A/S. http://www.hornsrev.dk/Miljoeforhold/miljoerapporter/ Investigations\_of\_harbour\_popoises.pdf.
- Stacey, P. J., S. Leatherwood & R. W. Baird, 1994. Pseudorca crassidens. Mammalian Species 456: 1–6.
- Tougaard, J., J. Carstensen, O. D. Henriksen, J. Teilmann & J. R. Hansen, 2004. Harbour porpoises on Horns Reef effects of the Horns Reef Wind Farm. Annual Status Report 2003. Commissioned by Elsam Engineering A/S, National Environmental Research Institute (NERI).
- Wood, F. G. & W. E. Evans, 1980. Adaptiveness and ecology of echolocation in toothed whales. In Busnel, R. & J. Fish (eds), Animal Sonar Systems. Plenum, New York.
- Zavala-Camin, L. A. & J. N. Antero da Silva, 1991. Histórico da pesquisa e pesca de atuns com espinhel no Brasil. Atlantica, Rio Grande 13: 107–114.
- Zavilov, P. O., I. Wainer & J. M. Absy, 1999. Sea surface temperature variability off southern Brazil and Uruguay as revealed from historical data since 1854. Journal of Geophysical Research 105: 21–32.
- Zollett, E. A. & A. J. Read, 2006. Depredation of catch by bottlenose dolphins (*Tursiops truncatus*) in the Florida king mackerel (*Scomberomorus cavalla*) troll fishery. Fishery Bulletin 104: 343–349.
- Zuur, A. F., E. N. Ieno & G. M. Smith, 2007. Analysing Ecological Data. Springer, New York.

# FISH HABITAT MAPPING

# Satellite observations of main oceanographic processes to identify ecological associations in the Northern Arabian Sea for fishery resources exploration

Himmatsinh U. Solanki · Pradip C. Mankodi · Rashmin M. Dwivedi · Shailesh R. Nayak

© Springer Science+Business Media B.V. 2008

Abstract Ecological associations are the inter-relationship between the species and their environment. Oceanographic processes like upwelling events and formation of eddies, rings, and fronts have been monitored using National Oceanic and Atmospheric Administration Advanced Very High Resolution (NOAA AVHRR) and Indian Remote Sensing Satellite-P4-Ocean Colour Monitor (IRS-OCM) data. Sea Surface Temperature (SST) and chlorophyll concentration (CC) images were derived from AV-HRR and OCM, respectively. Upwelling event was monitored using AVHRR-SST by detecting the differences in surface water temperature. The formation of eddies, rings, cyclonic eddies, and anticyclonic eddies and their biological responses were studied using CC. Eddies and rings were found with high phytoplankton production in the form of bloom, which provide grazing ground for fishes. The anticyclonic eddies were found with very low CC, indicating the biological deserts in the ocean. The

# P. C. Mankodi

Faculty of Science, Maharaja Sayajirao University of Baroda, Fatehgunj, Vadodara, Gujarat 390002, India

impacts of these processes on fish catch were studied using fishing operations data procured from Fishery Survey of India. In this paper, the occurrence of different oceanographic processes, their persistence, and relevance with catch statistics of fishery resources in the study area are discussed. The study explains the potentials of satellite remote sensing to establish the habitat linkage between oceanographic processes and fishery resources.

**Keywords** Oceanographic processes · Satellite · Remote sensing · Fisheries

# Introduction

Marine earth observations (EO) from satellites are particularly suitable for sampling and monitoring large areas. The major EO products about the ocean's surface include temperature distribution and chlorophyll concentration. Several Remote Sensing techniques can provide information regarding surface circulation features that affect or define fish habitats. These include the location and evolution of frontal boundaries, upwelling areas, currents, and circulation patterns in general. Optical and thermal characteristics of surface waters can be used as natural tracers of dynamic patterns. Understanding the physical and biological processes, as well as their interactions, is a central goal for fisheries management over continental

Guest editor: V. D. Valavanis Essential Fish Habitat Mapping in the Mediterranean

H. U. Solanki (⊠) · R. M. Dwivedi · S. R. Nayak Marine Water Resources Group, Space Applications Centre (ISRO), Ahmedabad 380015, India e-mail: himmatsinh@sac.isro.gov.in

shelf areas. A complex suite of seasonal physical processes influences phytoplankton productivity and fisheries production.

Satellite remote sensing applications in fisheries have concentrated on the measurements of ocean temperature, ocean color, and computation of ocean water transport based on satellite-measured wind stress (Laurs & Burcks, 1985). Examples of potential use of satellite imagery in the eastern North Pacific fisheries were given by Fiedler et al. (1985). Yamanaka et al. (1998) described the utilization of satellite imagery in Japanese fisheries. Njoku et al. (1986) reviewed applications of thermal infrared imagery in oceanography. Satellite imageries and concurrent albacore catch examined by Laurs et al. (1984) demonstrated that the distribution and availability of albacore are related to oceanic fronts. They substantiate the conventional wisdom of many fishermen who use temperature and/or color "breaks" to locate potentially productive fishing areas for albacore. Authors speculated that the behavior mechanisms related to feeding might be responsible for tuna aggregation on the warm side of temperature front. To support this argument the authors use Coastal Zone Colour Scanner (CZCS) measurements along with knowledge that tuna are visual feeder. Maul et al. (1984) combined in situ observation from four research vessels, CPUE (catch-per-unit-effort) for Atlantic blue fin tuna, visible (CZCS) and thermal infrared (GOES, NOAA) satellite data of Gulf of Mexico. The boundaries gulf loop current was located using satellite data during 1980 in fishing areas. CPUE was analyzed and a threefold increase in tuna catch in 1980 over that in 1979 was observed using available satellite infrared and visible imagery. Sugimoto & Tameish (1992) observed that warm and cold streamers entrained the periphery of the warm core ring, which form excellent fishing ground for pelagic fish such as skipjack, mackerel, flying squid, and saury. Stretta (1991) used a variety of satellite data as input in a proposed model for tuna fishing in the Gulf of Guinea region. Podestra et al. (1993) found that the probability of very high catch rates in US longline fishery for swordfish in the Atlantic was greater in the vicinity of SST fronts. Solanki et al. (1998a, b, c) used AVHRR sea surface temperature (SST) data to delineate thermal feature to locate potential fishing grounds and to study seasonal variability in fishery resources based on the patterns of ocean features observed in thermal imagery in the Arabian Sea.

Solanki et al. (2001a) synergistically analyzed SeaWiFS and AVHRR data. They found that ocean color features coincided with thermal boundaries at some locations. This indicates that physical and biological processes are closely coupled at these locations. High fish catch points were found in the vicinity of coincided boundaries. An approach for integration of chlorophyll concentration and SST features has been developed by Solanki et al. (2000) using OCM chlorophyll concentration and AVHRR SST. Some preliminary results of synergistic application of chlorophyll and SST have been demonstrated by Solanki et al. (2001b) for exploring the pelagic resources in the water of Gujarat coast. Gill nets were used for fishing in suggested Potential Fishing Zones (PFZs). Pomfret catch was found to increase twofold. OCM chlorophyll concentration images and AVHRR SST images were used by Solanki et al. (2003a, b) for fishery forecast. Comparatively high CPUE was observed in the PFZs forecast areas as compared to other areas in the Northern Arabian Sea.

# Materials and methods

#### Study area

Figure 1 shows the location of the study area, which is a high productive region, off the Gujarat Coast in the Northern Arabian Sea that supports extensive fishing grounds. Gujarat State has the longest coastline of 1,640 km among the maritime States of India. The continental shelf area along the State (Latitude 20-23° N) is about 90,200 km<sup>2</sup>, the largest shelf area among the Indian maritime States with a maximum continental shelf width of about 191 miles. The gradient of the shelf area is 1:1,769 at the maximum width and 1:537 at the minimum width. The powerful cyclonic Somalia current grazes the Saurashtra coast during the southwest monsoon. During the northeast monsoon, off-shore winds along the Kathiawar peninsula induce the primary production and high fish production.

OCM data for chlorophyll concentration and AVHRR data for SST computation were used. PFZs fish catch data, collected by the survey vessels (*Matsya Nireekshani* and *Matsya Mohini*) of Fishery





Survey of India (FSI), were used in the study (Anonymous, 1996). The major species caught were ribbon fish, catfish, horse mackerel, sciaenids, decapterids and nemipterids, and squids. Fish catch data were normalized and classified in terms of CPUE. The fish catch classification was based on mean  $(\mu)$ and standard deviation (SD). Mean ( $\mu$ ) of catch is considered as normal catch in the area. The details of statistical analysis, fishing gear, and species caught during fishing operation are discussed by Solanki et al. (2005). The catch points were classified with a combination of mean and standard deviation. Gujarat State fisheries data was available for daily trips. They were normalized as kg/hr with consideration of fishing hours. The catch composition consists of horse mackerels, lesser sardines, ribbon fishes, squids, and Sciaenis.

Satellite sensor data analysis

#### OCM data analysis

The retrieval of ocean color parameters such as phytoplankton pigment (i.e., chlorophyll concentration) and suspended matter in near shore waters involves two major steps. The first is known as atmospheric correction of visible channels to obtain normalized water leaving radiance and the second is the application of bio-optical algorithms for water parameters retrieval. The process of retrieving water leaving radiance  $L_w$  from the total radiance measured at the sensor  $L_t$  is usually referred as atmospheric correction. The ocean color parameters such as chlorophyll concentration and suspended matter concentration are estimated from the retrieved spectral

### Atmospheric correction of IRS-P4 OCM imagery

In oceanic remote sensing, the total signal received at the satellite altitude is dominated by radiance contribution through atmospheric scattering processes and only 8-10% of the signal corresponds to oceanic reflectance. Therefore, it becomes mandatory to correct for atmospheric effect, to retrieve any quantitative parameter from space. A long wavelength approach suggested by Gordon et al. (1985) and Mohan et al. (1998) was adopted for atmospheric correction of optical data. It has been shown that for near infrared (NIR) channels, the water leaving radiance coming out of ocean can be approximately considered equal to zero (Gordon et al., 1985). The radiance received by a satellite sensor at top of the atmosphere (TOA) in a spectral band located at a wavelength  $\lambda_i$ ,  $L_t(\lambda_i)$  can be divided into following components:

$$L_{t}(\lambda_{i}) = L_{a}(\lambda_{i}) + L_{r}(\lambda_{i}) + T(\lambda) * L_{g}(\lambda_{i}) + t(\lambda_{i}) \\ * L_{w}(\lambda_{i})$$

where  $L_{\rm a}$  and  $L_{\rm r}$  are radiance generated along the optical path by scattering in the atmosphere due to aerosol and Rayleigh scattering,  $L_{\rm g}$  is the specular reflection or sun glint component, and  $L_{\rm w}$  is the water leaving radiance.

