

# Role of hydro-climatic and demographic processes on the spatio-temporal distribution of cephalopods in the western Mediterranean

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**ABSTRACT:** Fluctuations in marine populations occur both in terms of abundance and distributional ranges, and this has major implications for marine ecology and fisheries management. However, little is known about the variability in, and factors influencing, spatial dynamics in marine groups other than fish. Using time series data from trawl surveys conducted in the western Mediterranean Sea from 1994 to 2012, we analysed the variability in population distribution (latitude, longitude and depth) of 2 cephalopod species with contrasting life histories, viz. the nekto-benthic squid *Illex coindetii* and the benthic octopus *Eledone cirrhosa*. We investigated the influence of demographic information (population density and mean individual size) together with environmental variables (including chlorophyll *a* concentration, runoff, precipitation, temperature and climate) to identify the main drivers shaping the cephalopod distributions in 4 shelf regions with contrasting oceanographic and geographic conditions. Marked inter-annual fluctuations were found in the distribution of the 2 species. In general, squid and octopus populations were affected by the same variables, but the effect of each variable depended on the species and study region. Different life strategies resulted in contrasting responses to the environment, with *I. coindetii* associated with variables contemporary to spring surveys. In contrast, *E. cirrhosa* was primarily affected by conditions during the previous winter. Vertical distribution was mainly explained by individual body length, while chlorophyll, temperature or local climate proved to be more important for geographical displacements.

**KEY WORDS:** Spatio-temporal distribution · Spatial ecology · *Illex coindetii* · *Eledone cirrhosa* · Demography · Hydro-climatic conditions

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## INTRODUCTION

Understanding the mechanisms shaping the fluctuations of marine populations has been the core of fisheries research since its beginnings in the last century (Hjort 1914). However, in the last few decades, there has been increasing evidence that changes in marine species abundance over time are often

accompanied by equally large-scale variations in spatial distribution patterns (Ciannelli et al. 2013 and references therein). This has significant implications for marine ecology (e.g. trophic interactions) and fisheries management. Additionally, the understanding of the complex relationships between abiotic and biotic processes is essential for a complete description and interpretation of the distributional changes

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in populations (Swain 1999). Thus, spatial distribution analyses (e.g. geostatistics, variograms, dispersal indices, spatially-explicit regression analyses) have been demonstrated to be efficient tools to identify patterns of variation in marine populations at different spatio-temporal scales, due to their direct link to habitat characteristics, environmental variables and biological processes such as recruitment, spawning, trophic migrations and species demography (Spencer 2008, Bachelier et al. 2009, Tamdrari et al. 2010).

Although spatial ecology studies have increased significantly for marine fish populations over recent years (e.g. Bachelier et al. 2009, Tamdrari et al. 2010, Engelhard et al. 2011), there are comparatively few studies on other harvested taxonomic groups such as cephalopods (see for instance Waluda & Pierce 1998, Wang et al. 2003, Smith et al. 2013). Cephalopods play a pivotal ecological role in marine ecosystems, being opportunistic predators feeding on a great variety of fishes and crustaceans, and are important prey of fishes, marine mammals and seabirds (Piatkowski et al. 2001 and references therein). The importance of cephalopods in fisheries has risen in recent decades (Hunsicker et al. 2010), with landings increasing steadily worldwide from the 1950s (FAO 2012). Owing to their rapid growth rates, short life span (most cephalopods are single-season breeders that die soon after reproduction takes place) and fast population turnover, cephalopods show high sensitivity to environmental changes, which result in important inter-annual fluctuations in population abundances (Boyle & Rodhouse 2005) that might affect entire ecosystem dynamics (André et al. 2010). In addition to this sensitivity to environmental conditions, other effects such as fishing impact, trophic interactions or migratory behaviour have been reported to affect the distribution and abundance of cephalopod populations (Caddy & Rodhouse 1998, Semmens et al. 2007, Hunsicker & Essington 2008).

Changes in spatial distribution are often related to migratory movements, which are very common in cephalopods either by vertical nycthemeral movements or spatial migrations related to feeding or spawning over extensive areas (Boyle & Rodhouse 2005). Currently, most available studies dealing with spatial movements in cephalopods have analysed the effects of environmental parameters on population abundance (Pierce et al. 1998, Balguerías et al. 2002, Denis et al. 2002) and structure (Ceriola et al. 2006, Lefkaditou et al. 2008). However, little attention has been devoted to investigate the effect of environmental and demographic processes on horizontal and vertical movements of cephalopod populations. To

shed light on these aspects, we analysed the populations of 2 cephalopod species from the Mediterranean Sea, the short-fin squid *Illex coindetii* (Ommastrephidae) and the horned octopus *Eledone cirrhosa* (Octopodidae). In that area, these species are the most frequent and abundant cephalopods (González & Sánchez 2002, Pertierra & Sánchez 2005, Pierce et al. 2010), having an important commercial value as by-catch (Sartor et al. 1998). Both species are mainly found on the lower continental shelf and upper slope between 50 and 400 m depth (Boyle & Rodhouse 2005), although they show contrasting life histories. *I. coindetii* is a fast-swimming nekto-benthic squid, but is usually associated with the bottom (Bakun & Csirke 1998, Sánchez et al. 1998, Quetglas et al. 2014). Spawning takes place all year, with seasonal peaks in spring and summer. Generalist diet and vertical nycthemeral movements and spring migrations towards the continental shelf are characteristic of populations from the Mediterranean Sea (Sánchez et al. 1998). In contrast, *E. cirrhosa* is a benthic octopus that crawls along the sea bottom (Boyle & Rodhouse 2005), with a diet based on decapod crustaceans, and strictly seasonal spawning occurs in spring after a migration shoreward. Recruits can also appear during spring, since *E. cirrhosa* has a maximum life span of 2 yr (Sánchez et al. 2004). Due to such contrasting life histories and habitats, we expect that these species would respond differently to environmental and demographic drivers, resulting in different inter-annual changes in their distributions.

The objective of the present study was to determine the key drivers that shape the spatio-temporal distribution of the 2 cephalopod species in the western Mediterranean. This is an oligotrophic and oceanographically heterogeneous area, highly influenced by the interchange of Atlantic and Mediterranean water masses through the Strait of Gibraltar (Millot 1999). Specifically, we aimed to analyse the effects of demography (population density and mean individual size) together with environmental variables (including chl *a* concentration, runoff, precipitation, hydrography and climate) on bathymetric and geographic changes in population distribution.

