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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

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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 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.*

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Essential Fish Habitat Mapping in the Mediterranean

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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 spatio-temporal 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

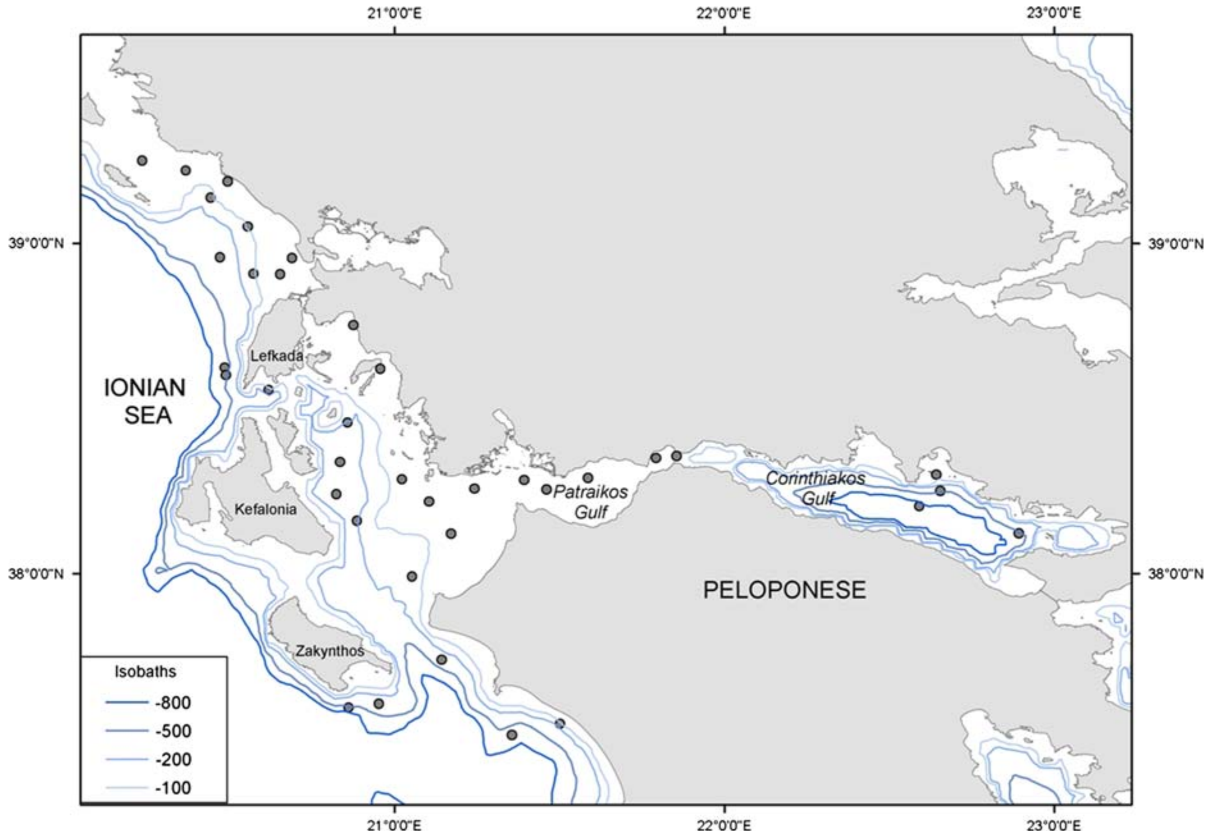


Fig. 1 Map of the area investigated showing the stations of MEDITS hauls in the Eastern Ionian Sea

(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 (~13.8°C) and salinity (~38.85 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 (~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^3) 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 (MEDITS). 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 common MEDITS 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^3) was downloaded through Ocean-color 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^2), 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^2) 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 inter-annual 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-at-maturity 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_{50} was also determined for males and females by year, using the logistic function (Fryer, 1991):

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

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_{50} can then be estimated from the following expression: $ML_{50} = \frac{v_1}{v_2}$. 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 (non-parametric 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_{50} estimates ranged

