

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

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**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

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

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Essential Fish Habitat Mapping in the Mediterranean

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## 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., 2001; Le Pape et al., 2003; 2007 and Valavanis 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.

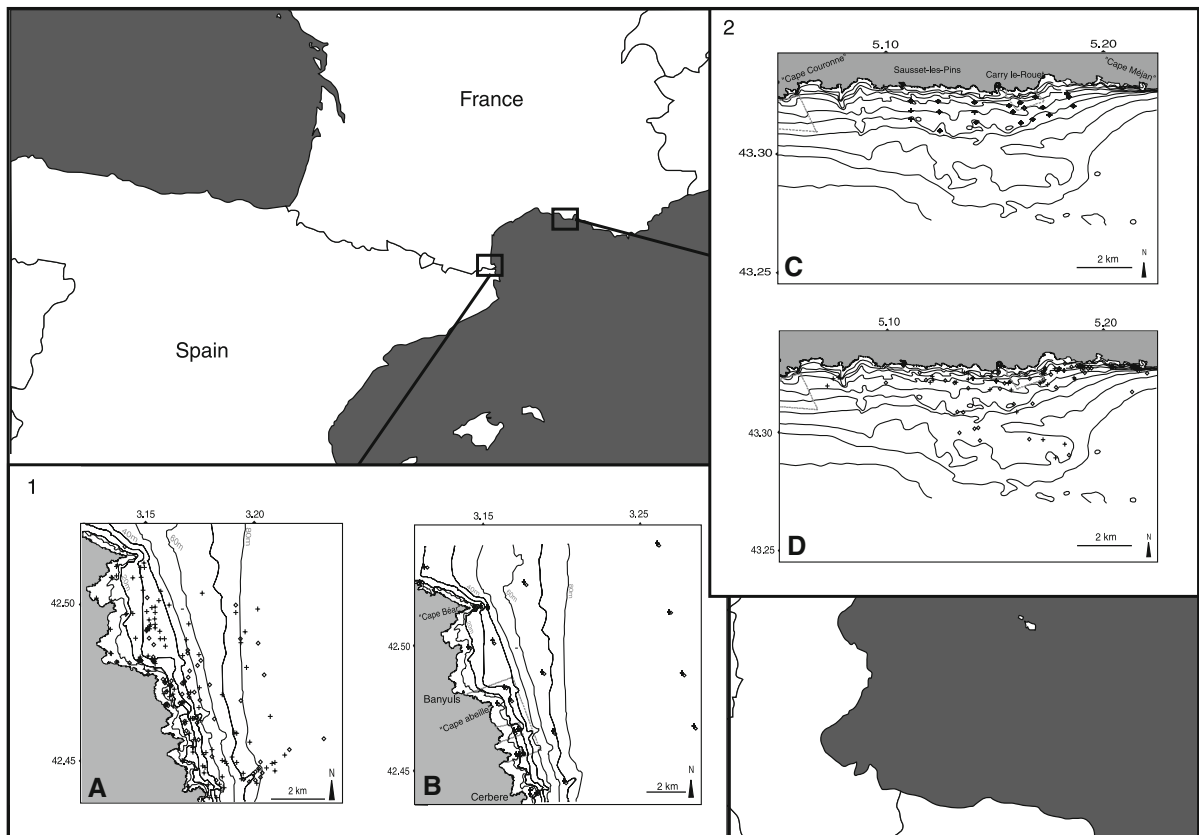
## Materials and methods

### Study area

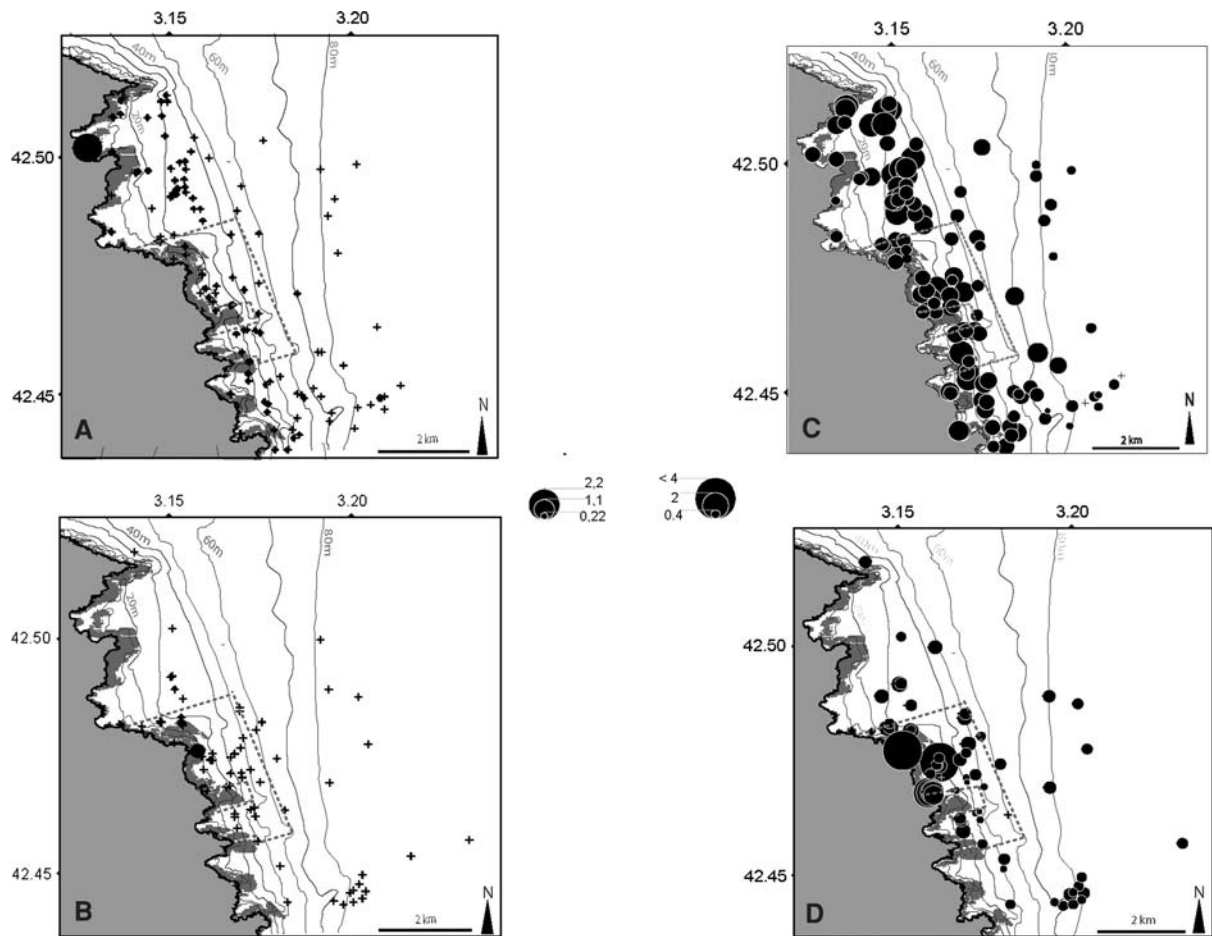
**Marine Reserve of Cerbère-Banyuls (France):** Established in 1974, the Marine Reserve of Cerbère-Banyuls (MRCB) extends over 1.85 square nautical miles, of which 0.185 square nautical miles are no-take (Fig. 1-1B). Adult fish community has been studied for over 20 years (since Bell, 1983). The area 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 no-take 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 (o)



**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  $\mu\text{m}$  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 ichthyoplankton 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/m <sup>2</sup> /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
<i>Posidonia</i> 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 Akaike'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  $17.446 \pm 3.769^\circ\text{C}$  