TOA radiance in OCM channels 765 and 865 nm mainly correspond to the contribution coming only from atmosphere, since water leaving radiance  $L_{w}$ (765 & 865 nm) can be safely assumed to be equal to zero. The Rayleigh scattering term  $(L_r)$  is computed using well-established theory. Once  $L_r$  is known then  $L_t$  is assumed equal to  $L_a$ , i.e., the aerosol path radiance. OCM payload has two channels at 765 and 865 nm in NIR and a relationship is obtained for the spectral behavior of the aerosol optical depth from these two bands. An exponential relationship for spectral behavior of aerosol optical depth has been used for atmospheric correction algorithm. The aerosol optical thickness has been extrapolated to visible channels using this exponential relation. Rayleigh scattering and sun glitter components were also computed based on the method by Mohan et al. (1998).

#### Bio-optical algorithms for OCM imagery

A number of bio-optical algorithms for chlorophyll retrieval have been developed to relate measurements of ocean radiance to the in situ concentrations of phytoplankton pigments. An empirical algorithm (also known as Ocean Chlorophyll 2 or OC2, O'Reilly et al., 1998) has been used with IRS-P4 OCM data, on the basis of results of a study on intercomparison of different bio-optical algorithms. This algorithm was modified as per regional retrieval of chlorophyll concentration (Chauhan et al., 2002). It has been found that this algorithm captures the inherent sigmoid relationship between  $R_{rs}490/R_{rs}555$ band ratio and Chlorophyll concentration C (where  $R_{\rm rs}$  is remote sensing reflectance). The algorithm was shown to retrieve low as well as high chlorophyll concentration which means a better retrieval. The algorithm operates with five coefficients and has following mathematical form:

$$log_{10} C = 0.341 - 3.001 * R + 2.811 * R^{2} - 2.04 * R^{3} \text{ for } 0.01 \text{ mg/m}^{3} \le C \le 50 \text{ mg/m}^{3}$$

where *C* is chlorophyll concentration in mg/m<sup>3</sup> and  $R = \log_{10} [R_{\rm rs} (490)/R_{\rm rs} (555)]$ , where  $R_{\rm rs}$  is remote sensing reflectance.

The chlorophyll concentration images were generated using the aforementioned processing approach. The software for generating chlorophyll concentration images is available for operational use at laboratory of Marine and Water Resources Group, Space Applications Centre, Ahmedabad.

#### AVHRR data analysis

The brightness temperature sensed at satellite height is influenced mainly by atmospheric moisture. The signal loss due to water vapor absorption is proportional to the radiance difference in the measurement made at two different channels of the thermal infrared. The multi-channel sea surface temperature (MCSST) approach suggested by McClain et al. (1985) was used to compute SST from AVHRR thermal infrared channels, i.e., Channel 4 (10.3– 11.3  $\mu$ m) and Channel 5 (11.5–12.5  $\mu$ m). In order to estimate SST accurately, it is necessary to eliminate the influence of emission from clouds besides the precise calibration and navigation. Prior to the SST estimation, pixels of full-resolution images are discriminated into cloud-free pixels or cloud-contaminated pixels using a cloud-filtering algorithm, i.e., threshold tests for reflectance, brightness temperature and brightness temperature difference between the split-window channels. SST is estimated from the brightness temperature of cloud-free pixels of the split-window channels using the following linear regression equation of the Multi-channel SST (MCSST) retrieval algorithm (McClain et al., 1985)

$$SST = a \cdot T_{11} + b(T_{11} - T_{12}) + c(T_{11} - T_{12}) \cdot (\sec \theta - 1) + d$$

where  $T_{11}$  is brightness temperature in 11 µm band,  $T_{12}$  is brightness temperature in 12 µm band,  $\theta$  is satellite zenith angle, and *a*, *b*, *c*, and *d* are coefficients of the linear regression equation. The coefficients of the equation for each satellite and for daytime or nighttime are provided on the web site of National Environmental Satellite Data and Information Service (NESDIS) of NOAA. After the estimation of SST, the estimated value in each pixel is compared with the climatology values of SST in order to eliminate unreasonable values of SST.

Preliminary geometric correction was carried out according to Narayana et al. (1995). This approach uses the satellite ephemeris. The precise geometric corrections were carried out using a set of ground control points (GCPs) located both on an image and on a Naval Hydrographic Office (NHO) bathymetric map. This geo-reference master image was used to image registration of AVHRR channels in order to generate geo-reference data set. Color-coded SST images were generated which indicate the distribution of SST in the northwest Arabian Sea. Same color scheme was applied to both chlorophyll and SST images to facilitate comparison between two parameters.

#### **Results and discussion**

# Satellite observation of coastal upwelling formation processes

Satellites are very useful to locate and monitor coastal upwelling, which required frequent observation over the large area. Time series AVHRR SST imagery for September and October 1995 were analyzed to study various phases of the upwelling process in the Arabian Sea. Figure 2 indicates monitoring of different upwelling phases occurred during the event. The coastal upwelling offshore Gujarat coast was initiated in September 1995. It is clearly observed in the images of SST derived from NOAA AVHRR data (September 28, 1995). This image indicates the maturation phase of upwelling extending from Okha to Diu. During this phase, the phytoplankton growth starts as nutrient supply in the euphotic zone, which enhances the primary production in the upwelling area. This phase creates favored fish feeding grounds as simultaneous zooplankton and herbivorous fish accumulate in the upwelling zone.

Figure 3 indicates weekly mean fish catch during the period of persistent upwelling. The fishing season usually starts after monsoon in September along the Gujarat Coast. Pre-upwelling weeks indicate that normal catch and fish catch decline during the initiation phase. As primary production increases due to availability of nutrient rich water during the maturation phase, an increase in fish catch during this phase and continued in stabilization phase is observed (Solanki et al., 1998a).

Satellite observations of cyclonic eddies and rings formation processes

The cold core eddies and rings can initially be characterized by low temperature and salinity, high nutrient concentration and great biological activity. Satellite observations are limited to SST and biological production (chlorophyll concentration). Rings transport both nutrients and biota. The transported nutrients are important in enhancing oligotrophic conditions. Eddy and ring formation was studied using time series OCM data. The area selected for this study was 20-23° N and 65-68° E. This area is known for eddy formation and high production during winter months (Banse, 1968). Eddies and rings were monitored for several months to study their formation and maturation. The general structure of eddies and rings and their evolution in time are shown in the Fig. 4. This figure indicates eddies and rings formation and decay stages. Four different eddies have been marked with serial numbers. The eddy marked "1" in Fig. 4 formed, developed, and decayed after 1 month. The eddy started forming on March 01, 2004, rotating in anticlockwise fashion and moving toward southwest







Fig. 3 Fish catch during different stages of upwelling along Gujarat Coast, India

direction, and formed an attached ring during March 21-25, 2004. The ring decayed on March 27, 2004. The feature marked "2" is a ring formed during March 3–5, 2004, in  $21-22^{\circ}$  N and  $67-68^{\circ}$  E remaining at the same area for about a month and decayed on March 27, 2004. This ring was highly energetic and supported high

production as nutrient supply was continuously available due to rotation of the feature. The feature marked "3" indicates a different stage of eddy formation. This is a weak eddy. It started forming on March 07, 2004, and was found decayed during March 25–27, 2004. The eddy feature marked "4" was observed for only a week. It formed on March 07, 2004 and decayed on March 15, 2004.

With time, mixing and heating modify the surface water properties related to quality and biological production. There are five physical mechanisms leading to the decay of eddies and rings: They are dispersion, instability, interaction with mean flow, small-scale friction, and surface wind mixing and heat exchanges. The sharp biological contrasts that exist at ring formation also decline with time. Chlorophyll concentration is a measure of the phytoplankton biomass and was found highest in the rings. Highest biomass occurs near the center of a ring and progressively declines toward the ring's edge (Fig. 4).



The potential of satellite observation allows its monitoring the formation, persistence of eddies, and their impacts on biological production. The observations

are shown on the images of eddies (Fig. 5). High CPUE points were found in the vicinity of eddies and comparatively poor catch points were found in non-



Fig. 5 Sequential images of OCM-derived chlorophyll concentration show eddy formation, their persistence, and their relevance to fish catch. White circles indicate classified

eddy areas. Eddies are a moving feature, and hence there is always transport and mixing of nutrients in these areas, which enhances the productivity.

Significance of cyclonic eddies and rings in Northern Arabian Sea

Cyclonic eddies transport nutrient-rich water to sea surface, and an important requirement is fulfilled for an abundant development of plankton in eddy regions. This serves as food for higher organisms, which in turn form the basis of nourishment for edible fish. In this study, a satellite observation of eddies and rings has provided an initial understanding of their behavior. With these data we can assess the influence of rings on the oceanic distribution of physical, chemical, and biological properties. In the ring formation process, a large volume of water is transported across the area. As the ring moves and decays, there is a partial exchange of this water with the surrounding one; thus the rings generate a flux of properties from shelf to open ocean and transfer organic material enhancing biological production.

fish-based mean ( $\mu$ ) and standard deviation (SD). Darker to lighter tone indicates the lower to higher chlorophyll concentration

Satellite observation of anti-cyclonic eddies

Clockwise rotation of eddies accumulate warm water in the center of the eddy. Anti-cyclonic eddies are considered as biological deserts as nutrient-poor warm water with low biological production is accumulated in the center of the eddy (Fig. 6). The area covered by the warm core eddy spread over around 100 km  $\times$  100 km area. The formation process was initiated in the third week of February 2003 and lasted for more than 2 weeks.

Monitoring of such ocean event using satellite is very useful for guiding fishermen to avoid operating in such areas. Although, fisheries data were not available for this study area, the structure of such water bodies is important for the life conditions in the ocean. Sun light and nutrients are the essential requirements for the development of phytoplankton growth which is the basis of food for zooplankton, which in turn feeds the higher organisms. An abundant plankton population consumes nutrients and descends dead into deeper layers. Because of the chemical decay processes, the decomposition constituents are again dissolved in the water and contribute





to accumulation of nutrients. Therefore, surface water layers near surface lose their nutrients if they are not replenished from deeper layers (upwelling). This is the case with anti-cyclonic eddies that are areas poor in nutrients and do not permit a significant development and growth of micro-organisms.

# Satellite observation of fronts

Fronts are important in the ocean dynamics since they are the regions where vertical advection and exchange of momentum are intense. The design of fishing strategies for maximum yields involves the **Fig. 7** A typical chlorophyll concentration image shows ocean color front with sharp gradient of chlorophyll concentration and its extent of distribution



detailed knowledge of the location of oceanic fronts where established algal blooms create regions of high biological productivity.

In oceanic front areas, there is a rapid change in temperature, chlorophyll, and salinity distribution, while the horizontal gradients of these properties are homogeneous in the surrounding water masses. Fronts have significant effect on biology. These systems tend to form zones of convergence of different water masses resulting in accumulation of planktonic organisms. This aggregation also affects distribution of secondary producers and pelagic herbivores (Laevastu & Hayes, 1981).