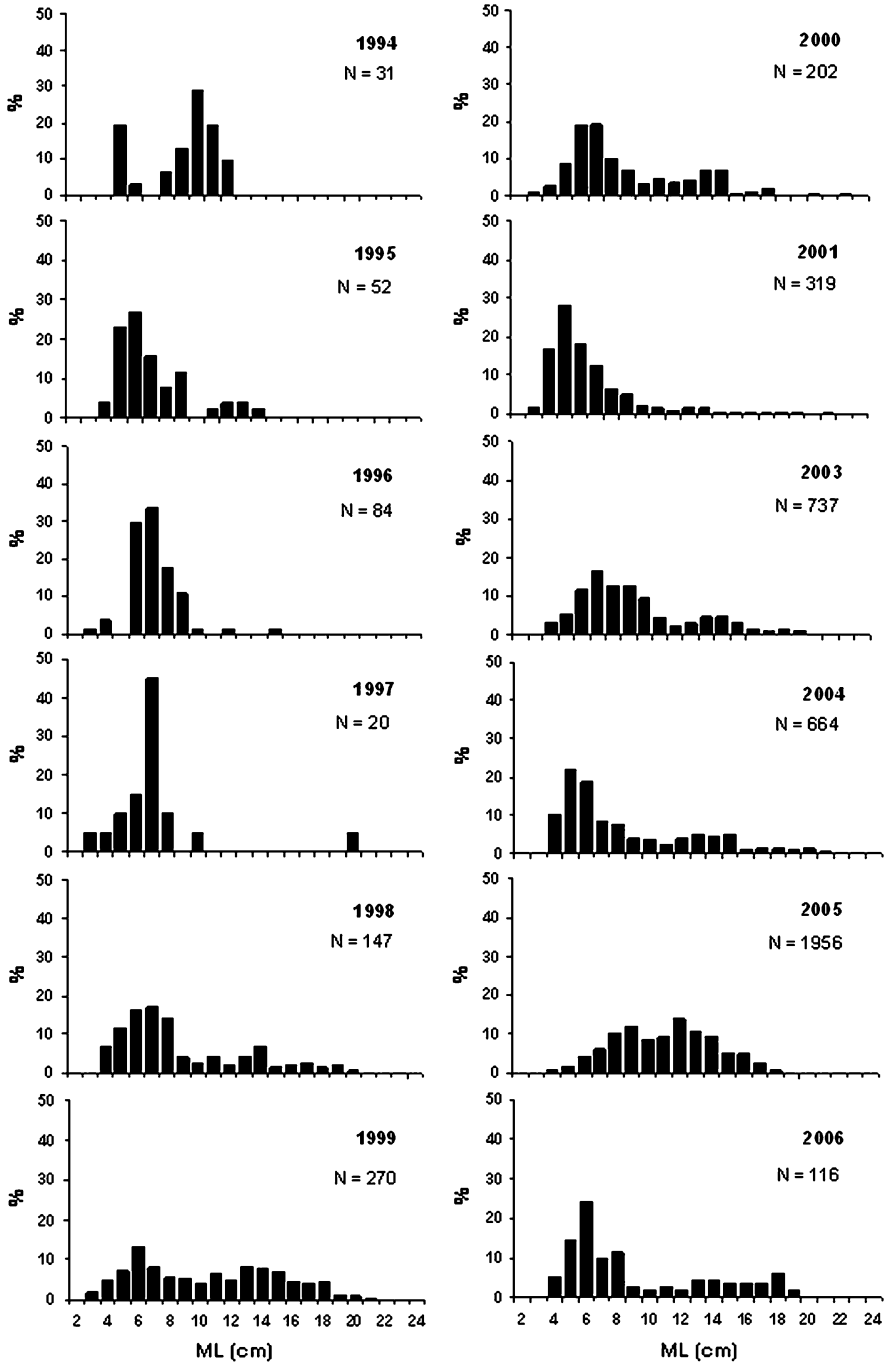


Fig. 2 Mantle length frequency distribution by year of MEDITS sampling in the Eastern Ionian Sea

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).

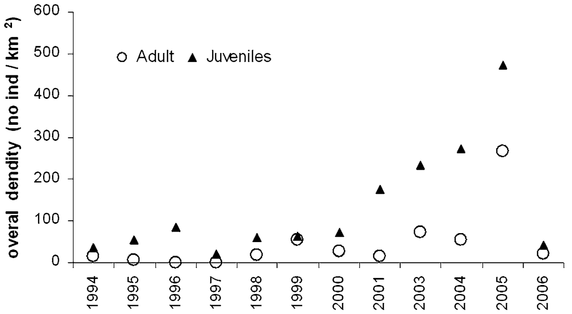


Fig. 3 Standardized in density estimates (in number of individuals per km^2) of *Illex coindetii* juveniles (immature ML < 10 cm) and adults (ML > 10 cm), in the Eastern Ionian Sea 1994–2006

