

# Concurrent changes in spatial distribution of the demersal community in response to climate variations in the southern Iberian coastal Large Marine Ecosystem

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**ABSTRACT:** Species inhabiting transitional areas in large marine ecosystems are highly sensitive to climate variations and thus of paramount importance as indicators of ecosystem changes. The spatiotemporal distribution of representative species of the demersal community in the southern Iberian coastal Large Marine Ecosystem was investigated using time series data from trawl surveys conducted in the Gulf of Cádiz. The geographic and bathymetric variability in the population distribution was analyzed. We investigated the influence of hydroclimatic (chlorophyll *a* concentration, sea surface temperature, precipitation, runoff, oceanic wind and meso- and large-scale climate indices) and population drivers (density) on species depth and location. Distribution shifts were more evident over the longitudinal gradient with species approaching and moving away from the Strait of Gibraltar. This contrasting behavior was segregated by depth and the hydrographical boundary of the Guadalquivir River runoff plume. On the shallow shelf (<100 m), a southeastward movement towards the Strait of Gibraltar was clear. This geographical shift was also observed in species from the deeper strata, occasionally coupled with depth changes. These movements were mainly associated with climate variability, in particular the North Atlantic Oscillation, whose effects were clearly species specific. Additionally, longitudinal variations of the community at a regional scale were related to a local climatic index that captured a pattern of covariation in local surface wind, temperature and precipitation. This study focuses on responses of several species with contrasting life histories (from Sparidae to Elasmobranchs) to hydroclimatic variability in the southern Iberian coastal Large Marine Ecosystem.

**KEY WORDS:** Demersal species · Spatial ecology · Species distribution · Geographic shifts · Climate indices · Southern Iberian coastal Large Marine Ecosystem

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## INTRODUCTION

Marine species can display changes in their spatial distribution in response to natural and anthropogenic stressors. Numerous studies have documented this

variability in the spatial patterns, particularly in fish populations (Perry et al. 2005, Nye et al. 2009, Pinsky et al. 2013). Numerical models have been useful to explore how ocean climate and other drivers may regulate the dynamics of marine ecosystems within

certain limits of predictability (Planque 2016). Most previous studies have focused on the mechanisms that regulate spatiotemporal changes in abundance or distribution, identifying 2 main categories of factors that control the spatial distribution: (1) external factors such as environmental conditions, anthropogenic impacts or species interactions; and (2) internal factors directly linked to the population status (demographic structure or density-dependent processes) (Planque et al. 2011).

Environmental and climatic variability have proved to have a strong influence on phenology at population and species levels (Edwards & Richardson 2004), abundance and distribution of fish through changes in population dynamics (habitat suitability, growth, survival, reproduction or recruitment) (Brander et al. 2003) and also responses at other trophic levels (Beaugrand et al. 2003). The impact of environmental variability often acts in a combined manner with the anthropogenic impacts, triggering synergistic effects (Hsieh et al. 2010, Hidalgo et al. 2011, Planque et al. 2011, Ciannelli et al. 2013). To disentangle these effects is challenging. However, biogeographic variations are sometimes clearly attributable to fluctuations in the environment or climate variability rather than other factors such as variability in life history or internal population properties (Perry et al. 2005, Engelhard et al. 2011, Pinsky et al. 2013, Punzón et al. 2016).

Seawater temperature is the most notable environmental driver influencing distributional changes at the global ocean scale (Cheung et al. 2010, 2012). Evidence of recent temperature increases has been linked to poleward shifts at the species level (Perry et al. 2005, Punzón et al. 2016) and even at the assemblage level (Dulvy et al. 2008, Kleisner et al. 2016) in the North Atlantic and adjacent areas. These thermal-induced changes are mostly observed at a large, or even global, spatial scale. However, at a smaller spatial scale, some other environmental components may have a profound impact on the temporal variation of species distribution. In this sense, chlorophyll *a* (chl *a*) concentration has been widely used as a proxy for marine productivity and several studies have shown its influence on distribution changes (e.g. Friedland et al. 2013, Puerta et al. 2014, Keller et al. 2016). In addition, more local-scale drivers such as freshwater inputs (precipitation or river discharge) may also alter water quality (e.g. salinity, nutrients), or even affect food availability (phytoplankton and zooplankton biomass) influencing species distribution (Sobrino et al. 2002). In contrast, density-dependent habitat selection can indirectly shape the rela-

tionship between population abundance and geographic distribution. Species population drivers (density) might also alter the spatial sensitivity to all the aforementioned local environmental factors, or trigger unexpected bathymetric changes in distribution when density dependence constrains geographic expansion (Bartolino et al. 2011).

Variability of complex temporal and spatial patterns in environmental factors is often aggregated into simpler measurements such as climate indices (Stenseth & Mysterud 2005, Nye et al. 2009, Nye et al. 2014), which make these indices a recurrent variable used in marine species distribution studies (Stenseth et al. 2003, Ottersen et al. 2010). Hydroclimatic information in the Northeast Atlantic is usually summarized at different spatial scales by (1) mesoscale climatic indices, incorporating local and regional information derived from a principal component analysis of atmospheric and sea surface variables. These indices have been widely used to explain changes in the distribution or the dynamics of marine species (Beaugrand et al. 2002, Molinero et al. 2005, Fernández de Puelles & Molinero 2007, Puerta et al. 2014). However, marine populations also may be affected by (2) the local effects of large-scale climate variability. In this context, the North Atlantic Oscillation (NAO) index has become useful in understanding the structure and variability in the functioning of marine ecosystems, from plankton to fish stocks (Beaugrand et al. 2003, Hurrell et al. 2003, Stenseth et al. 2003).

Located in the southern part of the Iberian coastal Large Marine Ecosystem (LME), the Gulf of Cádiz is an archetypal area of interest given its transitional geographical location between the open waters of the Atlantic Ocean and the semi-enclosed waters of the Mediterranean Sea. As such, it is characterized by the confluence of physical and ecological processes of contrasting geographic origin. Previous studies have shown that this area of the southern Iberian coastal LME is highly dynamic due to the exchange of water masses and is sensitive to oceanographic and climatic impacts (Vargas et al. 2010, Plomaritis et al. 2015). The influence of climatic and environmental variables on the spatial distribution of several lower trophic groups (Baldó et al. 2006, Ruiz et al. 2006, Drake et al. 2007, Prieto et al. 2009), and commercially important species in the Gulf of Cádiz (Sobrino et al. 2002, Catalán et al. 2006), has already been proven. Additionally, it has been proved that catch rates of pelagic species are controlled by environmental and climatic variables in the adjacent waters of Portugal (Leitão 2015,

Teixeira et al. 2016). However, there is still a need for a comprehensive understanding of the influence of climate–ocean variability in the spatial distribution of the whole demersal community in the Gulf of Cádiz.

The main aim of the present study was to investigate the spatiotemporal distribution of the demersal community in the water mass exchanges area of the Gulf of Cádiz in the southern Iberian coastal LME. Species spatial shifts could be used to explore and understand historical changes in the ecosystem, and to assess future effects in response to climate–ocean variations. Our purpose was thus to analyze the temporal stability and variability of the mean geographical and bathymetric location of the demersal community in response to hydroclimatic (chl *a* concentration, sea surface temperature, precipitation, runoff, oceanic wind components, mesoscale and large-scale climate variations) and density-dependent drivers. In particular, we aim to identify which species or groups showed a distribution change and which drivers could be held responsible for such observed displacements.