In remote sensing images, the fronts represent boundary between two water masses of different properties. The fronts can be easily delineated in SST and in the ocean color images due to variation in SST and chlorophyll concentrations (Figs. 6, 7). The various types of shape of fronts are significant to fishery resources (Solanki et al., 2001a). For example, the meandering types of fronts occupy larger areas than linear fronts. Fronts with high SST or chlorophyll gradients act as boundary for resources distributions. Fish populations aggregate in frontal boundaries due to accumulation of planktonic organisms. Relevance of oceanic front with fishery resources has been documented by Laurs et al. (1984), Maul et al. (1984) and Solanki et al. (2001a, 2003a, b). The details of statistical analysis of fish catch data and species distribution with reference to habitat have been discussed by Solanki et al. (2005).

### Conclusion

Oceanographic spatio-temporal processes are important to fishery resources accumulation. Such processes were identified on satellite images of ocean color and SST derived from IRS-OCM and NOAA, respectively. Important upwelling areas with low SST/high chlorophyll were identified and monitored from formation to stable phases. Fish catch was found to decline during initiation phase, while it increased during maturation and stabilization phases. Cyclonic eddies yielded high biological production leading to high catch inside the eddy areas, while anti-cyclonic eddies were found with low chlorophyll concentration. The frontal structures were identified with high chlorophyll concentrations indicating high biological production and high fish catch. Such satellite observations are useful to monitor ecological associations.

Acknowledgments The authors are grateful to Dr. R. R. Navalgund, Director, Space Applications Centre (SAC), and Dr. K. L. Majumdar, Deputy Director, Remote Sensing and Image Processing Area (RESIPA, SAC) for their interest and encouragement during the execution of this work.

### References

- Anonymous, 1996. Fish catch Statistics Report for Year 1995. The Commissioner of Fisheries, Fisheries Department, State Government, Gujarat State, Gandhinagar.
- Banse, K., 1968. Hydrography of the Arabian Sea Shelf of India and Pakistan, and effect on demersal fisheries. Deep Sea Research 15: 45–79.
- Chauhan, P., M. Mohan, P. Matondkar, B. Kumari & S. Nayak, 2002. Surface chlorophyll-a estimation using IRS-P4 OCM data in the Arabian Sea. International Journal of Remote Sensing 23: 1663–1676.
- Fiedler, P. C., G. B. Smith & R. M. Laurs, 1985. Fisheries application of satellite data in the eastern North Pacific. Marine Fisheries Review 46: 1–13.
- Gordon, H. R., R. W. Austin, D. A. Clark, W. A. Hovis & C. S. Yentsch, 1985. Ocean color measurements. Advances in Geophysics 27: 297–333.
- Laevastu, T. & T. Hayes, 1981. Fisheries oceanography. Fishing News Books, Norwich, England: 199.
- Laurs, R. M. & J. T. Burcks, 1985. Living marine resources applications. Advances in Geophysics 27: 419–452.
- Laurs, R. M., P. C. Fiedler & M. Montegomery, 1984. Albacore catch distributions relative to environmental features observed from satellite. Deep Sea Research 31: 1085–1099.
- Maul, G. A., M. Roffer & F. M. Sousa, 1984. Remotely sensed oceanographic patterns and variability of blue fin tuna catch in the Gulf of Mexico. Oceanologica Acta 7: 469–479.
- McClain, P. C., W. G. Pichel & C. C. Walton, 1985. Comparative performance of AVHRR based multi channel sea surface temperature. Journal of Geophysical Research 90: 11587–11601.
- Mohan, M., P. Chauhan, A. Mathur & R. M. Dwivedi, 1998. Atmospheric correction of MOS-B data using long wavelength and PCI based approaches. Scientific Report, SAC/RESA/MWRD/IRSP3/SN/02/98: 14–22.
- Narayana, A., H. U. Solanki, B. G. Krishna & A. Narain, 1995. Geometric correction and radiometric normalisation of NOAA AVHRR data for fisheries application. International Journal of Remote Sensing 16: 765–771.
- Njoku, E. G., T. P. Barnett, R. M. Laurs & A. C. Vasano, 1986. Advances in satellite sea surface temperature

279

measurement and oceanographic applications. Journal of Geophysical Research 90: 11571–11586.

- O'Reilly, J. E., S. Maritonena, B. G. Mitchell, D. A. Siegal, K. L. Carder, S. A. Graver, M. Kahru & C. R. McClain, 1998. Ocean color chlorophyll algorithms for SeaWiFS. Journal of Geophysics 103: 24937–24963.
- Podestra, G. P., J. A. Browder & J. J. Hoey, 1993. Exploring the association between swordfish catch rates and thermal fronts on US longline grounds in the Western North Atlantic. Continental Shelf Research 13: 253–277.
- Solanki, H. U., R. M. Dwivedi & A. Narain, 1998a. Satellite observations of coastal upwelling in the Northern Arabian Sea and its impact on fishery resources. Proceedings of the International Symposium on Information Technology in Oceanography (ITO, 1998), October 1998, Goa, India: 12–16.
- Solanki, H. U., R. M. Dwivedi & S. R. Nayak, 1998b. Relationship between IRS MOS-B derived chlorophyll and NOAA AVHRR SST: a case study in the North West Arabian Sea, India. Proceedings of 2nd International workshop on MOS-IRS and Ocean Colour. Institute of Space Sensor Technology, Berlin, Germany: 327–339.
- Solanki H. U., R. M. Dwivedi & S. R. Nayak, 2000. Generation of composite image using OCM chlorophyll and NOAA AVHRR SST for locating potential fishing grounds. In Proceedings PORSEC 2000 vol II, 669–672.
- Solanki H. U., R. M. Dwivedi & S. R. Nayak, 2001a. Synergistic analysis of Sea WiFS chlorophyll and NOAA AVHRR derived SST features for marine living resources. International Journal of Remote Sensing 22(8): 3877–3882.
- Solanki H. U., R. M. Dwivedi & S. R. Nayak, 2001b. Application of OCM chlorophyll and AVHRR SST for fishery forecast: Preliminary results off Gujarat coast. Indian Journal of Marine Science 30(3): 132–138.
- Solanki, H. U., R. M. Dwivedi & S. R. Nayak, 2003a. Application of remotely sensed closely coupled biological and physical process for marine fishery resources exploration. Journal of Society of Indian Remote Sensing 31: 67–70.
- Solanki, H. U., R. M. Dwivedi, S. R. Nayak, V. S. Somvanshi, D. K. Gulati & S. K. Pattnayak, 2003b. Fishery forecast using OCM chlorophyll concentration and AVHRR SST: Validation results of Gujarat Coast, India. International Journal of Remote Sensing 24: 3691–3699.
- Solanki, H. U., P. C. Mankodi, S. R. Nayak & V. S. Somvanshi, 2005. Evaluation of remote-sensing-based potential fishing zones (PFZs) forecast methodology. Continental Shelf Research 25: 2163–2173.
- Solanki, H. U., M. Raman, B. Kumari, R. M. Dwivedi & A. Narain, 1998c. Seasonal trends in the fishery resources off Gujarat: salient observations using NOAA-AVHRR. Indian Journal of Maine Sciences 27: 438–442.
- Stretta, J. M., 1991. Forecasting models for tuna fishery with Aerospatiale remote sensing. International Journal of Remote Sensing 12: 771–779.
- Sugimoto, T. & H. Tameish, 1992. Warm core rings and their role on the fishing ground formation around Japan. Deep Sea Research 39: 183–201.
- Yamanaka, I., S. Ito, K. Niwa, R. Tanabe, Y. Yabuta & S. Chikuni, 1998. The fisheries forecasting system in Japan for coastal pelagic fish. FAO Fisheries Technical Paper 301: 372.

## FISH HABITAT MAPPING

# Modelling potential habitat of the invasive ctenophore *Mnemiopsis leidyi* in Aegean Sea

Apostolos Siapatis · Marianna Giannoulaki · Vasilis D. Valavanis · Andreas Palialexis · Eudoxia Schismenou · Athanassios Machias · Stylianos Somarakis

© Springer Science+Business Media B.V. 2008

Abstract The invasive ctenophore *Mnemiopsis leidyi* was accidentally introduced into the Black Sea in the early 1980s and it was first sighted in the Aegean Sea (Eastern Mediterranean) in the early 1990s. This article presents a first attempt to develop a predictive spatial model based on *M. leidyi* presence data and satellite environmental data from the Aegean Sea during early summer, in order to identify those areas in the Greek Seas and the entire Mediterranean basin that

Guest editor: V. D. Valavanis Essential Fish Habitat Mapping in the Mediterranean

A. Siapatis · A. Machias Institute of Marine Biological Resources, Hellenic Centre for Marine Research, Aghios Kosmas, 16777 Helliniko, Greece

M. Giannoulaki (🖂) · E. Schismenou · S. Somarakis Institute of Marine Biological Resources, Hellenic Centre for Marine Research, Thalassocosmos, 71003 Heraklion Crete, Greece e-mail: marianna@her.hcmr.gr

V. D. Valavanis · A. Palialexis Marine GIS Laboratory, Institute of Marine Biological Resources, Hellenic Centre for Marine Research, Thalassocosmos, 71003 Heraklion Crete, Greece

A. Palialexis · E. Schismenou Department of Biology, University of Crete, Vassilika Vouton, P.O. Box 2208, 71409 Heraklion Crete, Greece could serve as potential habitat for the species. Generalized additive models (GAM) were applied. The final GAM model indicated higher probability of finding M. leidyi present in depths of 65-135 m and sea surface temperature values of 21-25°C. Furthermore, the significant interaction between photosynthetically active radiation (PAR) and sea level anomaly (SLA) indicated a higher probability of M. leidvi presence in low values of PAR and SLA. In the next step, the final GAM was applied in a prediction grid of mean monthly satellite values for June 2004-2006 in order to estimate probability of M. leidyi presence in the Hellenic Seas and the whole Mediterranean basin at a GIS resolution of 4 km. In the Aegean Sea, species potential habitat included areas influenced by the Black Sea Water (e.g. Thracian Sea, Limnos-Imvros plateau), gulfs that are affected by river runoffs, such as the Thermaikos, Strymonikos and Patraikos gulfs, or areas with strong anthropogenic influence such as the Saronikos gulf. Areas with the same environmental conditions as those in Aegean Sea have been indicated in certain spots of the Levantine Sea as well as in coastal waters of Egypt and Libya, although their spatial extent varied largely among years examined. However, the occurrence of conditions that are linked to high probability of M. leidyi presence does not necessarily mean that these areas can support successful reproduction, high population or bloom levels, since these depend on a combination of temperature, salinity, food availability and the abundance of predators.

