

Mesoscale spatio-temporal dynamics of demersal assemblages of the Eastern Ionian Sea in relationship with natural and fisheries factors[★]

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Abstract – Data from the MEDITS bottom trawl surveys in the Eastern Ionian Sea, covering a depth range of 28 to 845 m were analysed for the period 1998–2008. For each trawling location, environmental and geographical parameters were recorded, while biomass, abundance, biodiversity and size-based metrics were estimated for the total megafaunal community, as well as for four taxonomic sub-communities (Osteichthyes, Chondrichthyes, Crustacea and Cephalopoda) which were expected to respond differently to environmental changes and fishing. In addition, biomass and abundance of ten species selected based on commercial interest, depth range and life history traits were explored, with particular emphasis on deep-sea species. Fishing effort data collected during the study period were analysed and showed a decreasing trend, mainly due to a decrease in the activity of static nets. The relation between the estimated parameters and environmental and spatial factors, as well as temporal (interannual) effects and the effect of fishing effort were explored using generalized additive models (GAMs). Results of GAMs showed that depth and location explained much of the variation in community metrics, probably reflecting mesoscale spatial features and species/communities requirements. Even though the different communities and species exhibited variant patterns in bathymetric and spatial distribution, some common aggregation patterns in productive areas were identified. Despite the relatively short time series, GAMs were effective in detecting increasing trends for several metrics; taking into account spatial factors further contributed to attributing the remaining deviance to temporal effects. These trends were partly explained by the observed decline of fishing effort, which is further supported by the fact that negative relations between several metrics and fishing effort were identified, for some of the selected communities and populations. Abundance, species richness and maximum length proved the most informative metrics concerning the effect of fishing. The current decline in fishing effort in the area seems to be a move in the right direction and should be complemented by additional measures aiming to prevent allocation of effort towards the deep sea.

Keywords: Biodiversity / Fisheries impacts / Demersal community / Survey indicators / Temporal trends / Mediterranean Sea

1 Introduction

The need to evaluate the status of marine ecosystems, biological resources and the effect of environmental and anthropogenic factors has led to the development of numerous community metrics for use as important scientific and managerial tools (Rice 2000; Rochet and Trenkel 2003). However, the sensitivity of each indicator may vary with ecosystem and pressure type, thus metrics should be selected to best address the needs of each study (Rice 2003; Cury and Christensen 2005).

Biomass and abundance indices and their spatio-temporal patterns of distribution may reflect community productivity and are often used to examine fisheries-induced (Rochet and Trenkel 2003) and other anthropogenic changes. Although their usefulness for assessing fishing impacts is questionable, species diversity metrics remain widely used because of (i) the declarations of several organizations on the needs to conserve biodiversity and (ii) the debate on the dependence of ecosystem functions and stability on species diversity (Rochet and Trenkel 2003). In addition, size-based indicators (e.g., mean or maximum lengths, percentiles of the length frequency distribution) are analysed and monitored, mainly because they are sensitive to fishing mortality at population and community levels (Shin et al. 2005) and/or fisheries induced evolution towards

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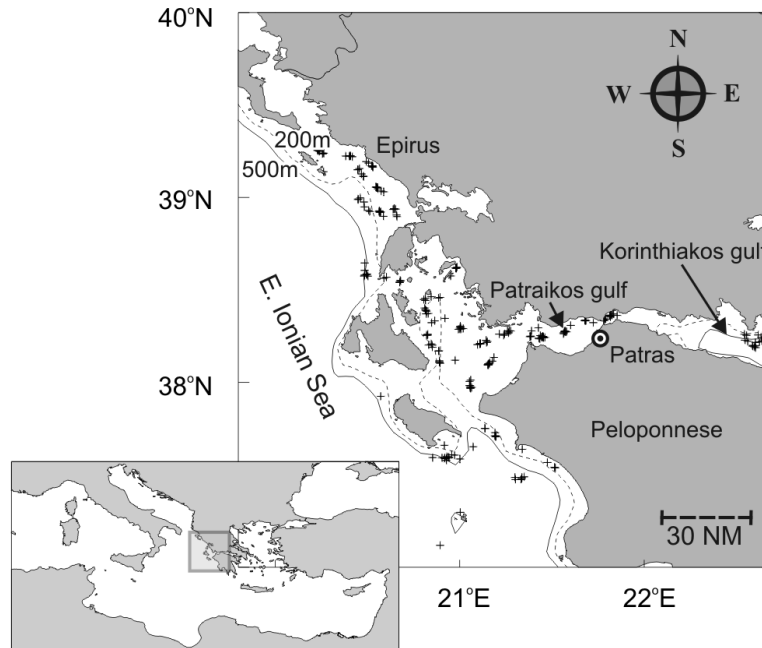


Fig. 1. Eastern Ionian Sea. Crosses indicate the positions of the MEDITS hauls. Isobaths are shown for 200 m (dashed line) and 500 m (solid line).

earlier reproduction (Law 2000). However, indirect effects through the food-web as well as environmental changes (e.g., eutrophication) may counteract the effect of fishing and thus the ability of such indices to detect fisheries effects (Rochet and Trenkel 2003). For example, the length distribution of the community is expected to be mostly related to the fishing effort; nevertheless it may also be sensitive to temporal recruitment variation. Thus, analysis of multiple indicators may be a better means of revealing the effects of fishing (Rice 2000). In addition, it can reveal patterns in species composition, relative abundance, distribution and migrations.

Spatial and bathymetric differences and patterns have been widely reported for the various metrics (e.g., Greenstreet and Hall 1996; Bianchi et al. 2000) and they mainly reflect species and/or life-stage preferences for specific habitats and environmental conditions (e.g., Rogers et al. 1999, Johnson et al. 2013) and, at the large scale, patterns in fishing pressure and/or productivity (Bianchi et al. 2000; Jennings et al. 2005). For example, in the Ionian Sea, differences in species distribution and abundance are evident both along the North/South and the West/North axes and were generally attributed to fishing activities, as well as hydrological characteristics (Politou et al. 2008a). Spatial patterns and depth gradients are also common in deep sea assemblages in terms of species composition, abundance and diversity (e.g., Gordon and Bergstad 1992; Koslow 1993; Lorance et al. 2002; Politou et al. 2003; D'Onghia et al. 2004; Dimech et al. 2008; Campbell et al. 2011). However, there doesn't seem to be a consistent pattern with depth; the metrics (e.g., number of species) may decrease (Moranta et al. 1998), increase (Magnussen 2002) or fluctuate (Sousa et al. 2006) depending on the ecosystem.

Furthermore, different taxonomic sub-communities are expected to show different responses on environmental gradients, including depth (Colloca et al. 2003; Politou et al. 2003).

Similarly they may respond differently to fishing or other pressures because (i) some may not be targeted by the fisheries, e.g., many species of crustaceans are not marketable in Greece (Machias et al. 2001; Thessalou-Legaki 2007) and (ii) they have different life history traits, e.g., chondrichthyes are generally large animals with low growth rate and fecundity and thus can only sustain low fishing mortality (Stevens et al. 2000), while most cephalopods are rather fast growing short-lived species (Caddy and Rodhouse 1998).

In the present study, we analysed the spatio-temporal patterns of a series of population and community metrics in the E. Ionian Sea throughout a 10 year period and studied their relationship with environmental and fishing factors. The study area extends over a wide bathymetric range and includes different species assemblages (Politou et al. 2003), which may respond differently to environmental variables and fishing intensity. However our goal was to analyse the system globally towards an integrative management approach; special emphasis was placed on the deep sea species, many of which are sensitive to fishing impact because of slow growth rates and low fecundity (Koslow et al. 2000). The aims of the study were to examine (i) spatial and temporal variation in the communities and their relationship with environmental variables and temporal trends in fishing activity and (ii) which metrics, taxonomic groups and/or species are more sensitive to fishing and can provide important information concerning its effect. We also discuss the management implications of our findings.

2 Materials and methods

2.1 Study area and fishing activity

The Eastern Ionian Sea (Fig. 1) is characterized by complex hydrography (Theocharis et al. 1993) and topography

since it includes numerous small and large islands, semi-enclosed gulfs and open waters. The continental shelf is narrow, especially to the western side of the area of this study while it is more extended in the semi-enclosed areas, with the exception of the deep Korinthiakos Gulf (Fig. 1). The Eastern Ionian is an oligotrophic sea, reflecting the overall oligotrophic condition of the Mediterranean Sea, the narrowness of the continental shelf and the regional circulation (Theocharis et al. 1993; Siokou-Frangou et al. 2010), with productivity varying locally, being higher in semi-enclosed gulfs than in offshore waters (Ramfos et al. 2006). As a consequence, spatial distributions of species and taxonomic groups have been found to be patchy (Politou et al. 2003; Politou et al. 2008b; Tserpes et al. 2008). Fisheries in the area are multi-species and multi-gear and most of the fleets operate on the shelf. However, there is some trawling for deep-sea shrimps (*Aristaeomorpha foliacea* and *Aristeus antennatus*), as well as longlining and gillnetting for blackspot seabream, *Pagellus bogaraveo*, and hake, *Merluccius merluccius* down to about 800 m (Mytilineou and Machias 2007). Overall, the main fishing activity involves static nets, which catch 63% of the landings (62% of Osteichthyes, 47% of Chondrichthyes, 84% of Cephalopods and 72% of Crustaceans) in the area (Anon. 2008). Bottom longlines catch approximately 47% of Chondrichthyes and ~10% of total landings while bottom trawls catch 27% of Crustaceans and ~5% of total landings (Anon. 2008). The remaining landings are mainly pelagic species, which are not included in the current analysis, and are caught with purse seines and pelagic longlines. Most of the commercial stocks were already considered overfished during the 1990s (Politou 2007) while the status of some, such as the red mullet (*Mullus barbatus*), striped mullet (*M. surmuletus*) and picarel (*Spicara smaris*) has improved in recent years (Anon. 2012; STECF 2012).