## MATERIALS AND METHODS

### Study area

The study area is located in the southern part of the Iberian coastal LME, encompassing the area of the Gulf of Cádiz at 36° to 37.25° N and 6° to 7.5° W. The Atlantic Ocean connects with the westernmost part of the Mediterranean Sea at the Strait of Gibraltar. The study area covers waters around the Gulf of Cádiz from the mouth of the Guadiana River that borders Portugal in Ayamonte (Huelva), to the Cape of Tarifa (Cádiz) (Fig. 1). This area spans 303 km of coast and covers 7224 km<sup>2</sup> of the southern Iberian coastal LME with depths ranging from 15 to 800 m.

Atmospheric conditions in this area are driven by large-scale frontal systems that cross the North Atlantic following an eastward path, determining the patterns of precipitation or wind. On a local scale, the orientation of the coastline and the local physiographic characteristics result in sheltering effects to the north component winds and funneling effects to south and east component winds due to the complex orography of the Strait of Gibraltar (Dorman et al. 1995).

Water masses in the Gulf of Cádiz area of the southern Iberian coastal LME are sorted along 3 bathymetric areas occupying particular depth intervals (Bellanco & Sánchez-Leal 2016): (1) inner shelf waters (<60 m depth), with strong coastal and atmospheric influence; (2) low-salinity Eastern North Atlantic Central Water (ENACW) related to the Gulf of Cádiz current (100–250 m); and (3) the near-bottom circulation dominated by the Mediterranean Outflow Water (MOW) (Sánchez et al. 2017). The oceanic surface circulation is anticyclonic, with short-term meteorologically induced variability that changes geostrophic streamlines and volume transport, while a counter-current flows over the inner shelf (Criado-Aldeanueva et al. 2006). This region is also influenced by freshwater runoff from the Guadalquivir and Guadiana rivers. The dense MOW is associated with a wide range of salinity and temperature occupying the deeper grounds tightly constrained by the topography, and forms a strong westward bottom current below the ENACW (Sánchez et al. 2017). The interaction of the MOW with topography

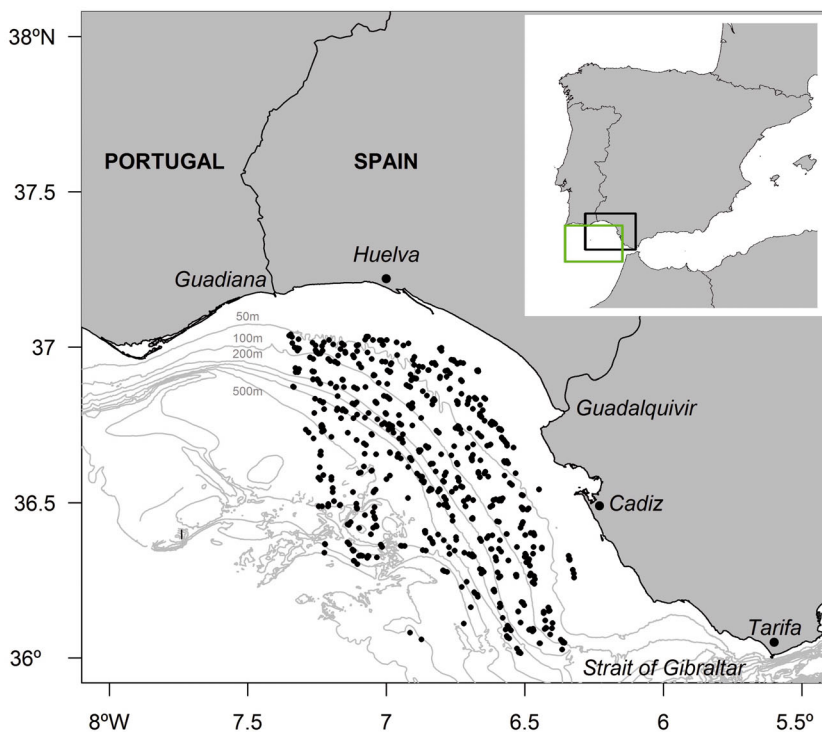


Fig. 1. Iberian Peninsula and the study area of the Gulf of Cádiz (black box) area of the southern Iberian coastal Large Marine Ecosystem. The locations of hauls during ARSA surveys (black points) and the region used to obtain environmental data (green box) are shown

and the entrainment process induces significant circulation in the surface layer (Bellanco & Sánchez-Leal 2016).

Regarding ecological communities, the shallow shelf (<100 m) is mainly characterized by Pleuronectiformes, pelagic species, families such as Triglidae or Sparidae, or by cephalopods such as *Octopus vulgaris*. The deep shelf (100–200 m) is the main area of distribution of commercial species such as *Merluccius merluccius* or the crustacean *Parapenaeus longirostris*. Elasmobranchs are well represented in the upper and middle slope (>200 m) as well as the crustacean *Nephrops norvegicus* (Sobrino et al. 1994).

### Sampling

Data on species abundance are derived from 1993–2012 monitoring bottom-trawl surveys conducted to evaluate demersal habitats of the continental shelf and slope of the Gulf of Cádiz area of the southern Iberian coastal LME (Arrastre demersal suratlántico español [ARSA; Spanish Southern Atlantic bottom-trawl surveys]; Sobrino et al. 1994). Sampling was conducted during late autumn following a common protocol (ICES 2010) and a random stratified scheme with 5 depth strata (15–30, 31–100, 101–200, 201–500 and 501–800 m). The number of hauls per stratum was proportional to the trawled surface (ca. 42 hauls per survey). Trawling duration was 60 min. All hauls were carried out during daylight hours using Baka 40/60 trawl gear with a 43.6 m footrope and a 60.1 m headline. An inner 20-mm-mesh codend liner was used to prevent the escape of small individuals. For each haul, sampling information (date, time, duration, initial and final longitude, latitude and depth, and trawled distance) was recorded. All the species were identified to the lowest taxon possible, weighed, counted and measured. Abundances were standardized to number of individuals per km<sup>2</sup> (density, dens). A set of 18 species from different taxonomic groups (fish, crustaceans and molluscs) was selected for the analyses according to the following criteria: (1) catchability (species effectively sampled by the net throughout the time series); (2) most representative species in terms of abundance and bio-

mass (Dulvy et al. 2008); (3) commercial interest. Table 1 shows the selection of representative species by taxonomic group and depth strata. This depth classification (SS: shallow shelf; DS: deep shelf; US: upper slope; US/MS: upper slope/middle slope) was based on ecological, oceanographic and geological information from the Gulf of Cádiz area of the southern Iberian coastal LME previously described by Sobrino et al. (1994), Lobo (1995), Baringer & Price (1997), Hernández-Molina et al. (2003) and Bellanco & Sánchez-Leal (2016).

### Environmental data

Two series of monthly records of all the environmental variables were used to analyze their possible influence on spatial distribution: (1) data representative of a delayed response in the demersal community (previous summer; June–July–August (S)) and (2) contemporary data to the survey (autumn; September–October–November (A)).