and  $19.097 \pm 3.353^\circ\text{C}$ , and high values of Chl-a concentration (between  $0.393 \pm 0.191 \text{ mg/m}^3$  and  $0.674 \pm 0.681 \text{ mg/m}^3$ ), high values of PAR (between  $48.817 \pm 11.420$  and  $52.279 \pm 9.269$ ) and mostly negative values of SLA (between  $-4.078 \pm 2.919 \text{ cm}$  and  $-2.355 \pm 2.026 \text{ cm}$ ) indicating anticyclonic eddies (e.g. convergence area).

In summer, SST is higher and more variable between  $20.442 \pm 2.321^\circ\text{C}$  and  $24.751 \pm 1.964^\circ\text{C}$ , 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  $2.615 \pm 2.920 \text{ cm}$  and  $3.440 \pm 2.364 \text{ cm}$ ) 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-A		PAR		SLA		IPUE of sparids		IPUE of Scorpaenids	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
MRCB	Spring	17.856	$\pm 3.363$	0.431	$\pm 0.185$	48.817	$\pm 11.420$	-2.355	$\pm 2.026$	1.685	$\pm 2.625$	0.067	$\pm 0.235$
	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	$\pm 9.269$	-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	$\pm 7.169$	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		PAR		SLA		Density of Sparids		Density of 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	±65.000	0.119	±0.700
	Summer	24.751	±1.964	0.174	±0.049	54.492	±4.011	2.850	±2.365	92.931	±606.893	1.627	±0.889
CBMP	Spring	19.097	±3.353	0.393	±0.19	52.1	±7.348	-2.95	±3.23	21.128	±31.743	0.184	±0.559
	Summer	23.972	±2.451	0.248	±0.18	55.15	±3.9	2.631	±2.15	3.171	±5.107	0.657	±1.559