**Keywords** *Mnemiopsis leidyi* · Ctenophores · Habitat modelling · Potential habitat · Generalized additive models · Satellite environmental data · Aegean Sea

### Introduction

The ctenophore *Mnemiopsis leidyi* A. Agassiz 1865 is a voracious zooplanktivorous species and its native habitat is found in estuaries and coastal regions along the eastern coast of North and South America (Javidpour et al., 2006). It was accidentally introduced into the Black Sea in the early 1980s (Vinogradov et al., 1989) possibly with ballast water from ship coming from the NW Atlantic coastal region. It has exhibited an explosive mass development there since 1988, and has expanded to the Azov, Marmara and Eastern Mediterranean Seas (Studenikina et al., 1991; Shiganova, 1993; Shiganova et al., 2001a).

This ctenophore is a polymorphic species with wide tolerance to environmental factors and high phenotypic variability (Javidpour et al., 2006) and it has been included in the International Union for Conservation of Nature (IUCN) list of 100 'World's Worst' invaders. Mnemiopsis leidyi strongly affected all levels of ecosystems and fishery in the Black, Azov and Caspian Seas (Shiganova et al., 2001a, 2003, 2004a, b). Mnemiopsis leidyi is one of the most carnivorous species among comb jellies and it is well adapted for rapid population growth, presenting high feeding, growth and reproduction rates (Finenko et al., 1995). As most planktonic ctenophores, M. leidyi is a simultaneous hermaphrodite and capable of selffertilization (Planka, 1974; Hirota, 1972; Reeve & Walter, 1976). It exhibits a totally planktonic life stage with early stages utilizing protozoa and microzooplankton while adults feed primarily on crustaceans (often copepods and cladocera), mollusc larvae, eggs and young fish larvae (Rapoza et al., 2005). In the Black Sea a sharp decline in icthyo- and mesozooplankton abundance was observed, followed by a change in species composition (Vinogradov et al., 1989, 1992; Shiganova, 1997; Konsulov & Kamburska, 1998; Kovalev et al., 1998) and an abrupt decline in the biomass of zooplanktivorous fish (Volovik et al., 1993; Prodanov et al., 1997; Shiganova, 1997, 1998) such as the Black Sea anchovy and the Mediterranean horse mackerel. These species spawn during summer and suffered from decreased zooplankton abundance (Shiganova et al., 2001a, b). By the late 1980s and early 1990s the pelagic ecosystem of the Black Sea had become a dead-end gelatinous food web and the reduction of *M. leidyi* populations in the Black Sea occurred after one of its predators, the ctenophore *Beroe ovata*, was introduced in the region (Rapoza et al., 2005).

The first occurrence M. leidyi in the Aegean Sea was recorded during late spring-summer 1990 in Saronikos Gulf (45-75 individuals/m<sup>2</sup>, Shiganova et al., 2001b). After 1991, M. leidyi swarms were observed in several coastal areas of the northern Aegean and few specimens were collected in offshore waters (Shiganova et al., 2001a). It is believed that the flow of Black Sea water mass to the northern Aegean Sea contributes to the dispersal of *M. leidyi* in the area. Further east, M. leidyi appeared in Mersin Bay in spring 1992 (Kideys & Niermann, 1994; Uysal & Mutlu, 1993), and in Syrian coastal waters in October 1993 (Shiganova, 1997). The individuals from these areas as well as from Saronikos gulf were probably introduced with ballast waters from ships because they were found near Latakia port (Mersin Bay) and Piraeus port (Saronikos gulf) (Shiganova et al., 2001a). In 1999, M. leidyi reached the Caspian Sea, where it is currently expanding at an even more rapid rate than in the Black Sea (Shiganova et al., 2001b). It has been recently found in the western Baltic Sea (Javidpour et al., 2006).

In Aegean Sea, *M. leidyi* has also been found in Lesvos island in the NE Aegean Sea in 1995 and in several coastal areas of the Aegean Sea (Skyros, Limnos and Alonissos islands and Halkidiki Peninsula) between 1991 and 1996 (Shiganova et al., 2001a). It is believed that the continuous flow of Black Sea water mass to the northern Aegean Sea and the dominant local circulation pattern has resulted in the dispersal of *M. leidyi* individuals to this area (Shiganova et al., 2004a). However no decrease in mesozooplankton biomass has been observed in the Aegean Sea after the appearance of *M. leidyi* in the area (Shiganova et al., 2001a).

The majority of the studies on the presence of *M. leidyi* in the Mediterranean and the Black Sea are referring mainly to species occurrence, life cycle and reproduction studies (Rapoza et al., 2005), population dynamics (Shiganova et al., 2001a, b, 2004a, b) and

the associated changes in the pelagic community structure (Shiganova, 1998; Shiganova et al., 2001a, 2004a, b). Although *M. leidyi* is a rapidly expanded invader with negative impacts in different ecosystems, there are no attempts to define the potential areas that could favour species presence. The prediction of an invasive species potential habitat has particular interest in a closed region such as the Mediterranean basin, which is characterized by strong anthropogenic influence and ecosystem degradation that could enhance the impact of the species into the ecosystem.

Spatial modelling of a species distribution in relation to environmental parameters appears to be a prospective approach to define areas with certain environmental characteristics that could potentially support species presence (Guisan & Zimmermann, 2000; Riou et al., 2001; Francis et al., 2005). It is increasingly becoming an effective tool for understanding the processes that affect the interannual variability in species distribution and provide essential information for management purposes. In addition, satellite environmental data may be used for modelling as proxies to infer spatial variations of environmental factors, allowing estimations in various years, periods and regions. Furthermore, new powerful statistical techniques and GIS tools have been created during the last decade and the use of such tools in the development of habitat distribution models has rapidly increased in ecology (Guisan & Zimmermann, 2000; Riou et al., 2001; Francis et al., 2005).

Thus, the present work is a first approach to develop a spatial model based on North Aegean Sea satellite data to determine the environmental conditions that characterize areas where *M. leidyi* is present and, based on this environmental interaction, to identify other potential areas that could support species presence in the Hellenic and Mediterranean Seas.

#### Materials and methods

#### Study area

The northern Aegean Sea is characterized by high hydrological complexity mostly related to the Black Sea waters (BSW) that enter the Aegean Sea through the Dardanelles strait as a surface current (Zervakis & Georgopoulos, 2002). Two anticyclonic systems dominate the area: one in the Samothraki plateau (the Samothraki gyre) and another one in the Strymonikos Gulf (Somarakis et al., 2002; Fig. 1). These gyres are considered permanent features in the area during early summer and are coupled with a cyclonic system located south of the island of Thasos. The overall circulation is mainly determined by the presence of the Limnos-Imvros stream (LIS), which carries waters of Black Sea origin into the Samothraki plateau (Somarakis et al., 2002; Fig. 1). The thickness of the BSW exiting the Dardanelles is less than 40 m; characterized by its very low salinity (<30 psu), in relation to the Aegean Sea waters (Zervakis et al., 2000). The outflow of BSW enhances local productivity and its advection in the Aegean Sea induces high hydrological and biological complexity (Isari et al., 2006, 2007; Somarakis & Nikolioudakis, 2007). The BSW layer undergoes modification of its characteristics by air-sea interaction and vertical diffusion through mixing with the underlying waters reaching gradually a salinity of 38 psu in the region of the Sporades Islands (central and western Aegean Sea).

The extent of the BSW plume is controlled by the prevailing wind conditions (Vlasenko et al., 1996). The wind field over the Aegean Sea is strong and its direction is largely controlled by orography. Semienclosed water bodies, common in Greek waters (many islands, irregular coastline, semi- or enclosed gulfs), are often highly influenced by wind patterns, producing in many cases local water movements that can favour bottom-up and top-down processes. Etesians (strong summer north-westerly winds) dominate the Aegean from mid-July to mid-September (Hyder et al., 2002). Furthermore, six main rivers discharge into the northern Aegean Sea (Axios, Aliakmon, Pinios, Strymon, Nestos and Evros) that end in large, semi-closed gulfs such as Thermaikos and Strymonikos Gulfs (Stergiou et al., 1997; Isari et al., 2006).

#### Sampling

Plankton specimens were collected during three research surveys during early summer in the northern Aegean Sea in June 2004–2006. Sampling design was based on a grid of stations spaced on parallel transects that were approximately 10 nautical miles apart (Fig. 1). A total of 205 stations were located at





five nautical mile intervals on each transect. Standard vertical plankton tows were carried out at each station, by a WP2 sampler (mouth opening:  $0.255 \text{ m}^2$ , mesh-size: 0.200-mm). *Mnemiopsis leidyi* specimens were identified and counted on board while zoo-plankton samples were preserved in 4% buffered formalin. Qualitative and quantitative analyses of ichthyoplankton samples were performed in the laboratory under a binocular microscope. The total number of *M. leidyi* and the total number of anchovy

eggs and larvae were determined and counted for each sample station.

#### Environmental data

The area is well monitored in terms of monthly satellite imagery. Sea surface temperature distribution (SST in °C) is available through the German Aerospace Agency's (DLR) satellite data archive (EOWEB), while sea surface chlorophyll concentration (CHLO in  $mg/m^3$ ) and photosynthetically active radiation (PAR in Ein/m<sup>2</sup>/day) are downloaded through Oceancolor Web, NASA's online Distributed Active Archive Centre. PAR is defined as the quantum energy flux from the sun in the spectral range 400-700 nm. Sea surface salinity distribution (SSS in psu from CMA BCC GODAS model, Liu et al., 2005) is available through the International Research Institute for Climate and Society (IRI—University of Columbia) online data distribution archive. Bathymetry is calculated through processing (kriging) of a point dataset derived from a blending of depth soundings collected from ships with detailed gravity anomaly information obtained from the Geosat and ERS-1 satellite altimetry missions (Smith & Sandwell, 1997). Sea level anomaly (SLA in cm) is available through AVISO website using their Live Access Server. These aforementioned parameters might be important either as a direct influence on the distribution of anchovy or as a proxy for other factors (Bellido et al., 2001). For example, SLA describes ocean processes, such as gyres, meanders and eddies (Larnicol et al., 2002; Pujol & Larnicol, 2005), which enhance productivity and often function as physical barriers differentiating the distribution of species or species life stages, whereas PAR, representing the amount of solar radiation useable for plants to photosynthesize (Frouin et al., 2003), might be indicative of the extent of the euphotic zone, with its lower limit defined as the depth to which PAR values are reduced to 0.1% of the surface measurements (Hader et al., 1994). The mean monthly values for June 2004-2006 of satellite imagery were estimated for all these variables (Valavanis et al., 2004).

#### Model estimation

Generalized Additive Models (GAMs) were used in order to define the set of the environmental parameters that describe the areas of *M. leidyi* presence in northern Aegean Sea in June 2004–2006. A GAM (Hastie & Tibshirani, 1990) is a generalized linear model with a linear predictor involving a sum of smooth functions of covariates (Wood, 2006). The main advantage of GAMs over traditional regression methods is their capability to model non-linearities using non-parametric smoothers (Hastie & Tibshirani, 1990; Wood, 2006). The selection of the GAM model followed the methodology proposed by Wood & Augustin (2002), using the 'mgcv' library in the R statistical software (R Development Core Team, 2005).