Sea surface temperature (SST) data were downloaded using Marine Geospatial Ecology Tools (MGET) v.0.8a28 (Roberts et al. 2010). SST AVHRR Pathfinder Version 5.0 products from 1993 to 2002 (Kilpatrick et al. 2001, Casey et al. 2010) were obtained from the NOAA National Oceanographic Data Center (NODC) ([www.nodc.noaa.gov/Satellite-Data/pathfinder4km/](http://www.nodc.noaa.gov/Satellite-Data/pathfinder4km/)). SST data from 2003 to 2015 were obtained from the MODIS Aqua sensor from

Table 1. Selection of representative species of the southern Iberian coastal Large Marine Ecosystem by depth strata and taxonomic group. SS: shallow shelf; DS: deep shelf; US: upper slope; US/MS: upper slope/middle slope

Depth strata	Group	Species	Abbreviation
<100 m (SS)	Fish	<i>Mullus surmuletus</i>	Msur
		<i>Pagellus acarne</i>	Paca
		<i>Pagellus erythrinus</i>	Pery
		<i>Spondylus cantharus</i>	Span
		<i>Trachurus trachurus</i>	Ttra
		<i>Citharus linguatula</i>	Clin
		<i>Dicologlossa cuneata</i>	Dcun
		<i>Chelidonichthys obscurus</i>	Cobs
100–200 m (DS)	Molluscs	<i>Octopus vulgaris</i>	Ovul
	Fish	<i>Conger conger</i>	Ccon
		<i>Merluccius merluccius</i>	Mmer
		<i>Parapenaeus longirostris</i>	Plon
200–300 m (US)	Crustaceans		
		<i>Scyllorhinus canicula</i>	Scan
		<i>Lophius budegassa</i>	Lbud
>300 m (US/MS)	Fish	<i>Lepidopus caudatus</i>	Lcau
		<i>Raja clavata</i>	Rcla
		<i>Etmopterus spinax</i>	Espi
		<i>Nephrops norvegicus</i>	Nnor

the NASA Goddard Space Flight Center Ocean Color Group (<http://oceancolor.gsfc.nasa.gov/>). Chl *a* concentration ( $\text{mg m}^{-3}$ ) was downloaded from <http://giovanni.gsfc.nasa.gov/giovanni/> as a proxy of food availability. Precipitation data (PP) were downloaded from the National Center for Environmental Prediction/National Center for Atmospheric Research (NCEP/NCAR) reanalysis fields provided by the NOAA/PSD (<https://www.esrl.noaa.gov/psd/>; Kalnay et al. 1996). The Guadalquivir River runoff records (RUN) were obtained from the Regional River Authority (Confederación Hidrográfica del Guadalquivir) database (<http://chguadalquivir.es/saih/>). Additionally, environmental variables were detrended for the seasonal cycle.

A local climatic index (LCI) quantifying the mesoscale hydroclimatic variability was estimated by summarizing the following variables over the southern Iberian coastal LME study region (Fig. 1) into the first axis of a principal component analysis (PCA) (Molinero et al. 2005): monthly anomaly fields of surface air temperature, SST, sea-level pressure, 500 hPa geopotential height and precipitation records from the NCEP/NCAR reanalysis project (Kalnay et al. 1996). The NAO index (from the previous summer and autumn) was obtained from <https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-pc-based> and included as a large-scale climatic index. The NAO refers to a redistribution of atmospheric mass between the Arctic and the subtropical Atlantic, and swings from one to the other producing large changes in surface air temperature, winds, storminess and precipitation over the North Atlantic Ocean as well as the adjacent continents (Hurrell & Deser 2009).

Additionally, oceanic winds over the region between 34° and 37.5° N latitude and 6° and 12° W longitude were included in our analysis. We used the Cross-Calibrated Multi-Platform ocean surface wind vector analyses (Atlas et al. 2011) as ocean wind data. These data provide a consistent, gap-free long-term time series of ocean surface wind vector analysis monthly fields. Data were retrieved from the NASA Physical Oceanography Distributed Archive Center. To filter out high-frequency variability, characterize the spatial patterns and extract a scalar wind index, an empirical orthogonal function analysis of the wind dataset was applied. In this context, it produces a number of weights or loadings (spatial maps) that explain the highest amount of variability and scores (or time series) that express the amplitude and sign of the spatial maps. As a vectorial magnitude, a fre-

quently used approach is to analyze either the zonal (*u*) or meridional (*v*) wind component. However, given the heterogeneity of the oceanic wind field in the Gulf of Cádiz area of the southern Iberian coastal LME (Sánchez et al. 2007a), we considered both components together. Both *u* and *v* can be combined as real variables in the input data matrix. After the analysis, the loadings matrix can be decomposed into a vectorial map modulated by a real time series (e.g. Sánchez et al. 2007b).

### Descriptors of spatial location

We explored 18 yr time series of scientific surveys analyzing trends in active movements of populations. Spatial indices of location (i.e. center of gravity, CG) in longitude, latitude and depth were calculated for each species and year as described by Woillez et al. (2009) and using the RGeostast package in R software (Renard et al. 2014, R Core Team 2015). CG is the mean location of a population and also the mean location of an individual fish taken at random in the field (each data location was weighted by fish density). CG was calculated as:

$$\text{CG} = \frac{\sum_{i=1}^N x_i s_i z_i}{\sum_{i=1}^N s_i z_i} \quad (1)$$

where  $z_i$  were sample values (density, dens) at locations  $x_i$ ,  $s_i$  were the areas of influence for longitude and latitude CG, and  $i = 1$  to  $N$ . The area of influence is defined as that containing the points in space closer to this sample than to others. It was obtained by overlaying a very fine regular grid and counting the grid points closer to the sample (in distance units) than to other samples. These areas act as weighting factors to avoid bias due to the geographical heterogeneity of the sampling design (random stratified scheme) (Woillez et al. 2009, ICES 2010, RGeostast package). The outer border of the domain can be a known or supposed boundary of the sample population (Woillez et al. 2009). The boundary defined by Sobrino et al. (1994) from ARSA surveys in the study area has been used.

### Data analysis

Linear models (LMs) were fitted to the CG longitude, latitude and depth time series to assess temporal trends for each species. We also used LMs on CG to estimate the rate of change and average shifts in



CG over time in accordance with Pinsky et al. (2013). The effect of environmental, climatic and density-dependent factors was investigated independently at the species-specific and community levels. Prior to analysis, correlation matrices and variance inflation factor (VIF) were used to detect collinearity among the explanatory variables. A cut-off VIF value of 5 was applied to drop collinear variables and to obtain the final set of covariates included in the statistical analyses (Zuur et al. 2009a). (1) At the species-specific level, the effects of the potential drivers on spatial indices were analyzed by means of LMs. (2) At the community level, effects of covariates were analyzed using the entire set of species and comparing different model structures: LMs that assume independence of observations and linear mixed-effects models (LMEMs) that take into account the dependence of data within each species. LMEMs have 2 components that contain explanatory covariates: the fixed term and the random term. The fixed term tests global effects in the community in a similar way to the LMs, while the random term allows the assessment of the effect of covariates by species identity (random grouping factor in our case) (Zuur et al.

2009b). To do that, 2 types of random effects were tested: (1) the effect in the intercept and (2) the effect in the intercept and slope. Model selection was based on a stepwise approach using Akaike's information criterion (AIC) as a measure of goodness of fit. Best model was selected as the one with significant covariates having the smallest AIC value for species-specific models (LMs) and for the community-based models (between LMs and LMEMs). Model assumptions were validated by checking residuals. Model analyses were performed using the *mgcv* and *nlme* packages in R software (R Core Team 2015).

## RESULTS

### Time trends in centers of gravity

Nearly 70% of species have shown temporal changes in the geographical distribution (longitude and latitude) (Figs. 2 & 3). The east–west coastline of the Gulf of Cádiz area of the southern Iberian coastal LME prevents northward shifts, but several populations underwent displacements towards the Strait of

Gibraltar (southeast) or the Portugal coast of the Iberian coastal LME (northwest). Those opposite patterns in distributional changes were observed around an apparent geographical boundary marked by the Guadalquivir River plume. While species with a mean CG located north of the Guadalquivir River mouth displayed an average shift towards the northwest of the Gulf of Cádiz area of the southern Iberian coastal LME (*Parapenaeus longirostris* or *Dicologlossa cuneata*), those with mean CG south of the river mouth showed the opposite pattern (e.g. *Pagellus acarne* or *Raja clavata*) (Fig. 3A).