## MATERIALS AND METHODS

### Study area

The study area covers the entire Mediterranean coast of the Iberian Peninsula, from its southernmost (Strait of Gibraltar) to the northernmost (Cape of

Creus) points, including the Balearic Islands (Fig. 1a). For data analysis, however, we considered 4 different regions characterized by contrasting oceanographic conditions. The first region comprises the eastern Iberian coast, from the Cape of Palos to the Cape of Creus, including the Ibiza Channel (Fig. 1b). This area is mainly influenced by the northern current of Mediterranean waters flowing southwards along the coast on their way back to the Strait of Gibraltar (Pinot et al. 2002, Monserrat et al. 2008). This current bifurcates in the Ibiza Channel, with a first branch continuing southward and a second branch flowing north-eastwards along the north-western slope of the Balearic Islands (Monserrat et al. 2008, Fig. 1a).

The second region covers the waters off the Balearic Islands, excluding the Ibiza Channel (Fig. 1c). We

additionally subdivided this region into north and south subareas, an operational subdivision which is further supported by known contrasting oceanographic conditions (López-Jurado et al. 2008, Monserrat et al. 2008). The northern subarea corresponds to the Balearic sub-basin and is surrounded by the Balearic Current, which is mainly influenced by atmospheric forcing and is characterized by cold and highly saline Mediterranean waters (Fig. 1a). By contrast, the southern subarea, included in the Algerian sub-basin, receives warmer and less saline Atlantic waters (Fig. 1a) and is mainly driven by density gradient forcing (Pinot et al. 2002).

The last region comprises the Alboran Sea, from the Strait of Gibraltar to the Cape of Gata (Fig. 1d). This region receives the input flow of Atlantic waters,

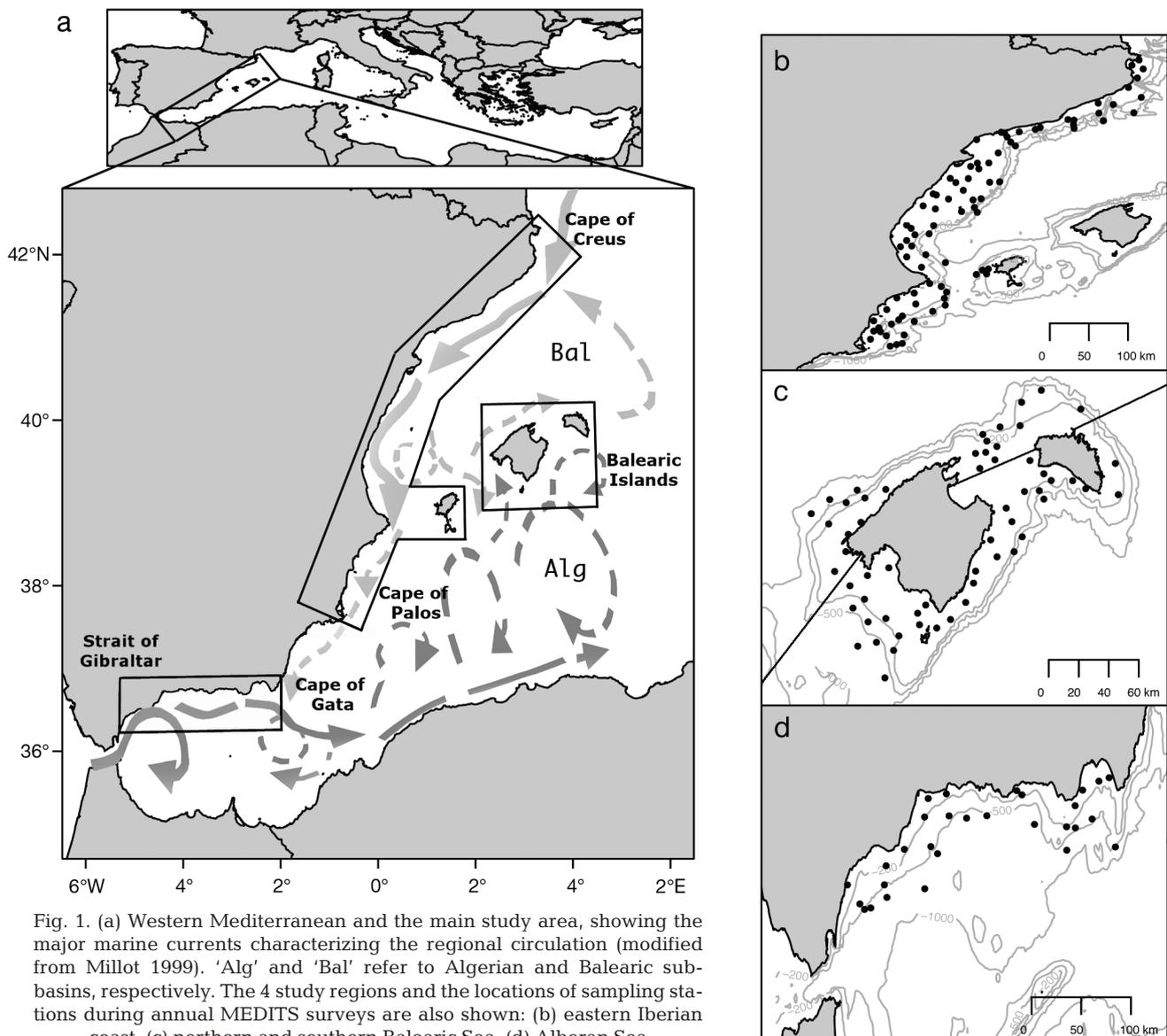


Fig. 1. (a) Western Mediterranean and the main study area, showing the major marine currents characterizing the regional circulation (modified from Millot 1999). 'Alg' and 'Bal' refer to Algerian and Balearic sub-basins, respectively. The 4 study regions and the locations of sampling stations during annual MEDITS surveys are also shown: (b) eastern Iberian coast; (c) northern and southern Balearic Sea; (d) Alboran Sea

which are trapped by 2 quasi-permanent anticyclonic gyres and a series of anticyclonic eddies that are developed due to the topography of the area (Millot 1999, 2005). The presence of fronts, eddies, upwelling systems and other oceanographic processes would act as a barrier for the dispersal or exchange between populations, especially for planktonic early life stages (Bouchet & Taviani 1992, Galarza et al. 2009).