As response variable (y), we used the binary presence/absence of M. leidyi. Independent variables included the cubic root of the depth, the natural logarithm of CHLO, the SST, the SSS, the SLA and the PAR. Bottom depth and CHLO presented high variability in their original values, and thus transformation was necessary to achieve uniform distribution for GAM development (Hastie & Tibshirani, 1990). The appropriate type of transformation was based on the inspection of Quantile–Quantile plots (QQ-plots) to check if variables under certain transformations follow the normal distribution. Environmental variables were ranked according to the above criteria and the best model was chosen based on a stepwise forward selection method. In addition, besides the environmental variables, the binary presence/absence of anchovy eggs and anchovy larvae was tested. For the construction of such a model that could successfully estimate probabilities of the M. leidyi presence, data collected over a wide range of environmental parameters should be collated. Therefore, pooled data from all three examined years were used, in order to obtain more possible observed conditions and ensure potentiality (ICES, 2005).

The output of the GAMs is smoothed fits for each environmental predictor. The individual models cannot be tested for significance using the P-values provided by 'mgcv' library since the true number of degrees of freedom is unknown. Therefore, the best GAM model was chosen based on a stepwise forward selection method that reduces the collinearity problem starting from a simple initial model with few explanatory variables (Sacau et al., 2005; Zuur personal communication). Specifically, models were compared based on the level of deviance explained (0-100%); the higher the better), the Akaike Information Criterion (AIC) and the Un-biased Risk estimator (UBRE, the lower the better). Furthermore, the degree of smoothing of each parameter was chosen based on the observed data and the Generalized Cross Validation method suggested by Wood (2006) and incorporated in the 'mgcv' library. A binomial error distribution and the natural cubic spline smoother were chosen as appropriate for the model. All first order interactions of the parameters included in the final model were tested.

In the next step, the final GAM was applied in a predictive mode in order to estimate the probability

of *M. leidyi* presence to each point of the area used for modelling for June 2004–2006, respectively. Therefore, a specific set of satellite conditions was attributed to a specific probability of *M. leidyi* presence. Moreover, the final GAM was applied in a prediction grid of mean monthly satellite values for June 2004–2006, estimated for the entire Hellenic Seas as well as for the whole Mediterranean basin, at a GIS resolution of 4 km. The areas with a specific set of satellite conditions corresponding to different probabilities (i.e. 25, 50 and 75%) of *M. leidyi* presence were plotted. The Surfer v8.0 of the Golden Software Inc. software was used for mapping.

#### Model validation

The predictive accuracy of the final model was tested by comparing M. leidyi presence and the results of the final GAM model (i.e. the predicted probabilities) concerning the northern Aegean Sea, region used for modelling for each examined year. For this purpose, the Receiver Operating Characteristic (ROC)-plots (Fieldings & Bell, 1997; Guisan and Zimmermann 2000) and the area under the Receiver Operating Characteristic Curve (AUC) were estimated. AUC has been used extensively in the species' distribution modelling literature, measuring the ability of a model to discriminate between those sites where a species is present and those where it is absent (Hanley & McNeil, 1982). It provides an indication of the usefulness of the models for indicating areas in terms of their relative importance as habitat for the particular species. The values of AUC ranges from 0 to 1, where a score of 1 indicates perfect discrimination, a score of 0.5 implies predictive discrimination that is no better than a random guess and values <0.5 indicate performance worse than random (Boyce et al., 2002; Elith et al., 2006). Estimations were made with the presence/absence library of the R statistical software.

#### Results

#### M. leidyi distribution in northern Aegean Sea

The distribution of *M. leidyi* in northern Aegean Sea (including both larvae and adult specimens) is shown in Fig. 2. Although its abundance and distribution

shows a large degree of interannual variability, the highest abundances were observed in Thermaikos and Strymonikos gulfs where large rivers outflow. The lowest abundances were recorded in June 2005  $(3-50 \text{ ind/m}^2)$ , whereas the highest in June 2004  $(4-188 \text{ ind/m}^2)$ . The wider and most southern distribution (up to N. Evoikos Gulf) of the species was observed in 2006 compared to the previous years. A comparison of the distribution of *M. leidyi* and the distribution of anchovy eggs, in the northern Aegean Sea showed contrasting spatial patterns (Fig. 2), with higher abundances of *M. leidyi* in areas presenting low abundances of anchovy eggs. This was more pronounced in Thermaikos gulf in 2004–2006, Strymonikos gulf in 2004 and N. Evoikos gulf in 2006.

# Model estimation

The final selected GAM model based on satellite data included as main effects: SST, Depth and the interactive effect of PAR and SLA, and they are described in Table 1. All variables selected in the final model were statistically significant. Despite the contrasting spatial pattern, possibly because it was not consistent in all areas and years, the entry in the final GAM model of the term "anchovy eggs presence" was found non-significant. The entry of the term "anchovy larvae presence" resulted in a minor reduction of the AIC (less than 0.5%), which implied that the inclusion of the latter term practically did not improve the final GAM model. Therefore these results a not included in Table 1.

The results of the final GAM model are shown as plots of the best-fitting smooths for the effect of the environmental parameters on M. leidyi presence (Fig. 3). The 95% confidence intervals were also plotted around the best-fitting smooths for the main effects. Interaction effects are shown as a perspective plot without error bounds. The y-axis reflects the relative importance of each parameter of the model and for the interaction effects this is presented on the z-axis (Fig. 3). It should be noted that the effect of each variable is the conditional effect, i.e. the effect of the variable given that all other variables are included in the model. Plots indicated higher probability of M. leidyi presence in depths of 65-135 m and SST of 21-25°C (the maximum temperature available). The interaction plot between PAR and SLA also indicated a higher probability of *M. leidyi* 





Mnemiopsis ind/m<sup>2</sup>

v	1 to 10
$\nabla$	11 to 25
$\bigtriangledown$	26 to 50
$\bigtriangledown$	51 to 200

Anchovy eggs ind/m<sup>2</sup>



Deringer

-					
Parameter	Res. Df	Res. deviance	Deviance explained %	AIC	P-value
Null model	560	638.45			
s(Depth)	552.641	603.8489	5.42	620.5676	$\ll 0.000$
s(Depth) + s(SST)	547.784	572.5161	10.3	598.947	$\ll 0.001$
s(Depth) + s(SST) + s(SLA:PAR)	522.65	468.20	26.70	544.9252	$\ll 0.000$
Total variation % explained			26.70		

Table 1 Analysis of deviance for GAM covariates and their interactions of the final model fitted

Level of significance was set to 0.05. The (:) sign denotes interaction. Res. Df, Residual d.f.; Res. deviance, residual deviance; AIC, Akaike information criterion value; *P*-value (chi-square), significance values



**Fig. 3** Coefficients of the generalized additive models (GAMs) for *M. leidyi* against (a) SST, (b) Bottom depth and (c) the interaction plot of PAR and SLA. Black thick lines indicate the value of GAMs coefficient, dotted lines represent

the confidence intervals at P = 0.05. The rug under the single variable effects plots indicates the density of points for different variable values

Table 2
Estimated area under the ROC curve (AUC) per year for *M. leidyi*

AUC	Sensitivity = specificity threshold
0.88	0.22
0.90	0.27
0.75	0.34
	AUC 0.88 0.90 0.75

N, Number of observations. Sensitivity equals specificity threshold is also shown. Sensitivity is defined as the probability that a model yields a positive prediction where species actually occurs (i.e. 1), whereas specificity is the probability that the species is absent (i.e. 0). The threshold at which sensitivity equals specificity coincides with the optimum probability threshold for model performance

presence in the lower values of PAR combined with the lower values of SLA.

#### Model validation

This final model that was based on pooled data from all years was tested for accuracy with the calculation of AUC value for each ROC plot corresponding to satellite data from each separate year. Results indicated good discrimination ability of the model according to Elith et al. (2006), as it exceeded 0.75 in all cases (Table 2). The model was applied in a predictive mode for the entire Hellenic Seas at a GIS resolution of 4 km, in order to map the areas that present environmental conditions similar to those found in northern Aegean Sea. Similar maps were drawn for the entire Mediterranean Sea (Figs. 4-6). The resulted maps indicated areas with environmental conditions that are associated with specific probability values i.e. 0-25, 25-50, 50-75 and 75-100% probability of *M. leidyi* presence in northern Aegean Sea.

# Discussion

Results show that the abundance of *M. leidyi* in the northern Aegean Sea exhibits a high degree of interannual variability and the highest abundances were generally observed in gulfs influenced by river runoffs such as Thermaikos and Strymonikos gulf (Figs. 1 and 2). Rivers outflows bring terrestrial input with subsequent increase in nutrients and local productivity, thus allowing the ecosystem to support higher abundance of zooplankton populations.

Experiments by Shiganova et al. (2004a) have shown that the species can feed and reproduce successfully in the environmental conditions of the northern Aegean Sea. Satellite environmental data describe sea surface conditions rather than describing the actual environment in which the species exists. However, according to the estimated GAM model there was a higher probability of M. leidyi presence in 60-140 m, 21-25°C, and low levels of PAR and SLA. Although difficult to interpret, this interaction effect is likely to indicate an association with waters of 'shallower' euphotic zone (possibly indicating more stratified water masses) combined with downward water movement. This could indicate that there is a positive effect of anticyclonic gyres in the northern Aegean Sea (known as retention areas for zooplankton and ichthyoplankton) as well as a summer effect, implied by the higher probability of M. leidyi presence in warmer, more stratified waters.

Furthermore, there is an indication for contrasting spatial occupation of *M. leidyi* and anchovy eggs (i.e. higher abundance of *M. leidyi* coinciding with low abundances of anchovy eggs and vice versa) in the northern Aegean Sea (Fig. 2). However, this was not consistent in all areas and years, being more pronounced during June 2004 and in Thermaikos gulf during June 2005. Pelagic cnidarians and ctenophores may compete with zooplanktivorous fish and fish larvae. In addition, M. leidyi is known to strongly compete with larval anchovy for food in Black Sea (Gordina et al., 2005) being, at the same time, a prominent predator of anchovy eggs and yolk-sac larvae (Shiganova et al., 2001a). This might partly explain the observed contrasting spatial patterns. However, because this contrasting spatial pattern in anchovy eggs and M. leidyi presence was not consistent in areas and years due to the spatiotemporal variability in the abundance of both species, the entry of this relationship into the GAM model was found non-significant.