Only in specific cases, these patterns were also coupled with depth changes, while in other cases this behavior was not observed, as detailed below by bathymetric stratum (Figs. 2 & 3B). In the shallow shelf (SS; <100 m), except for *D. cuneata*, Sparidae species (*P. acarne*, *Pagellus erythrinus*, *Spondyllosoma cantharus*), *Mullus surmuletus*, *Trachurus trachurus* and Scorpaeniformes species (*Chelidonichthys obscurus*) are widely

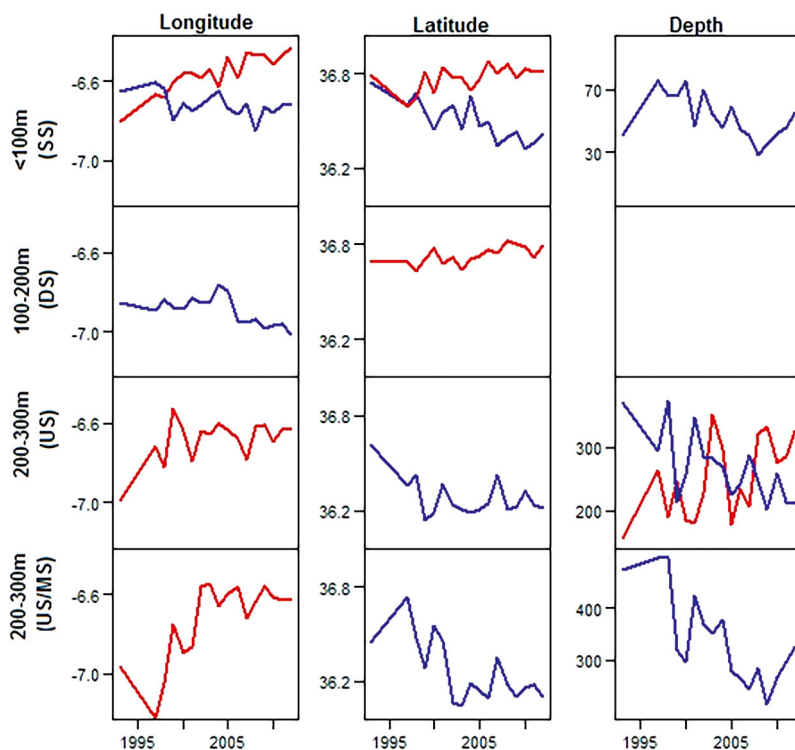


Fig. 2. Time series of changes in the mean center of gravity patterns in longitude, latitude and depth, for species grouped by significant trend (Fig. 3) and depth stratum (y-axis). Red and blue lines show positive and negative trends, respectively. SS: shallow shelf; DS: deep shelf; US: upper slope; US/MS: upper slope/middle slope

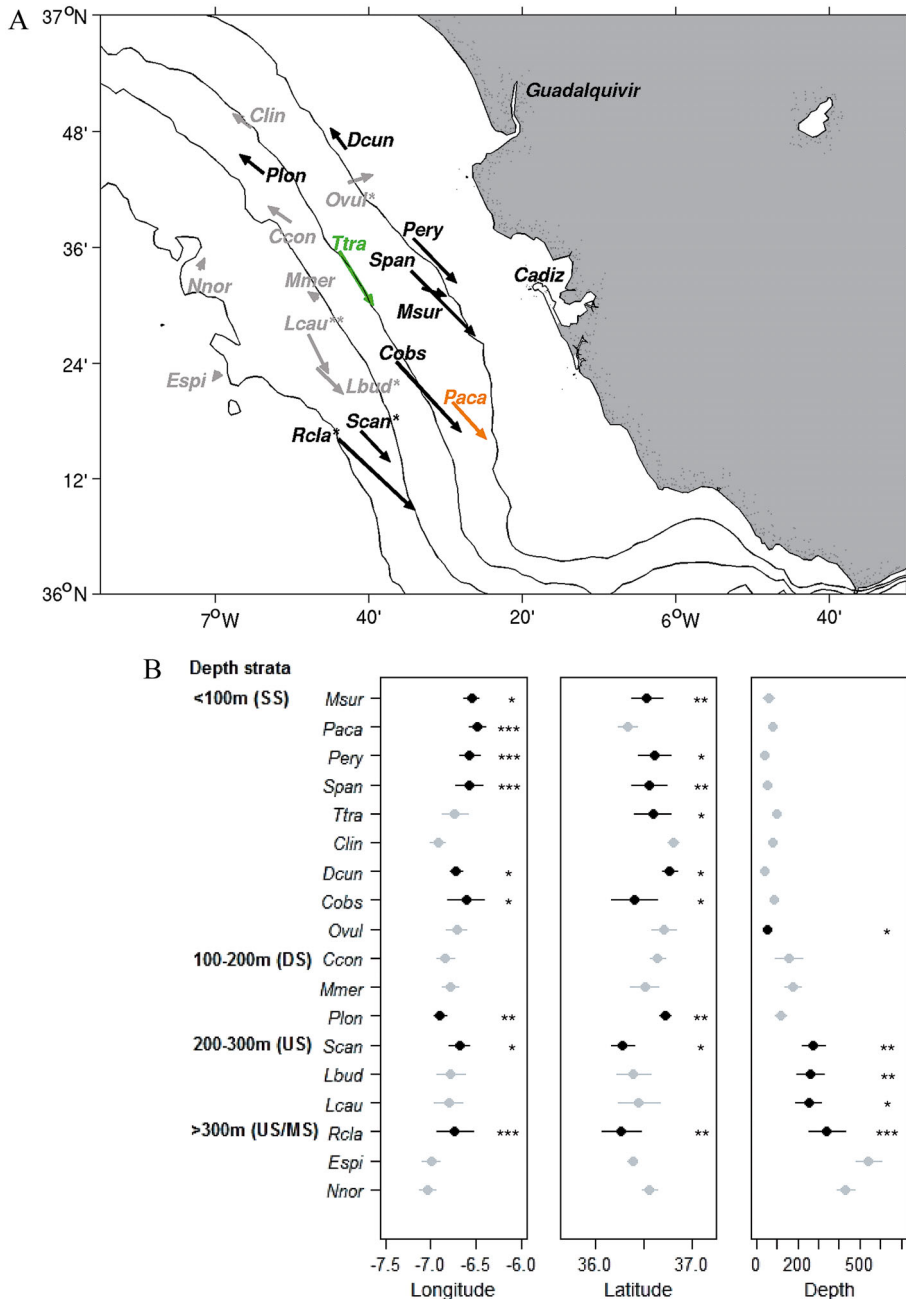


Fig. 3. (A) Vectors show the average shift of the centre of gravity (CG) in latitude and longitude for each species examined from waters of the southern Iberian coastal Large Marine Ecosystem (from lineal models fitted to CG time series). Color scale—black: significant shift in latitude and longitude; orange: significant shift in longitude; green: significant shift in latitude; grey: no significant shift. Isobaths (right to left, respectively): 20, 100, 200 and 500 m. \*: Significant shift to shallower waters. \*\*: Significant shift to deeper waters. Species abbreviations are compiled in Table 1. (B) Mean and standard deviation in CG in longitude, latitude and depth by species and bathymetric stratum. Black symbols: significant trend. Level of significance: \*p < 0.05; \*\*p < 0.01; \*\*\*p < 0.001

distributed and their CG in longitude and latitude showed a clear southeastward movement towards the Strait of Gibraltar. This movement was not

reflected in depth. Indeed, these species exhibited very low bathymetric variability, except the cephalopod *Octopus vulgaris*, which moved to shallower waters without any significant geographical displacement.

