



Contribution to the Themed Section: 'Seascape Ecology' Original Article

Community – environment interactions explain octopus-catshark spatial overlap

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The octopus *Eledone cirrhosa* and the catshark *Scyliorhinus canicula* present the same feeding habits and distributional preferences in the Mediterranean Sea. We explore patterns of spatial overlap between these species to address coexistence and infer possible competition from spatial patterns in the western Mediterranean Sea. A spatially explicit modelling approach revealed that spatial overlap mainly responded to the distribution of shared resources, where coexistence is allowed by different ecological processes. Catshark (k-strategy) was highly abundant and widely distributed. However, the fluctuating population dynamics of octopus (r-strategy) explained the variations in spatial patterns of overlap. Spatial structuring across the study area was observed both in population distributions and in species interactions (coexistence or exclusion). Areas with high resources in terms of specific prey items (Catalan Sea) or alternative supplies, such as niche opportunities and ecosystem functions defined by community diversity (Balearic Islands), favoured species coexistence. Sea surface temperature showed opposite effects on overlap in northern and southern regions of the study area, which were not related to differences in species sensitivity. We suggest a surface trophic link, where different phytoplankton communities at each region might have opposite responses to temperature. This triggers contrasting mechanisms of food transfer to deeper benthic communities that subsequently facilitates species overlap. Characterizing how benthic and pelagic seascape properties shape species interactions across space and time is pivotal to properly address community spatial dynamics and move towards ecosystem-based management for sustainable fisheries and conservation planning.

Keywords: benthic-pelagic coupling, coexistence, competition, *Eledone cirrhosa*, Mediterranean, *Scyliorhinus canicula*, spatial distribution, species interactions.

Introduction

Species and populations are typically non-randomly allocated in the nature. How they are distributed is a cornerstone in our knowledge of marine ecosystems, not only for addressing ecological and biogeographic questions but also for management and conservation, forecasting and assessment of global change impacts (Dambach and Rödder, 2011; Albouy *et al.*, 2014). Often, species distribution research has focused on the relationships between abundance and

environmental conditions. Other factors such as resource availability, community complexity, or interactions among species are more usually than not ignored, despite their importance in dictating spatial patterns of species across different seascapes (Ciannelli *et al.*, 2008; Kordas *et al.*, 2011; Johnson *et al.*, 2013). Multispecies and ecosystem models are an exception because they take into account and quantify interspecific and trophic relationships. However, spatial patterns of foodwebs and ecosystem functioning

are usually excluded due to difficulties in the parameterization and the lack of spatial information on all ecosystems compartments (Kempf *et al.*, 2013 and references therein).

The aforementioned limitations of species distribution modeling are manifest in cephalopod research. Recent studies addressed the keystone role of cephalopods in foodwebs (Coll *et al.*, 2008, 2013; André *et al.*, 2010; Gasalla *et al.*, 2010), but usually trophic interactions are described based on stomach contents and prey–predator relationships without spatial context (e.g. Staudinger *et al.*, 2013; Rodhouse *et al.*, 2014 and references therein). There is particularly a dearth of information on competition between cephalopods and other taxonomic groups (but see for instance Butler and Lear, 2009; Link and Auster, 2013). Trophic interactions are crucial in shaping the population dynamics and distributions of cephalopods (Rodhouse *et al.*, 2014; Stewart *et al.*, 2014; Puerta *et al.*, 2015). However, the high dependence of cephalopods on environmental fluctuations (Pierce *et al.*, 2008; Rodhouse *et al.*, 2014) may mask the effect of species interactions in distributional patterns.

In this study, we explore the patterns in spatial overlap between an octopus, *Eledone cirrhosa*, and one of its putative competitors, the catshark *Scyliorhinus canicula*, in the western Mediterranean Sea. Both species are common in the Mediterranean and especially abundant in the western basin (Belcari *et al.*, 2002; Ellis *et al.*, 2009). They are found mainly on the lower continental shelf and the upper slope between 50 and 400 m depth and across all types of substrates (Boyle and Rodhouse, 2005; Gouraguine *et al.*, 2011; Pennino *et al.*, 2013; Puerta *et al.*, 2015). Additionally, the two species exhibit size segregation in depth distributions, with juveniles inhabiting shallower waters, between 100 and 200 m depth (Belcari *et al.*, 2002; Gouraguine *et al.*, 2011; Puerta *et al.*, 2014a). The octopus and the catshark are bottom dwelling and most active at night (Cobb *et al.*, 1995; Sims *et al.*, 2001). They are opportunistic feeders with similar diets (Boyle *et al.*, 1986; Valls *et al.*, 2011; Martinho *et al.*, 2012; Puerta *et al.*, 2015), mainly preying on decapod crustaceans, usually crabs.

Similarities in the distribution and feeding habits between octopus and catshark can suggest a potential competition for resources. However, while inferring imprints of competition from spatial patterns is challenging, studies indicate that competition effects can be discernible from local to regional (few hundred km) geographical ranges (Gotelli *et al.*, 2010; Araújo and Rozenfeld, 2014). Additionally, habitat and/or feeding overlap do not necessarily imply competition, except for instance when resources are in short supply (Hofer *et al.*, 2004; Link and Auster, 2013). Overlap and competition among species also vary with the environmental and community context (Hofer *et al.*, 2004; Orrock and Watling, 2010; Boström-Einarsson *et al.*, 2014; Cormon *et al.*, 2014) due to the spatial variation of population density, resource availability, fishing impact, or species sensitivity to changing habitat conditions.

In this paper, the patterns in spatial overlap between octopus and catshark are assessed in relation to environmental, trophic, and community indicators, along with density-dependent effects. Here we combine three issues of species interactions and spatial distributions, which have been poorly investigated in empirical systems. We examine the interaction (i) between two species of different taxonomic groups, (ii) at the population level (Link and Auster, 2013 and references therein), and (iii) including biotic factors that can dictate their interactions (e.g. species diversity; Johnson *et al.*, 2013) at broad spatio-temporal scales. For this purpose and attempting to infer possible interspecific competition from spatial patterns, a spatially explicit model is used to assess species coexistence at both

local and regional scales in the western Mediterranean. We hypothesize that seascapes with high resources in terms of productivity and diversity will favour the spatial overlap by lessening competitive interactions.