2.2 Data

Catch data from the MEDITS bottom trawl surveys in the E. Ionian Sea (including Patraikos and Korinthiakos Gulfs, Fig. 1) during summer in the periods 1998–2001, 2003–2006 and 2008 were used in this study. Existing MEDITS data for the years before 1998 were not considered since the survey design was improved in that year and we chose to be more consistent instead of including possible sampling biases. The MEDITS survey, which targets fish, crustaceans and cephalopods, follows a standardized protocol with fixed trawl locations (stations) and haul durations of 30 and 60 min in shallow (<200 m) and deep (>200 m) waters, respectively (Bertrand et al. 2002a). Catches are sorted to the species level and total biomass and numbers of individuals per species are recorded. The sizes (total length of fish, carapace length of crustaceans and mantle length of cephalopods to the mm) of all individuals of each species, or of a representative sample (at least 50 individuals, according to the MEDITS protocol) in cases when catches are high, are measured.

A CTD (until 2001: Sea-Bird 19; from 2003: Sea-Bird 19 + SeaCat profiler v3.0) was used to measure the vertical temperature and salinity profiles at each station. In total, 241 hauls at depths of 28 to 845 m were analysed, representing

approximately 28 hauls each year. Some hauls had to be excluded because of missing environmental data.

Days-at-sea of gears targeting the demersal community (bottom trawls, longlines and static nets) from five ports in the area defined in the framework of the EU Data Collection Regulation (DCR) and other studies in support of the Common Fishery Policy (“Patterns and propensities in Greek fishing effort and catches”, “Investigation of the fishing effort of the Greek commercial fishery”, Anon. 2001) were used to estimate total fishing effort for each year during the study period (Labropoulou 2007; Anon. 2008). In the Ionian Sea, trip duration is always less than 24 h, thus days-at-sea corresponds to actual fishing days. Due to the multi-species nature of the fisheries, most species are targeted by several gears; thus, the total fishing effort (sum of the effort of each gear) was considered a more appropriate representation of the actual fishing pressure exerted on the megafaunal community.

2.3 Data analysis

Trends in fishing effort for the three gears considered, as well as for the total fishing effort, were examined with linear regressions.

For each sampling station, after excluding pelagic species occurring incidentally in the catches, abundance and biomass were standardized per hauled area (km^{-2}) using the swept area method from the MEDITS protocol (Bertrand et al. 2002a,b), i.e., taking into account wing spread and the distance travelled by the trawl. Based on the standardized values, a series of community and diversity metrics was calculated for each year to assess the impact of environmental, fishing and spatio-temporal factors on the mega-faunal community in the E. Ionian Sea. Specifically, we estimated (i) values of biomass and abundance indices (kg km^{-2} and N km^{-2} , respectively) which were natural log transformed to reduce the effect of extreme values, (ii) three diversity indices from Hill’s series (N_0 , N_1 and N_2 ; Hill 1973) and (iii) four size-based indicators (L_{mean} : mean length; L_{max} : maximum length; $L_{0.05}$: length of the 5% of the length frequency of the community; $L_{0.95}$: length of the 95% of the length frequency of the community). Concerning the diversity metrics, N_0 is the number of species, N_1 , the exponential of Shannon H' index, is more sensitive to changes in rare species, and N_2 , the inverse of Simpson’s evenness index, is more sensitive to abundant species and to the evenness of the community (Greenstreet and Hall 1996; Greenstreet and Rogers 2006; and references therein). Primer-5 software (Clarke and Warwick 1994) was used to calculate these metrics, which were estimated for the whole benthodemersal megafaunal community, as well as for four taxonomic sub-communities i.e. Osteichthyes, Chondrichthyes, Crustaceans and Cephalopods.

Further, we calculated the log abundance and biomass for 10 abundant benthic and demersal populations, which were frequently present, i.e., in at least 15% of the hauls, and were selected based on the following criteria: commercial interest, depth range (mainly deep sea species) and life history (slow growth and/or low fecundity, e.g., Chondrichthyes) in order to represent as many species categories as possible. Specifically, we included (i) species of both high (e.g.,

Table 1. List of species considered and their main characteristics. Depth range refers to the bathymetric distribution of the species in the study area; main range is also indicated in parenthesis.

Scientific name	Common name	Depth range (m) (main range)	Behaviour	Commercial interest	Occurrence (%)
Osteichthyes					
<i>Pagellus bogaraveo</i>	Blackspot seabream	42–655 (>300)	demersal	High	27.4
<i>Helicolenus dactylopterus</i>	Blackbelly rosefish	98–692 (>300)	benthic	Medium	34.9
<i>Merluccius merluccius</i>	Hake	30–735 (all)	demersal	High	85.5
<i>Lepidorhombus boscii</i>	Four-spot megrim	100–659 (>250)	benthic	High	23.7
<i>Spicara smaris</i>	Picarel	28–337 (<150)	demersal	Medium	47.7
Chondrichthyes					
<i>Squalus blainville</i>	Longnose spurdog	77–659 (>250)	demersal	Medium	23.2
<i>Raja clavata</i>	Thornback ray	36–659 (<350)	demersal	Medium	52.3
Crustacea					
<i>Nephrops norvegicus</i>	Norway lobster	66–647 (100–550)	benthic	High	16.6
<i>Plesionika heterocarpus</i>	Arrow shrimp	97–655 (250–550)	demersal	No	20.3
<i>Liocarcinus depurator</i>	Blue-leg swimcrab	36–586 (<150)	benthic	Low	37.3

Merluccius merluccius hake, *Nephrops norvegicus* Norway lobster) and low (e.g., *Plesionika heterocarpus* arrow shrimp, *Liocarcinus depurator* blue-leg swimcrab) commercial interest, (ii) deep sea (e.g., *Pagellus bogaraveo* blackspot seabream, *Helicolenus dactylopterus* blackbelly rosefish, *Lepidorhombus boscii* four-spot megrim) and shallow water (e.g., *Spicara smaris* picarel) species and (iii) two abundant chondrichthyans (*Squalus blainville* longnose spurdog, *Raja clavata* thornback ray). Commercial interest was defined based on the records of Hellenic Statistical Service. Depth range comes from the MEDITS survey and species behaviour was defined based on the literature, remotely operated vehicle (ROV) observations and the authors' experience. The main ecological characteristics of these species, as well as their commercial interest, are listed in Table 1. We did not consider size-based metrics for these species since in some stations their abundance was too low to derive reliable length distribution and length metrics.

We used generalized additive models, GAMs, to explore the relationships between the aforementioned population and community metrics and (i) bottom depth, (ii) geographical location at haul positions, i.e. latitude, longitude and their interaction, (iii) temperature and salinity averaged for the 5 m layer above the seabed in each station, (iv) time (year) and (v) fishing effort (expressed as total days-at-sea for all gears combined during the year of sampling). The model we applied was of the form:

$$E(\text{metric}) = s(\text{Depth}) + s(\text{Latitude}) + s(\text{Longitude}) \\ + s(\text{Latitude} * \text{Longitude}) + s(\text{Temperature}) \\ + s(\text{Salinity}) + s(\text{Year}) + s(\text{Fishingeffort}) \quad (1)$$

where “s” is the smooth function and * denotes interaction.

A Gaussian distribution and identity link were assumed and the natural cubic spline smoother was used for the independent variable smoothing and fitting GAM. The “mgcv” package in the R statistical software (v. R2.13.1; R Development Core Team 2011) was used to apply GAMs (Wood 2006). The correlation among the explanatory variables was low (correlation coefficient <|0.2|, except in the case of depth with temperature (correlation coefficient = -0.48) and fishing effort with year (correlation coefficient = -0.48). Since

fishing effort values were aggregated annually, either year or effort was considered in the model, also given their correlation. Concerning geographical coordinates, we included either the effect of the interaction of latitude with longitude or separately latitude and/or longitude in the models. Only significant terms were considered for each model. Validation graphs (e.g., QQ-plot and residual plot against the original explanatory variables) were inspected in order to detect any model misspecification. We explored the effect of each explanatory variable alone, as well as the combined effects of all variables in order to detect the best model explaining the variation in the data. The final models were selected based on the deviance explained and the minimization of the Akaike information criterion (AIC) (Burnham and Anderson 2002), while models with $\Delta AIC < 2$ ($\Delta AIC = AIC_i - AIC_{\min}$, where AIC_i is the AIC of the custom model and AIC_{\min} is the minimum AIC observed) were also considered as substantially explaining the data (Burnham and Anderson 2002). In some cases, in order to further identify temporal effects or the effect of fisheries, an additional model was also considered where fishing effort or year was also significant and the model more complex but not the best, provided that it explained substantial amount of the observed variability and that the increase in AIC in comparison to AIC_{\min} was lower than 2%. Furthermore, in order to derive a robust conclusion on whether the temporal effects revealed by GAMs showed increasing, decreasing or no particular trend, we examined the Pearson's correlation of these effects with year.

3 Results

The examination of the fishing effort showed that total effort has declined with a statistically significant negative trend since the year 2000 ($y = -18.058x + 36933$, $R^2 = 0.626$, p -value = 0.034; Fig. 2). This decline is mainly due to a decrease in fishing effort of static nets, ($y = -21.513x + 43770$, $R^2 = 0.877$, p -value = 0.002; Fig. 2). Fishing efforts of bottom trawls and longlines have also declined since 2003, but without presenting a statistically significant trend.