A common geographic pattern could not be drawn for the deep shelf (DS) of the southern Iberian coastal LME. Most species showed no significant displacement except *P. longirostris*. This crustacean displayed a statistically significant movement towards the northwest along the 100–200 m stratum. Furthermore, elasmobranchs occupying the deepest strata (upper slope and middle slope; US and MS) and southernmost mean location (*Scyliorhinus canicula* and *R. clavata*) moved to the southeastern area of the Gulf of Cádiz area of the southern Iberian coastal LME (Fig. 3) and towards shallower areas. It is also worth noting that all species from the 200–300 m stratum (US) displayed temporal changes in bathymetry. *Lophius budegassa* and *Lepidopus caudatus* displayed antagonist behavior towards deepest and shallower waters, respectively, without any significant geographical displacement (Fig. 3).

### Time trends of environmental covariates

Variability in the environmental time series is shown in Fig. 4. SST, PP and RUN data revealed the expected differences between dry summer and wet autumn in the study area of the southern Iberian coastal LME.

Empirical orthogonal function analysis primarily decomposed the wind dataset into 3 orthogonal basis functions (W1, W2 and W3)

with a spatial pattern displayed for the first 2 modes, W1 (51% variance explained) and W2 (22%), in Fig. 5. The variance explained for the third mode was

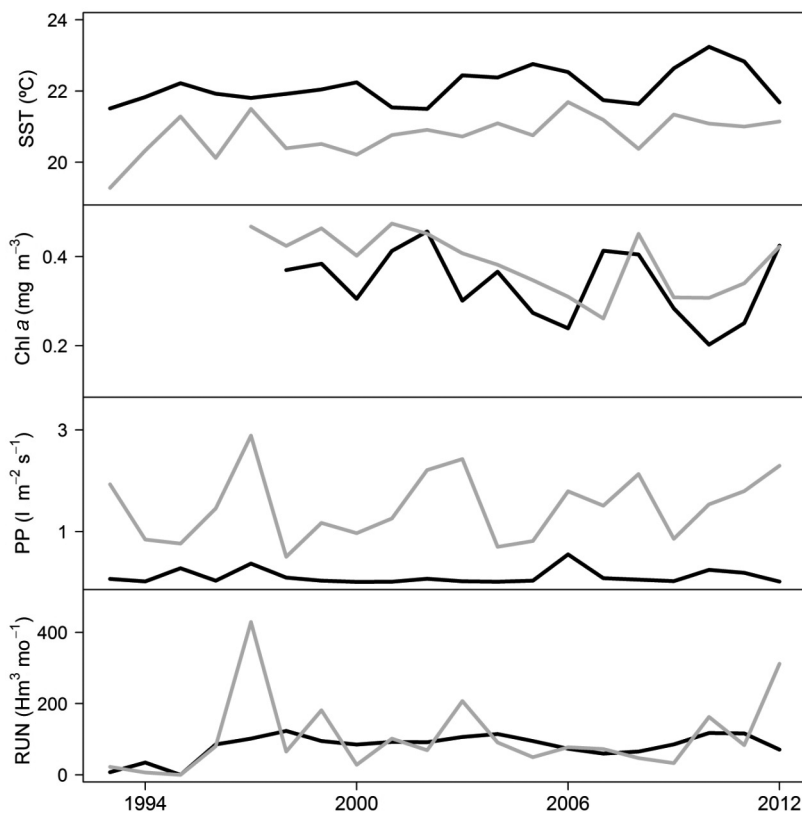


Fig. 4. Time series of environmental variables: sea surface temperature (SST), chlorophyll *a* concentration (chl *a*), precipitation (PP) and Guadalquivir River runoff (RUN), during summer (black lines) and autumn (grey lines) for the Gulf of Cádiz area of the southern Iberian coastal Large Marine Ecosystem

minimal (W3, 7%). The first function gives information about large-scale southwest–northeast wind components, while the second function reports on southeast–northwest wind components at a regional scale (Gulf of Cádiz area of the southern Iberian coastal LME).

The LCI (PC1 58% of total variance; Table 2) is negatively linked to air and water temperatures and atmospheric pressure variables, while precipitation records are positively correlated to this axis. Therefore, high LCI values are associated with wet conditions, low atmospheric pressure and low temperatures, in line with the summer and autumn patterns observed in the study area of the southern Iberian coastal LME.

The correlation matrix confirmed the clear and opposite trends between chl *a* and SST with a particularly high and negative correlation in summer (Fig. 6). LCI was also negatively correlated with SST and positively correlated with the orthogonal basis function of winds W2 and chl *a* in both seasons,

which directly link LCI variability with local wind patterns (southeast–northwest component, W2) and productivity. A lack of statistically significant correlation between NAO and the regional environmental variables was also evident (Fig. 6). Based on these correlations and VIF analysis (not shown), the final set of environmental covariates to be included in the analysis was: NAO, LCI, RUN, the wind function W1 from both seasons and W2 from autumn.

### Effects of the environmental variables and population density

#### Species-specific effects

Table 3 displays the best LM for each response variable (CG in latitude, longitude and depth). In general, the NAO was the most frequent explanatory covariate related to the distributional variability of species. LCI, dens or RUN also influenced changes in CG in some populations. The wind modes (W1 and W2) were not significant explanatory covariates in the best LMs.

Variations in CG in longitude were mostly influenced by the NAO, but delayed or contemporary responses were species dependent. This index mostly influenced species inhabiting the shallower strata (<100 m and 100–200 m). A negative response to the NAO index in summer (NAO\_S) was observed in longitudinal changes on *M. surmuletus* and *P. erythrinus*. By contrast, the other 7 species showed positive effects related to changes in longitude (Table 3). Additionally, the NAO exclusively affected latitudinal changes, positively in the case of *P. erythrinus* and negatively in the case of *M. merluccius* and *S. canicula*. Regarding depth variations, the positive effect of the NAO index in autumn (NAO\_A) was related to movements of *O. vulgaris* to shallower waters.

LCI negatively influenced variations in longitude of *O. vulgaris* and movements in depth for *P. acarne* and *Conger conger*. Density-dependent covariate (dens) had less recurrent influence, but showed negative effects in longitude for *Nephrops norvegicus* and in depth for *L. budegassa*. Only *P. erythrinus* showed a positive effect of dens in relation to depth. RUN in summer only negatively affected changes in depth for *C. conger*.