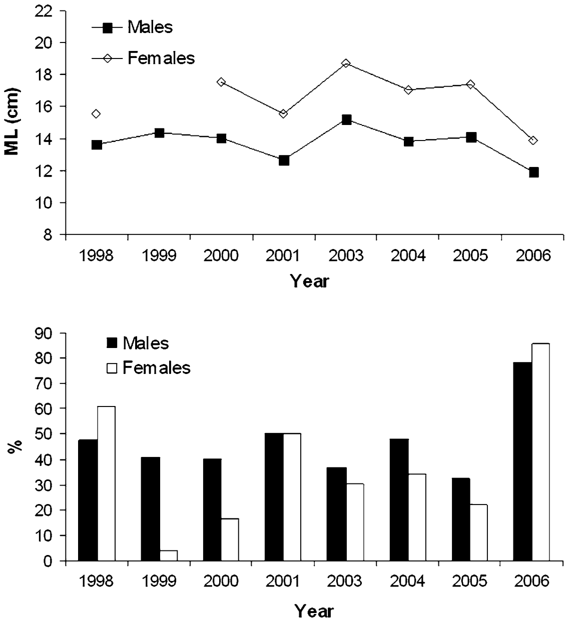


Fig. 4 Variation of ML_{50} (top) and percentage of matures among individuals with ML more than 10 cm (bottom), estimated for *Illex coindetii* males and females sampled during the MEDITS surveys 1998–2006

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

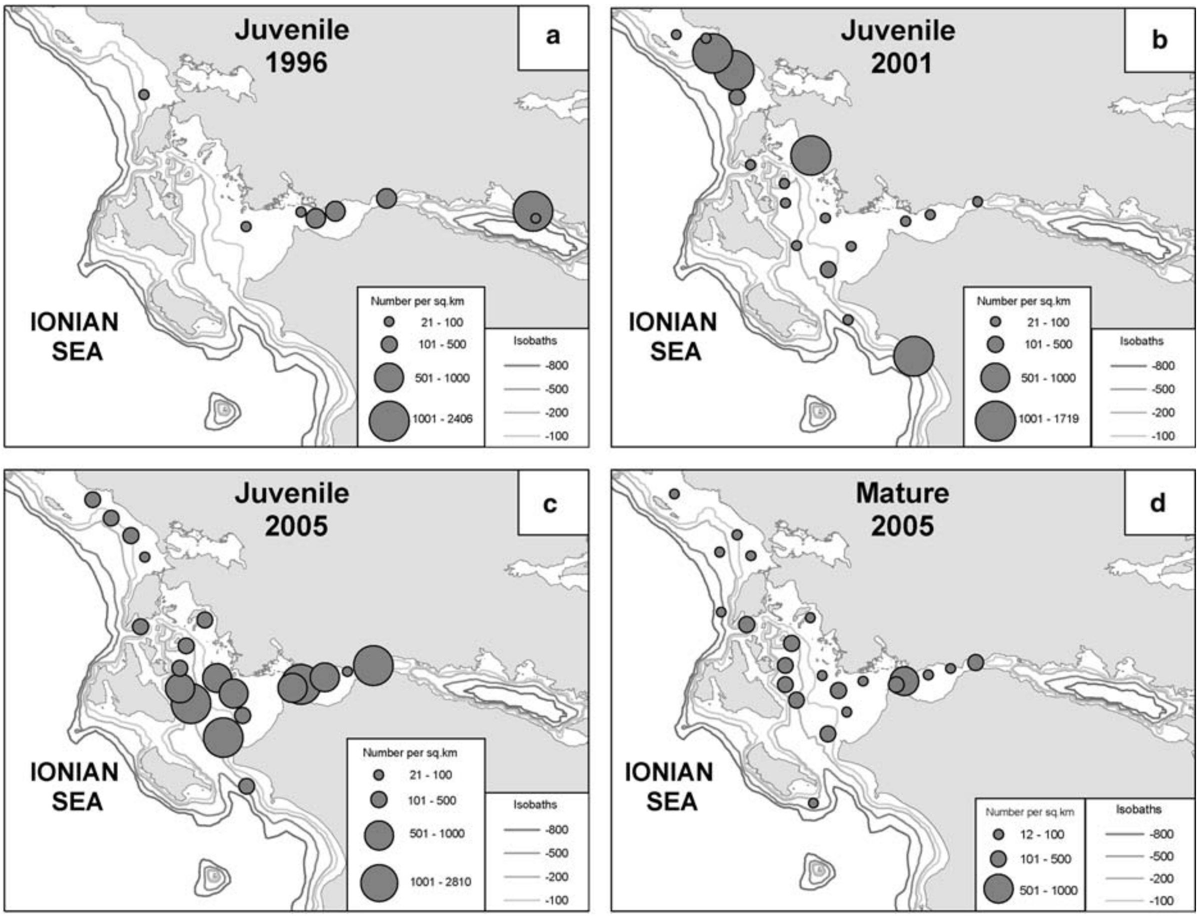


Fig. 5 Standardized catch data of *Illex coindetii* juveniles during MEDITS surveys of 1996 (**a**), 2001 (**b**), 2005 (**c**) and for mature individuals during 2005 survey (**d**), in the Eastern Ionian Sea