Table 2. GAMs of metrics of the total community of the E. Ionian Sea: deviance explained (%) by each one of the explanatory variables when considered alone, and total deviance explained (%) by the final selected model(s). The best models were selected based on the minimization of *AIC* and corresponding ΔAIC . *Bi*: biomass; *N*: abundance; N_0 , N_1 and N_2 : diversity indices from Hill's series; for definition of the remaining length metrics see text; *D*: depth; *S*: salinity; *T*: temperature; *Lon*: longitude; *Lat*: latitude; *Y*: year; *E*: fishing effort; “:” denotes interaction; “*” indicates statistically significant effect ($p < 0.05$); (a) principal model; (b): additional model; *r*: Pearson's correlation coefficient of year with the effect of year.

Metrics	Explanatory variables (deviance explained %)									Best model	
	<i>D</i>	<i>S</i>	<i>T</i>	<i>Lat</i>	<i>Lon</i>	<i>Lat:Lon</i>	<i>Y</i>	<i>E</i>	variables	dev. expl. %	<i>r</i> (<i>p</i> -value)
$\ln Bi$	26.2*	1.4	32.8*	9.6*	36.9*	46.1*	6.4*	7.9*	<i>Lat:Lon + T + Y</i>	59.9	1 (<0.001)
$\ln N$	45.6*	1.7*	48.5*	18.8*	53*	64.2*	5.3*	0.2	<i>Lat:Lon + D + Y</i>	70.4	0.94 (<0.001)
N_0	49.8*	1.7	41.6*	14.6*	49.9*	62.9*	1.3	0.0	<i>Lat:Lon + D + Y</i>	65.7	1 (<0.001)
N_1	17.4*	7.7*	10.5*	17.2*	14.4*	46.7*	0.0	0.1	<i>Lat:Lon</i>	46.7	
N_2	11.6*	7.4*	8.3*	15.3*	11.7*	39.7*	0.0	0.1	<i>Lat:Lon + D</i>	40.4	
L_{mean}	43.0*	0.0	52.4*	13*	62.9*	69.8*	1.7	2.5	<i>Lat:Lon + Y</i>	71.6	0.78 (<0.001)
$L_{0.05}$	27.5*	13.5*	17.6*	17.6*	31.6*	46.2*	0.8	2.8	<i>Lat:Lon + D + Y</i>	52.6	0.63 (<0.001)
$L_{0.95}$	36.3*	1.4	34.5*	2.2	40.4*	55.5*	0.7	3.1	<i>Lat:Lon + D</i>	56.5	
L_{max}	21.9*	2.7	11.7*	15.5*	14.9*	37.3*	2.1	2.8	(a) <i>Lat:Lon + E</i> (b) <i>Lat:Lon + Y</i>	40.6 39.5	0.92 (<0.001)

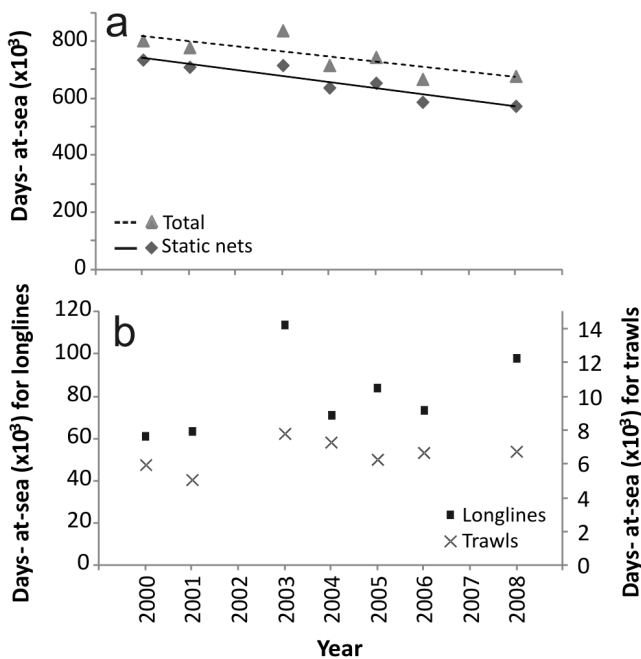


Fig. 2. Fishing effort (days-at-sea) in the E. Ionian Sea during the period 2000–2008. (a) Total fishing effort and fishing effort of static nets; (b) fishing effort of longlines (left axis) and trawls (right axis). Lines illustrate statistically significant trends.

Temperature in the 5 m layer above the seabed ranged from 13.5 to 21.5 °C throughout the study period, being relatively higher at shallow depths and always below 16 °C in stations deeper than 100 m. Salinity above the seabed ranged from 36.4 to 44.2, with 88% of the values being between 38.4 and 39.4. Even though these parameters varied locally, no spatio-temporal patterns, linear or non-linear, were identified for temperature and salinity.

The data set analysed comprised 248 species, including 128 Osteichthyes, 29 Chondrichthyes, 62 Crustacea and 29 Cephalopoda. The data used in GAM analysis, annual box-plots of biomass, abundance and mean length of the total com-

munity (all species combined) during the study period are presented in Figure 3. In addition, biomass, abundance indices and mean lengths of the four sub-communities examined (Osteichthyes, Chondrichthyes, Crustacea and Cephalopoda) are presented as annual box-plots in Figure S1 of the Appendix, while means and standard errors of these metrics for the 10 species examined are illustrated in Figure S2.

The final GAMs of the metrics of the total community explained 40–72% of the deviance (Table 2). The deviance explained by each factor alone may give a general idea on the distribution of explanatory power among the explanatory variables. In general, depth and geographical coordinates (the interaction of longitude with latitude) explained much of the deviance of the community metrics, when considered alone and in most cases they were included in the final selected models (Table 2, Fig. 4). The abundance increased slightly with depth to about 400 m and then decreased sharply. Diversity metrics, N_0 and N_2 decreased with depth, but a peak was apparent for species richness (N_0) at around 400 m (Fig. 4). For N_1 , the depth effect was not significant when added to the effect of geographical coordinates. $L_{0.05}$ also decreased with depth, revealing the existence of a higher proportion of small-sized individuals/species in deeper water between 300 and 700 m depth, though coexisting with a high proportion of large individuals/species, as revealed by the effect of depth on the $L_{0.95}$ which increased up to 500 m. Local effects were observed for all the metrics examined. Positive effects on biomass corresponding to geographical coordinates in the Patraikos Gulf (approximately 38.3N/21.5E; see Figs. 1 and 4) were obvious, while diversities also maximized in the Patraikos Gulf and in areas eastern to the islands of the central E. Ionian Sea (approximately 38.5 N/21E; see Figs. 1 and 4). For several metrics, the effect of temperature taken alone was significant, but it was only included in the final model for biomass, which presented low values at low temperatures. On the contrary, salinity contributed very little to the deviance explained. The effect of year was significant only in two cases when considered alone (in biomass and abundance), but it was included as a significant factor in the finally selected models for six metrics. Specifically, increasing trends (positive correlation) were apparent for

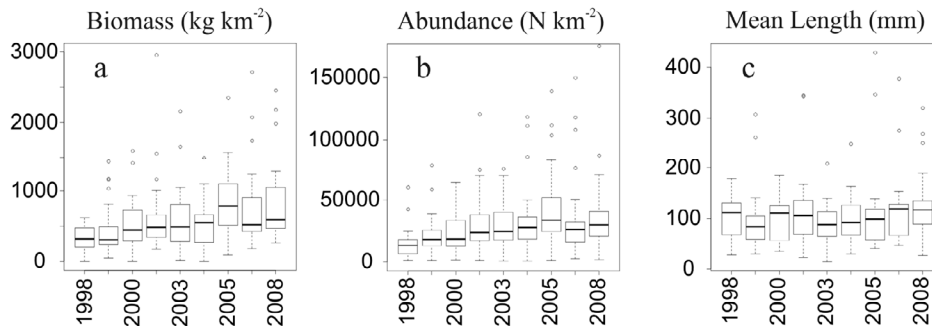


Fig. 3. Annual box-plots for biomass (a) and abundance (b) indices as well as mean length (c) of the total community.

abundance, biomass, N_0 , $L_{0.05}$, L_{mean} and L_{max} , throughout the study period (Table 2, Fig. 4). Fishing effort contributed only to the selected model for L_{max} , which declined with increasing effort (Fig. 4).

Geographical coordinates and depth were also the main factors in the selected models in the analysis of the Chondrichthyes sub-community (Table 3). GAMs fitted most of the metrics well (34–65%), but did not adequately describe L_{mean} and $L_{0.05}$, since the deviance explained was low (<22%). Biomass and abundance were low on the continental shelf and peaked between 300 and 700 m, decreasing with further depths. All diversity metrics were low between 0 and 200 m and increased sharply afterwards, with maxima at 400 m (Fig. S3). Positive effects on biomass and abundance were also obvious for areas corresponding to the Patraikos Gulf and to offshore areas (low longitudes). Increasing temporal trends were obvious for abundance, N_0 and L_{max} . A clear negative relation of abundance with fishing effort and one not so obvious for L_{max} were revealed.

The GAMs for the Osteichthyes sub-community explained even higher percentages of the deviance (44–81%; Table 3). As in previous analyses, geographical coordinates and depth contributed the most, but year or fishing effort was also included in several final selected models. Contrary to what was observed in Chondrichthyes, abundance and diversity metrics declined with depth, while $L_{0.95}$ increased. The remaining size-based metrics fluctuated presenting peaks at intermediate depths (L_{max} at 200–600 m; L_{mean} at 450 m and 700 m; $L_{0.05}$ at depths >200 m). Although peaks in the different size-based metrics are observed at different depths, it is noticeable that the lowest values are usually observed at shallower depths. Biomass and particularly abundance were maximal in Patraikos Gulf and off the coasts of Epirus. Biomass, abundance, number of species (N_0) and L_{max} increased during the survey period, while L_{max} and N_0 decreased at increased fishing effort (Fig. S4).