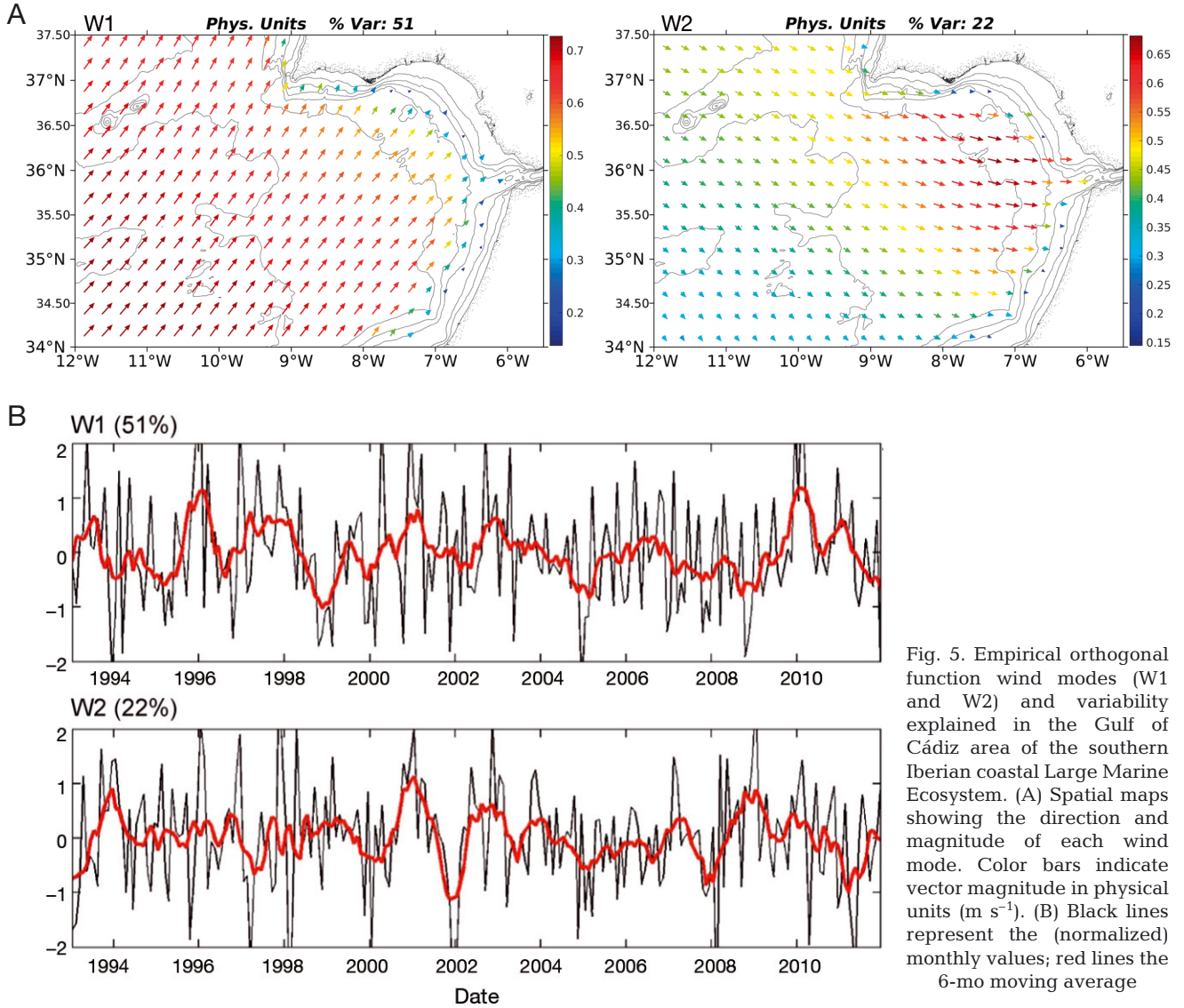


Fig. 5. Empirical orthogonal function wind modes (W1 and W2) and variability explained in the Gulf of Cádiz area of the southern Iberian coastal Large Marine Ecosystem. (A) Spatial maps showing the direction and magnitude of each wind mode. Color bars indicate vector magnitude in physical units ( $\text{m s}^{-1}$ ). (B) Black lines represent the (normalized) monthly values; red lines the 6-mo moving average

#### Effects on the community

Table 4 displays the best LMs and LMEMs that fit CG in longitude including significant variables for the entire set of species. The LMEM with random intercept and slope minimized AIC and contained LCI as a significant explanatory variable of the fixed term and a different effect of NAO\_S for each species (random grouping factor). LCI had a negative effect and evidenced a regional and common pattern on the entire community of the southern Iberian coastal LME with high LCI related to westward movements of the whole community and eastward displacements to lower LCI values. By contrast, each species had a different sensitivity to large-scale climate variation from the previous sum-

mer (NAO\_S) on the variation of CG in longitude. Fig. 7 shows the sign and the relative importance of the random effect and evidenced that, at the community level, the NAO\_S effect was segregated by bathymetric strata. NAO\_S effects were mostly negative for species belonging to the shallower stratum (SS; <100 m), mainly for *M. surmuletus* or *P. erythrinus*. The effects were positive for species of deeper strata such as *Merluccius merluccius* or *P. longirostris*, but not in the case of *L. caudatus*. The results at the community level (Fig. 7, Table 4) were in accordance with species-specific models (Table 3). However, there was no statistical evidence (LM or LMEM) for drivers that could explain changes in CG in latitude or CG in depth at the community level.

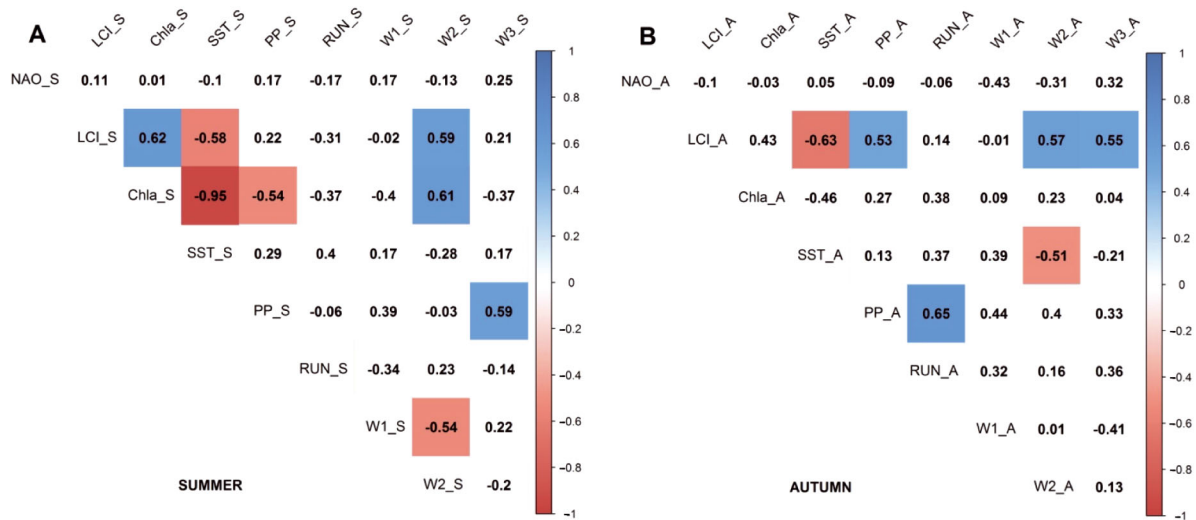


Fig. 6. Pearson correlation coefficients among climate indices (NAO: North Atlantic Oscillation; LCI: local climatic index) and environmental variables (chl *a*: chlorophyll *a*; SST: sea surface temperature; PP: precipitation; RUN: Guadalquivir River runoff; W1, W2 and W3: wind modes) in (A) summer and (B) autumn for the study period (1993–2012). Blue: significant positive correlation; red: significant negative correlation ( $p < 0.05$ ); unshaded: no significant correlation

Table 2. Percentage of the total variance associated with the principal components PCA1 (local climatic index, LCI) and PCA2 of the analyzed time series and the correlation coefficients of aggregated variables (loadings) of the southern Iberian coastal Large Marine Ecosystem. SST: sea surface temperature; SAT: surface air temperature; GHP: 500 hPa geopotential height; SLP: sea-level pressure; PP: precipitation