Modelling the relationship of *M. leidyi* presence with satellite environmental data from the northern Aegean Sea provided a map of these areas in the Hellenic Seas and the entire Mediterranean basin with certain environmental conditions related to certain probabilities of *M. leidyi* presence. Areas indicated in the Hellenic Seas varied in their spatial extent annually, depending on the environmental conditions. In the Aegean Sea, areas that have been Fig. 4 Map of the probability of potential M. leidyi presence in the Greek region, based on GAM model from northern Aegean Sea. GIS resolution used for prediction is 4 km of mean monthly satellite values from (a) June 2004, (b) June 2005 and (c) June 2006





0 to 0.25

0.25 to 0.5

0.50 to 0.75

indicated were characterized by BSW influence (e.g. Thracian Sea, Limnos-Imvros plateau), including gulfs that are affected by river runoffs such as

Thermaikos and Strymonikos gulf or have strong anthropogenic influence such as Saronikos gulf (Fig. 4). In the Ionian Sea, the main areas were

#### Fig. 5 Eastern

Mediterranean Sea: Map of the probability of potential *M. leidyi* presence based on GAM model from Aegean Sea. GIS resolution used for prediction was 4 km of mean monthly satellite values from (**a**) June 2004, (**b**) June 2005 and (**c**) June 2006



Patraikos gulf and the coastal waters between the islands and the mainland, areas characterized by shallow, productive waters and river runoffs. Areas have also been indicated in the Turkish coastal waters of the Aegean Sea that are strongly associated with the BSW, such as the Saros Bay and the area around the island of Imvros as well as areas like the Edremit gulf and the gulf of Izmir (Figs. 4 and 5). Known

records of the species in Saronikos Gulf since late spring-summer 1990 (Shiganova et al., 2001a) as well as from other coastal areas of the Aegean Sea (Skyros, Limnos and Alonissos islands, Halkidiki Peninsula) between 1991 and 1996 (Shiganova et al., 2001a) and Izmir Gulf (Kideys & Niermann, 1994) generally confirm the areas indicated by the model as potential *M. leidyi* habitat. Fig. 6 Western

Mediterranean Sea: Map of the probability of potential future *M. leidyi* presence based on GAM model on records from Aegean Sea. GIS resolution used for prediction was 4 km of mean monthly satellite values from (**a**) June 2004, (**b**) June 2005 and (**c**) June 2006



Maps for the entire Mediterranean Sea (Figs. 5 and 6) indicated areas with similar environmental characteristics to those in the Aegean Sea. It is well understood that the spatial and seasonal extent of these areas is affected by the variability in climate and the environment, thus estimation was restricted to early summer (June) and estimated for three different years (Figs. 5 and 6). In the Eastern Mediterranean basin, areas have been indicated in the Levantine: the Syrian and the Lebanese coastal waters, the Turkish southeast coastal waters, such as the Gulf of Antalya and the Gulf of Mersin, and offshore eastern Cyprus.

*M. leidyi* in Mersin Bay in spring 1992 (Uysal & Mutlu, 1993; Kideys & Niermann, 1994) and in the Syrian coastal waters in October 1993 (Shiganova, 1997; Shiganova et al., 2001a, b), but it is unknown if there is a persistent, reproducing, local population. Although the model explains only a small fraction of total deviance (26.70%), the areas indicated are

Areas have also been indicated in the coastal waters

of Egypt and Libya, although their spatial extent

varied largely from year to year. Data from the

Eastern Mediterranean confirm the presence of

shallow, productive areas, influenced by river runoffs,

being under strong anthropogenic influence (e.g. big commercial ports) or by the BSW mass, which most likely contributes to the dispersal of *M. leidyi* to the northern Aegean Sea. Although there was a lack of adequate data, areas indicated by the model are mostly areas of known presence of M. leidyi. The model could be further improved by adding data from other areas like the Black Sea region and by taking into account the temporal variation in the environmental parameters (e.g. weekly differences), the abundance of anchovy eggs as well as the abundance of competitor species and predators. The seasonal abundance of *M. leidyi* largely depends on the combination of favourable conditions regarding temperature, salinity, food availability and predators' abundance; therefore the occurrence of M. leidyi in the Aegean Sea and the eastern Mediterranean does not necessarily mean that the species in the area can reproduce, reach high populations or bloom levels, causing ecosystem effects similar to the ones occurred in the Black Sea. For example, the occurrence of high temperatures during the winter period is very important to M. leidyi's successful reproduction (Shiganova et al., 2001a).

The case of the western Mediterranean Sea presents particular interest because, as of this study, there are no reported records of the species presence. Mapping indicated those regions that present environmental characteristics similar to those where the species occurs in the northern Aegean Sea. Derived areas include the Adriatic Sea, the coastal waters of the Ligurian and the Tyrrhenian seas, the straits of Sicily, coastal areas in Tunisia and Libya (e.g. the Gulf of Benghazi, the Gulf of Gabes and the Gulf of Shirte, Figs. 5 and 6), as well as the Gulf of Lions and the Catalan Sea. Future plans of establishment of oil pipe lines in the region (i.e. Adriatic Sea) could increase the risk of the invasion of M. leidyi with ballast waters to the western Mediterranean. It should be noted that all these areas seem to have environmental conditions that potentially, but not necessarily, could support the species presence, such that the species can both successfully reproduce and reach high populations or bloom levels.

The areas indicated in the western Mediterranean coincide with the major spawning grounds and fishing grounds of small pelagics and especially anchovy (i.e. the Adriatic Sea, the Gulf of Lions, the Catalan Sea and the Gulf of Tunis, see García Lafuente et al., 2002; Cuttitta et al., 2003; Sabates et al., 2007; Palomera et al., 2007). Since experience from the Black Sea has shown that high abundances of *M. leidyi* (Shiganova et al., 2001a) involve a high risk for alterations in the local food web and in the abundance of zooplanktivorous fish populations, such as anchovy (Volovik et al., 1993; Prodanov et al., 1997; Shiganova, 1997; 1998), it is important to examine through future work the possible dispersion pathways of *M. leidyi* to the western Mediterranean.

Furthermore, future work may involve the examination of whether local conditions (e.g. temperature, salinity, prey's availability and/or predators' abundance) in the Mediterranean Sea could favour *M. leidyi's* successful reproduction, high populations or bloom levels during all year round that might possibly lead to an alteration of the food web in a similar way to the case of the Black Sea.

Acknowledgements The study was partially financed by the Commission of the European Union (EnviEFH-FP6-22466: Environmental Approach to Essential Fish Habitat Designation). Authors thank the captain and the crew of RV "Philia" for their assistance during the surveys and Alain F. Zuur (Highland Statistics, Ltd.) for his help and statistical advice regarding data analysis.

#### References

- Bellido, J. M., G. J. Pierce & J. Wang, 2001. Modelling intraannual variation in abundance of squid *Loligo forbesi* in Scottish waters using generalised additive models. Fisheries Research 52: 23–39.
- Boyce, M. S., P. R. Vernier, S. E. Nielsen & F. K. A. Schmiegelow, 2002. Evaluating resource selection functions. Ecological Modelling 157: 281–300.
- Cuttitta, A., V. Carini, B. Patti, A. Bonanno, G. Basilone, S. Mazzola, J. Garcia Lafuente, A. Garcia, G. Buscaino, L. Aguzzi, L. Rollandi, G. Morizzo & C. Cavalcante, 2003. Anchovy egg and larval distribution in relation to biological and physical oceanography in the strait of Sicily. Hydrobiologia 503: 117–120.
- Elith, J., C. H. Graham, R. P. Anderson, M. Dudik, S. Ferrier, A. Guisan, R. J. Hijmans, F. Huettmann, J. R. Leathwick, A. Lehmann, J. Li, L. G. Lohmann, B. A. Loiselle, G. Manion, C. Moritz, M. Nakamura, Y. Nakazawa, J. Mc. C. Overton, A. T. Peterson, S. J. Phillips, K. S. Richardson, R. Scachetti-Pereira, R. E. Schapire, J. Soberon, S. Williams, M. S. Wisz & N. E. Zimmermann, 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography 29: 129–151.
- Fieldings, A. H. & J. F. Bell, 1997. A review of methods for the assessment of prediction errors in conservation presence: absence models. Environmental Conservation 24: 38–49.

- Finenko, G. A., G. I. Abolmasova & Z. A. Romanova, 1995. Intensity of the nutrition, respiration and growth of *Mnemiopsis mccradyi* in relation to grazing conditions. Biologia Morya 21: 315–320.
- Francis, M. P., M. A. Morrison, J. Leathwick, C. Walsh & C. Middleton, 2005. Predictive models of small fish presence and abundance in northern New Zealand harbours. Estuarine Coastal and Shelf Science 64: 419–435.
- Frouin, R., B. A. Franz & P. J. Werdell, 2003. The SeaWiFS PAR product. In Hooker, S. B. & E. R. Firestone (eds), Algorithm Updates for the Fourth SeaWiFS Data Reprocessing, NASA/TM 2003–206892 22: 46–50.
- García Lafuente, J., A. García, S. Mazzola, L. Quintanilla, A. Delgado, A. Cuttitta & B. Patti, 2002. Hydrographic phenomena influencing early life stages of the Sicilian Channel anchovy. Fisheries Oceanography 11: 31–44.
- Gordina, A. D., J. A. Zagorodnyaya, A. E. Kideys, L. Bat & H. H. Satilmis, 2005. Summer ichthyoplankton, food supply of fish larvae and impact of invasive ctenophores on the nutrition of fish larvae in the Black Sea during 2000 and 2001. Journal of Marine Biological Association of the United Kingdom 85: 537–548.
- Guisan, A. & N. E. Zimmermann, 2000. Predictive habitat distribution models in ecology. Ecological Modelling 135: 147–186.
- Hader, D. P., R. C. Worrest, H. D. Kumar & R. C. Smith, 1994. Effects of increased solar ultraviolet radiation on aquatic ecosystems. United Nations Environment Programme, Environmental Effects of Ozone Depletion, 1994 Assessment. http://sedac.ciesin.org/ozone/UNEP/UNEP94toc.html
- Hanley, J. A. & B. J. McNeil, 1982. The meaning and use of the area under a Receiver Operating Characteristic (ROC) curve. Radiology 143: 29–36.
- Hastie, T. & R. Tibshirani, 1990. Generalized Additive Models. Chapman and Hall, London.
- Hirota, J., 1972. Laboratory culture and metabolism of the ctenophore *Pleurabrachia bachei* A. Agassiz. In Takenouti, A. Y. (ed.), Biological Oceanography of the Northern North Pacific Ocean. Idemitsu Shoten: 465–484.
- Hyder, P. W., J. H. Simpson, S. Christopoulos & Y. Krestenitis, 2002. The seasonal cycles of stratification and circulation in the Thermaikos Gulf Region of Freshwater Influence (ROFI), north-west Aegean. Continental Shelf Research 22: 2573–2597.
- ICES, 2005. Report on the Study Group on Regional Scale Ecology of Small Pelagic Fish (SGRESP). ICES CM/ 2005/G:06.
- Isari, S., S. Psarra, P. Pitta, P. Mara, M. O. Tomprou, A. Ramfos, S. Somarakis, A. Tselepides, C. Koutsikopoulos & N. Fragopoulu, 2007. Differential patterns of mesozooplankters' distribution in relation to physical and biological variables of the Northeastern Aegean Sea (eastern Mediterranean). Marine Biology 151: 1035–1050.
- Isari, S., A. Ramfos, S. Somarakis, C. Koutsikopoulos, A. Kallianiotis & N. Fragopoulu, 2006. Mesozooplankton distribution in relation to hydrology of the Northeastern Aegean Sea, eastern Mediterranean. Journal of Plankton Research 28: 241–255.
- Javidpour, J., U. Sommer & T. Shiganova, 2006. First record of *Mnemiopsis leidyi* A. Agassiz 1865 in the Baltic Sea. Aquatic Invasions 1: 299–302.