The Crustaceans were more abundant at the continental slope between 200 and 700 m depth (Fig. S5). Their diversities reached maximum values at 400–500 m and showed a tendency to decrease in deeper waters (>600 m). All length metrics also increased with depth. Local effects were apparent for several metrics, however a common positive effect on biomass, abundance, diversities and L_{max} was observed for coordinates corresponding to areas to the east of the islands of the central E. Ionian Sea (approximately 38.5 N/21.2 E; see Figs. 1

and S5). The effect of year was included in the final models of six out of nine metrics (Table 3, Fig. S5). Biomass and abundance increased from 1998 to 2004 and decreased thereafter in combination with a decline of diversity (N_0 and N_1). Overall, throughout the study period, no correlation was found between year and the effect of year on biomass, weak negative correlation was found for abundance while for diversity (N_0 and N_1) a negative correlation was apparent (Table 3). In contrast, L_{mean} and $L_{0.05}$ showed an increasing trend throughout the whole period (positive correlation; Table 3). The effect of fishing effort was significant in only three cases: specifically, concerning the abundance and N_0 , complex effects were detected consisting of an increase from low to intermediate values of fishing effort, a decline thereafter and a further increase in high effort values, while a clear negative effect was apparent for $L_{0.95}$ (Table 3, Fig. S5).

Depth was the main factor for most metrics applied to Cephalopods, and its effect was often stronger than the geographical effect, as implied by the % deviance explained (Table 3). A negative effect was observed for abundance and biomass with increasing depth and similar effects were apparent with diversity metrics after a peak at around 300 m depth. In general, length metrics increased with depth and declined only in the deepest range below about 450 m (Fig. S6). Furthermore, all metrics decreased with increasing longitude. Year was significant for all metrics but N_1 and N_2 (Fig. S6), and a generalized increasing trend (positive correlation) was observed throughout the study period. Fishing effort was significant in an alternative model for L_{mean} , $L_{0.05}$ and $L_{0.95}$ only. For these metrics its effect was generally negative, although it fluctuated a great deal (Fig. S6).

The directions of change of the metrics examined for the total community and the sub-communities (i) throughout the study period and (ii) as a response to fishing effort are synthesized in Table 4. The directions of changes are based on the smooth terms shown in Figures 4 and S3–S6 and on alternative models to the best ones with year or fishing effort contributing as significant factors. In general, most metrics increased with year and decreased at high values of fishing effort for the whole community, as well as for the Osteichthyes, Chondrichthyes and Cephalopoda sub-communities (Table 4). Nevertheless, fishing effort was less frequently significant than year and in several cases there was no clear pattern. The combination of increasing trends throughout the study period and decreasing responses with fishing effort was strong for Chondrichthyes and

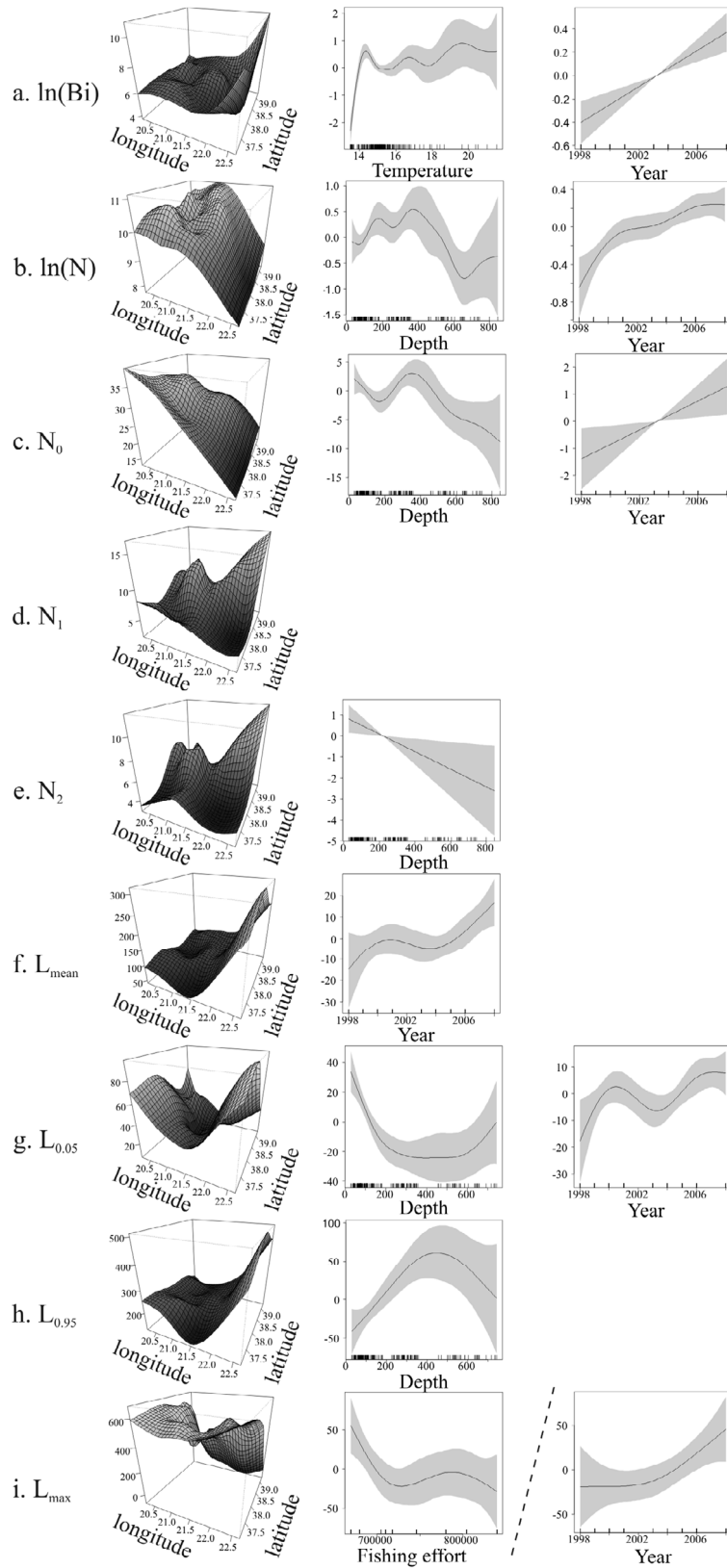


Fig. 4. Estimated smooth terms of the parameters contributing to the selected GAMs for metrics of the total community. $\ln(Bi)$: natural logarithm of biomass; $\ln(N)$: natural logarithm of abundance; N_0 , N_1 and N_2 : diversity indices from Hill's series; for definition of the remaining length metrics see text. Diagonal dashed lines indicate alternative models (see Table 2 for more information). Grey areas are 95% confidence intervals. Rug plots indicate the distribution of the observed values.

Table 3. GAMs of metrics of the Chondrichthyes (A), Osteichthyes (B), Crustacean (C) and Cephalopod (D) sub-communities of the E. Ionian Sea: deviance explained (%) by each one of the explanatory variables when considered alone, and total deviance explained (%) by the final selected model(s). The best models were selected based on the minimization of *AIC* and corresponding ΔAIC . Some additional ecologically interpretable models were selected and are indicated in *italics*. *Bi*: biomass; *N*: abundance; N_0 , N_1 and N_2 : diversity indices from Hill's series; for definition of the remaining length metrics see text; *D*: depth; *S*: salinity; *T*: temperature; *Lon*: longitude; *Lat*: latitude; *Y*: year; *E*: fishing effort; “:” denotes interaction; “*” indicates statistically significant effect ($p < 0.05$); (a) principal model; (b): additional model; *r*: Pearson's correlation coefficient of year with the effect of year.