### Sampling

Squid and octopus abundance data were collected in the framework of the International Bottom Trawl Surveys in the Mediterranean (MEDITS program) following a common protocol (Bertrand et al. 2002), during the Spanish surveys carried out annually since 1994. The time series available depends on the study region: 1994 to 2012 in the Alboran Sea and the eastern Iberian coast, and 2001 to 2012 in the Balearic Sea. Sampling was done during late spring or early summer at the same predefined stations, following a stratified random sampling design based on different bathymetric strata (10–50, 50–100, 100–200, 200–500 and 500–800 m), with the number of hauls per stratum proportional to its area. An average of 151 hauls was carried out each year, with proportionally few differences between regions. An experimental trawl net (GOC 73) with a stretched mesh size in the cod-end of 20 mm was used for sampling, with ca. 16.4 and 2.8 m of horizontal and vertical openings, respectively (estimated using the SCANMAR system). Trawling duration was 30 and 60 min at depths shallower and deeper than 200 m, respectively. For each haul, sampling information (date, time, initial and final latitude, longitude and depth, duration, trawled distance, vertical and wing opening of the net) was recorded, together with the number of individuals and size (dorsal mantle length, DML; to the nearest 0.5 cm) of the 2 cephalopod species. Abundances were standardized to number of individuals per km<sup>2</sup>, and mean DML of a population (weighted by number of individuals) was calculated as a proxy of the relative contribution of juvenile or adult individuals in the population.

### Environmental data

To investigate putative environmental drivers affecting the spatial distribution of the 2 cephalopods, different oceanographic and climatic related param-

eters were tested. Two series of monthly records, i.e. spring data contemporary to the survey and data from the previous winter to account for delayed responses, were used as suggested by the results of relevant studies in the NW Mediterranean (e.g. Lloret et al. 2001, Quetglas et al. 2011). Chl *a* concentration (downloaded from <http://disc.sci.gsfc.nasa.gov/giovanni>) as a proxy of food availability, together with sea surface temperature (SST) and precipitation data from the NCEP/NCAR reanalysis fields provided by the NOAA/OAR/ESRL PSD (Kalnay et al. 1996) were obtained for each of the 4 regions. Owing to the important role played by the Ebro River in the marine productivity (Estrada 1996, Lloret et al. 2004) and on the abundance of demersal cephalopods (Lloret et al. 2001, Pertierra & Sánchez 2005) in the eastern Iberian coastal region, runoff information (available at [www.chebro.es](http://www.chebro.es)) was also included in the analyses for this specific area.

The North Atlantic Oscillation (NAO) was included as a large-scale climatic index (both winter and spring NAO indices based on principal component analysis, PCA, were available at <https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-pc-based>). The NAO averages out meteorological conditions across time and space and integrates different aspects of climate such as air temperature, wind speed and precipitation. This has been demonstrated to influence the inter-annual variability of very different ecological traits of marine populations (growth and mortality rates, recruitment success) together with abundance and distribution of different species (Drinkwater et al. 2003, Stenseth et al. 2003, Straile & Stenseth 2007), even in our study area (Massutí et al. 2008). At a meso-scale level, a local climatic index (LCI) already used in the western Mediterranean (Fernández de Puelles & Molinero 2007, 2013, Hidalgo et al. 2011) was also calculated for each study region. This index quantifies the meso-scale hydroclimatic variability, synthesizing the following variables by means of the first axis of a PCA (for details, see Molinero et al. 2005): monthly anomaly fields of surface air temperature, SST, atmospheric sea level pressure, 500 hPa geopotential height and precipitation records (Kalnay et al. 1996). High LCI values are associated with higher temperatures, drier conditions and weaker winds compared to low LCI values. This regional climate variability has been demonstrated to have a direct effect on zooplankton biomass in the Balearic Sea, with critical influence on its variability during winter conditions (Fernández de Puelles & Molinero 2007, 2008).

### Spatial distribution descriptors and data analysis

Spatial indices were calculated for each species, region and year, to characterize the location (centre of gravity, CG) and occupation of space (inertia,  $I$ ) in longitude, latitude and depth, as described by Woillez et al. (2007). The average location of the population was estimated using the CG, the mean location of an individual taken at random in the field.  $I$ , or mean square distance between such an individual and the CG, describes the spatial dispersion of the population around its CG. Where  $z(x)$  is the density of a population at location  $x$ , the CG is estimated from the data through discrete summations over sample locations as

$$CG = \frac{\int xz(x)dx}{\int z(x)dx} \quad (1)$$

and  $I$  is calculated as its variance:

$$I = \text{Var}(\bar{x}) = \frac{\int (x - CG)^2 z(x)dx}{\int z(x)dx} \quad (2)$$

These statistics only depend on positive density values but not on 0 values; that is, in the case of 0, its numerical contribution to the CG is also 0 (Woillez et al. 2007). When sampling is geographically heterogeneous, as in our case, it is recommended to use areas of influence around each sample (sum of points of the space that are closer to this sample than the others) as weighting factors of CG and  $I$  to ensure that displacements of CG are not due to unbalanced sampling areas or changes in sampling design over time (Woillez et al. 2007). However, we did not use them because no remarkable inter-annual variations were observed in our results. Similarly, it is worth noting that isotropy and anisotropy indices, which are often used to describe whether the spatial direction of population dispersion around its CG is identical or not (Woillez et al. 2007), were not calculated in our study. They proved uninformative in all our study regions because the coastal morphology and orientation restricted the spatial distribution of the species.

Spatial distribution studies of marine populations around islands imply having average estimated positions on land in some cases, as well as buffering of potential changes in distribution on opposed sides of the islands. This geographical limitation was circumvented with the additional split of the Balearic Sea region into northern and southern sub-areas, which is also consistent with the oceanographic differences mentioned above.

For each cephalopod species and region, generalized additive models (GAMs) were fitted on the time series of longitude, latitude and depth CG to describe

the putative temporal linear or non-linear trends over time. Secondly, we applied generalized linear models (GLMs) to analyse the potential relationships of environmental (described above) and demographic predictors with the time series of CG. As demographic information, we used the mean population density (ind. km<sup>-2</sup>) and the mean DML (weighted by number of individuals) to account for density-dependent and size-dependent variations, respectively, in spatial distribution. GLMs were selected in this case, as non-linear relationships were not expected between location descriptors and the covariates, but also because they would be difficult to interpret. Prior to the GLM analysis, we applied variance inflation factor (VIF) analysis to detect collinear variables. A cut-off VIF value of 5 was applied to variables, in which case they were removed for the next VIF analyses until getting the final subset of covariates to include in the GLMs (Zuur et al. 2009). Model selection was based on a stepwise approach obtained using Akaike's information criterion (AIC) as a measure of goodness of fit, with the best model having the smallest AIC value. Finally, model residuals were checked to fulfil the normality assumption and absence of temporal autocorrelation in both GAMs and GLMs. All analyses were developed using R statistical software (R Development Core Team 2013).