Methods

Biological data

Data on species abundance were collected from the Spanish trawl surveys carried out as part of the Mediterranean International Trawl Survey (MEDITS) project, which has been conducted since 1994. The geographical range of the surveys covers the entire Spanish western Mediterranean Sea, including the Balearic Islands (Figure 1). The MEDITS surveys are performed annually between May and July during day-time. An experimental trawl gear (GOC 73) is used to ensure high catchability of demersal species (Bertrand *et al.*, 2002). Sampling followed an international standardized protocol (Bertrand *et al.*, 2002), with predefined stations based on bathymetric strata (10–50, 50–100, 100–200, 200–500, and 500–800 m) that were approximately replicated each year. For the present study, we included surveys performed from 2001 to 2012 and stations sampled for at least 5 of the 12 available years. Sampling information (date, time, position, depth, duration, distance trawled, vertical, and wing opening of the net) and species weight and number were recorded.

Using the information of each sampling station, the abundances of *E. cirrhosa* and *S. canicula* were transformed to standardized densities (individuals km⁻²). Similarly, total prey densities were calculated; a broad group of benthic crustaceans were selected as potential prey items based on previous research (Valls *et al.*, 2011; Puerta *et al.*, 2015). Community indicators such as total species biomass (g km⁻²) and the Shannon–Wiener diversity index (H') were also calculated per station. Only macrofaunal species (fish, crustaceans, and cephalopods) were included in the calculations of these two indicators, since other taxonomic groups were neither identified nor recorded consistently over time and space. These taxonomical groups account for ~88% of the survey catches. These community indicators can be also interpreted as a proxy of the fishing effort across the study area, since the main consequences of fishing impact is the degradation of the community by diminishing species diversity and biomass (Worm and Lotze, 2009; Coll *et al.*, 2012). Finally, the densities of octopus and catshark were summed across the entire sampling area in each year to estimate plausible population sizes and investigate density-dependent effects on species overlap.

Environmental data

Sea surface temperature (SST, °C) and chlorophyll *a* concentration (Chl_a, mg m⁻³) were obtained from satellite remote sensing data for each sampling station and year. Using 8-day composites files of 4 km resolution, we extracted Chl_a and SST values in a 9-km radius around each sampled station and calculated monthly averages back from the date of sampling. This spatio-temporal resolution allows characterizing the local oceanography of the study area and minimizes cloud impact on the measurements. Environmental data were obtained from different sensors to cover the temporal range of collected biological data. SST dataset were supplied by AVHRR (2001–2002) and MODIS (2003–2012) sensors (NASA's Goddard Space Flight Center), while Chl_a dataset were obtained from Sea WiFS (2001–2002) and MODIS (2003–2012) sensors (NOAA CoastWatch Program). Differences in measurement between sensors are negligible (Walton *et al.*, 1998; Kilpatrick *et al.*,

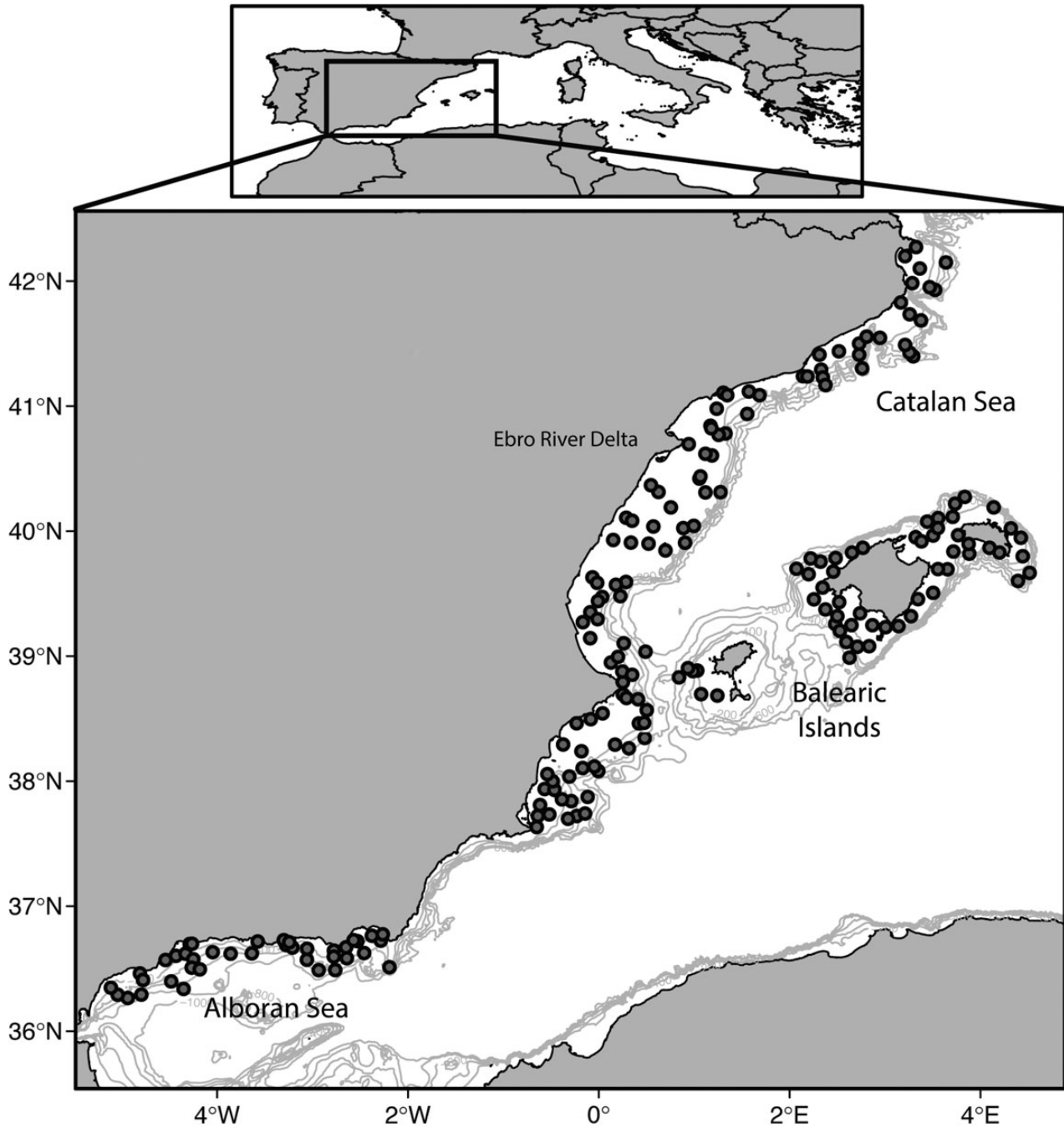


Figure 1. Sampling stations in the western Mediterranean Sea. Isobaths from 200 to 1000 m are shown.