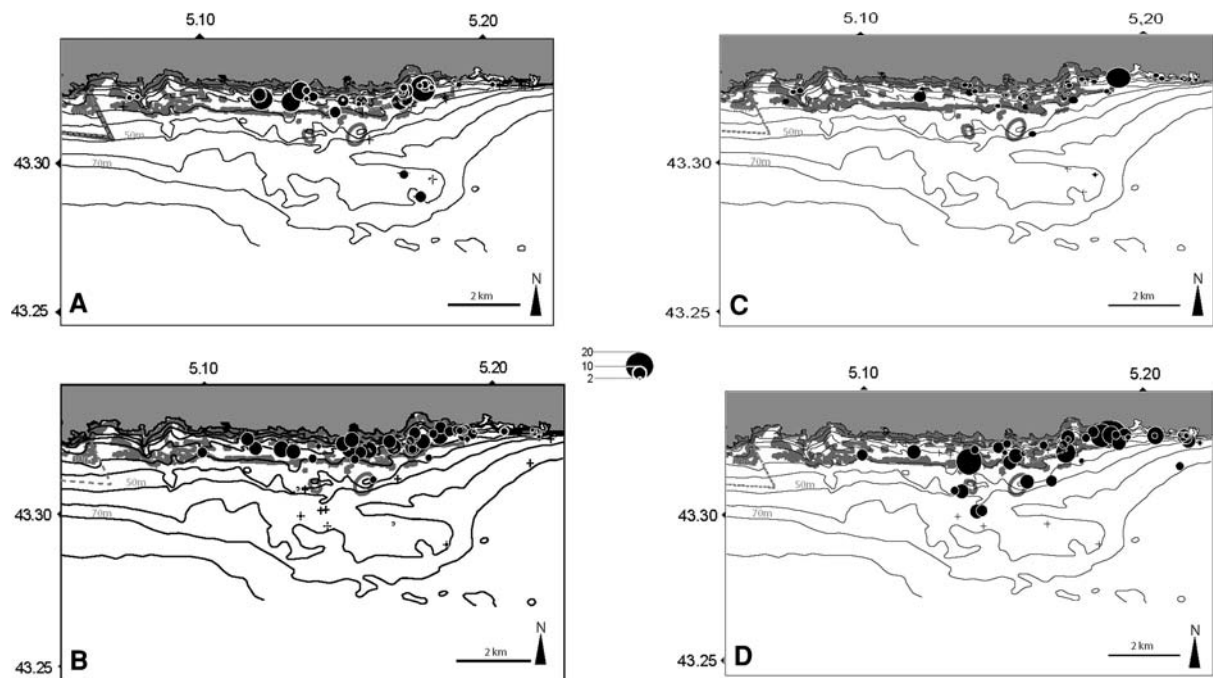
Mean and SD were calculated from data resulting from Larvae sampling effort