	PCA1 (58 %)	PCA2 (32 %)
SST	-0.42	-0.51
SAT	-0.43	-0.50
GHP	-0.55	0.05
SLP	-0.40	0.52
PP	0.41	-0.47

## DISCUSSION

This study illustrates spatiotemporal changes in the distribution of key demersal species in the Gulf of Cádiz area of the southern Iberian coastal LME, which were mainly driven by hydroclimatic variability. Changes were more evident over the longitudinal gradient with species moving closer to and away from the Strait of Gibraltar or from the Guadalquivir River plume. Additionally, these distributional changes depended on the species mean location regarding the runoff plume of the Guadalquivir River. This different behavior was also segregated by depth. In the shallow shelf (<100 m), a southeastward movement towards the Strait of Gibraltar was clear, whereas species from the deeper strata additionally underwent bathymetric shifts. Our study also evidenced

that those movements were mainly associated with large-scale climate variability (NAO). The sign and strength of the NAO effect was clearly species specific. Furthermore, the mesoscale climate index (LCI) largely controlled longitudinal variations at a regional scale. In contrast with the absence of directional trends in other areas of a similar small size (e.g. Gulf of Lions in the Northwestern Mediterranean Sea, Morfin et al. 2012), significant spatial shifts of species distributions and communities were observed in the southern Iberian coastal LME mainly related to hydroclimatic variability. The confluence of physical and ecological processes with synergistic influence over different spatial and temporal scales could explain the particular sensitivity of these systems to regional and global climate variability.

The southeastward movement (i.e. towards the Strait of Gibraltar) was the most remarkable trend, followed by several species from the shallow shelf, particularly Sparidae species, *Chelidonichthys obscurus*, *Mullus surmuletus* and *Trachurus trachurus* (<100 m) and 2 elasmobranchs from the deeper strata (upper slope and middle slope; >200 m). In contrast, a northwestward shift was detected for the wedge sole *Dicologlossa cuneata* in the shallow shelf and for the deep-water rose shrimp *Parapenaeus longirostris* in the deep shelf. Although river runoff did not have a significant role in these shifts, the geographical boundary marked by the Guadalquivir River plume (Caballero et al. 2011) might play an ecological differentiation role since these opposite trends matched the mean location of species in rela-

Table 3. Best linear models (LMs), including statistically significant covariates, for the variability in centers of gravity (longitude, latitude and depth) for each species. Results for those with no significant variables are not shown. Explanatory covariates: NAO (North Atlantic Oscillation); LCI (local climatic index); RUN (Guadalquivir River runoff); dens (density). S: summer; A: autumn; E: estimate; I: intercept;  $r^2$ : coefficient of determination. SS: shallow shelf; US: upper shelf; US/MS: upper slope/middle slope of the southern Iberian coastal Large Marine Ecosystem. Level of significance: \* $p < 0.05$ ; \*\* $p < 0.01$ ; \*\*\* $p < 0.001$

Depth strata	Species	Longitude		Latitude		Depth	
		Covariate (E)	$r^2$	Covariate (E)	$r^2$	Covariate (E)	$r^2$
<100 m (SS)	<i>Mullus surmuletus</i>	NAO_S (-0.05)*	0.32				
	<i>Pagellus acarne</i>						
	<i>Pagellus erythrinus</i>	NAO_S (-0.07)*	0.36			LCL_A (-6.50)*	0.32
	<i>Spondyllosoma cantharus</i>	NAO_A (0.08)*	0.33	NAO_S (0.11)***	0.41	dens (27.04)**	0.40
	<i>Trachurus trachurus</i>	NAO_A (0.08)**	0.38				
	<i>Citharus linguatula</i>	NAO_S (0.04)*	0.25				
100–200 m (DS)	<i>Dicologlossa cuneata</i>						
	<i>Chelidonichthys obscurus</i>						
	<i>Octopus vulgaris</i>	LCL_S (-0.10)*	0.44			NAO_A (7.56)*	0.29
	<i>Conger conger</i>					LCL_A (-60.54)***, RUN_S (-1.89)***	0.70
200–300 m (US)	<i>Merluccius merluccius</i>	NAO_S (0.05)*	0.30	NAO_S (-0.08)*	0.28		
	<i>Parapenaeus longirostris</i>	NAO_S (0.04)**	0.26				
	<i>Scyllorhinus canicula</i>	NAO_A (0.06)*	0.40	NAO_A (-0.06)*	0.27		
	<i>Lophius budegassa</i>						
	<i>Lepidopus caudatus</i>						
>300 m (US/MS)	<i>Raja clavata</i>						
	<i>Etmopterus spinax</i>	NAO_A (0.07)**				dens (-234.0)**	0.50
	<i>Nephrops norvegicus</i>	dens (-0.75)**	0.54				

tion to this geographical boundary (Fig. 3A). This suggests that the external impact on species distribution was spatially segregated into 2 ecotones: east and west of the river plume. These regions have already been differentiated by mesoscale hydrological conditions (Muñoz et al. 2015). Additionally, the river plume also determines habitat characteristics through an indirect but strong influence in marine sedimentary environments (Lobo et al. 2014). Muddy and muddy-sandy bottoms have been associated with *D. cuneata* and *P. longirostris* population distributions (Ardizzone et al. 1990, Jiménez et al. 1998), and are more abundant west of the river mouth (Fernández-Salas et al. 2015). This could explain the mean distributions of these species west of the river found in our results. In contrast, in the case of very mobile species with a wider distribution area than our study area, such as the mid-size pelagic *T. trachurus*, this displacement might correspond to a fraction of the population. In that regard, Murta (2000) hypothesize that individuals from Spanish waters of the Gulf of Cádiz are well discriminated from the population of the Algarve and Moroccan waters, and could have a Mediterranean origin. However, information about spatial distribution of this species or about its connectivity with Mediterranean waters remains scarce in this area. Regarding depth changes, only *Octopus vulgaris* in the shallow shelf showed a significant displacement, most likely due to the variability of rainfall in the Gulf of Cádiz area of the southern Iberian coastal LME (Sobrino et al. 2002). It is also interesting to note that geographical shifts were linked to bathymetric displacements in the upper slope species. Most species moved to shallower waters, in contrast to well-known shifts to deeper areas in response to global ocean warming (Perry et al. 2005, Dulvy et al. 2008, Punzón et al. 2016). This suggests that additional environmental or demographic factors not included in the study may affect deeper strata.

Table 4. Best linear model (LM) and linear mixed-effects models (LMEMs) including significant explanatory covariates to explain variability in centers of gravity of longitude for the entire set of species of the southern Iberian coastal Large Marine Ecosystem. Explanatory covariates: NAO (North Atlantic Oscillation); LCI (local climatic index). S: summer. Species was the random grouping factor. Estimates (standard error); Corr: correlation term between the random intercept and slope; SD: standard deviation. Level of significance: \* $p < 0.05$ ; \*\* $p < 0.01$ ; \*\*\* $p < 0.001$

Model	AIC	Fixed effects		Random effects	
		Intercept	LCI_S		
LM	97.99	0.53 (0.03)***	−0.05 (0.02)*		
Random intercept LMEM	93.55	0.53 (0.03)***	−0.05 (0.02)*	(1 species)	
				SD intercept	0.08
				SD residual	0.28
Random intercept and slope LMEM	89.22	0.53 (0.03)***	−0.05 (0.02)*	(NAO_S species)	
				SD intercept	0.09
				SD slope (NAO_S)	0.08
				SD residual	0.26
				Corr	0.34

Environmental variables such as SST, chl *a* or freshwater inputs have been the most recurrent explanatory variables in fish distribution studies (Perry et al. 2005, Puerta et al. 2014, Punzón et al. 2016). According to Perry et al. (2005), runoff and precipitation might also have indirect implications on trophic levels through changes in food availability.