2001). Due to the strong seasonality of the western Mediterranean Sea and the rapid increase in SST during spring and summer (Santoleri *et al.*, 1994), we applied generalized additive models (GAMs) to remove temporal trends in SST values associated with the differences in the dates of surveys. Residuals of SST were retained to be included as an explanatory variable in the model approach.

Data analysis

Overlap index

Spatial overlap between octopus and catshark was calculated as the natural logarithm of multiplied densities (x) of the two species at

each sampling station (defined by latitude, ϕ and longitude, λ) and year (y), as following:

$$O_{(\phi,\lambda),y} = \log(x_{sp1,(\phi,\lambda),y} \cdot x_{sp2,(\phi,\lambda),y}).$$

Only stations where at least one of the species was present were included in the calculation of overlap. Before this calculation, species densities were standardized to make the overlap index dependent only on spatial variability, rather than interannual variability of population abundances. Standardization was performed

as follows:

$$\frac{x_{(\phi,\lambda),y} - \bar{x}_y}{\sigma_y^2} + \min(x_y),$$

where the density of each species at a station and year $x_{(\phi,\lambda),y}$ is demeaned and divided by standard deviation of density in the corresponding year. The minimum density value in the year y was then added to ensure (i) the overlap index were >0 (even if only one of the species were found) and (ii) the normal distribution of data.

In contrast to previous studies, the contribution of neighbour stations to density value at a given station were not taken into account (Ciannelli and Bailey, 2005; Hunsicker et al., 2010), because the distances that the two species move from their dwelling areas (<20 km; Cobb et al., 1995; Rodríguez-Cabello et al., 2004, 2007; Boyle and Rodhouse, 2005) are shorter than the average distance between sampling stations.

Model formulation

GAMs were used to explore the influence of density-dependent effects (population size), trophic resources (prey densities), community indicators (total biomass and diversity), and environment (SST, Chl a) on species overlap. In heterogeneous systems, local conditions experienced by individuals across the geographic gradient can be very different from the mean averaged conditions in the entire region (Bachele et al., 2009; Bartolino et al., 2011; Ciannelli et al., 2012; Puerta et al., 2015). Therefore, we applied a spatially explicit GAM where linear relationships between overlap index and the covariates are assumed, but these relationships are allowed to change smoothly in relation to the geographical position.

In the model formulation,

$$\begin{aligned} O_{(\phi,\lambda),y} = & s_1(\phi, \lambda) + s_2(\text{depth}_{(\phi,\lambda)}) + te(\phi, \lambda, \text{size}) + s_3(\phi, \lambda) \\ & \times \text{prey}_{(\phi,\lambda),y} + s_4(\phi, \lambda) \times \text{biomass}_{(\phi,\lambda),y} + s_5(\phi, \lambda) \\ & \times H_{(\phi,\lambda),y} + s_6(\phi, \lambda) \times \text{SST}_{(\phi,\lambda),y} + s_7(\phi, \lambda) \\ & \times \text{Chl}a_{(\phi,\lambda),y} \end{aligned}$$

geographic position (longitude ϕ , latitude λ) and depth were included as smoothing functions denoted by s . The spatially explicit terms were included for log-transformed prey densities (prey) and total biomass in the community (biomass), diversity index (H), residual SST, and Chl a concentrations. The variation in overlap (response) explained by the spatially explicit terms depends on the weighted sum of the same smoothing function evaluated at different covariate values. Additionally, the effects of population size (size) were tested independently for the two species. To do that, we used the formulation above in two different models, including octopus or catshark annual densities in the size term in each case. This allows evaluating density-dependent effects at different population sizes and testing the contribution of each species to overlap patterns, since large differences in the population abundances between species were observed in the preliminary analysis. A tensor product smoother (te) was included for the size term. Tensor products are more appropriate for interactions fitted over covariates with different units (combining different smoothers, a two-dimensional thin plate regression for ϕ , λ , and univariate cubic regression spline for size). This formulation assumes gradual changes in the overlap distribution related to variations in the population size. To reduce

overfitting, the knots for univariate and two-dimensional smoothers were restricted to 4 and 20, respectively.

Starting from the full model above, a backward stepwise approach was performed by removing one term at a time. Full and reduced models were compared using Akaike information criterion (AIC) as a measure of goodness of fit and genuine cross validation (gCV) as a measure of the complete out-of-sample predicted mean squared error. The latter criterion determines which model was optimal for predictions. The best model was selected by minimizing both AIC and gCV criteria. Standard model diagnostics and residuals checking were performed for homogeneity of variance, the absence of temporal autocorrelation and violation of normality assumptions. Observations and model residuals were also checked for the lack of spatial correlation applying directional variograms and spatial plots to evaluate the best model. Additionally, the coefficients of regression (slopes) between the overlap index and each of the spatially explicit covariates were extracted from the best model. These coefficients (significant slopes based on 95% confidence interval) display the strength of the effect of a given covariate in the overlap at each geographical position. All calculations and models were coded in R software (version 3.1.2.), using the *vegan* and *mgcv* libraries.

Results

Spatial patterns in biotic and environmental factors

Spatial variability of the biotic and environmental factors in the study area is shown in Figure 2. Prey densities are patchily distributed, with higher abundances in the northern area of the mainland (Catalan Sea) and the Balearic Islands. These areas also presented higher community diversity values, especially in the islands. Total community biomass was larger in the southern area (Alboran Sea) and the islands. Chl a concentrations remained very low across the entire region, except in the Alboran Sea close to the Strait of Gibraltar. Finally, a north-south gradient of increasing temperatures is observed from residual SST.