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′)

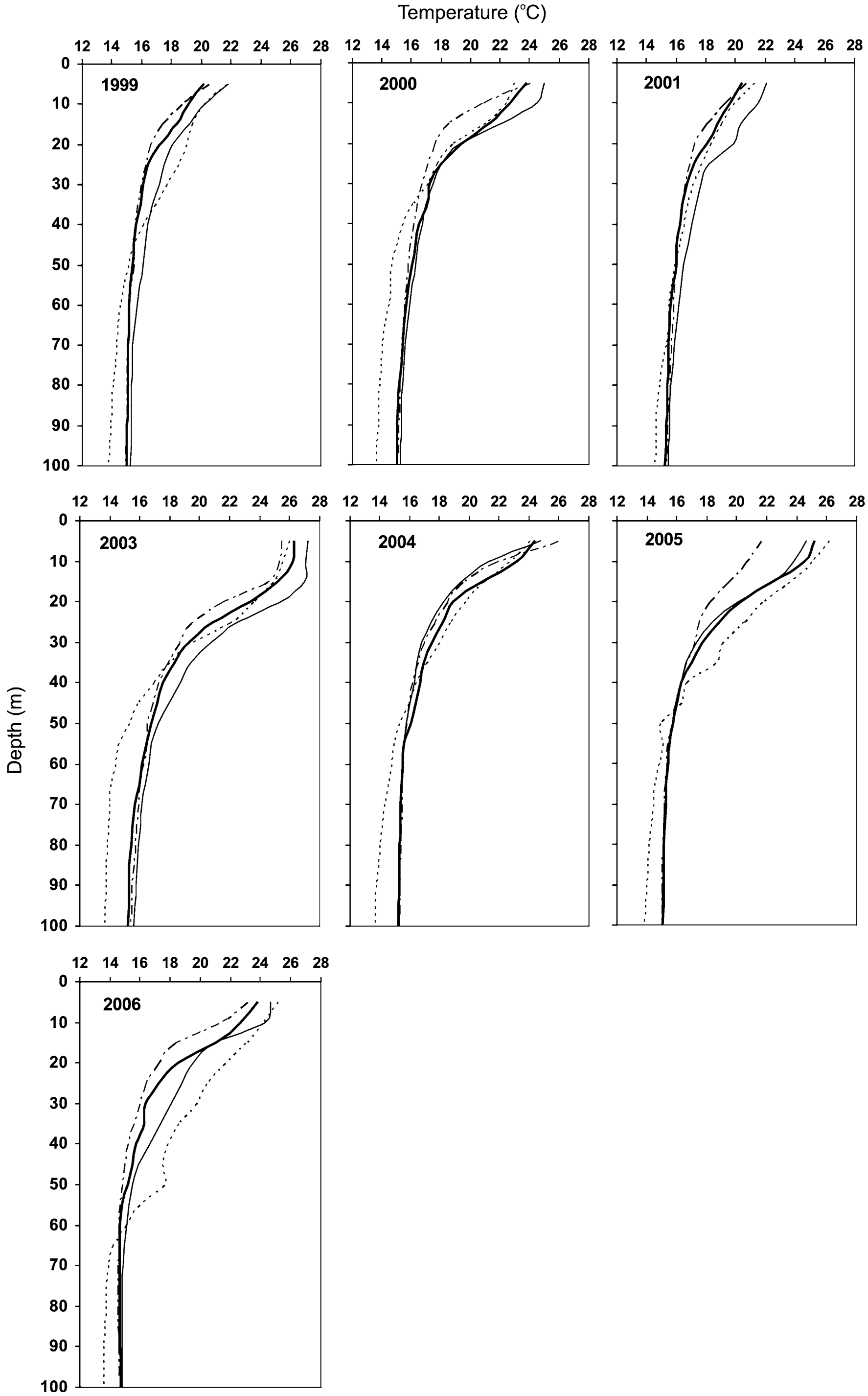


Table 2 Area under curve (AUC) estimates for GAM and MAXENT models for different *Illex coindetii* life stages