## RESULTS

### Time series of distribution descriptors

The CG of both cephalopod populations showed marked inter-annual fluctuations in longitude, latitude and depth (Fig. 2). Variation in latitudinal and longitudinal changes was proportional to the area covered in each region, being smoother in the Balearic Sea compared to the Alboran Sea and eastern Iberian coast. The most important movements, which were obviously restricted by the shape of the continental shelf, were those parallel to the coast, with perpendicular displacements being comparatively reduced (Fig. S1 in the Supplement at [www.int-res.com/articles/suppl/m514p105\\_supp.pdf](http://www.int-res.com/articles/suppl/m514p105_supp.pdf)). In the case of *Eledone cirrhosa* from the Alboran Sea, there was a significant positive linear trend in both latitude and longitude ( $p < 0.05$  in both cases) indicating a net displacement northeastwards.

Depth changes between both cephalopod species were correlated in the Alboran Sea (correlation coefficient,  $r = 0.39$ ) and the eastern Iberian coast ( $r = 0.43$ ). In these 2 regions, depth was also correlated

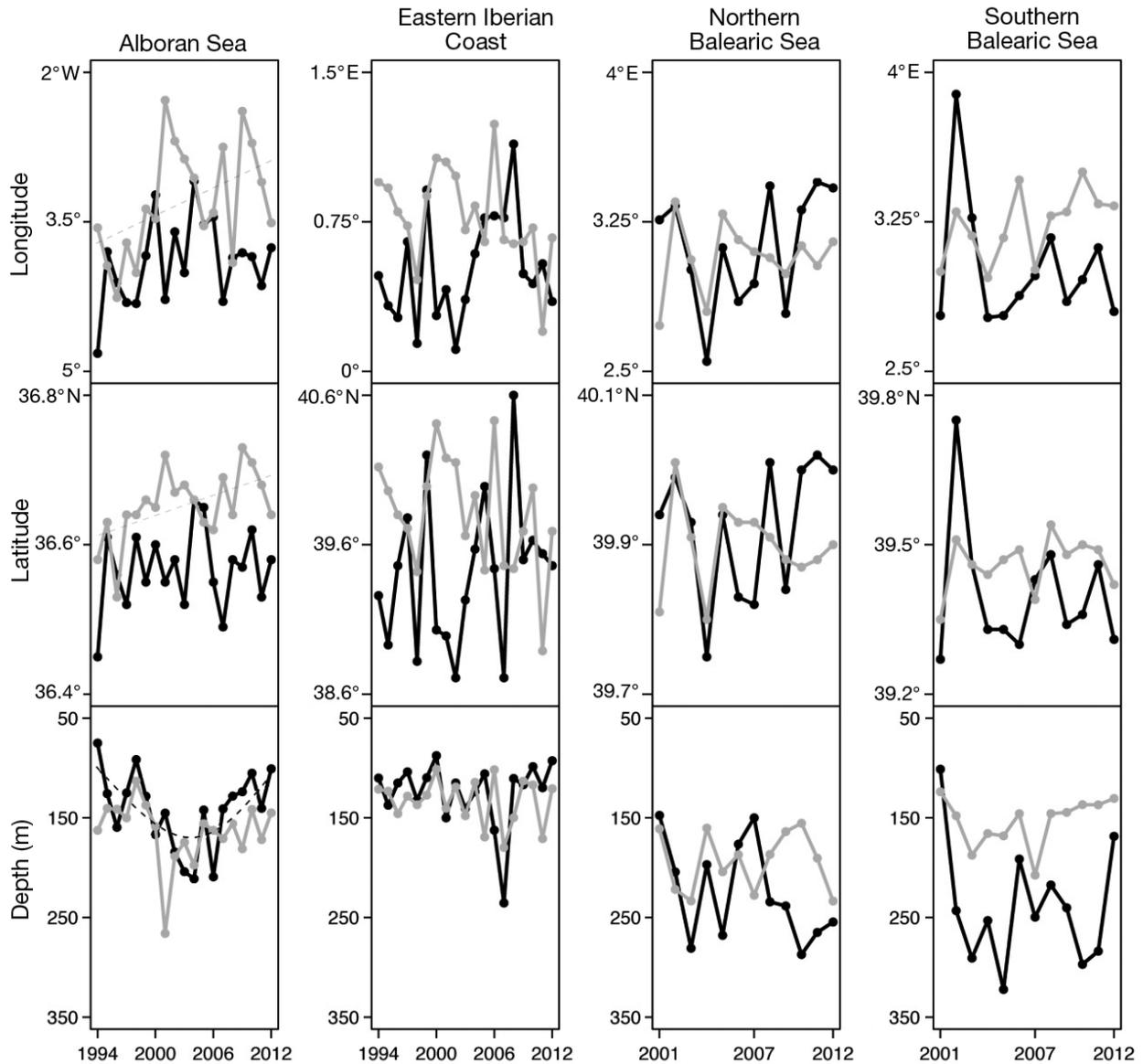


Fig. 2. Time series of changes in centres of gravity of *Illex coindetii* (solid black line) and *Eledone cirrhosa* (solid grey line) in longitude, latitude and depth for each study region. Significant linear and non-linear trends ( $p < 0.05$ ) are described by dashed lines. Scales of latitude and longitude are proportional to the area covered by each region

with latitudinal and/or longitudinal movements ( $p < 0.05$ ), suggesting that changes in depth were partially determined by the continental shelf topography. This synchrony between species was absent in the Balearic Sea, but there was instead a synchrony between the northern and southern areas in both cephalopods (*Illex coindetii*:  $r = 0.64$ ; *E. cirrhosa*:  $r = 0.48$ ). With the only exception of *E. cirrhosa* from the Alboran Sea, mean depth in the 2 species was always higher in the Balearic Sea than in the 2 mainland regions. There was only a significant non-linear trend in inter-annual variation of depth distribution in the case of *I. coindetii* from the Alboran Sea ( $p <$

$0.05$ ), with depth increasing from 75 m in 1994 to 210 m in 2004 and decreasing subsequently down to 100 m in 2012 (Fig. 2).