Spatial patterns in overlap

A total of 1297 samples taken during 2001–2012 were included in the analysis (108 ± 14 trawls per year). Densities of catshark were much higher ($250\text{--}800$ individuals km^{-2}) than those of octopus ($60\text{--}170$ individuals km^{-2}). Spatial distribution of species densities and overlap index is shown in Figure 3. The distribution of high-density areas in octopus followed the deep continental shelf from the Catalan Sea down to the Balearic Islands, where intermediate densities were found (Figure 3a). Very low densities were detected in the Alboran Sea. In contrast, the catshark distribution showed high-density values across the entire study region, except the inshore waters in the central coast of the mainland under the influence of Ebro river run-off (Figure 3b). Areas of high species overlap mainly covered the Catalan Sea and the Balearic Islands (Figure 3c), and appeared to coincide with the distribution of *S. canicula*.

Model selection

Two model formulations were tested. They only differed in the inclusion of octopus or catshark population size, but the model outcomes and effects of covariates were the same. In both cases, all predictor covariates were retained except Chl a , which did not present significant effects on the overlap index (Table 1). The density-dependent effects of population size greatly improved the model fits. However, inclusion of octopus population size resulted in a better fit in terms of AIC, gCV, and deviance explained

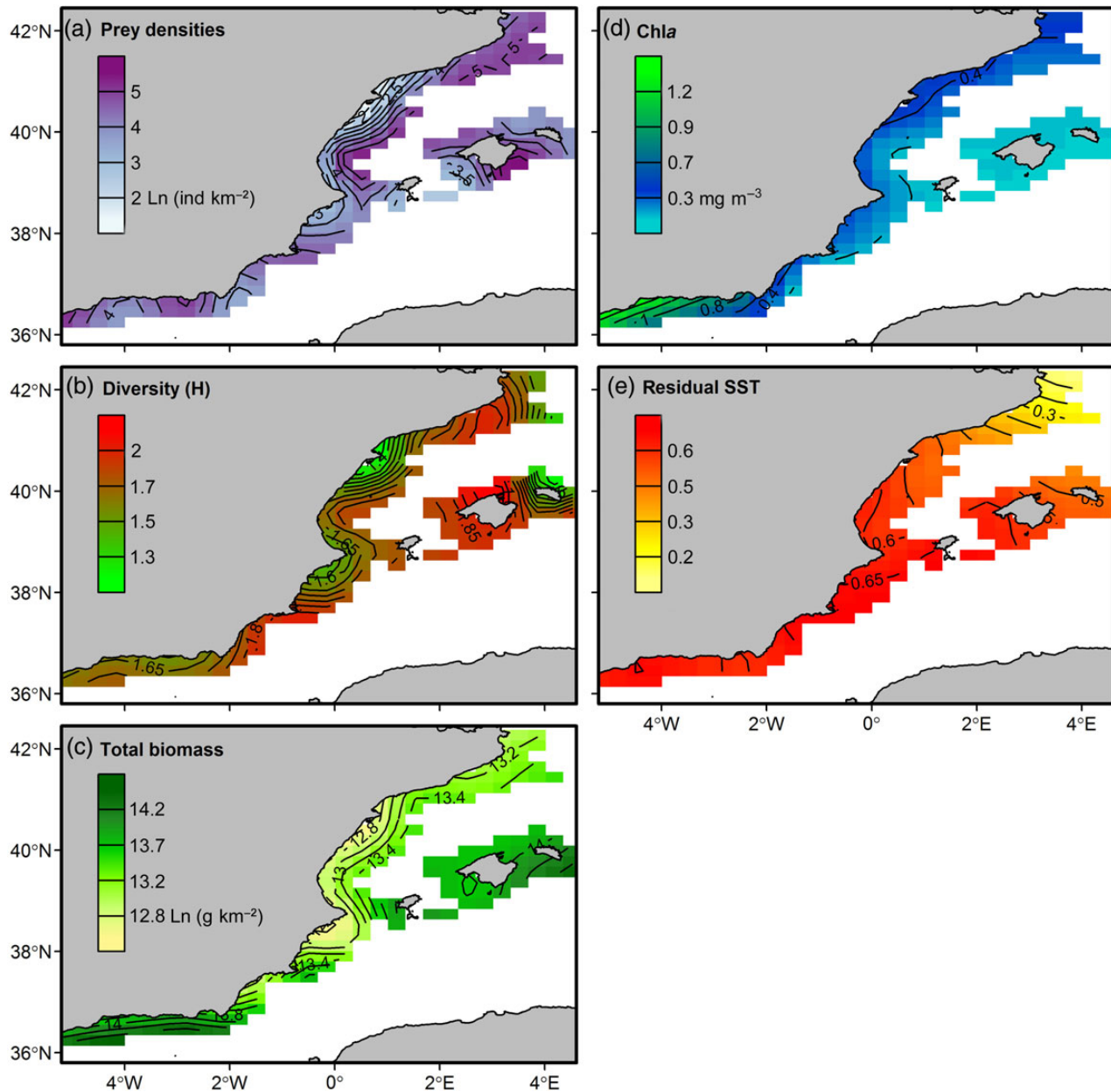


Figure 2. Spatial variability across the study area of the resources (prey densities), community indicators (Shannon–Wiener diversity index, H ; total biomass) and environmental (chlorophyll a concentration, Chla; residual SST) factors. This figure is available in black and white in print and in colour at *ICES Journal of Marine Science* online.

(61.8%). Therefore, the best model selected included the spatially explicit effects of prey densities, total biomass, diversity, and residual SST, along with density-dependent effect of the octopus population size and a mean bathymetric and geographic effect. Directional variograms (90 and 135 directions) of overlap index data showed a noticeable spatial autocorrelation. However, the model residuals did not show any dependence pattern (Supplementary Figure S1). Since spatial correlation structure disappeared from the model, it should not influence the estimates and uncertainty.

Density-dependent effect of population size

Increases in the annual population size of octopus resulted in gradual changes in the overlap with catshark (Figure 4). Two spatial patterns were detected in relation to the variation in the

overlap distribution. First, the overlap increased in the regions where high overlap values were previously detected, the Balearic Islands and the Catalan Sea. The Alboran Sea and the central coast of the mainland stayed uniform with low overlap values regardless of population size. Second, considering only the high overlap areas, overlap values increased from the boundaries to the centre of overlap area as the population size increased.