Metrics	Explanatory variables (deviance explained %)								Best model		
	<i>D</i>	<i>S</i>	<i>T</i>	<i>Lat</i>	<i>Lon</i>	<i>Lat:Lon</i>	<i>Y</i>	<i>E</i>	variables	dev. expl. %	<i>r</i> (<i>p</i> -value)
A. Chondrichthyes											
<i>ln Bi</i>	35.1*	4.7*	12.1*	7.9*	25.5*	43.3*	0.9	0.3	Lat:Lon + D	47.5	
<i>ln N</i>	39.2*	3.5	12.3*	7.3*	25.9*	46.9*	1.9	0.9	(a) Lat:Lon + D + Y (b) Lat:Lon + E	54.7 53.8	0.77 (<0.001)
N_0	49.7*	8.5*	16.1*	15.9*	36.2*	57.2*	1.3	0.2	Lat:Lon + D + Y	64.6	1 (<0.001)
N_1	34.3*	5.6	9.3*	9.2*	24.3*	44.1*	1.0	0.1	Lat:Lon + D	48.7	
N_2	22.9*	7.8	6.8*	9.2*	17.1*	34.3*	0.6	0.0	Lat:Lon + D	39.1	
L_{mean}	4.8	2.7	5.1	2.7	8.1*	8.0*	0.0	5.0	Lat:Lon	8.0	
$L_{0.05}$	14.3*	6.6	3.1	0.1	4.1	5.1	3.2	2.6	D + S	22.6	
$L_{0.95}$	0.0	1.6	36.4*	1.4	36.5*	81.2*	8.1	11.2*	Lat:Lon	81.2	
L_{max}	12.8*	6.3	16.1*	1.1	0.0	2.5	4.9*	14.1*	(a) D+T+E (b) D + T + Y	40.4 34.4	0.47 (<0.001)
B. Osteichthyes											
<i>ln Bi</i>	28.4*	1.6	29.3*	13.2*	35*	50.9*	5.2*	6.8*	(a) Lat:Lon + E (b) Lat:Lon + Y	56.1 54.5	1(<0.001)
<i>ln N</i>	46.1*	1.4	37.7*	22.2*	44.4*	60*	6.8*	4.5	Lat:Lon + D + Y	68.8	0.90 (<0.001)
N_0	54.4*	5.3*	44.6*	19.6*	41.7*	66.3*	2.3*	0.4	(a) Lat:Lon + D + Y (b) Lat:Lon + D + E	69.5 69.0	1 (<0.001)
N_1	32.1*	12.1*	25.5*	14.8*	21.5*	57.4*	0.3	0.6	Lat:Lon + D	60.7	
N_2	23.9*	11.5*	20.1*	12.5*	20.1*	50.7*	0.4	0.5	Lat:Lon + D	52.8	
L_{mean}	71.2*	1.8	43.8*	22.3*	48.6*	73.9*	0.0	0.0	Lat:Lon + D	80.6	
$L_{0.05}$	13.0*	0.3	0.5	14.4*	6.7	39.9*	0.3	3.1	Lat:Lon + D	44.4	
$L_{0.95}$	62.8*	2.3	28*	30.9*	44*	72.4*	0.0	0.1	Lat:Lon + D	75.6	
L_{max}	20.4*	0.9	11.5*	22.2*	18.3*	40.4*	4.2*	1.6	(a) Lat:Lon + D + Y (b) Lat:Lon + D + E	47.1 47.1	0.92 (<0.001)
C. Crustacea											
<i>ln Bi</i>	32.7*	7.9*	21.5*	30.0*	31.3*	66.0*	2.5	0.3	Lat:Lon + D + Y	73.6	0 (0.94)
<i>ln N</i>	31.7*	8.9*	18.4*	23.4*	23.5*	52.5*	4.8*	3.1	(a) Lat:Lon + D + Y (b) Lat:Lon + D + E	62.6 60.5	-0.25 (<0.001)
N_0	20.6*	5.2*	12.8*	12.9*	10.4*	30.8*	7.1*	4.0*	(a) Lat:Lon + T + D + Y (b) Lat:Lon + T + D + E	46.4 43.1	-0.56 (<0.001)
N_1	15.7*	4.6*	0.2	5.5*	6.7	15.5*	7.6*	1.6	Lat:Lon + D + Y	31.0	-0.68 (<0.001)
N_2	18.6*	3.4*	0.0	5.8	1.9	11.3	4.2*	0.2	D + S	20.2	
L_{mean}	38.9*	0.8	12.5*	20.1*	26.5*	47.3*	5.6*	4.0	Lat:Lon + D + Y	58.1	0.94 (<0.001)
$L_{0.05}$	20.0*	0.4	13.5*	3.6*	20.3*	25.4*	8.7*	4.5*	Lat:Lon + D + Y	39.7	0.89 (<0.001)
$L_{0.95}$	45.4*	0.2	13.5*	26.2*	30.8*	45.9*	2.0	4.5	Lat:Lon + D + E	63.9	
L_{max}	39.3*	0.4	7.4*	25.5*	24.5*	54.7*	0.2	0.0	Lat:Lon + D	68.5	
D. Cephalopoda											
<i>ln Bi</i>	64.0*	8.6*	45.7*	17.0*	46.2*	66.5*	2.1*	0.2	Lat:Lon + D + Y	73.1	0.85 (<0.001)
<i>ln N</i>	77.4*	3.4*	58.2*	16.0*	60.6*	81.5*	0.2	0.0	Lat:Lon + T + D + Y	87.8	0.70 (<0.001)
N_0	64.0*	4.7*	36.8*	16.3*	40.8*	65.1*	2.1*	0.0	Lat:Lon + D + Y	71.8	0.82 (<0.001)
N_1	44.4*	6.4	19.3*	9.9*	29.1*	42.4*	0.4	0.2	Lat:Lon + D	48.4	
N_2	29.8*	6.7	7.4*	1.2	15.9*	29.0*	0.2	0.2	D	29.8	
L_{mean}	52.0*	1.2	9.2*	18.3*	13.6*	52.8*	5.1*	0.9	(a) Lat:Lon + D + Y (b) Lat:Lon + D + E	64.8 64.0	0.89 (<0.001)
$L_{0.05}$	39.5*	0.9	12*	16.6*	12.8*	50.3*	9.0*	3.5*	(a) Lat:Lon + D + Y (b) Lat:Lon + D + E	72.4 70.8	0.74 (<0.001)
$L_{0.95}$	51.6*	9.0	20.1*	24.6*	35.9*	57.8*	12.7*	8.5	(a) D + E (b) D + Y	57.6 55.3	0.98 (<0.001)
L_{max}	21.0*	1.5	1.2	6.5*	4.6	28.9*	4.8	0.0	Lat:Lon + D + Y	36.4	0.68 (<0.001)

Table 4. Directions of changes throughout the study period (Y) and at high values of fishing effort (E) of the metrics considered for the total community and for the four sub-communities, as revealed by GAM analysis. The effect of the best model with significant effect of Y or E was considered. Bi : biomass; N : abundance; N_0 , N_1 and N_2 : diversity indices from Hill's series; for definition of the remaining length metrics see text; NS: non-significant effect; *: significant effect but with no clear trend; ly: indicates that the direction of change refers only to the last years of the dataset.

Metrics	Total Community		Chondrichthyes		Osteichthyes		Crustacea		Cephalopoda	
	Y	E	Y	E	Y	E	Y	E	Y	E
$\ln Bi$	↗	*	NS	NS	↗	*	↗↘	*	↗	NS
$\ln N$	↗	*	↗	↘	↗	*	↗↘	*	↗	NS
N_0	↗	NS	↗	↘	↗	↘	ly↘	*	↗	NS
N_1	NS	NS	NS	NS	NS	↘	ly↘	↗	NS	NS
N_2	NS	NS	NS	NS	NS	↘	ly↘	NS	NS	NS
L_{mean}	↗	*	NS	NS	NS	NS	↗	NS	↗	↘
$L_{0.05}$	↗	*	NS	NS	NS	NS	↗	↘↗	↗	↘
$L_{0.95}$	NS	NS	NS	↘	NS	NS	NS	↘↗	↗	*
L_{max}	↗	↘	↗	↘	↗	↘	↗	NS	↗	NS

present but not so strong for Osteichthyes and Cephalopoda. In contrast, the Crustacean sub-community presented more complex responses, and often showed decreasing temporal trends and positive effect of increased fishing effort. L_{max} , and to a lesser extent abundance and N_0 , were the metrics that to which year and effort most often contributed significantly for sub-communities (Table 4). In contrast, N_1 and N_2 , i.e., diversity indices, showed lesser changes with year and effort.

GAM analysis of the biomass and abundance indices of the selected species explained a large part of the deviance (45–90%; Table 5). There is a strong depth effect for every species, with a peak in biomass (Fig. S7) and abundance (not shown as very similar to the effect on biomass) depending on species preferred habitat. Similarly, the effect of geographical factors was also species specific, with several species presenting high biomasses in areas previously identified as important for the total community and the four sub-communities (e.g., *M. merluccius*, *R. clavata*, *L. depurator* in the Patraikos Gulf; Fig. S7). Temporal trends and/or the effect of fishing proved significant for the biomass of six out of the ten species. For *H. dactylopterus*, a commercially important benthic deep sea fish species, the increase of fishing effort had a negative, almost linear, effect on its biomass (Fig. S7). *S. smaris*, a shallow water commercial species, presented a more complex effect with fishing effort, while the two crustaceans *P. heterocarpus* and *L. depurator* seemed to be favoured by high values of fishing effort. For the rest of the species, fishing effort was not included in the final selected models. Concerning temporal trends, increases in biomass were observed for three (*H. dactylopterus*, *M. merluccius* and *S. smaris*) out of the five bony fish species examined. Decreasing trends were observed for all three crustacean species considered, especially for *N. norvegicus*, since biomasses of *P. heterocarpus* and *L. depurator* increased during the first years and declined afterwards, presenting relatively weak negative correlations overall (Table 5, Fig. S7). Concerning the two elasmobranches examined, (*S. blainville* and *R. clavata*), only geographical and bathymetric factors were included in the selected models. Biomass of *S. blainville* and *R. clavata* peaked at 350 and 250 m, respectively.

4 Discussion

Spatial and temporal patterns of population and community metrics of the E. Ionian Sea megafaunal communities were related to geographical, environmental and fishing factors. In general, Generalized Additive Models have proved powerful tools for examining the effect of such factors (e.g., Katsanevakis 2006; Tserpes et al. 2011). In our case, they were able to explain large part of the variability for several metrics across the total community, the four taxonomic sub-communities, and the ten selected populations, despite the inherent high noise characterizing bottom trawl surveys (Gaertner et al. 2005). Location, i.e., the interaction between latitude and longitude, and bottom depth were the factors with the highest explanatory power in the models of the majority of the subsets and metrics examined. Although, in some of the final models, either location or (more commonly) depth dropped out and when both were kept, their explanatory power was clearly not additive. This comes from the correlation between location and depth, in particular with a fixed station protocol, where the locations convey the depth information.