	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 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

Discussion

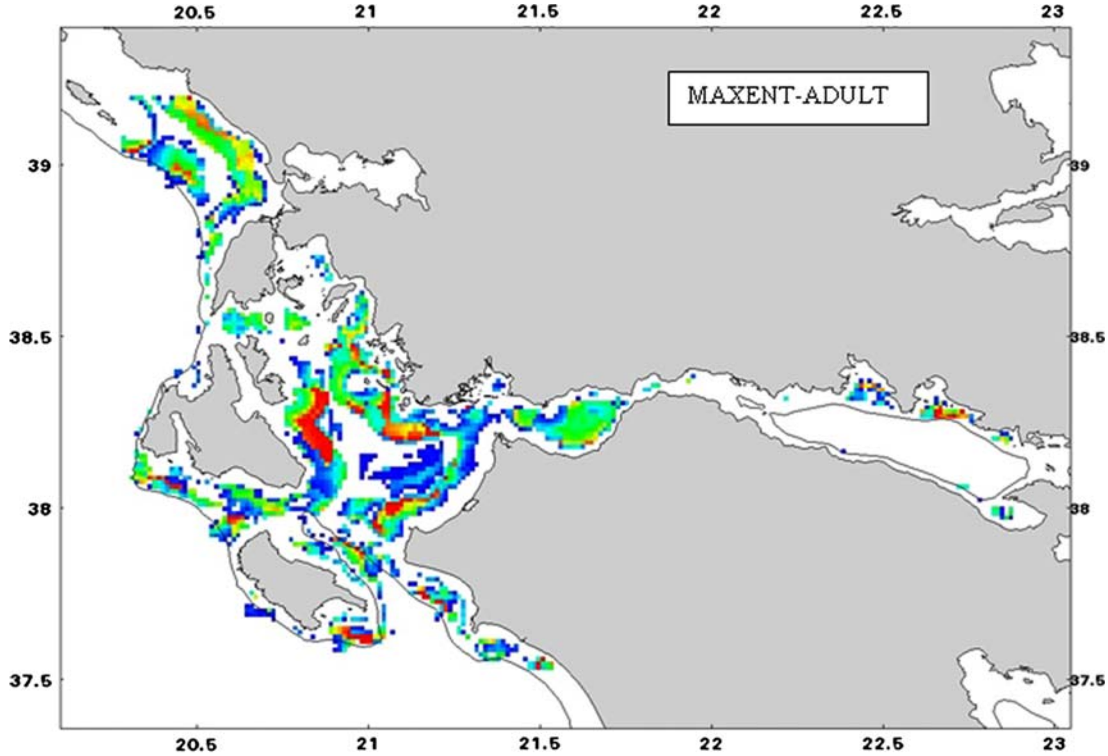
Variation in population structure and size-at-maturity

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 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	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