Spatially explicit effects

Significant slopes were found between the overlap index and all covariates included as spatially explicit terms in the model, showing contrasting local effects across the study area (Figure 5). Positive effects of prey densities were observed in the Catalan Sea and the islands, where the maximum overlap

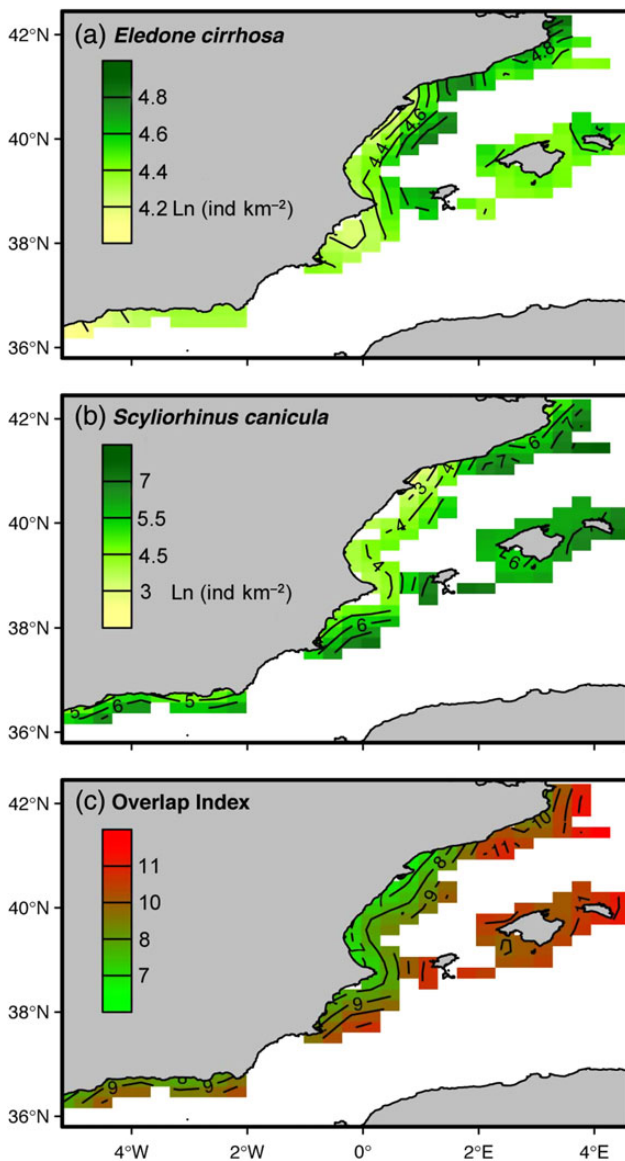


Figure 3. Spatial distribution of log-transformed densities of octopus (*Eledone cirrhosa*) and catshark (*Scyliorhinus canicula*) and the overlap index estimated for the two species. This figure is available in black and white in print and in colour at ICES Journal of Marine Science online.

between the species was observed. In contrast, the positive effects of total biomass in the community were generalized across the entire region. However, the strength of this effect was higher in the areas with maximum overlap. A different pattern was observed for the effects of the community diversity. Positive effects were present in the islands and continuing southwards throughout the mainland coast, following approximately the boundary of the overlap distribution. Additionally, negative effects of diversity were detected in the most southwestern region, close to the Strait of Gibraltar. Finally, both negative and positive effects were also observed related to residual SST. In the Catalan Sea, the overlap was negatively influenced by temperature, while the southern boundary of the overlap distribution and part of the Alboran Sea presented positive effects. The colder and warmer SST records characterized, respectively, these two regions.

Discussion

The spatial patterns of the octopus *Eledone cirrhosa* and the catshark *Scyliorhinus canicula* revealed that the overlap of these two species increased as their shared prey densities (benthic crustaceans) increased. Competition between the species could be expected as resource limitation might occur at small spatial and temporal scales in the western Mediterranean Sea. Oligotrophy, pronounced seasonality in productivity (Estrada, 1996; Bosc et al., 2004; D'Ortenzio and Ribera d'Alcalà, 2009) and degradation of habitat conditions, community, and species interactions by fishing pressure (Coll et al., 2006, 2012; Corrales et al., 2015) can all lead to food limitations. Our model approach allows considering spatial patterns in a relative broad geographic area, while the species overlap and its drivers are evaluated at local scales where imprints of competitive interactions can be still discernible (Araújo and Rozenfeld, 2014). However, deducing processes from spatial patterns are still a challenge in ecological research and inferences should be taken with caution. The results showed that spatial and diet overlap does not necessarily imply competition and a constraint in the species-specific distributions. This is in accordance with the theoretical framework of species interactions which indicates that species overlap at broad scales are only evident when actually there is no negative relationship between those species (Gotelli et al., 2010; Araújo and Rozenfeld, 2014). As we hypothesized, different ecological mechanisms allow for successful coexistence of species with the same resource requirements (Hofer et al., 2004). Density-dependent, environmental, trophic, and community factors play a role in the coexistence between the octopus and the catshark across the study area.

Overlap was not spatially homogeneous and distribution. Catshark showed much higher densities than octopus across the study area. Additionally, the spatial pattern in the overlap was similar to the catshark distribution. However, variability in octopus population size better described variations in overlap patterns. The differences in the species life history strategies may explain those patterns. Catshark is a long-lived species (k-strategy), which usually presents densities close to carrying capacity and successive coexisting generations. The long lifespan and the demographic buffering support more steady populations over time, and higher success in fluctuating environments (Reznick et al., 2002 and references therein). Opposite traits (r-strategy) define the cephalopod life cycles. The short lifespan with no overlap among generations, make populations very sensitive to changing conditions (Pierce et al., 2008), especially at local scales (Puerta et al., 2014b). They display high fluctuations as a consequence.