Depth is known as one of the most influential factors on the distribution, abundance (e.g., Macpherson 2003; Politou et al. 2003; Tserpes et al. 2011) and other population and community metrics (e.g., Moranta et al. 1998; Lorange et al. 2002). However, depth-related patterns are ecosystem specific, especially for biodiversity (e.g., Moranta et al. 1998; Lorange et al. 2002, Magnussen 2002) and, as also seen in our case, they further depend on the sub-communities examined (e.g., Colloca et al. 2003). The total megafaunal community and the sub-community of Osteichthyes present similar patterns in abundance, with high spatial and bathymetric fluctuations and local peaks, but generally decline in deeper waters. This similarity is mostly due to the dominance of fin-fish in the total community as these make up 74% of the total biomass in our study, underlining the interest of exploring sub-communities separately. Indeed, variant patterns were observed for the remaining categories, in line with previous studies in the area (Politou et al. 2003); the abundance of

Table 5. GAMs for abundance and biomass of selected species of the E. Ionian Sea: deviance explained (%) by each one of the explanatory variables when considered alone, and total deviance explained (%) by the final selected model(s). Best models were selected based on the minimization of *AIC* and corresponding ΔAIC . Some additional ecologically interpretable models were selected and are indicated in *italics*. *Bi*: biomass; *N*: abundance; *D*: depth; *S*: salinity; *T*: temperature; *Lon*: longitude; *Lat*: latitude; *Y*: year; *E*: fishing effort; “:” denotes interaction, “*” indicates statistically significant effect ($p < 0.05$); (a) principal model; (b): additional model; *r*: Pearson’s correlation coefficient of year with the effect of year.

Metrics	Explanatory variables (deviance explained %)									Best model		
	<i>D</i>	<i>S</i>	<i>T</i>	<i>Lat</i>	<i>Lon</i>	<i>Lat * Lon</i>	<i>Y</i>	<i>E</i>	variables	dev. expl. %	<i>r</i> (<i>p</i> -value)	
<i>Pagellus bogaraveo</i>												
log(<i>Bi</i>)	48.8*	1.0	13.9*	21.8*	8.1*	60.8*	0.2	0.1	Lat:Lon + D	68.6		
log(<i>N</i>)	45.4*	0.9	14.8*	18.2*	16.9*	57.4*	0.0	0.1	Lat:Lon + D	63.4		
<i>Helicolenus dactylopterus</i>												
log(<i>Bi</i>)	67.2*	11.3*	17.3*	42.2*	19.4*	76.0*	1.8*	0.3	(a) Lat:Lon + D + Y	90.1	0.92 (<0.001)	
									(b) <i>Lat:Lon + D + E</i>	89.7		
log(<i>N</i>)	74.1*	16.4*	21.8*	32.1*	33.6*	77.3*	1.7*	0.2	(a) Lat:Lon + D + E	89.5	1 (<0.001)	
									(b) Lat:Lon + D + Y	89.1		
<i>Lepidorhombus boscii</i>												
log(<i>Bi</i>)	54.4*	7.4	15.7*	30.4*	41.7*	72.6*	0.6	0.1	Lat:Lon + D	77.7		
log(<i>N</i>)	58.3*	7.7	16.8*	29.3*	41.5*	72.1*	0.4	0.0	Lat:Lon + D	76.8		
<i>Merluccius merluccius</i>												
log(<i>Bi</i>)	20.7*	2.4*	2.6*	24.8*	19.8*	49.4*	5.8*	3.8	Lat:Lon + D + Y	60.9	0.94 (<0.001)	
log(<i>N</i>)	38.9*	1.9*	13.5*	22.6*	16.8*	57.1*	6.9*	5.0*	Lat:Lon + D + Y	67.1	0.95 (<0.001)	
<i>Spicara smaris</i>												
log(<i>Bi</i>)	31.6*	14.4*	11.2*	40.4*	38.4*	68.4*	1.5	0.0	(a) Lat:Lon + D + Y	74.6	1 (<0.001)	
									(b) Lat:Lon + D + E	75.0		
log(<i>N</i>)	52.2*	17.5*	24.6*	37.7*	38.5*	71.3*	1.2	0.6	(a) Lat:Lon + D + Y	79.0	1 (<0.001)	
									(b) Lat:Lon + D + E	79.2		
<i>Squalus blainville</i>												
log(<i>Bi</i>)	54.9*	7.7	13.8*	11.4*	36.7*	60.5*	0.0	0.5	Lat:Lon+D	67.4		
log(<i>N</i>)	59.3*	8.4*	14.3*	9.3*	37.2*	64.4*	0.2	0.1	Lat:Lon+D	73.8		
<i>Raja clavata</i>												
log(<i>Bi</i>)	24.5*	4.3	13.1*	10.9*	16.9*	43.5*	0.1	0.0	Lat:Lon+D	45.5		
log(<i>N</i>)	33.5*	4.7*	13.9*	13.7*	18.8*	51.8*	1.1	0.3	Lat:Lon+D	58.7		
<i>Nephrops norvegicus</i>												
log(<i>Bi</i>)	20.4*	0.9	9.7	14.2*	23.8*	43.3*	1.4	0.9	Lat:Lon + D + Y	47.5	-0.99 (<0.001)	
log(<i>N</i>)	23.0*	0.9	11.4*	17.2*	26.8*	48.5*	1.1	0.8	Lat:Lon + D + Y	54.1	-1 (<0.001)	
<i>Plesionika heterocarpus</i>												
log(<i>Bi</i>)	45.0*	7.5	13.1*	19.8*	33.2*	58.5*	3.6	0.8	(a) Lat:Lon + D + Y	63.2	-0.22 (<0.001)	
									(b) <i>Lat:Lon + D + E</i>	61.6		
log(<i>N</i>)	52.0*	10.6*	15.7*	21.2*	33.4*	62.5*	3.5	0.8	Lat:Lon + D + Y	67.6	-0.27 (<0.001)	
<i>Liocarcinus depurator</i>												
log(<i>Bi</i>)	36.3*	9.1*	11.5*	15.1*	25.9*	54.7*	4.5*	3.8*	(a) Lat:Lon + D + T + Y	63.3	-0.68 (<0.001)	
									(b) Lat:Lon + D + T + E	62.5		
log(<i>N</i>)	36.8*	9.1*	12.3*	15.0*	26.7*	55.6*	4.4*	3.8*	(a) Lat:Lon + D + T + Y	64.1	-0.65 (<0.001)	
									(b) Lat:Lon + D + T + E	63.5		

Osteichthyes and Cephalopods decreased with depth, whereas those of Chondrichthyes and of Crustaceans increased, especially below 200 m. Such results may prove important for spatial management of selected sub-communities or species. The upper slope 250–700 m appeared to be the habitat with the highest biomass for Chondrichthyes. It is noteworthy that three of the shark species recorded at these depths are categorized as vulnerable in the IUCN (2012) red list, i.e. *Oxynotus centrina*, *Squalus acanthias* and *Centrophorus granulosus*, and one more (*Galeorhinus galeus*) even though recorded at shallow waters is also known to occur on the upper slope. Thus, maintaining biological diversity may require management of the fishing mortality of these vulnerable species in this depth zone. Moreover, spatial variation in $L_{0.05}$ can be used to identify nursery grounds: for Osteichthyes, low $L_{0.05}$ was obvious at around 200 m depth, reflecting the high proportions of juvenile fish, mainly *Merluccius merluccius*, in this depth zone, in line with previous studies (Tserpes et al. 2008). In addition, L_{\max} increased with depth for all sub-communities, as did L_{mean} and $L_{0.095}$ except for Chondrichthyes. These patterns suggest that the deeper-bigger pattern known at species level (Macpherson and Duarte 1991) exists for wider taxonomic groups, as mentioned by previous authors (e.g., Papiol et al. 2012), although not for the overall community, at least to 800 m (Stefanescu et al. 1992).

Furthermore, spatial patterns or variations are common across ecosystems (Magnussen 2002; Macpherson 2003; Gaertner et al. 2005; Sousa et al. 2006) and were also identified in our study in the E. Ionian Sea. For example, local peaks of biomass and abundance for the whole community and several taxa (e.g., Chondrichthyes, Osteichthyes, *M. merluccius*, *Raja clavata*) were observed in coordinates corresponding to the Patraikos Gulf (approximately 38.3N/21.5E; Fig. 1), probably reflecting the relatively high productivity of this area (Ramfos et al. 2006) explained by the presence of river deltas and estuaries. As concerns diversities of the total community, other than the Patraikos Gulf, these were also maximized in areas east of the central E. Ionian Sea islands, probably owing to increased diversities of the Crustacean sub-community. These patterns are probably related to habitat preferences of the species/community and reflect the synergistic effect of other environmental factors, some of which (e.g., productivity, currents, substrate) may not have been included in the analysis.

Despite this, the remaining environmental factors examined, even though significant in many cases when considered alone (especially bottom temperature), were seldom included in the final selected models for the metrics considered. Temperature is correlated with depth, so when depth was included in the final models, the additional contribution of temperature was not significant. Furthermore, it seems that due to the relatively stable thermal conditions observed below 100 m depth in the study area, temperature may play only a secondary role in explaining patterns in community distribution in deeper waters, at least to the community level. Concerning salinity, its non-inclusion in the final models may be due to the narrow range of the majority of records, which results in minor effects on the communities/species. Furthermore, spatial factors and bathymetry additionally act as proxies for salinity and

temperature, at least to certain extent, and this is also true for several other environmental factors. In this context, even though some of the parameters included in the GAMs may be well related to community distributions, they may not reveal direct cause-and-effect information but may integrate the effect of other environmental variables such as water mass characteristics, productivity and food availability, which are known to affect spatial and bathymetric patterns (e.g., Papiol et al. 2012; Abelló et al. 1988). Nevertheless, a certain part of the variability was not explained by the factors considered in the analysis, and including additional environmental parameters (e.g., substrate type, Katsanevakis et al. 2009) would probably increase the explanatory power of the models, if available.