- Kideys, A. E. & U. Niermann, 1994. Occurrence of *Mnemi-opsis* along the Turkish coast. ICES Journal of Marine Science 51: 423–427.
- Konsulov, A. S. & L. T. Kamburska, 1998. Ecological determination of the new Ctenophora – *Beroe ovata* invasion in the Black Sea. Proceedings of the Institute of Oceanology of Varna 2: 195–198.
- Kovalev, A. V., S. Besiktepe, J. Zagorodnyaya & A. Kideys, 1998. Mediterraneanization of the Black Sea zooplankton is continuing. In Ivanov, L. & T. Oguz (eds), Ecosystem Modeling as a Management Tool for the Black Sea. Kluwer Academic Publishers, The Netherlands.
- Larnicol, G., N. Ayoub & P. Y. Le Traon, 2002. Major changes in Mediterranean Sea level variability from 7 years of TOPEX/Poseidon and ERS-1/2 data. Journal of Marine Systems 33: 63–89.
- Liu, Y., R. Zhang, Y. Yin & T. Niu, 2005. The application of ARGO data to the global ocean data assimilation operational system of NCC. Acta Meteorological Sinica 19: 355–365.
- Palomera, I., M. P. Olivar, J. Salat, A. Sabates, M. Coll, A. Garcia & B. Morales-Nin, 2007. Small pelagic in the NW Mediterranean Sea: an ecological review. Progress in Oceanography 74: 377–396.
- Planka, H. D., 1974. Ctenophora. Reproduction of Marine Invertebrates 1: 201–265.
- Prodanov, K., K. Mikhailov, G. Daskalov, K. Maxim, A. Chashchin, A. Arkhipov, V. Shlyakov & E. Ozdamar, 1997. Environmental Impact on Fish Resources in the Black Sea. In Ozsoy, E. & A. Mikaelyan (eds), Sensitivity of North Sea. Baltic Sea and Black Sea to Anthropogenic and Climatic Changes. Kluwer, Dordrecht: 163–181.
- Pujol, M. I. & G. Larnicol, 2005. Mediterranean sea eddy kinetic energy variability from 11 years of altimetric data. Journal of Marine Systems 58: 121–142.
- R Development Core Team 2005. R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing. http://www.R-project.org
- Rapoza, R., D. Novak & J. H. Costello, 2005. Life-stage dependent, in situ dietary patterns of the lobate ctenophore *Mnemiopsis leidyi* Agassiz 1865. Journal of Plankton Research 27: 951–956.
- Reeve, M. R. & M. A. Walter, 1976. A large-scale experiment on the growth and predation potencial of ctenophore populations. In Mackie, G. O. (ed.), Coelenterate Ecology and Behavior. Plenum: 187–199.
- Riou, P., O. Le Pape & S. I. Rogers, 2001. Relative contributions of different sole and plaice nurseries to the adult population in the Eastern Channel: application of a combined method using generalized linear models and a geographic information system. Aquatic Living Resources 14: 125–135.
- Sabates, A., M. P. Olivar, J. Salat, I. Palomera & F. Alemany, 2007. Physical and biological processes controlling the distribution of fish larvae in the NW Mediterranean. Progress in Oceanography 74: 355–376.
- Sacau, M., G. J. Pierce, J. Wang, A. I. Arkhipkin, J. Portela, P. Brickle, M. B. Santos, A. F. Zuur & X. Cardoso, 2005. The spatio-temporal pattern of Argentine shortfin squid *Illex argentinus* abundance in the southwest Atlantic. Aquatic Living Resources 18: 361–372.

- Shiganova, T. A., 1993. Ctenophore *M. leidyi* and ichthyoplankton in the Sea of Marmara in October of 1992. Oceanology 33: 900–903.
- Shiganova, T. A., 1997. *M. leidyi* abundance in the Black Sea and its impact on the pelagic community. In Ozsoy, E. & A. Mikaelyan (eds), Sensitivity of North Sea, Baltic Sea and Black Sea to anthropogenic and climatic changes. Kluwer Academic Publishers, Dordrecht: 117–130.
- Shiganova, T. A., 1998. Invasion of the Black Sea by the ctenophore *M. leidyi* and recent changes in pelagic community structure. Fisheries Oceanography 7: 175–390.
- Shiganova, T. A., Y. V. Bulgakova, E. I. Musaeva, Z. A. Mirzoyan & M. L. Martynyuk, 2003. Ctenophore invaders *Mnemiopsis leidyi* (A. Agassiz) and *Beroe ovata* Mayer 1912 and their effect on pelagic ecosystem of northeastern Black Sea. Biological Bulletin N3.
- Shiganova, T. A., E. D. Christou, J. V. Bulgakova, I. Siokou-Frangou, S. Zervoudaki & A. Siapatis, 2004a. Distribution and biology of the invader *M. leidyi* in the Northern Aegean Sea, comparison with indigenous species *Bolinopsis vitrea*. In Dumont, H., T. Shiganova & U. Niermann (eds), Aquatic Invasions in the Black, Caspian and Mediterranean Seas. NATO Science Series 4. Earth and Environmental Sciences. Kluwer Academic Publishers: 113–135.
- Shiganova, T. A., H. J. D. Dumont, A. Mikaelyan, D. Glazov, M. Y. V. Bulgakova, E. I. Musaeva, P. Y. Sorokin, L. A. Pautova, Z. A. Mirzoyan & E. I. Studenikina, 2004b. Interaction between the invading ctenophores *Mnemiopsis leidyi* (A. Agassiz) and *Beroe ovata* (Mayer 1912), and their influence on the pelagic ecosystem of the Northeastern Black Sea. In Dumont, H., T. Shiganova & U. Niermann (eds), The Ctenophore *Mnemiopsis leidyi* in the Black, Caspian and Mediterranean Seas and Other aquatic Invasions. NATO Science Series 2. Environment. Kluwer Academic Publishers: 33–70.
- Shiganova, T. A., A. Kamakin, D. P. Zhukova, V. B. Ushivtzhev, A. B. Dulimov & E. I. Musaeva, 2001a. New invader in the Caspian Sea - ctenophore *Mnemiopsis* and its initial effect on the pelagic ecosystem. Oceanology 41: 542–549.
- Shiganova, T. A., Z. A. Mirzoyan, E. A. Studenikina, S. P. Volovik, I. Siokou-Frangou, S. Zervoudaki, E. D. Christou, A. Y. Skirta & H. J. Dumont, 2001b. Population development of the invader ctenophore *Mnemiopsis leidyi* in the Black Sea and other seas of the Mediterranean basin. Marine Biology 139: 431–445.
- Smith, W. H. F. & D. T. Sandwell, 1997. Global sea floor topography from satellite altimetry and ship depth soundings. Science 277: 1956–1962.
- Somarakis, S., P. Drakopoulos & V. Filippou, 2002. Distribution and abundance of larval fishes in the northern Aegean

Sea—eastern Mediterranean—in relation to early summer oceanographic conditions. Journal of Plankton Research 24: 339–357.

- Somarakis, S. & N. Nikolioudakis, 2007. Oceanographic habitat, growth and mortality of larval anchovy (*Engraulis encrasicolus*) in the northern Aegean Sea (eastern Mediterranean). Marine Biology 152: 1143–1158.
- Stergiou, K. I., E. D. Christou, D. Georgopoulos, A. Zenetos & C. Souvermezoglou, 1997. The Hellenic Seas: physics, chemistry, biology and fisheries. Oceanography and Marine Biology: An Annual Review 35: 415–538.
- Studenikina, E. I., S. P. Volovik, I. A. Miryozan & G. I. Luts, 1991. The ctenophore *M. leidyi* in the Sea of Azov. Oceanology 3: 722–725.
- Uysal, Z. & E. Mutlu, 1993. Preliminary note on the occurrence and biometry of ctenophore *Mnemiopsis leidyi* finally invaded Mersin Bay. Turkish Journal Zoology 17: 229–239.
- Valavanis, V. D., S. Georgakarakos, A. Kapantagakis, A. Palialexis & I. Katara, 2004. A GIS environmental modeling approach to Essential Fish Habitat designation. Ecological Modelling 178: 417–427.
- Vinogradov, M. E., V. V. Sapozhnikov & E. A. Shushkina, 1992. The Black Sea ecosystem. Moscow. Russia. Nauka: 112.
- Vinogradov, M. E., E. A. Shushkina, E. I. Musaeva & P. Y. Sorokin, 1989. Ctenophore *M. leidyi* (A. Agassiz) (Ctenophora: Lobata) - new settler in the Black Sea. Oceanology 29: 293–298.
- Vlasenko, V. I., N. N. Stashchuk, V. A. Ivanov, E. G. Nikolaenko, O. Uslu & H. Benli, 1996. Influence of the water exchange through Dardanelles on the thermohaline structure of the Aegean Sea. Bulletin de l'Institut Oceanographique. Monaco 17: 147–165.
- Volovik, S. P., I. A. Mirzoyan & G. S. Volovik, 1993. *M. leidyi*: biology, population dynamics, impact to the ecosystem and fisheries. ICES Biological Oceanography Committee 69: 1–11.
- Wood, S. N., 2006. Generalized Additive Models. An Introduction with R. Chapman & Hall, New York.
- Wood, S. N. & N. H. Augustin, 2002. GAMs with integrated model selection using penalized regression splines and applications to environmental modelling. Ecological Modelling 157: 157–177.
- Zervakis, V. & D. Georgopoulos, 2002. Hydrology and circulation in the Northern Aegean Sea throughout 1997 and 1998. Mediterranean Marine Science 3: 5–19.
- Zervakis, V., D. Georgopoulos & P. G. Drakopoulos, 2000. The role of the North Aegean in triggering the recent Eastern Mediterranean climatic changes. Journal of Geophysical Research 105: 26103–26116.

### FISH HABITAT MAPPING

# A GIS-based tool for storage, selection and visualization of time series 4D marine datasets

Ricardo N. Fernandes · Vasilis D. Valavanis

© Springer Science+Business Media B.V. 2008

**Abstract** We present an initial attempt for the development of a distributed and scalable GIS-like tool for the storage, selection and visualization of 4D marine datasets. The aim of this tool is to standardize the variety of data available for the water column and support non-technical marine biologists in manipulating 4D marine datasets. The tool is developed towards answering specific environmental and biological questions regarding ocean processes and essential fish habitat mapping in three dimensions.