High overlap values (i.e. high densities of the two species) were detected in the northern mainland (Catalan Sea) and the Balearic Islands, indicating a low or lack of competition in these areas. In contrast, the low overlap areas corresponded to low densities of catshark and octopus and were not affected by species population size. Catshark was only absent in the central coast of the mainland, where low biomass and diversity were also observed. These patterns in the community indicators agree with the high fishing pressure observed nearby the Ebro river mouth (Coll et al., 2012; Navarro et al., 2015, 2016). Due to the long-living strategy, elasmobranchs are very sensitive to long-term disturbances such as fishing pressure since populations present low resilience and recovery (Guijarro et al., 2012; Barausse et al., 2014; Navarro et al., 2015, 2016; Quetglas et al., 2016). In accordance with previous research (Cartes et al., 2013; Navarro et al., 2015, 2016), these results point the high fishing pressure of this area as responsible for the decline of elasmobranch

Table 1. Comparison of full and reduced GAMs of overlap index.

Model	AIC	gCV	Dev (%)
$O_{(\phi,\lambda)} = s_1(\phi,\lambda) + s_2(\text{depth}_{(\phi,\lambda)}) + \text{te}(\phi,\lambda,\text{size.S}) + s_3(\phi,\lambda)*\text{prey}_{(\phi,\lambda),y} + s_4(\phi,\lambda)*\text{biomass}_{(\phi,\lambda),y} + s_5(\phi,\lambda)*H_{(\phi,\lambda),y} + s_6(\phi,\lambda)*\text{SST}_{(\phi,\lambda),y} + s_7(\phi,\lambda)*\text{Chla}_{(\phi,\lambda),y}$	4720.57	2.43	60.70
$O_{(\phi,\lambda)} = s_1(\phi,\lambda) + s_2(\text{depth}_{(\phi,\lambda)}) + \text{te}(\phi,\lambda,\text{size.S}) + s_3(\phi,\lambda)*\text{prey}_{(\phi,\lambda),y} + s_4(\phi,\lambda)*\text{biomass}_{(\phi,\lambda),y} + s_5(\phi,\lambda)*H_{(\phi,\lambda),y} + s_6(\phi,\lambda)*\text{SST}_{y(\phi,\lambda),y}$	4717.79	2.41	60.50
$O_{(\phi,\lambda)} = s_1(\phi,\lambda) + s_2(\text{depth}_{(\phi,\lambda)}) + \text{te}(\phi,\lambda,\text{size.S}) + s_3(\phi,\lambda)*\text{prey}_{(\phi,\lambda),y} + s_4(\phi,\lambda)*\text{biomass}_{(\phi,\lambda),y} + s_5(\phi,\lambda)*H_{(\phi,\lambda),y}$	4719.72	2.39	60.40
$O_{(\phi,\lambda)} = s_1(\phi,\lambda) + s_2(\text{depth}_{(\phi,\lambda)}) + \text{te}(\phi,\lambda,\text{size.E}) + s_3(\phi,\lambda)*\text{prey}_{(\phi,\lambda),y} + s_4(\phi,\lambda)*\text{biomass}_{(\phi,\lambda),y} + s_5(\phi,\lambda)*H_{(\phi,\lambda),y} + s_6(\phi,\lambda)*\text{SST}_{(\phi,\lambda),y} + s_7(\phi,\lambda)*\text{Chla}_{(\phi,\lambda),y}$	4704.83	2.43	61.80
$O_{(\phi,\lambda)} = s_1(\phi,\lambda) + s_2(\text{depth}_{(\phi,\lambda)}) + \text{te}(\phi,\lambda,\text{size.E}) + s_3(\phi,\lambda)*\text{prey}_{(\phi,\lambda),y} + s_4(\phi,\lambda)*\text{biomass}_{(\phi,\lambda),y} + s_5(\phi,\lambda)*H_{(\phi,\lambda),y} + s_6(\phi,\lambda)*\text{SST}_{(\phi,\lambda),y}$	4700.87	2.38	61.80
$O_{(\phi,\lambda)} = s_1(\phi,\lambda) + s_2(\text{depth}_{(\phi,\lambda)}) + \text{te}(\phi,\lambda,\text{size.E}) + s_3(\phi,\lambda)*\text{prey}_{(\phi,\lambda),y} + s_4(\phi,\lambda)*\text{biomass}_{(\phi,\lambda),y} + s_5(\phi,\lambda)*H_{(\phi,\lambda),y} + s_6(\phi,\lambda)*\text{SST}_{(\phi,\lambda),y}$	4708.82	2.40	61.20

Full model of overlap index ($O_{(\phi,\lambda)}$) includes longitude (ϕ), latitude (λ), depth, *E. cirrhosa* (size.E) or *S. canicula* (size.S) population size, prey densities (prey), total biomass in the community (biomass), diversity (H), sea surface temperature (SST) and chlorophyll concentration (Chla) as covariates. Dev, deviance explained; AIC, Akaike Information Criterion; gCV, genuine Cross Validation. Best model is in bold.