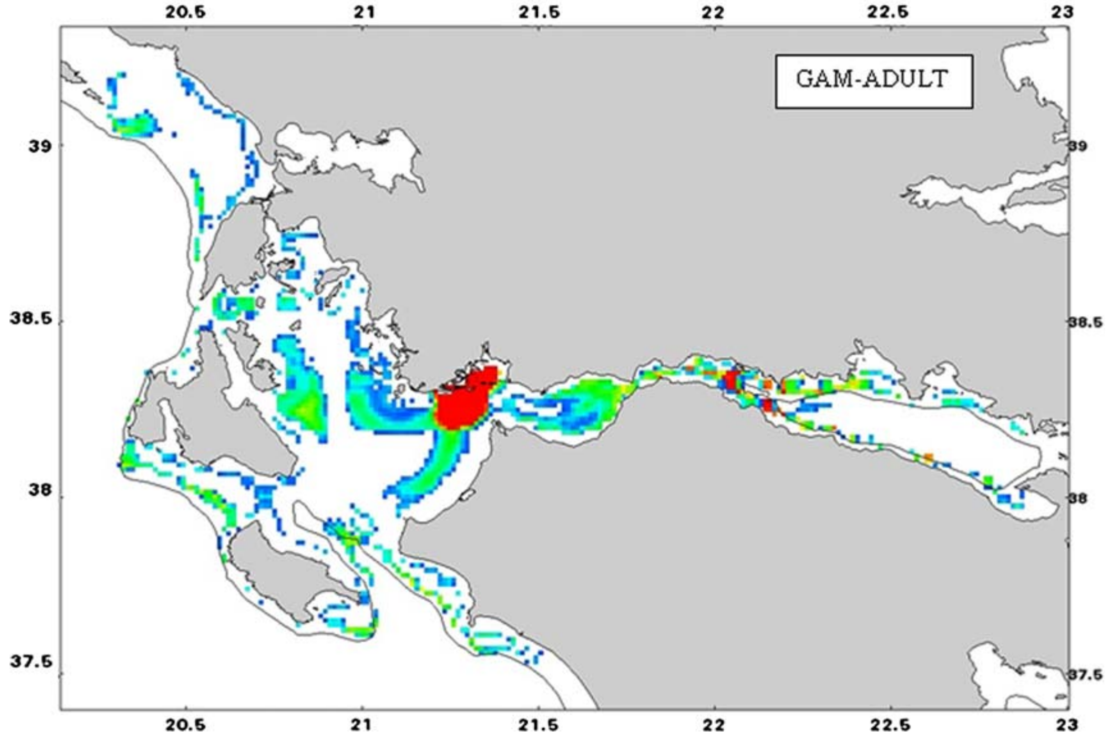


Fig. 7 General MAXENT (top) and GAM (bottom) probability map estimates for adult *Illex coindetii* using summer surveyed MEDITS data 1998–2006