### 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 “l’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)

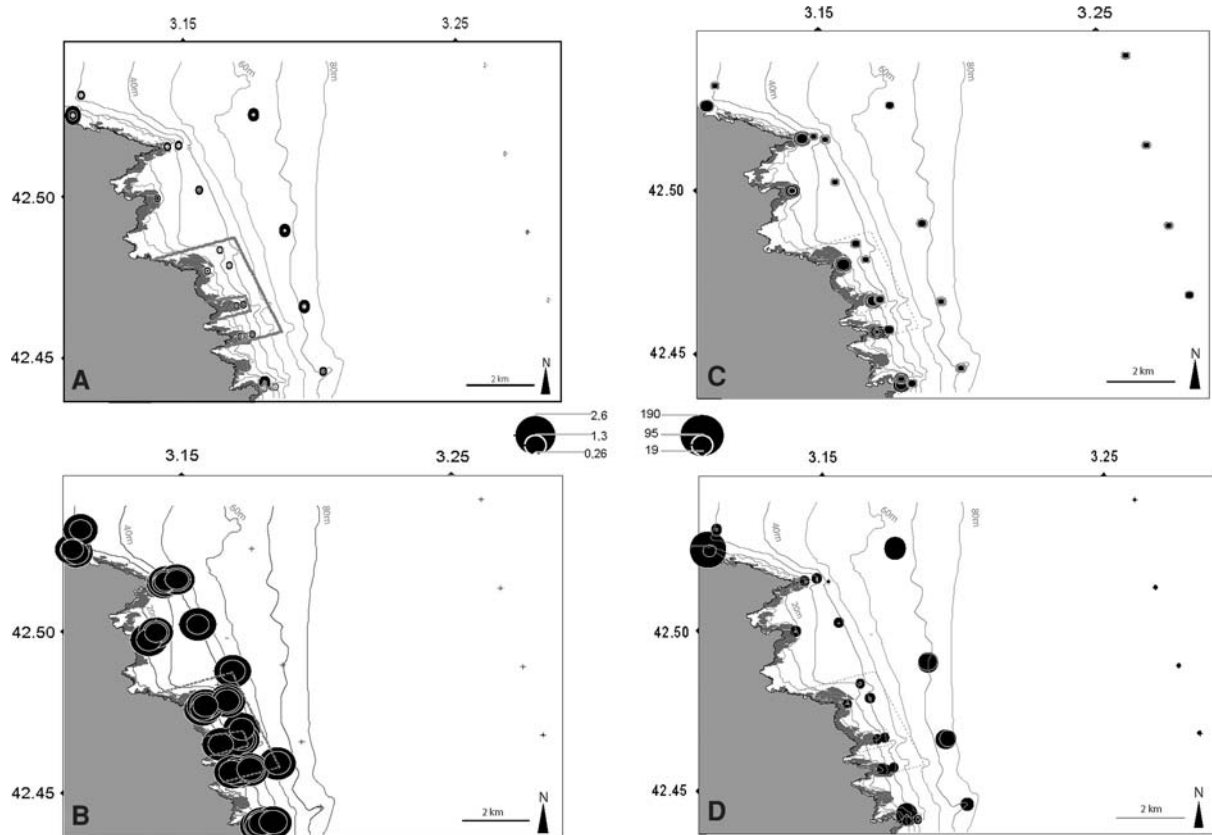
9.768). A density gradient was observed between the coastal station, middle shore and off-shore stations (Fig. 3C, D).

### Larval stage

Scorpaenids larvae were caught in both areas and periods. In MRCB, mean larval density was greater in summer ( $1.627 \pm 0.889$  larvae/1000 m<sup>3</sup>) than in spring ( $0.119 \pm 0.700$  larvae/1000 m<sup>3</sup>). 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 ( $0.657 \pm 1.559$  larvae/1000 m<sup>3</sup>). As in MRCB, larvae were more abundant in coastal stations than offshore (Fig. 5A, B).

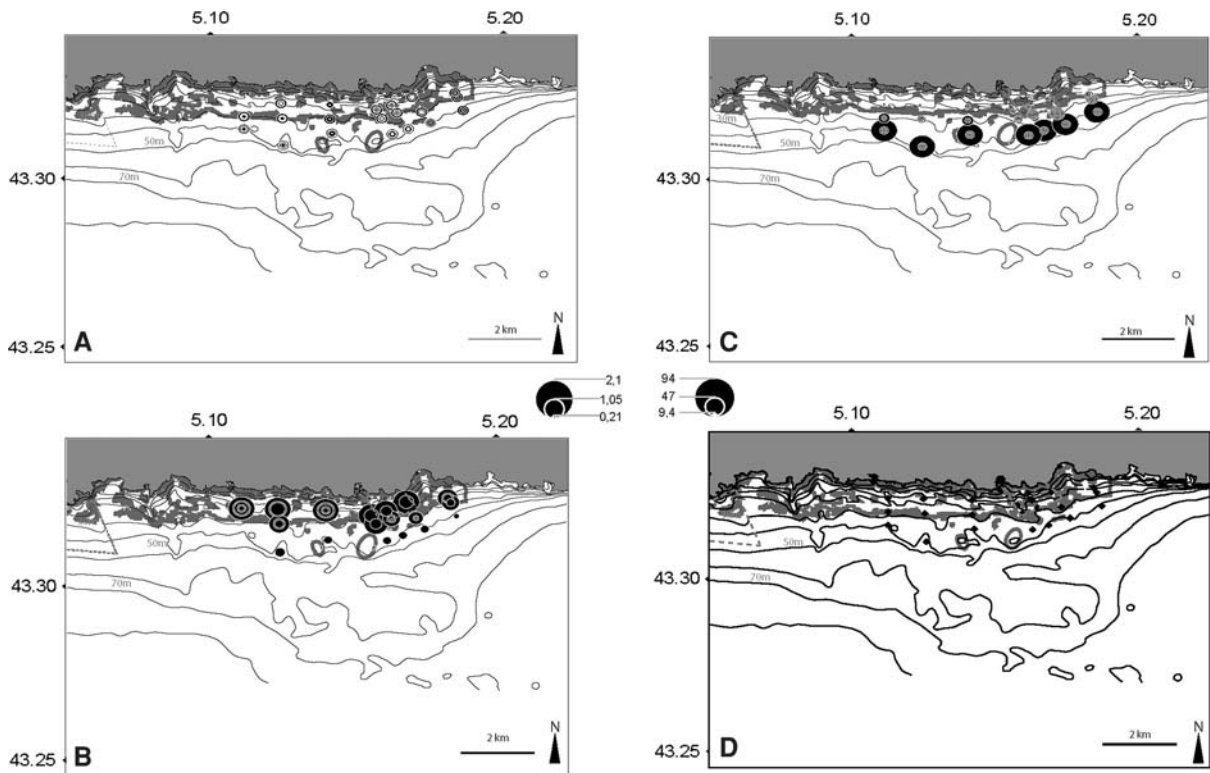
Sparid larvae were caught in both areas and periods. In MRCB, mean larval density was greater in summer ( $92.931 \pm 606.893$  larvae/1000 m<sup>3</sup>) than in spring ( $27.956 \pm 65.000$  larvae/1000 m<sup>3</sup>). Larvae were more abundant in coastal stations than offshore even if substantial 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 ( $21.128 \pm 31.743$  larvae/1000 m<sup>3</sup>) than in summer ( $3.171 \pm 5.107$  larvae/1000 m<sup>3</sup>). 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