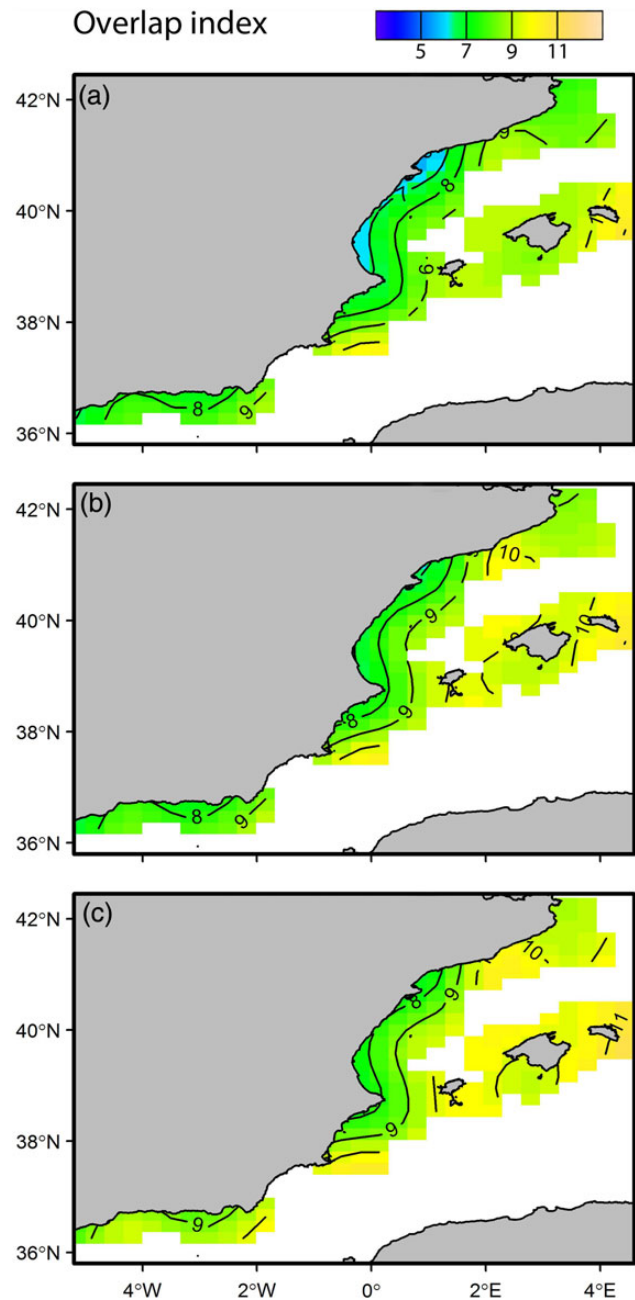


Figure 4. Changes in the spatial patterns of overlap index between octopus and catshark, with increases in the octopus population size. (a) Population size = 3000 ind km². (b) Population size = 9000 ind km². (c) Population size = 20 000 ind km². This figure is available in black and white in print and in colour at ICES Journal of Marine Science online.

populations, along with changes in salinity that can lessen habitat suitability. In contrast, the fast-living strategy makes cephalopod populations highly resilient and therefore, their spatial distribution is mainly forced by the short-term environmental variability, being no affected by fishing impact (Caddy and Rodhouse, 1998; Coll et al., 2013; Navarro et al., 2015; Quetglas et al., 2016). The high hydro-dynamism and varying conditions in the southern area (Alboran Sea) may make this area less suitable to cephalopods (Puerta et al., 2015). High densities in prey and catshark and low in octopus found in the Alboran Sea could also reflect a prior

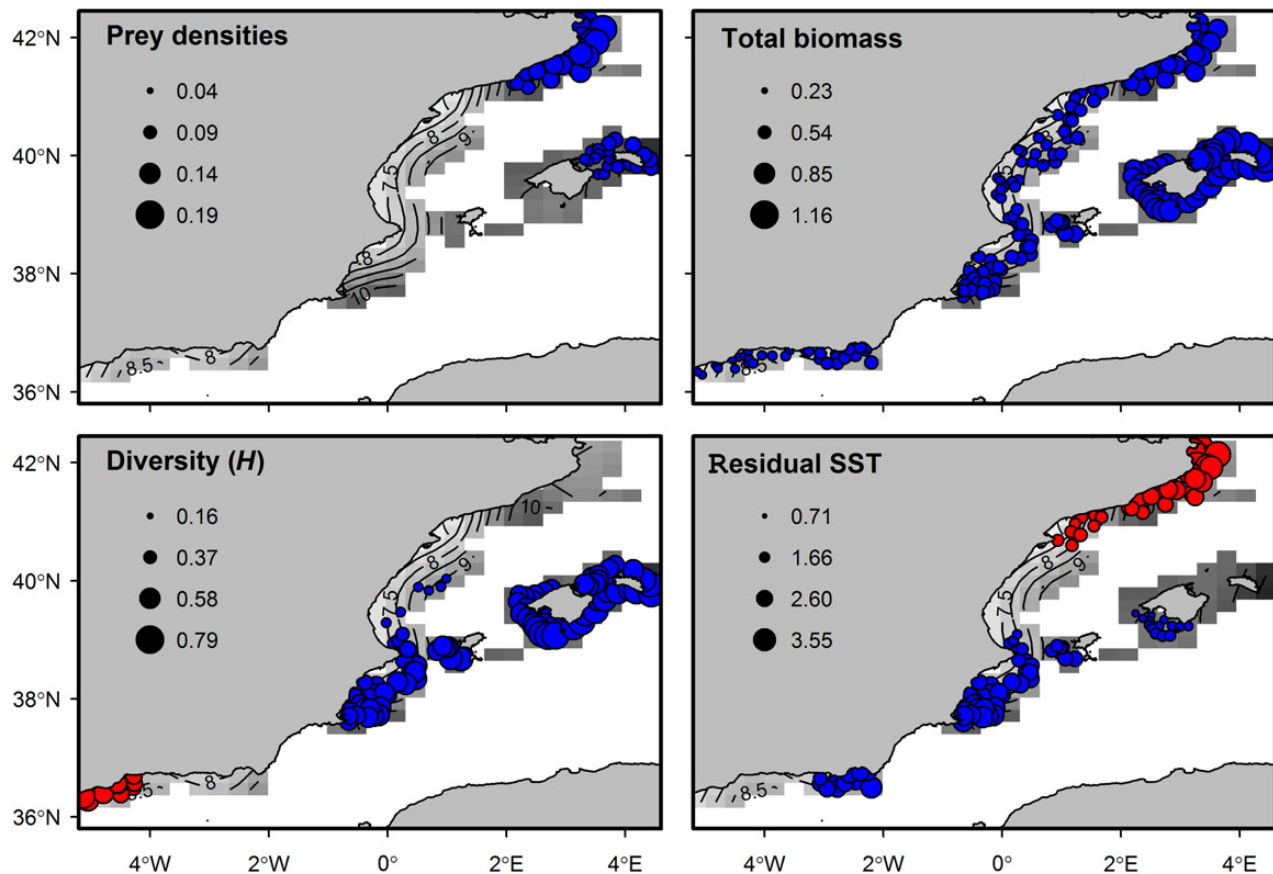


Figure 5. Spatially explicit effects of resources (prey densities), community indicators (Shannon – Wiener diversity index, H ; total biomass), and environmental (residual SST) factors on the overlap index. Only significant positive (blue) and negative (red) effects (regression slopes based on 95% confidence interval) are shown. Patterns of spatial overlap are presented (grey contour), with high and low values of overlap indicated by dark and light grey shading, respectively. This figure is available in black and white in print and in colour at *ICES Journal of Marine Science* online.

competitive exclusion process in this area. However, the effects of other factors not considered in this study, e.g. substrate, predation, or local seasonality in octopus populations (Vargas-Yáñez *et al.*, 2009; Puerta *et al.*, 2014b) cannot be discarded.