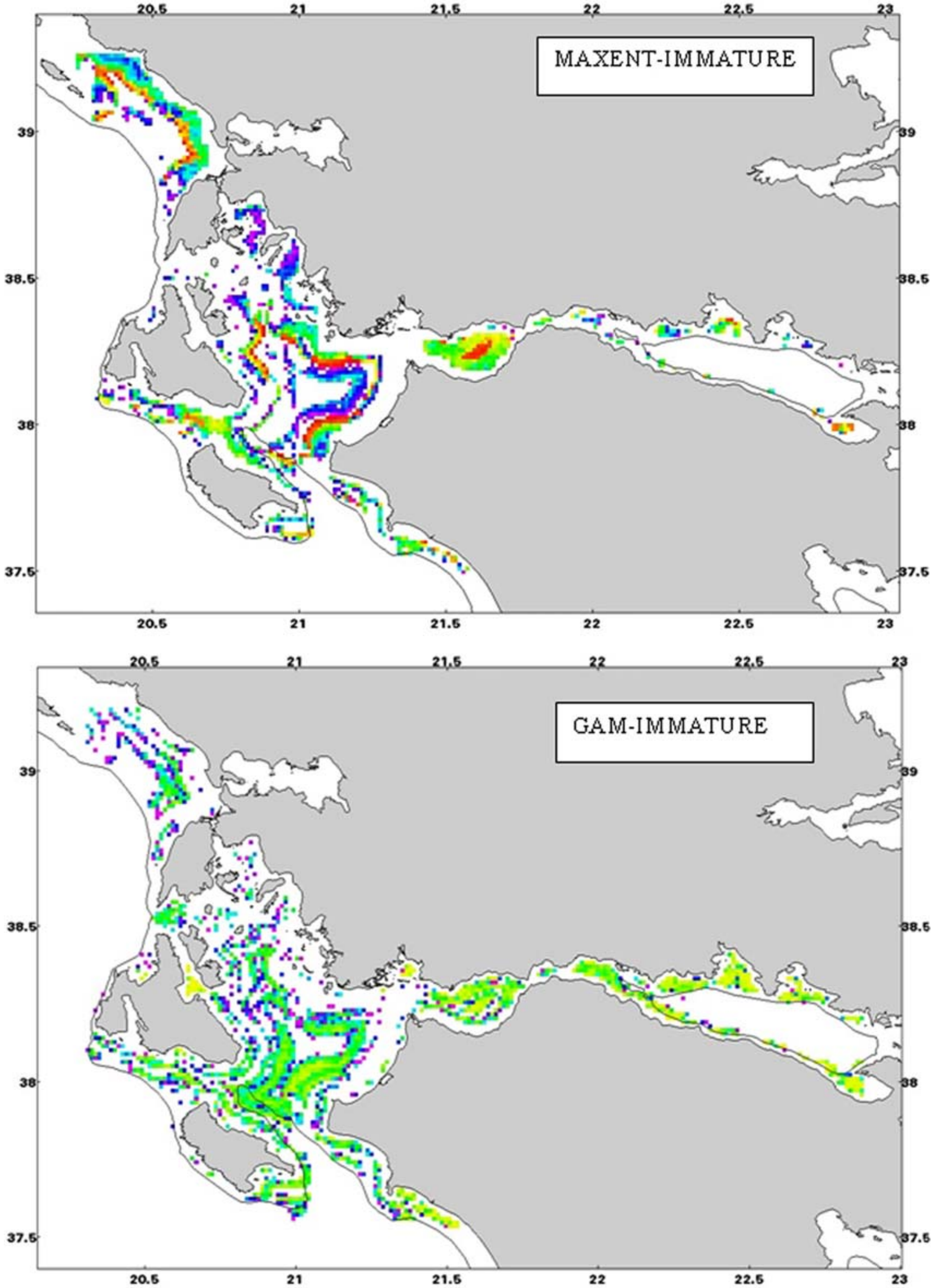


Fig. 8 General MAXENT (top) and GAM (bottom) probability map estimates for immature *Illex coindetii* using summer surveyed MEDITS data 1998–2006

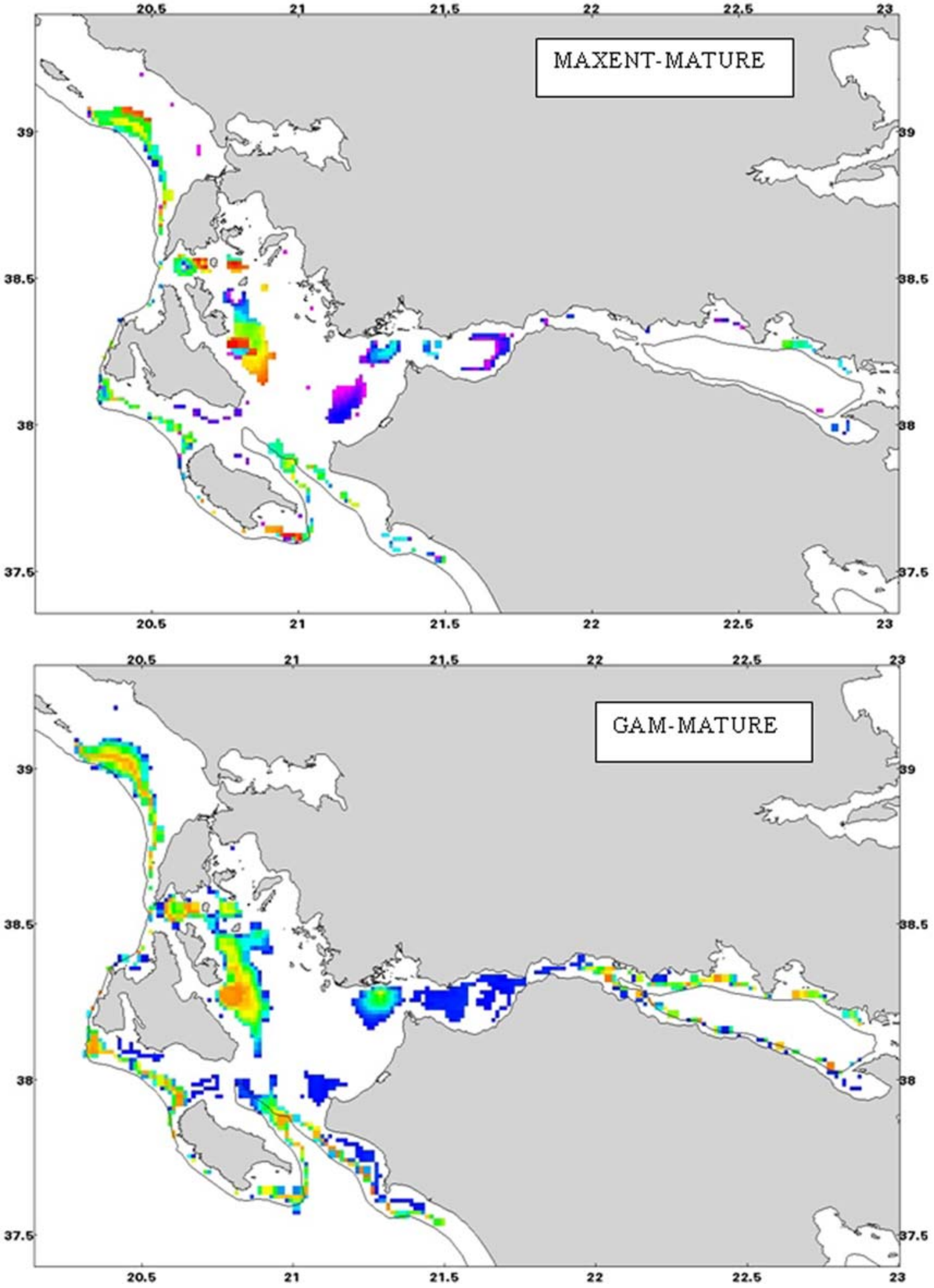


Fig. 9 General MAXENT (top) and GAM (bottom) probability map estimates for mature *Illex coindetii* using summer surveyed MEDITS data 1998–2006