**Keywords** Geographic information systems (GIS) · Marine datasets · Database · 3D graphics · 4D visualization

# Introduction

Extensive amounts of accumulated and diverse marine datasets need to be commonly organized, accessed and queried by marine scientists (Su et al., 2000). The result of these queries should be displayed using sophisticated techniques, such as 3D graphics

Guest editor:	V. D. Valavanis	
Essential Fish	Habitat Mapping in the M	Iediterranean

R. N. Fernandes (⊠) · V. D. Valavanis Marine GIS Laboratory, Institute of Marine Biological Resources, Hellenic Centre for Marine Research, Thalassocosmos, 71003 Heraklion Crete, Greece e-mail: ricardo@her.hcmr.gr and animations (Chen et al., 2004). Three-dimensional visualizations can contain more information at once and are therefore more suitable for presenting large datasets (Schonhage et al., 2000). However, taking into account another important factor, time (as the fourth dimension) is still one of the challenges in the field. Thus, there is a need for a powerful, yet simple to use, GIS-based tool that stores time series of marine datasets, performs analytical GIS functions (i.e. data selection using certain criteria defined by the user) and visualizes the results in 3D animations. These analytical functions may be used to answer specific questions, such as the spatiotemporal relations between different environmental variables (e.g. 3D mapping of upwelling, fronts, gyres and essential fish habitats).

In many disciplines, large data collections are increasingly emerging as one of the most important resources. In domains as diverse as global climate change, high energy physics and computational genomics, the data volume already reaches terabytes and will soon approach petabytes. User groups with data access and mining needs are often large and almost always geographically distributed (Moore et al., 1998). The accumulated large amount of marine datasets, coming from diverse sources such as remote sensing or electronic sensors, must be efficiently stored to be queried by marine scientists according to specific criteria (e.g. where are the areas that simultaneously have a temperature between 10 and 15°C, salinity greater than 35 psu and chlorophyll greater than  $0.003 \text{ mg/m}^3$ ) and must display the result of these queries in 3D graphics.

Recently, several 3D visualization tools have been developed for terrestrial (Jasnoch et al., 2001; Dunbar, 2003; Grunwald & Barak, 2003) and marine applications (Su & Sheng, 1999; Campbell, 2002; McCann, 2002). Most of these tools visualize specific data formats, although the current stream of applications makes use of latest technologies in datametadata organization, such as the eXtensible Markup Language (XML). The GIS-based tool described here follows this current stream of applications focusing on the development of a 'light' multi-platform tool to be easily used by marine biologists. The tool aims to answer specific biological questions with the capability to store, select and visualize time series 4D (latitude, longitude, depth and time) marine datasets in a distributed and heterogeneous environment (i.e. with different types of equipment or platform, accessing data stored in one or more remote servers). Here, the architecture, the various features of the application as well as the tools used to develop it are described and its functionality is explained.

# Characteristics

The tool has been implemented as a client/server architecture, since this is a versatile, message-based and modular infrastructure which assures usability, flexibility, interoperability and scalability (Kinshuk et al., 2001). The main characteristics of this 4D tool are:

A. Distributed. Since the GIS-based tool may have many users (often referred to as clients), it was built to allow many clients to query datasets stored in one or more remote servers, although it can operate in a centralized way, as well (both the client and the server residing in the same machine). Query results are stored in the user's computer and may be displayed in 3D graphics.

B. Heterogeneous. Since users work with different types of hardware and operating systems, the tool was implemented in Java programming language to support this heterogeneity by being able to be easily transferable and run on any platform.

C. Simple. The user interface is one of the most important parts of any tool, because it is the connection between the tool and the user (Preece et al., 1994). Therefore, the tool's interface, based on the graphical user interface (GUI) paradigm, was conceived to be very simple and intuitive to be used by non-technical users. After just a few trials, users start to familiarize themselves with the tool's interface and its functionalities.

D. Scalable. Since diverse datasets accumulate over time, the tool is able to easily absorb additional data. With the current design of the tool, it is possible to have up to 12 servers capable of storing and querying data simultaneously (i.e. in a parallel way), allowing users to add more servers according to their current needs and the existing volume of data.

E. High-performance. Since a large amount of marine datasets is accessed and queried by many users across different sites and is displayed on local screens as 3D graphics, high computing power is required. Consequently, the tool had been implemented in a way that ensures high performance and usability through the use of Java 3D because of its optimization towards real-time 3D rendering and ability to take advantage of native graphics hardware.

To build all the features mentioned above, the following components have been employed: under a distributed and heterogeneous environment, Java was the natural choice as the programming language, since it is simple, distributed, portable and multithreaded (Gosling, 1995), and thus very suited to implement the logical layer of the tool. Swing and Java 3D were used to develop the user interface, i.e. the presentation layer of the tool. For the persistence layer, MySQL was chosen because of its well proven scalability, flexibility and high performance. The connection layer, between the client and the server, was assured by Java Database Connectivity (JDBC), the industry standard for connectivity between the Java programming language and a wide range of databases. All components are open source and available in the public domain.

#### Functionality

The tool's functionality has been divided into four steps (Fig. 1), each performing a well-defined task. Such modularization of the functionality helps the user utilizing the tool, leading him step-by-step through the analysis process.

A. Transformation/standardization. Usually, marine datasets are collected from heterogeneous sources


Fig. 1 The data flow through the tool's four-stage functionality

(e.g. remote sensing or electronic sensors) and represented in a variety of different formats. Therefore, the first step is to represent these marine datasets in a standardized format using XML. One of the major benefits of using XML is based on its capability to represent not only data itself but also the nature and structure of that data (metadata). This combination of data and metadata in the same file means XML has considerable advantages (e.g. data quality control or data formatting errors) over traditional data structures (Good, 2005). Marine datasets in any format may be transformed and imported into the system, as long as they contain information about the latitude, longitude, depth, the value of the attribute measured (e.g. salinity, temperature, etc.) and the date of the measurements. For each existing marine dataset, the equivalent in XML is generated with the help of tools especially developed for this purpose, some of them freely available in the public domain. Such tools are easy to use and guide the user



Fig. 2 Example of a 3D graphics showing results from a query of multiple variables

during the transformation process without requiring in-depth knowledge about XML.

B. Import. After the datasets have been transformed into XML, they are imported into the underlying MySQL database. The import process is automated and the user just needs to select the relevant XML files that will be checked for their validity, in terms of structure and range of values, through the use of an XML schema definition (XSD).

C. Selection. Having populated the database, the user may perform queries and apply criteria in order to select the data subsets of interest (e.g. where are the areas were a specific fish species was captured with a weight greater than 1.5 kg and the temperature of the water was below 17°C, during 2006) and save the selection results in his computer.

D. Visualization. Finally, after having performed a certain query, the user may visualize the query result in 3D graphics (Fig. 2). The user can manipulate the 3D display by standard visualization capabilities (e.g. rotation, pan and zoom in/out) but also perform more advanced operations, like navigating through time when displaying the graphics or create an animation (movie) from the sequence of graphics.

## Conclusion

This tool merges expertise from computer and marine sciences (i.e. bioinformatics) in order to facilitate the understanding of the ever-changing marine world through the manipulation and visualization of a high variety of 4D marine datasets (latitude, longitude, depth and time). Targeting users in the marine biology domain, the system aims to facilitate biological questions, such as where optimum living environmental conditions for a species are located or where certain productivity-enhancing ocean processes occur. After a period of evaluation and feedback by end-users, their suggestions will be implemented towards the improvement of the tool. In addition, future work will include the enabling of the tool for web-based usage (as a Java applet) or the embedding of the Web Feature Service standard of the Open Geospatial Consortium. The tool is freely distributed through the following website: http://arch.her.hcmr.gr.

Acknowledgements The development of this GIS-based tool was supported by the Sixth Framework Programme of the European Union through the Marie Curie Action ECOSUMMER. We thank the two referees that greatly improved earlier versions with constructive comments.

## References

- Campbell, B., P. Collins, H. Hadaway, N. Hedley & M. Stoermer, 2002. Web3D in ocean science learning environments: Virtual big beef creek. In Wagner, M. G., K. S. Candan & M. T. Beitler (eds), Proceedings of the Seventh International Conference on 3D Web Technology, Tempe Arizona: 85–91.
- Chen, S. C., X. Wang, N. Rishe & M. A. Weiss, 2004. A webbased spatial data access system using semantic R-trees. Information Sciences 167: 41–61.
- Dunbar, M., 2003. 3D visualization for the analysis of forest cover change. Proceedings of the ISPRS Commission IV Joint Workshop on Challenges in Geospatial Analysis, Integration and Visualization, Stuttgart, Germany.
- Good, J., 2005. The benefits and practicalities of using extensible markup language (XML) for the interfacing and

control of object-oriented simulations. In Zerger, A. & R. M. Argent (eds), MODSIM 2005 International Congress on Modelling and Simulation. Modelling and Simulation Society of Australia and New Zealand: 655–661.

- Gosling, J., 1995. Java: An Overview. Sun Microsystems. http://research.sun.com/features/tenyears/volcd/papers/ 7Gosling.pdf. Accessed 12-04-2008.
- Grunwald, S. & P. Barak, 2003. 3D geographic reconstruction and visualization techniques applied to land resource management. Transactions in GIS 7: 231–241.
- Jasnoch, U., V. Coors & U. Kretschmer, 2001. Virtual tourist guide. GIM International 15: 39–41.
- Kinshuk, H. H., N. Albi, A. Patel & C. Jesshope, 2001. Clientserver architecture based integrated system for education at a distance. In Ruokamo, H., O. Nykanen, S. Pohjolainen & P. Hietala (eds), Intelligent Computer and Communications Technology—Learning in On-line Communities. Proceedings of the Tenth International PEG Conference, Tampere University of Technology: 57–61.
- McCann, M., 2002. Creating 3D oceanographic data visualizations for the web. In Wagner, M. G., K. S. Candan & M. T. Beitler (eds), Proceedings of the Seventh International Conference on 3D Web Technology, Tempe Arizona: 179–184.
- Moore, R., C. Baru, R. Marciano, A. Rajasekar & M. Wan, 1998. Data-intensive computing. In Foster, I. & C. Kesselman (eds), The Grid: Blueprint for a Future Computing Infrastructure. Morgan Kaufmann Publishers, San Francisco: 105–129.
- Preece, J., Y. Rogers, H. Sharp, D. Benyon, S. Holland & T. Carey, 1994. Human-computer Interaction. Addison-Wesley, Wokingham, UK.
- Schonhage, B., A. van Ballegooij & A. Eliens, 2000. 3D gadgets for business process visualization—A case study. Proceedings of the Fifth Symposium on Virtual Reality Modeling Language (Web3D-VRML). Monterey California: 131–138.
- Su, S. & Y. Sheng, 1999. Visualizing upwelling at Monterey bay in an integrated environment of GIS and scientific visualization. Marine Geodesy 22: 93–103.
- Su, Y., J. Slottow & A. Mozes, 2000. Distributing proprietary geographic data on the world wide web: UCLA GIS database and map server. Computers and Geosciences 26: 741–749.