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

### 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%).

### 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

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

Stage	Location	Data type	Season	Variables ( <i>P</i> -value)	Deviance explained	<i>N</i>
Adult	MRCB + CBMP	P/A		s(PAR) (<0.05) + s(POS) (<0.01) + s( <b>CHL-A</b> ) ( <b>0.84</b> ) + s(SLA) (<0.05)	18.4%	316
	MRCB	IPUE	Spring	s(PAR) (<0.01) + s( <b>DEP</b> ) ( <b>0.071</b> )	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( <b>SST</b> ) ( <b>0.077</b> ) + s( <b>CHL-A</b> ) ( <b>0.152</b> ) + s( <b>SLA</b> ) ( <b>0.083</b> )	51.4%	71
	Larvae	MRCB + CBMP	P/A		s(SLA) (<0.01) + s(ROC) (<0.01) + s(CHL-A w) (<0.01)	14.1%
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

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

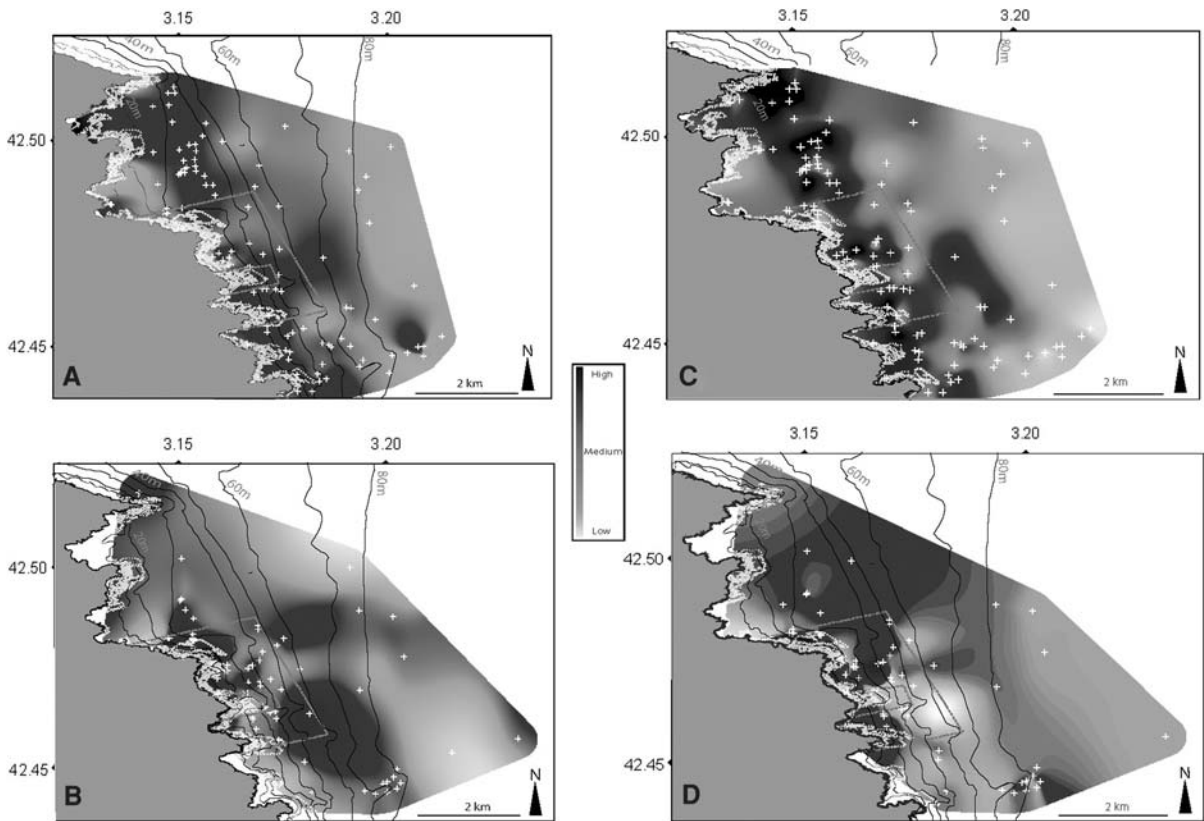
Stage	Location	Data type	Season	Variables ( <i>P</i> -value)	Deviance explained	<i>N</i>
Adult	MRCB + CBMP	P/A		s( <b>POS</b> ) ( <b>0.058</b> ) + s(SAN) (<0.05) + s(SLA) (<0.01) + s( <b>DEP</b> ) (<0.01)	29.8%	316
	MRCB	IPUE	Spring	s(POS) (<0.01) + s( <b>ROC</b> ) ( <b>0.146</b> ) + s( <b>DEP</b> ) (<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( <b>DEP</b> ) (<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%
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( <b>PAR</b> ) ( <b>0.078</b> )	11.4%	125
			Summer	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°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).