On the contrary, either the year or the fishing effort were often significant and were included in the final selected models, despite being rarely significant when considered alone, especially fishing effort. GAMs were effective in detecting non-linear temporal trends and effects of fishing pressure after testing for spatial and bathymetric factors. Specifically, the term Year was almost always included in the final models when it showed significant effect when considered alone, while it was additionally included in the final models for 13 metrics (total community: N_0 , L_{mean} , $L_{0.05}$, L_{\max} ; Chondrichthyes: abundance, N_0 ; cephalopods: abundance, L_{\max} ; *Spicara smaris*: biomass, abundance; *Nephrops norvegicus*: biomass, abundance; *P. heterocarpus*: abundance) despite not being significant as a single term. Even though long time series (few decades) are usually required to detect population and community changes related to changes in fishing practices, several studies have revealed effects of fishing in shorter periods (<10 years, e.g., Bianchi et al. 2000). In our case, GAMs revealed responses to fishing despite the examined time series being relatively short. The metrics were better related to temporal trends than to fishing effort. Effort is difficult to measure and absolute values of fishery statistics may not be complete or fully reliable, especially in a multi-gear fishery like that in the E. Ionian Sea. Thus, although clearly not causal, time (year) might be a better reflection of the (cumulative) change in fishing pressure. An increase in most of the examined metrics was observed throughout the study period, with the exception of abundance indices and diversities for the Crustaceans sub-community and species examined, which declined especially during the most recent years. Since the effect of fishing effort was negative for several of the metrics, we assume that the declining fishing effort of the Greek fishing fleet (Fig. 2) has contributed to the observed increase in biomass, abundance, species richness and some of the length-related metrics. However, one cannot ignore the possible contribution of other processes which may favour ecosystem productivity resulting in bottom-up effects (Rochet et al. 2010) and/or recruitment success. These may include (i) anthropogenic activities (e.g., aquaculture; Machias et al. 2006), (ii) changes in climatic indices such as the North Atlantic Oscillation index, which has been shown to affect species abundance and distribution, including those of deep-sea species (e.g., Cartes et al. 2009) at least to the population level, and (iii) hydrological changes (e.g., changes in water mass: Souvermezoglou and Krasakopoulou 2005; Bensi et al. 2013). Even though we have not detected a temporal trend in temperature and salinity

in our dataset, we cannot exclude e.g., changes in the centre of gravity of the distribution of some deep-sea species, or other responses. Thus, possible links with climatic changes and the mechanisms involved, remain to be examined.

The effect of fishing was found to linearly affect abundance and N_0 of Chondrichthyes, which are more sensitive to fishing pressure (Stevens et al. 2000; ICES 2005) suggesting that this sub-community can be used as an indicator for the effects of fishing on the study ecosystem. This was also the case for *Helicolenus dactylopterus*, which declined linearly with increasing fishing effort. *H. dactylopterus* is a benthic species, sensitive because of its low growth rate, low fecundity and the distribution of juveniles in areas of intensive fishing activity (D'Onghia et al. 1996; Mytilineou et al. 2006; Sequeira et al. 2009), and important effects of fishing for this species have also been identified in the Central Mediterranean (Dimech et al. 2012). In the North Sea, *R. clavata* has been proposed as an indicator species for which reference points of overexploitation of the community could be defined (ICES 2005). However, in our study, its abundance was not found to respond to fishing effort nor to vary with time over the studied period (where effort decreased); nor did *Squalus blainville* the other Chondrichthyes analysed as a single species. Possibly a longer time series is required to reveal changes in the abundance of these long-lived species. Our results highlight that species with different life history traits respond to fishing pressure in different ways; Chondrichthyes which are generally long-lived species are negatively related to fishing effort whereas some short-lived decapods respond positively and can recover rapidly in abundance and biomass. Specifically, two of the crustacean species considered, *Plesionika heterocarpus* and *Liocarcinus depurator*, seemed to increase in abundance and biomass at high values of fishing effort. This may be caused by indirect trophic effects caused by the removal of their predators (e.g., large fish and octopuses) by fishing, i.e., the predation mortality of these crustaceans would be relaxed at high fishing effort. In addition, since these species are partly scavengers, the positive effects may also be related to a direct increase of food supply from (i) discards and (ii) “non-catch” mortality of benthos in the towpath of the fishing gear (e.g., Catchpole et al. 2006). More complex effects were observed for the whole crustacean sub-community, possibly because of both trophic and fisheries effects, as crustaceans include targeted and non-commercial species with a great diversity of feeding strategies, from scavengers (e.g., *L. depurator*) to small particulate feeders (e.g., *P. heterocarpus*) (Bozzano and Sardà 2002; Cartes et al. 2002). An additional factor contributing to these effects is that a considerable fraction (27%) of the crustacean landings in the area are caught by trawlers (Anon. 2008), the effort of which did not significantly decline during the survey period. It is also worth noting that after 2003 Italian trawlers started targeting deep-sea shrimps in the E. Ionian Sea (Mytilineou and Machias 2007), which may further reflect the decline of *N. norvegicus* during this period. Therefore, monitoring different sub-communities and species may improve appraisals of the effect of fishing, which may be masked in metrics for the whole community because of contrasting life history traits, trophic position and different fishing techniques. Our findings allow us to suggest that a combination of the trends observed in the

abundance of severely affected by fisheries, long-lived and/or low growth rate species (e.g., Chondrichthyes as a group and *H. dactylopterus*) and of some short-lived decapod crustaceans (e.g., *P. heterocarpus*) which proliferate from fishing, may be used in management as indicators of the effect of fishing on the deep-sea resources.

The metrics examined here showed variable sensitivity to fisheries and/or time. Such effects were more common on abundance indices, the number of species (N_0) and some of the length metrics, especially the one related to the lengths of the larger individuals, i.e. L_{max} . The reduction of abundance indices and N_0 caused by increased fishing pressure reflects the direct removal of targeted and non-targeted catch. Specifically, a reduction of species richness at high values of fishing effort does not necessarily imply local extinction of populations, but is in line with the decreased abundance which further decreases the probability of a species to be caught within a sample. However, the improving sorting ability of the personnel on-board scientific survey as years go by cannot be excluded as a possible bias that may have affected the documented increase of species richness during the survey period. Regarding length metrics, the negative effect of high values of fishing effort on large individuals is related to (i) the increased mortality in populations, so that a lower proportion of individuals reach old age and large size (Shin et al. 2005) and (ii) possible evolutionary effects such as selection of early reproduction (Law 2000).

The present study suggests that the E. Ionian Sea megafaunal assemblages have improved during the study period in line with recent stock assessments in the area which report recovery of previously overexploited stocks. Specifically, based on F/F_{msy} and B/B_{msy} (F : fishing mortality; B : stock biomass; msy : maximum sustainable yield), it has been shown that the stock biomasses of *Spicara smaris*, *S. flexuosa*, *Mullus barbatus*, *M. surmuletus* and *Merluccius merluccius* have increased (Anon. 2012; STECF 2012). Our approach underlines that keeping fishing effort at an appropriate overall level may have measurable ecological effects within a short time frame. The currently decreasing trend of fishing effort is mainly an outcome of the decline in the number of fishing vessels, particularly of small scale fisheries, during the study period (Anon. 2008). This seems to substantially contribute to the goal of achieving good environmental status as defined by the Marine Strategy Framework Directive (MSFD) (EU 2010). In particular, biomass, abundance and several size-based indicators, which are related to descriptors 1 (biological diversity) and 3 (exploited species) of the MSFD have increased for the total community as well as for Chondrichthyes, Osteichthyes, Cephalopods and several commercial species. In other words, the improvement of the state of the community seems to involve several taxonomic groups including those sensitive to fishing, e.g., Chondrichthyes (Stevens et al. 2000), as well as fast growing ones e.g., Cephalopods (Caddy and Rodhouse 1998). The observed changes may or may not be sufficient to achieve the overarching goals of e.g., exploiting commercial species at levels capable of producing MSY and maintaining biological diversity. In terms of management, keeping effort at an appropriate level does not explicitly imply effort regulation, and a number of other management tools have been used

to this end (e.g., Worm et al. 2009; Colloca et al. 2013). In the East Ionian Sea, we found strong spatial patterns in fish, crustacean and cephalopod distributions, so that reducing the fishing mortality of a particular population or sub-community might be achievable by setting fishing restrictions in the area where the populations or community is most abundant. In this framework, the metrics used here might allow the identification of the preferred habitats of species and sub-communities and allow management measures to be taken. Finally, taking into account a possible fishing effort reallocation towards deeper waters resulting from EU regulation 1967/2006 (which prohibits trawling within 1.5 nautical mile of the coast and thus reduces available coastal fishing grounds; Tserpes et al. 2011) as well as the increasing interest for deep-sea resources (Mytilineou and Machias 2007), the above results could be useful in designing management plans, particularly under the concept of an ecosystem approach.

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Electronic supplementary materials

Figure S1: Annual box-plots for biomass and abundance indices and mean length for the four sub-communities examined. Figure S2: Annual means and standard errors of biomass and abundance indices and mean length of the ten species examined.

Figures S3–S7: Estimated smooth terms of the parameters contributing to the selected GAMs for metrics of the four sub-communities and ten species examined.

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Annexes: Lists of species included in the analysis

Table A1. List of Osteichthyes species included in the analysis.