*I*-values of the 2 cephalopod populations also displayed marked inter-annual fluctuations in latitude, longitude and depth (Fig. S2 in the Supplement). Latitudinal and longitudinal *I*-values were also proportional to the area covered in each region, being higher in the Alboran Sea and the eastern Iberian coast compared to the Balearic Sea. By contrast, *I*-values of depth were comparatively higher in the Balearic Sea, owing to the wider depth range of both species in the archipelago.

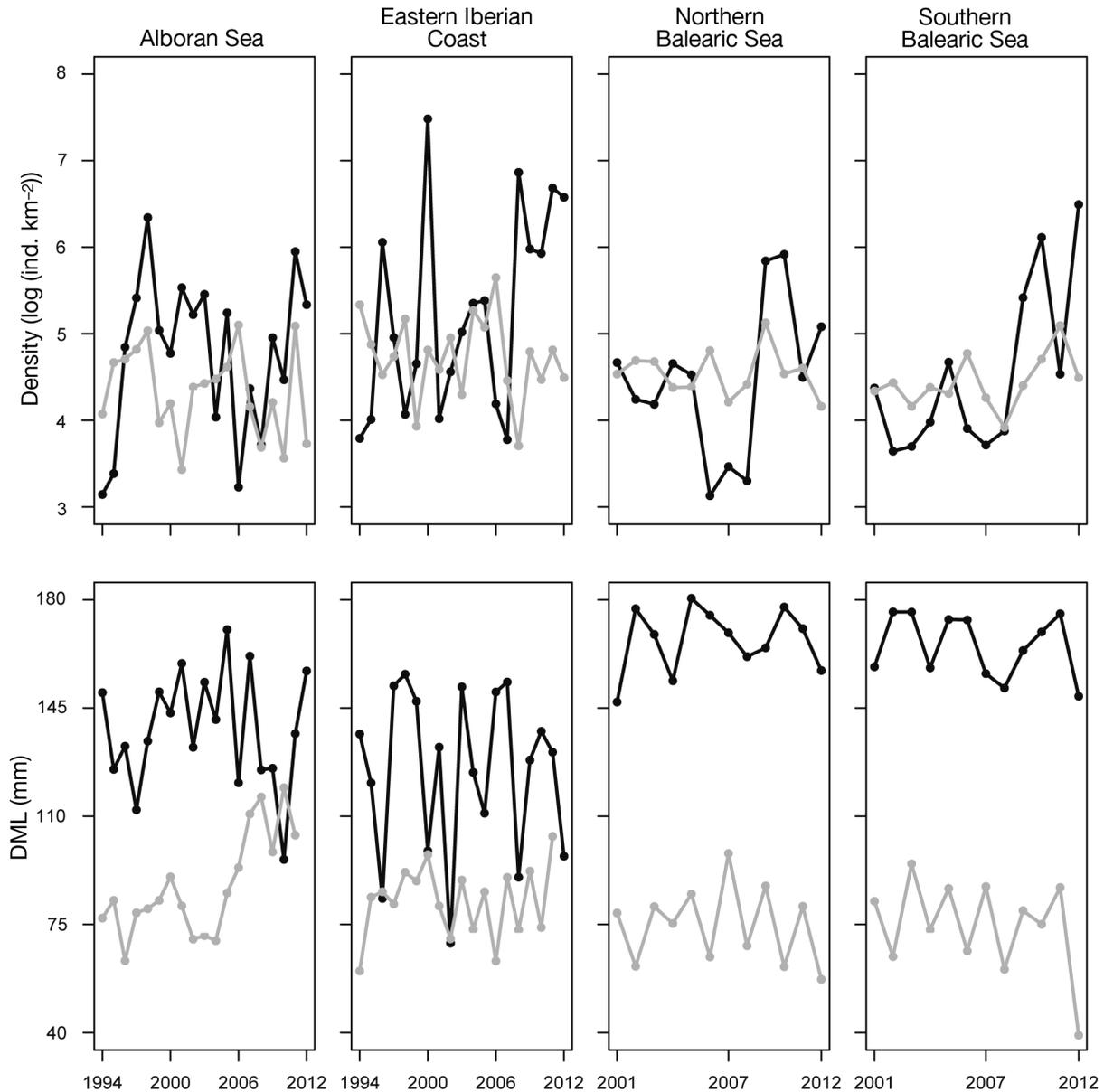


Fig. 3. Changes in annual population mean density and dorsal mantle length (DML) of *Illex coindetii* (black line) and *Eledone cirrhosa* (grey line) for each study region

#### Time series of demographic and environmental covariates

Temporal variation of the demographic covariates depended on the species and the region considered (Fig. 3). In the Balearic Sea, for instance, the 2 species showed lower fluctuations in both population density and individual size, compared to the other 2 regions. In all cases, inter-annual changes in population density were higher in squids than in octopuses. There were no clear patterns for density and size, with the only exception being the mean size of *E. cirrhosa* in

the Alboran Sea, which increased progressively from 70 to 119 mm between 2004 and 2011, reaching the highest values of the whole series. Other generalities included the higher squid sizes in the Balearic Sea throughout the time series and the increase in squid density in all areas since 2009. Finally, it was observed that high densities of squid on the eastern Iberian coast were negatively correlated with size ( $r = -0.47$ ), which might be explained by the inter-annual variation in the strength of recruitment.