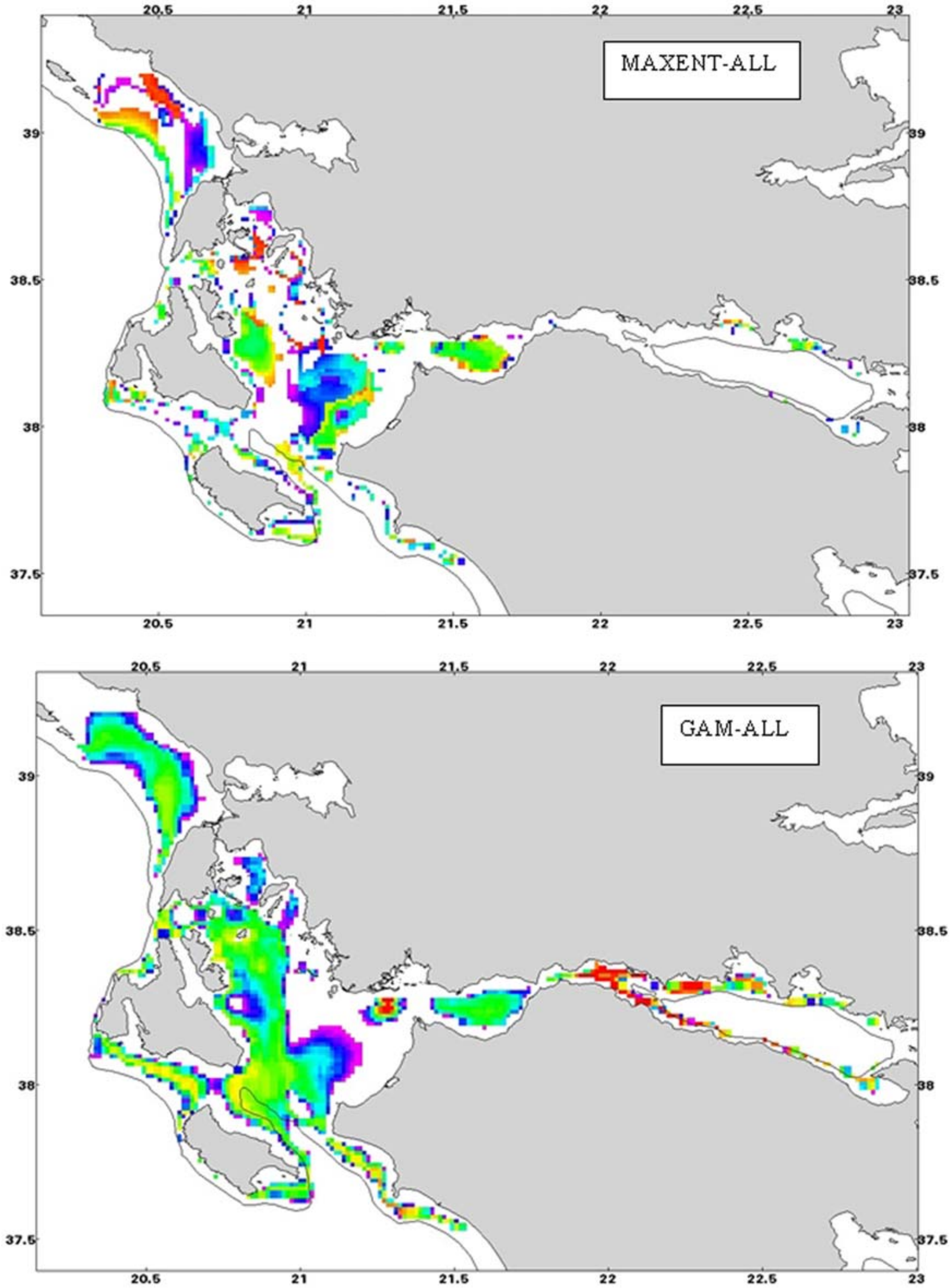


Fig. 10 General MAXENT (top) and GAM (bottom) probability map estimates for both juvenile and adults (including mature) *Illex coindetii* using summer surveyed MEDITS data 1998–2006

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 age-at-maturity. The interranual variability of $ML_{50,}$ 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_{50} 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.

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