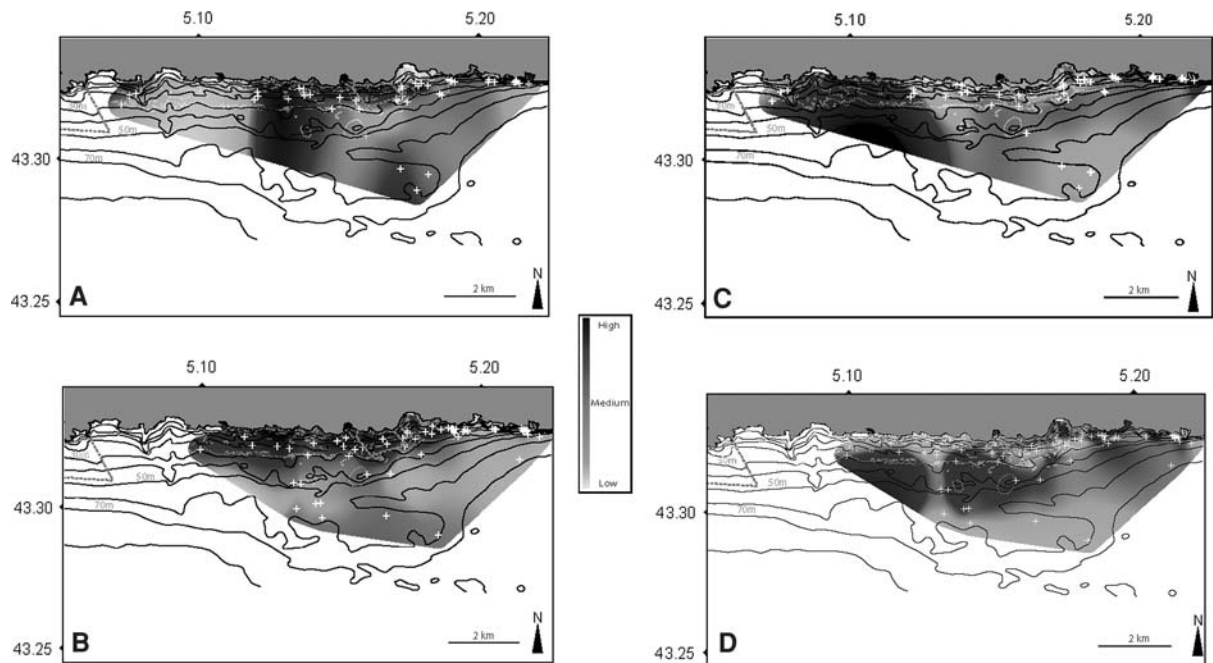
#### Larval habitat

In MRCB, sparids larval models explained between 58.4% and 69.6% of deviance (Table 4) with a positive correlation with SST ( $13^{\circ}\text{C} < \text{TV} < 15^{\circ}\text{C}$  and  $\text{TV} > 19^{\circ}\text{C}$ ), Chl-a concentration (negative Slope,  $\text{TV} = 0.48 \text{ mg/m}^3$ ) (Table 6) and the percentage of sand (negative Slope,  $\text{TV} = 80\%$ ) in spring. The summer situation was explained by the distribution of Chl-a concentration (positive slope,  $\text{TV} = 0.18 \text{ mg/m}^3$ ), SLA (positive Slope,  $\text{TV} = 1.5 \text{ cm}$ ), percentage of sand (positive Slope,  $\text{TV} = 75\%$ ) and SST (positive Slope,  $\text{TV} = 23^{\circ}\text{C}$ ). 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,  $\text{TV} = 57$ ). 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  $0.18 \text{ mg/m}^3$ , 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.