The time series of environmental covariates (chl *a*, precipitation and LCI) during spring and the pre-

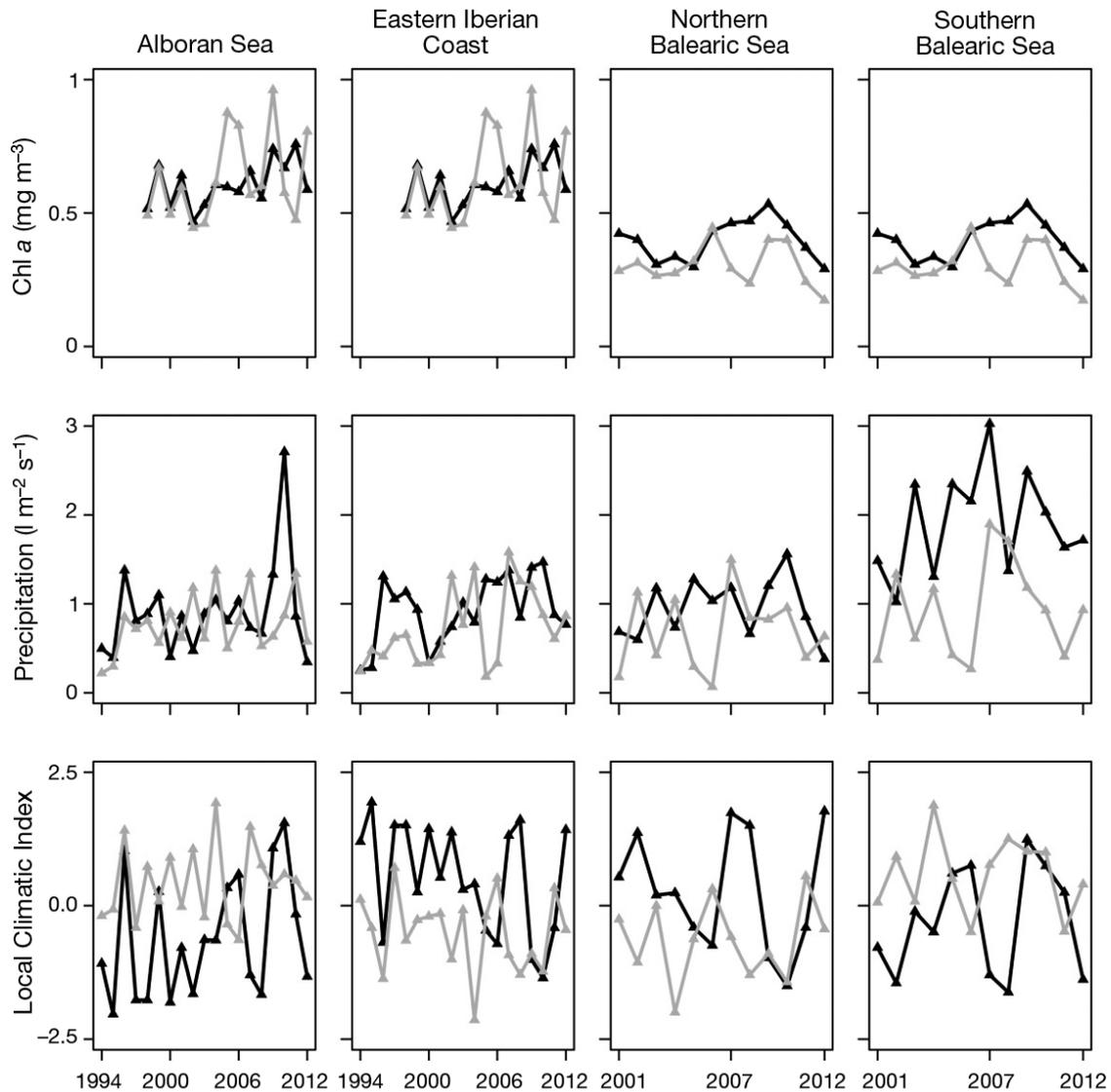


Fig. 4. Interannual variability in chl *a* concentration, precipitation and local climatic index during winter (black line) and spring (grey line) for each study region

vious winter displayed saw-toothed inter-annual fluctuations without any clear general trends (Fig. 4). In agreement with northwestern Mediterranean phenology, winter chl *a* values were higher than spring values. The opposite pattern occurred for precipitation, corresponding with the rain and drought periods of the Mediterranean climate. As expected, the LCI also showed important dissimilarities between the spring and previous winter time series.

#### Demographic and environmental effects

For each species and region, Table 1 displays the best GLM for each response variable (latitude, longi-

tude, depth), with the statistically significant covariates included in the model. In general, the 2 cephalopod species responded to the same set of variables, indicating sensitivity to the same demographic (DML and density) and environmental (precipitation, LCI, chl *a*) drivers. However, the responses were not homogeneous, evidencing clear contrasting effects depending on the species and region. The main contrast between the 2 species was the general association of *I. coindetii* distribution with contemporary spring environmental variables, while *E. cirrhosa* was more influenced by the previous winter processes. Different explanatory variables influenced distributional changes in each region. However, we did not find significant influences of covariates for

Table 1. Summary of variability in centres of gravity of *Illex coindetii* and *Eledone cirrhosa* obtained with the best generalized linear model (GLM) including significant explanatory variables. Note that model results are not shown for those with no significant variables. Explanatory variables are CHL: chlorophyll; DEN: density; DML: dorsal mantle length; EBR: Ebro run-off; LCI: local climate index; NAO: North Atlantic Oscillation Index; PP: precipitation; SST: sea surface temperature; spr: spring; win: winter; Int: GLM-intercept. Level of significance: ·p < 0.1, \*p < 0.05, \*\*p < 0.01, \*\*\*p < 0.001

Descriptor	<i>Illex coindetii</i>				<i>Eledone cirrhosa</i>			
	Variable	Estimate	SE	R <sup>2</sup>	Variable	Estimate	SE	R <sup>2</sup>
<b>Alboran Sea</b>								
Latitude	(Int)	37.38	0.34	0.34				
	NAOspr*	-0.03	0.01					
	SSTspr*	-0.06	0.02					
Longitude	(Int)	1.87	2.36	0.23	(Int)	-12.55	4.33	0.40
	CHLwin·	-2.09	1.12		PPspr*	1.20	0.37	
	SSTwin·	-0.39	0.18		SSTspr*	0.64	0.30	
Depth	(Int)	100.18	20.90	0.03	DEN*	-0.01	0.00	
	PPspr*	54.59	24.84					
<b>Eastern Iberian coast</b>								
Latitude					(Int)	41.30	0.60	0.24
					DML*	-0.02	0.01	
Longitude					(Int)	1.76	0.35	0.28
					DML*	-0.01	0.00	
Depth	(Int)	-615.15	248.75	0.55	(Int)	65.36	37.82	0.12
	EBRspr*	0.14	0.04		DML·	0.83	0.45	
	DEN*	-0.03	0.01					
	SSTspr*	47.62	16.57					
<b>Northern Balearic Sea</b>								
Depth	(Int)	-12.85	161.31	0.61	(Int)	189.23	7.36	0.32
	CHLspr**	-670.60	180.41		LCIwin*	16.48	6.63	
	LCIwin**	-41.02	11.82					
	DML*	2.72	1.02					
<b>Southern Balearic Sea</b>								
Latitude	(Int)	37.41	0.38	0.77	(Int)	39.58	0.05	0.28
	CHLspr*	-1.62	0.52		CHLwin*	-0.34	0.15	
	PPspr***	0.29	0.05					
	DML***	0.01	0.00					
Longitude	(Int)	-1.54	1.46	0.44	(Int)	3.84	0.23	0.40
	PPspr*	0.42	0.16		LCIwin*	0.12	0.04	
	DML*	0.03	0.01		DML*	-0.01	0.00	
Depth	(Int)	-572.07	260.89	0.42	(Int)	44.52	29.58	0.55
	LCIspr·	46.02	22.26		LCIwin*	-13.84	5.66	
	DML*	4.75	1.54		PPwin*	26.56	9.97	
				DML·	0.72	0.38		