<i>Acantholabrus palloni</i>	<i>Epigonus denticulatus</i>	<i>Pagrus pagrus</i>
<i>Argentina sphyraena</i>	<i>Epigonus telescopus</i>	<i>Paralepis speciosa</i>
<i>Arnoglossus imperialis</i>	<i>Epinephelus aeneus</i>	<i>Peristedion cataphractum</i>
<i>Arnoglossus kessleri</i>	<i>Epinephelus guaza</i>	<i>Phycis blennoides</i>
<i>Arnoglossus laterna</i>	<i>Eutrigla gurnardus</i>	<i>Phycis phycis</i>
<i>Arnoglossus rueppelli</i>	<i>Gadella maraldi</i>	<i>Psetta maxima</i>
<i>Arnoglossus thori</i>	<i>Gadiculus argenteus</i>	<i>Scophthalmus rhombus</i>
<i>Aspitrigla cuculus</i>	<i>Gaidropsarus mediterraneus</i>	<i>Scorpaena elongata</i>
<i>Aspitrigla obscura</i>	<i>Gaidropsarus</i> spp.	<i>Scorpaena notata</i>
<i>Aulopus filamentosus</i>	<i>Gnathophis mystax</i>	<i>Scorpaena porcus</i>
<i>Bellotia apoda</i>	<i>Gobius niger</i>	<i>Scorpaena scrofa</i>
<i>Benthocometes robustus</i>	<i>Gobius paganellus</i>	<i>Scorpaena</i> sp.
<i>Benthoema glaciale</i>	<i>Gobius</i> spp.	<i>Serranus cabrilla</i>
<i>Blenniidae</i>	<i>Helicolenus dactylopterus</i>	<i>Serranus hepatus</i>
<i>Blennius ocellaris</i>	<i>Hoplostethus mediterraneus</i>	<i>Solea impar</i>
<i>Boops boops</i>	<i>Hymenocephalus italicus</i>	<i>Solea kleini</i>
<i>Bothus podas</i>	<i>Lepidopus caudatus</i>	<i>Solea</i> spp.
<i>Callanthias ruber</i>	<i>Lepidorhombus boscii</i>	<i>Solea vulgaris</i>
<i>Callionymus lyra</i>	<i>Lepidorhombus whiffiagonis</i>	<i>Sparus aurata</i>
<i>Callionymus maculatus</i>	<i>Lepidotrigla cavillone</i>	<i>Sphoeroides cutaneus</i>
<i>Callionymus risso</i>	<i>Lepidotrigla dieuzeidei</i>	<i>Spicara flexuosa</i>
<i>Callionymus</i> spp.	<i>Leusueurigobius friesii</i>	<i>Spicara maena</i>
<i>Capros aper</i>	<i>Lophius budegassa</i>	<i>Spicara smaris</i>
<i>Caranx rhonchus</i>	<i>Lophius piscatorius</i>	<i>Stomias boa</i>
<i>Carapus acus</i>	<i>Macrorhamphosus scolopax</i>	<i>Symbolophorus veranyi</i>
<i>Centracanthus cirrus</i>	<i>Merlangius merlangus</i>	<i>Symphodus</i> spp.
<i>Centrolophus niger</i>	<i>Merluccius merluccius</i>	<i>Symphurus ligulatus</i>
<i>Cepola macrophthalmia</i>	<i>Microchirus ocellatus</i>	<i>Symphurus nigrescens</i>
<i>Cerastocopelus maderensis</i>	<i>Microchirus variegatus</i>	<i>Symphurus</i> spp.
<i>Chlorophthalmus agassizii</i>	<i>Micromesistius poutassou</i>	<i>Synchiropus phaeton</i>
<i>Citharus linguatula</i>	<i>Molva dipterygia</i>	<i>Syngnathus acus</i>
<i>Coelorhynchus coelorhynchus</i>	<i>Monochirus hispidus</i>	<i>Syngnathus</i> spp.
<i>Conger conger</i>	<i>Mugil cephalus</i>	<i>Synodus saurus</i>
<i>Dactylopterus volitans</i>	<i>Mullus barbatus</i>	<i>Trachinus araneus</i>
<i>Deltentosteus quadrimaculatus</i>	<i>Mullus surmuletus</i>	<i>Trachinus draco</i>
<i>Dentex dentex</i>	<i>Muraena helena</i>	<i>Trachinus radiatus</i>
<i>Dentex gibbosus</i>	<i>Nettastoma melanurum</i>	<i>Trigla lucerna</i>
<i>Dentex macrophthalmus</i>	<i>Nezumia sclerorhynchus</i>	<i>Trigla lyra</i>
<i>Dentex maroccanus</i>	<i>Notacanthus bonapartei</i>	<i>Trigloporus lastoviza</i>
<i>Diplodus annularis</i>	<i>Ophichthus rufus</i>	<i>Trisopterus minutus capelanus</i>
<i>Diplodus vulgaris</i>	<i>Pagellus acarne</i>	<i>Uranoscopus scaber</i>
<i>Echelus myrus</i>	<i>Pagellus bogaraveo</i>	<i>Zeus faber</i>
<i>Epigonus constanciae</i>	<i>Pagellus erythrinus</i>	

Table A2. List of Chondrichthyes, Crustaceans and Cephalopod species included in the analysis.

Chondrichthyes	<i>Ebalia granulosa</i>	<i>Pontocaris lacazei</i>
<i>Centrophorus granulosus</i>	<i>Ergasticus clouei</i>	<i>Pontophilus norvegicus</i>
<i>Centrophorus uyato</i>	<i>Ethusa mascarone</i>	<i>Pontophilus spinosus</i>
<i>Chimaera monstrosa</i>	<i>Eurynome aspera</i>	<i>Processa canaliculata</i>
<i>Dalatias licha</i>	<i>Gennadas elegans</i>	<i>Rissoides desmaresti</i>
<i>Dasyatis pastinaca</i>	<i>Goneplax rhomboides</i>	<i>Rissoides pallidus</i>
<i>Etmopterus spinax</i>	<i>Homola barbata</i>	<i>Scyllarides latus</i>
<i>Galeorhinus galeus</i>	<i>Inachus communissimus</i>	<i>Solenocera membranacea</i>
<i>Galeus melastomus</i>	<i>Inachus dorsettensis</i>	<i>Squilla mantis</i>
<i>Heptranchias perlo</i>	<i>Inachus sp.</i>	<i>Stenopus spinosus</i>
<i>Mustelus mustelus</i>	<i>Inachus thoracicus</i>	
<i>Myliobatis aquila</i>	<i>Latreillia elegans</i>	Cephalopoda
<i>Oxynotus centrina</i>	<i>Liocarcinus depurator</i>	<i>Abralia veranyi</i>
<i>Raja asterias</i>	<i>Lysmata seticaudata</i>	<i>Alloteuthis media</i>
<i>Raja brachyura</i>	<i>Macropipus tuberculatus</i>	<i>Alloteuthis subulata</i>
<i>Raja clavata</i>	<i>Macropodia longipes</i>	<i>Bathypolypus sponsalis</i>
<i>Raja miraletus</i>	<i>Macropodia longirostris</i>	<i>Eledone cirrhosa</i>
<i>Raja montagui</i>	<i>Macropodia rostrata</i>	<i>Eledone moschata</i>
<i>Raja naevus</i>	<i>Maja goetziana</i>	<i>Illex coindetii</i>
<i>Raja oxyrinchus</i>	<i>Maja squinado</i>	<i>Loligo forbesi</i>
<i>Raja polystigma</i>	<i>Medaeus couchi</i>	<i>Loligo vulgaris</i>
<i>Raja radula</i>	<i>Munida iris</i>	<i>Neorossia caroli</i>
<i>Raja rondeleti</i>	<i>Munida rugosa</i>	<i>Octopus macropus</i>
<i>Raja undulata</i>	<i>Munida sp.</i>	<i>Octopus salutii</i>
<i>Scyliorhinus canicula</i>	<i>Nematocarcinus ensifer</i>	<i>Octopus vulgaris</i>
<i>Squalus acanthias</i>	<i>Nephrops norvegicus</i>	<i>Pteroctopus tetracirrhus</i>
<i>Squalus blainville</i>	<i>Palicus caronii</i>	<i>Rondeletiola minor</i>
<i>Torpedo marmorata</i>	<i>Parapenaeus longirostris</i>	<i>Rossia macrosoma</i>
<i>Torpedo nobiliana</i>	<i>Parthenope macrochelous</i>	<i>Scaevurgus unicolor</i>
<i>Torpedo torpedo</i>	<i>Parthenope massena</i>	<i>Sepia elegans</i>
	<i>Pasiphaea sivado</i>	<i>Sepia officinalis</i>
Crustacea	<i>Penaeus kerathurus</i>	<i>Sepia orbignyana</i>
<i>Alpheus glaber</i>	<i>Pilumnus spinifer</i>	<i>Sepietta neglecta</i>
<i>Aristaeomorpha foliacea</i>	<i>Pisa armata</i>	<i>Sepietta oweniana</i>
<i>Aristeus antennatus</i>	<i>Plesionika acanthonotus</i>	<i>Sepietta spp.</i>
<i>Bathynectes maravigna</i>	<i>Plesionika antigai</i>	<i>Sepiolo affinis</i>
<i>Calappa granulata</i>	<i>Plesionika edwardsii</i>	<i>Sepiolo intermedia</i>
<i>Calappa pelii</i>	<i>Plesionika giglioli</i>	<i>Sepiolo ligulata</i>
<i>Calocaris macandreae</i>	<i>Plesionika heterocarpus</i>	<i>Sepiolo rondeleti</i>
<i>Chlorotocus crassicornis</i>	<i>Plesionika martia</i>	<i>Sepiolo spp</i>
<i>Dorippe lanata</i>	<i>Polycheles typhlops</i>	<i>Todaropsis eblanae</i>
<i>Dromia personata</i>	<i>Pontocaris cataphractus</i>	