According to the species range hypothesis, populations living at distributional boundaries are more influenced by environmental changes because habitat conditions are less suitable there than in the core distribution area (Rosenzweig, 1991; Brunel and Boucher, 2006). In a similar way, species overlap was more sensitive to population size effects in the boundaries of high overlap areas, i.e. Catalan Sea and Balearic Islands, where prey densities were lower compared with the core. As predator population sizes increased, their spatial overlap first increased in the boundaries, which might reflect a strategy to reduce competition and diversify diets (see below). In contrast, under high-population densities, the species overlap extended to the central area, where higher prey densities were found. In accordance with these results, positive effects of prey were observed in the high overlap areas. These results reinforced our hypothesis of shared resources as a mechanism for spatial overlap, where coexistence is allowed by other ecological processes. Despite the considerable fishing pressure reported in the Catalan Sea (Moranta *et al.*, 2008; Quetglas *et al.*, 2012; Navarro *et al.*, 2015, 2016), intermediate and high values of biomass and diversity, respectively, were observed in this area. The Catalan Sea is one of the most productive areas in the western Mediterranean due to the influence of the upwelling

and nutrient-rich waters from the Gulf of Lions (Estrada, 1996; D’Ortenzio and Ribera d’Alcalà, 2009) that can supply enough resources to maintain prey and competitor populations at relatively high densities.

Very high diversity was observed around the Balearic Islands, where the high overlap was more related to this factor than to prey densities. High species diversity is associated with complex, diverse, and “healthy” seascapes in structure and functioning (Thrush *et al.*, 2006; Foley *et al.*, 2010 and references therein). This pattern is in agreement with the lower fishing pressure and better state of conservation observed in the islands compared with the mainland areas (Moranta *et al.*, 2008; Quetglas *et al.*, 2012; Navarro *et al.*, 2015, 2016). These systems provide more opportunities to exploit different resources, thus favouring species coexistence (Bonin *et al.*, 2009; Geange and Stier, 2010). Opportunistic species with wide range of prey items, such as octopus and catshark, may show slightly different feeding habits to avoid competition in high resource and complex ecosystems. For instance, in addition to benthic crustaceans, the two species also consume polychaetes, molluscs, or small fishes (Valls *et al.*, 2011; Puerta *et al.*, 2015). These results are in agreement with the regional effect observed for total biomass in the community, which showed a general increment in overlap when resources (specific prey items and others) are higher.

In the western Mediterranean, trophic pathways are the most plausible link between surface conditions, such as SST, and benthic

communities (Cartes *et al.*, 2009; Fanelli *et al.*, 2013). Residual SST showed contrasting spatial effects on overlap along the temperature–geographic gradient. Similar SST spatial effects were also detected in the distribution of the two species (Supplementary Figure S2), suggesting a common response to SST in the benthic community. This response is likely related to differences in the foodwebs and the energy transfer efficiency between northern and southern regions of the study area (Fanelli *et al.*, 2013). Benthic communities are mainly supported by surface primary production throughout vertical flux of organic matter (Turner, 2015 and references therein), which in turn depend on the type of phytoplankton community (Guidi *et al.*, 2009). In the western Mediterranean, phytoplankton composition change seasonally from a dominance of large cells during winter and spring blooms to a higher contribution of the pico-size fraction in summer (Agawin *et al.*, 1998, 2000; Arin *et al.*, 2005). Residuals of SST indicated that northern and southern areas were at different stages of the seasonal transition during spring (Figure 2). Therefore, opposite spatial effects of SST might reflect different mechanisms supplying resources from surface to deeper benthic communities via primary producers that lastly favour species overlap.

Lower values and negative spatial effects of SST observed in the Catalan Sea might be associated with the influence of colder and nutrient-richer waters from the Gulf of Lions over time (Miquel *et al.*, 2011; Heimbürger *et al.*, 2013; Estrada *et al.*, 2014) that trigger the spring bloom (Estrada, 1996; D’Ortenzio and Ribera d’Alcalá, 2009). In contrast, the southern areas are warmer and more oligotrophic, showing no blooms (D’Ortenzio and Ribera d’Alcalá, 2009). At the residual SST observed here, pico-phytoplankton community is expected to be already dominant (Agawin *et al.*, 1998, 2000; Partensky *et al.*, 1999; Arin *et al.*, 2005). Warmer temperatures increase productivity and turnover rates of pico-size cells (Agawin *et al.*, 1998, 2000), which might explain the positive effects of SST. Regardless of the mechanism, the rapid vertical fluxes (few days from subsurface production to seabed, Peterson *et al.*, 2005) might favour the octopus–catshark overlap. It is worth noting that during spring, a deep chlorophyll maximum is also observed under the thermocline (Estrada, 1996), which may also influence the benthic community.

The present study highlights the necessity of a deeper knowledge in species interactions combining small and large spatial scales. Distribution and interaction patterns between species arose from local variability in the seascapes across geographical ranges, where community and trophic features play an important role. However, some other factors should be considered in future research to improve the inference of competitive interactions from spatial patterns. For instance, information on fishing pressure could provide more accurate description of the spatial pattern in overlap. Additionally, the segregation by size described for the two species can also play a role in the octopus–catshark competitive interactions. The results described a spatial structuring not limited to population distributions and also observed for the species interactions (coexistence or exclusion). Areas with high resources in terms of specific prey items (Catalan Sea) or alternative supplies, such as niche opportunities and ecosystem functions, defined by community diversity (Balearic Islands) favoured species coexistence. Our study also suggests that pelagic seascapes (surface temperature and primary production) are not independent of the benthic realm, and the dynamic benthic–pelagic coupling needs to be taking into account in oligotrophic systems such as the Mediterranean Sea. Characterizing species interactions across space and time is pivotal to properly

address community spatial dynamics and move towards ecosystem-based management (Sexton *et al.*, 2009; Foley *et al.*, 2010; Link and Auster, 2013) for sustainable fisheries and conservation planning.

Supplementary data

Supplementary material is available at the ICESJMS online version of the manuscript.

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