some combinations (Table 1, no reported models), such as changes in latitude and longitude for both species in the northern Balearic Sea or for *I. coindetii* on the eastern Iberian coast.

The influence of individual size was the most frequent explanatory variable related to distributional changes. Although it showed no influence in the Alboran Sea, it gave rise to contrasting responses between species in the other regions. Size effects on *I. coindetii*, for instance, were always positive in all descriptors (latitude, longitude and depth) from the

Balearic Sea, indicating a northeast displacement of the population and a movement of large individuals to deeper waters. By contrast, the effects on *E. cirrhosa* depended on the distributional parameter analysed, being negative for latitude and longitude but positive for depth both on the eastern Iberian Coast and in the southern Balearic Sea. Contrary to size, population density only affected the squid distribution from the eastern Iberian coast and that of octopus from the Alboran Sea. In the first case, negative effects of depth indicated higher densities of squid at shallower waters, while negative effects of longitude for octopus indicated increased population densities related to westward movements.

Independently of the distributional parameter considered, the effect of freshwater inputs (precipitation and Ebro run-off) was always positive, whereas the effect of chl *a* was always negative. Precipitation induced displacements of *I. coindetii* to deeper waters in the Alboran Sea, while a similar response was observed on the eastern Iberian coast with the river run-off impact. In the southern Balearic Sea, precipitation conditioned latitudinal and longitudinal movements, causing a slightly net movement of the squid population to the northeast. In the case of *E. cirrhosa*, precipitation induced longitudinal and depth changes in the Alboran Sea and southern Balearic Sea, respectively. Concerning chl *a*, *I. coindetii* populations from the northern Balearic Sea showed a highly negative effect with depth. The same

negative response was observed in latitudinal changes in the southern Balearic Sea for the 2 species.

The SST and LCI showed clear contrasting influences depending on the region and species considered. The LCI affected exclusively the Balearic Sea regions, which in turn were not affected by the SST. In contrast, SST did affect both the Alboran Sea and the eastern Iberian coast. In the Alboran Sea, SST had negative effects on latitude and longitude in *I. coindetii*, but positive longitudinal effects in *E. cirrhosa*. Except longitudinal effects on the octopus

populations from the southern Balearic Sea, the LCI induced depth-related changes in all other cases. In the northern Balearic Sea, however, such effects were negative in the squid but positive in the octopus. In the southern Balearic Sea, by contrast, the effects on depth were positive in the squid but negative in the octopus.

## DISCUSSION

Our study reports clear inter-annual changes in the spatial distribution of 2 of the main cephalopod species harvested in the western Mediterranean Sea, viz. the squid *Illex coindetii* and the octopus *Eledone cirrhosa*, and provides a comprehensive overview of their space occupation in the study area. We demonstrate that these distributional active movements were associated with both the population demography (density- and size-dependent variations) and environmental processes (e.g. productivity, hydrography and climate). In general, squid and octopus populations were affected by the same variables, but their responses differed depending on the species and regions. Besides the inherent complexity of interactions and synergies present in most ecological processes, some of the environmental variables appeared to be principally associated with specific study regions (e.g. LCI to the Balearic Sea). This reinforces our initial reasoning of splitting those regions according to their different oceanographic conditions. Also, the contrasting responses in distributional changes exhibited by the squid and octopus are a consequence of their contrasting life history strategies. As a demersal, fast-swimming squid, *I. coindetii* presents a strong sensitivity to oceanographic features (Boyle & Rodhouse 2005, Pierce et al. 2008), which was reflected in our results by a clear association with the contemporary (spring) environmental variables. By contrast, the benthic octopus *E. cirrhosa* was preferentially affected by conditions during the previous winter, which is in accordance with previous work reporting lag-time responses to environmental drivers on this species (Lloret et al. 2001, Quetglas et al. 2011) and other octopuses (Sobrino et al. 2002, Vargas-Yáñez et al. 2009).

Demographic factors, such as population density or individual size, have been widely studied in cephalopods, but are usually considered as responses instead of drivers (e.g. Waluda & Pierce 1998, Chen et al. 2006, Perdichizzi et al. 2011). Despite the importance of population density in spatial distribution analysis, this was only associated with longitude in *E. cirrhosa*

and depth in *I. coindetii* from the Alboran Sea and eastern Iberian coast, respectively. The mean individual size, which was the main factor driving population displacements, induced homogeneous positive bathymetric responses in the 2 species. This suggests that populations with predominantly small-sized individuals are often distributed in shallow waters, whereas populations dominated by adults are distributed through deeper habitats. This is in accordance with the life history of the 2 cephalopods in the western Mediterranean, with small individuals of *E. cirrhosa* mainly located between 100 and 200 m depth and larger individuals at greater depths (Sánchez et al. 2004). Juveniles of *I. coindetii* are dispersed in the water column during spring, displaying diel vertical migrations, whereas adults are found close to the bottom (Sánchez et al. 1998, Quetglas et al. in press). Furthermore, the population density of *I. coindetii* was negatively correlated with depth on the eastern Iberian coast and also with the mean DML of the population, suggesting the influence of strong recruitment events at shallow depths. Size effects on latitude–longitude were negative for the octopus population from the eastern Iberian coast. This indicates a displacement of populations dominated by small individuals of *E. cirrhosa* towards the mouth of the Ebro River, likely related to years of strong recruitment. We did not find significant effects of Ebro runoff on these movements, although results from previous authors (Lloret et al. 2001, Quetglas et al. 2011) support a strong relationship between food availability around river mouths and recruitment success of this octopus in the western Mediterranean.