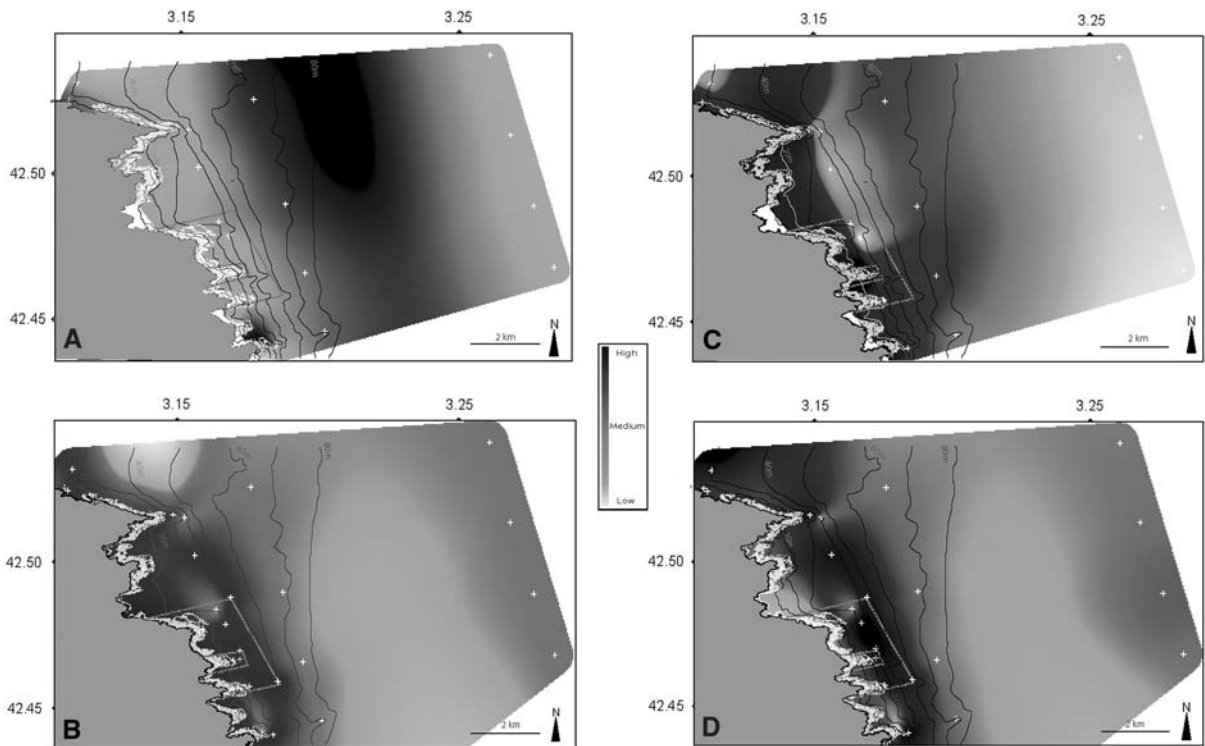
### Habitat characterisation

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

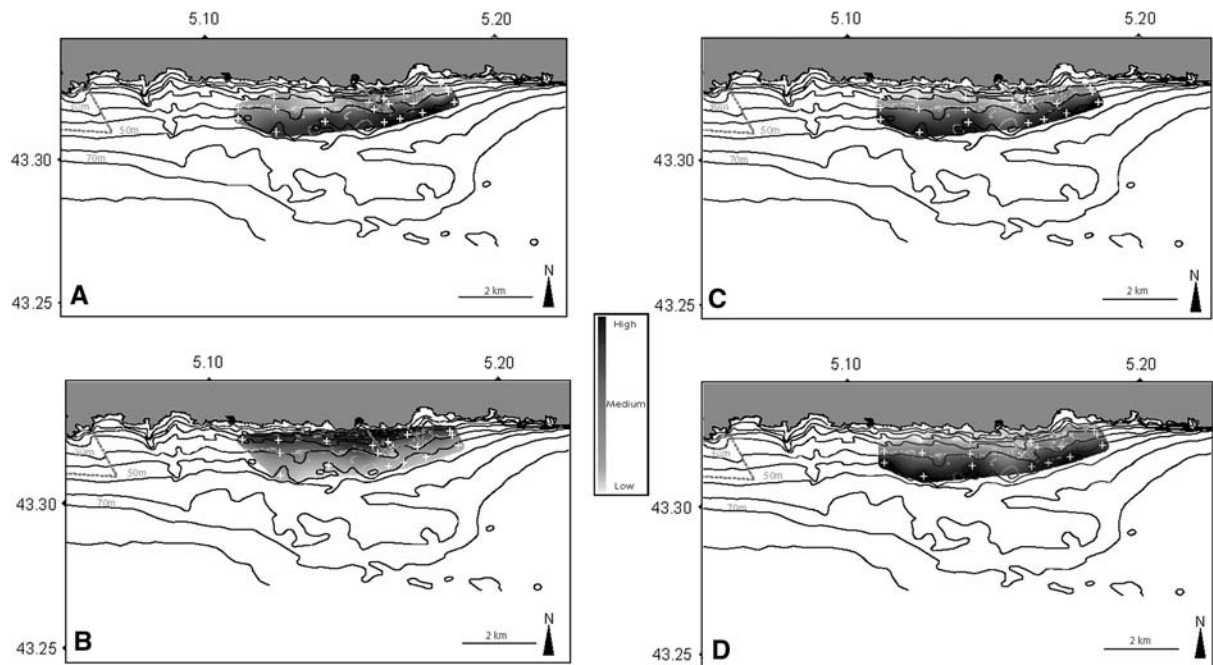


**Fig. 8** Suitable habitats in *Marine Reserve of Cerbère-Banyuls* for sparid larvae (A and B) and scorpaenids larvae (C and D), in spring (A and C) and in summer (B and D).

& 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

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 wind-driven 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** Trends and Threshold Value (TV) of variables resulting from GAM plot of model for each taxa, stage and area

Taxa	Stage	Data type	Location	Season	Variables	Trend	TV	Variables	Trend	TV	Variables	Trend	TV			
Sparidae	Adult	P/A	MRCB+CBMP		PAR	-	50	POS	-	20%	CHL-A	+	0.4 mg/ m <sup>3</sup> SLA			
			MRCB	SPR	PAR	-	40	DEP	±	30/45 m						
				SUM	POS	±	2/4%	CHL-A	+	0.34 mg/m <sup>3</sup>	SLA	+	3 cm SAN			
			CBMP	SPR	CHL-A	+	0.6 mg/m <sup>3</sup>	SLA	-	-2 cm				40%		
				SUM	SAN	+	30%	SST	-	19°C	CHL-A	+	0.4 mg/ m <sup>3</sup> SLA	+	2 cm	
		Larvae	P/A	MRCB+CBMP		SLA	±	-7/-2 cm	ROC	-	2%	CHL-A	-	0.3 mg/ m <sup>3</sup>		
Scorpaenidae		Density	MRCB	SPR	SST	±/+	13/15/19°C	CHL-A	-	0.48 mg/m <sup>3</sup>	SAN	-	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	-	57						
				SUM	SAN	+	45%									
		Adult	P/A	MRCB+CBMP		POS	+	20%	SAN	-	70%	SLA	±	-2/ 4 cm DEP	-	38 m
			IPUE	MRCB	SPR	POS	+	12%	ROC	-	5%	DEP	-	40 m		
Larvae				SUM	POS	+	3.5%	ROC	+	5%						
			CBMP	SPR	SST	+	21°C	POS	+	40%	PAR	+	60			
				SUM	DEP	-	25 m	PAR	+	52	POS	+	45%			
		P/A	MRCB+CBMP		CHL-A	-/+	0.3/0.6 mg/m <sup>3</sup>									
		Density	MRCB	SPR	CHL-A	+	0.55 mg/m <sup>3</sup>									
				SUM	CHL-A	-	0.18 mg/m <sup>3</sup>									
		CBMP	SPR	CHL-A	-	0.3	PAR	±	47/60							
			SUM	SLA	-	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 *Merluccius* 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 assess 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.

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## 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.
- Aleman, 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*. RAMOGE 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 sole *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.
- García-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.
- García-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.
- García-Charton, J. A., A. Perez-Ruzafa, P. Sanchez-Jerez, J. T. Bayle-Sempere, O. Renones & D. Moreno, 2004. Multi-scale spatial heterogeneity, habitat structure, and the effect of marine reserves on Western Mediterranean rocky reef fish assemblages. Marine Biology 144: 161–182.
- García-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'ichtyofaune 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. Cottonneq, 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. Gordo & 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. Scientia 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 Puellas, 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 non-linear 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. Flatfish-habitat 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.