SST is the most studied environmental driver and has been shown to have considerable effects on cephalopod abundance and distribution (Pierce et al. 2008 and references therein). In our case, SST only affected populations from the mainland regions but not those from the Balearic Sea, where the LCI may account for thermal variability (see below). SST mainly influences the Alboran Sea region, where contrasting responses were observed in the 2 species. While *I. coindetii* tended to displace to cooler waters, *E. cirrhosa* displacements seemed to be more associated with warmer temperatures. Depending on the species considered, cephalopod responses to temperature can be highly variable (Vargas-Yáñez et al. 2009 and references therein). However, temperature variations might also act as a proxy for other related oceanographic processes at different spatial and temporal scales other than those investigated here. Particularly, the Alboran Sea is characterized by an intense mixing of Atlantic and Mediterranean waters

(Millot 1999), the presence of several upwelling processes and fronts that favour nutrient enrichment and primary production (Estrada 1996), and advection of water masses from distant places that trigger retention/dispersion of early life stages (Bouchet & Taviani 1992, Galarza et al. 2009). These processes have been found to highly influence the distribution and abundance of cephalopods worldwide (Semmens et al. 2007 and references therein). Thus, geographic population displacements in the Alboran Sea may also respond to this intense oceanographic variability, also explaining the influence of spring variables in the benthic species *E. cirrhosa* (an opposite pattern to that observed in the other regions).

Food availability has also traditionally been analysed in many cephalopod studies, with chl *a* as the most used proxy for marine productivity (Pierce et al. 2008 and references therein). Chl *a* was associated with several population displacements in all regions, except the eastern Iberian coast, despite being the most productive region (Estrada 1996). However, our results suggest that local-scale processes on the eastern Iberian coast, such as river input pulses, can be more relevant for local primary production than the regional enrichment processes associated with the influence of water masses coming from the Gulf of Lion (Estrada 1996). Several studies suggest that rainfall also indirectly affects food availability for cephalopods due to changes in water quality and salinity (Lefkadiou et al. 1998, Sobrino et al. 2002). In the Alboran Sea, rainfall can affect the availability of cephalopod prey as a consequence of changes in water quality (e.g. turbidity, pollutants; Sobrino et al. 2002), which remains consistent with our results. In the case of the Balearic Sea, our results agree with previous studies reporting the strong effect of precipitation on marine food webs through important variations in nutrient concentrations and phytoplankton and zooplankton biomass (Fernández de Puellas & Molinero 2007, 2008). Thus, in highly oligotrophic regions such as the southern Balearic Sea, the distribution of cephalopods seems to be especially sensitive to trophic-related drivers, such as chl *a* and precipitation.

Large-scale climatic variability, including NAO, has been reported to influence population dynamics of many cephalopods, especially ommastrephids (Zuur & Pierce 2004, Waluda et al. 2006). However, in agreement with more recent studies (Keller et al. 2012, Quetglas et al. 2013), we found negligible effects of NAO on the distribution of cephalopods from the western Mediterranean. By contrast, the LCI was a recurrent driver in the Balearic Sea. The

relevance of LCI in the Balearic Sea has already been reported for different taxonomic groups (Fernández de Puellas & Molinero 2007, Hidalgo et al. 2011), including cephalopods (Keller et al. 2012). Winter local climate determines the regional hydrographic pattern around the Balearic Islands, affecting productivity and food availability in the upper trophic levels (Hidalgo et al. 2011). During low LCI winters, cold winds reinforce the mixing of the water column, strengthen trophic food webs and increase spatial and temporal coverage of favourable trophic conditions under a general oligotrophic system (Fernández de Puellas & Molinero 2007, 2008). In our results, the LCI strongly influenced the bathymetric distribution of both cephalopods and the geographic variability of *E. cirrhosa* in the Balearic Sea. However, the sign of this effect in the archipelago varies between species as well as between subareas, a pattern already observed for other species (Guijarro et al. 2008, 2009, Hidalgo et al. 2008, 2009) that might be related to differences in local hydrography between the north and south of the archipelago.

Finally, the lack of environmental influences in the *I. coindetii* populations from the northern Balearic Sea and the eastern Iberian coast suggests 2 non-exclusive causes. Firstly, connectivity between populations from these 2 regions may occur for a highly mobile species such as *I. coindetii*, as has been documented for some fishes (Galarza et al. 2009, Hidalgo et al. 2009). Therefore, squid responses to environmental drivers might be masked by occasional arrival of individuals from neighbouring subpopulations. Secondly, we could not identify the precise spatial scale at which a key environmental driver is affecting the population distribution (Ciannelli et al. 2013), particularly in the case of the eastern Iberian coast. Besides the importance of the spatial scale, we also recognize that population displacements for both species may be associated with drivers other than the ones analysed here. For instance, we did not consider seabed information (e.g. substrata, shelf shape) that could be pivotal for understanding the mechanisms affecting the distribution of benthic species such as *E. cirrhosa* (Boyle & Rodhouse 2005). Factors such as predator-prey relationships or fishing effort may also exert a relevant influence on distributional patterns of marine species, as has already been observed in fish populations (Bartolino et al. 2012, Hunsicker et al. 2013). Additionally, available data based only on spring trawl surveys presents some limitations. The spawning peak of both species occurs in spring with a migration to shallower areas (Sánchez et al. 1998, 2004). Inter-annual variability in the spawning time

may thus bias the estimations of mean DML and influence the displacement of populations.

In summary, our study shed new light on the scarcely investigated issue of determining the drivers shaping the spatio-temporal displacement of cephalopod populations. Despite the common sensitivity to the same drivers in the 2 species studied, effects of demographic and environmental variables varied between species and regions. The mean DML mainly explained bathymetric changes, while SST, local climate or chl *a* was more relevant for geographical displacements. Our study improves our knowledge on the population dynamics of cephalopods and enhances the need for a deeper understanding of the complex interactions between physical and biological processes. This constitutes an important step to improve cephalopod assessment and management in the framework of current climate change, which is expected to disrupt the distribution patterns of marine populations in areas considered especially sensitive, such as the Mediterranean Sea (Coma et al. 2009). Displacements in spatial distribution and their association with environmental variables can help to forecast population dynamics to implement sustainable fishery management programmes and identify essential habitats or potential marine reserves. These applications can have special importance for cephalopod stocks, which in most cases still remain unmanaged.

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