Traditionally, regional temperature changes have explained differences in observed shifts away from warming waters (Pinsky et al. 2013, Punzón et al. 2016) and chl *a* had a great influence on spatial movements in the nearby western Mediterranean Sea (Puerta et al. 2014). Additionally, wind-induced larval transport has been also associated with recruitment success of several marine species. Wind-forcing mechanisms can affect residual currents and hydrodynamic transport and, consequently, determine interannual differences in development conditions and dispersal of eggs and larvae (Bradbury & Snelgrove 2001, Bolle et al. 2009). In this sense, interannual fluctuations in the duration of intense easterly winds has been related to recruitment failure of the pelagic species *Engraulis encrasicolus* in the Gulf of Cádiz (Ruiz et al. 2006). However, in the present study, their influences are captured by the local (LCI) and global (NAO) climate indices that are able to capture the environmental variability effect on fish distributions (see below). Finally, although stronger density-dependent effects were potentially expected on the distributional shift in accordance with other studies (Spencer 2008, Puerta et al. 2014), this effect was minimal. Density was the only driver affecting bathymetric displacements of *Lophius budegassa* with shallower distribution in years of high population density. This response most likely occurs to avoid intraspecific competition, which has already been observed in other benthic species (Swain & Wade 1993, Marshall & Frank 1995). Additionally, the negative and significant correlation found between density and mean size in the case of this species (Fig. A1 in

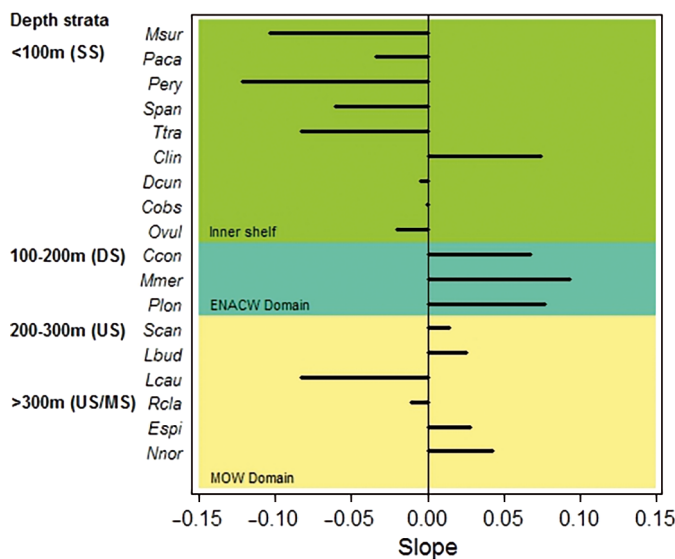


Fig. 7. Species-specific slopes of the random effects of the North Atlantic Oscillation index in summer (NAO\_S) in the random intercept and slope lineal mixed-effect model for the center of gravity in longitude (Table 4). Water mass depth distributions in the eastern Gulf of Cádiz area of the southern Iberian coastal Large Marine Ecosystem from Bellanco & Sánchez-Leal (2016). Species abbreviations are compiled in Table 1. SS: shallow shelf; DS: deep shelf; US: upper slope; MS: middle slope; US/MS: upper slope/middle slope; ENACW: Eastern North Atlantic Central Water; MOW: Mediterranean Outflow Water



the Appendix), show that these density-dependent effects could be also related to interannual variation in the strength of recruitment, i.e. changes in relative ontogenic habitat occupation (Martin et al. 2010, Bartolino et al. 2011).

Climate indices over different spatial scales are the main drivers shaping the species distribution in the present study. It is known that climate indices are able to capture a broad and diverse range of environmental processes across spatial and temporal scales (Stenseth et al. 2002, 2003, Stenseth & Mysterud 2005). The local climate index used here (LCI) summarizes the regional climatic information in the Gulf of Cádiz area of the southern Iberian coastal LME, with positive values related to wet conditions, low temperature, northwesterly wind component and high chl *a* concentration (as a proxy of primary productivity). This climatic pattern depicted by positive values of LCI promotes the most important upwelling system in the Gulf of Cádiz area of the southern Iberian coastal LME, located in the vicinity of the Portuguese Cape San Vicente, to the east of Cape Santa Maria (Criado-Aldeanueva et al. 2006). However, another wind-induced upwelling has also been described in the area during easterlies events (negative values of LCI), located at the southwestern end of the Strait of Gibraltar (Vargas et al. 2003, Prieto et al. 2009). The prevalence of negative values of LCI (easterlies) in summer could prevent upwelling phenomena in the western zone of our study area, and benefit its formation in the southeastern-most part of the Gulf of Cádiz area of the southern Iberian coastal LME. This mechanism might affect shallower water masses and could be behind these distributional variations towards the Strait of Gibraltar. Alternatively, positive LCI values might be more related to changes towards the Portuguese coast. The variability in upwelling systems along the southwest coast of the Iberian Peninsula has important implications for the productivity of the shelf in the Gulf of Cádiz area of the southern Iberian coastal LME. This suggests that interannual variation in the strength and location of upwelling systems in summer is a common regional driver that triggers longitudinal displacements recorded at the community level and contrasts with species-specific effects of the NAO.

Regarding large-scale climatic influence, the NAO was the most recurrent driver on species displaying geographical shifts, particularly in longitude. However, the NAO effects differ in strength, direction and season depending on the species, with a delayed response in some cases and a contemporary effect in others. For instance, the NAO in summer correlates

with opposite effects on longitudinal changes segregated by depth strata (Table 4), suggesting that the response of species of the different strata is associated with different physical and/or ecological processes already influenced by the NAO. The influence of the large-scale NAO index on ecological processes through parameters such as wind strength, precipitation, SST and salinity in the North Atlantic is well documented (Stenseth et al. 2002, Hurrell et al. 2003, Stige et al. 2006). However, contrasting the findings reported in other geographical areas (Fromentin & Planque 1996, Beaugrand et al. 2003), our results detected a lack of association between the NAO and wind modes or other local environmental variables. The topographic characteristics of the Gulf of Cádiz area of the southern Iberian coastal LME shelter it from the main offshore winds and a dissimilar wind pattern and surface circulation has been described on either side of Cape San Vicente (Portugal) (Sánchez et al. 2006). This characteristic together with spatiotemporal scale differences between local variables and this large-scale index might explain this absence of relationship. It is known that the NAO integrates several mechanisms through which this climate index often outperforms local weather variables to explain climate-related variation in life history traits or abundance: the time window, the spatial window and the weather composition component window of climate (Stenseth & Mysterud 2005). This multiscale perspective of the NAO is consistent with our results and with the confluence of complex hydrobiological processes in the Gulf of Cádiz area of the southern Iberian coastal LME, which probably confers it a special sensitivity to climate. Therefore, we argue that other hydrodynamic and oceanographic mechanisms, extended over much larger and deeper areas, and not included in our study, are indirectly affected by NAO dynamics and could influence species distributions.

In this sense, depth-segregated responses to the NAO matched the spatial distribution of water masses in the eastern Gulf of Cádiz area of the southern Iberian coastal LME seabed (Fig. 7): the shelf water mass (<100 m), strongly influenced by coastal and atmospheric events; the ENACW that flows in the deep shelf (100–250 m); and the MOW that occupies the deeper grounds (>250 m) (Bellanco & Sánchez-Leal 2016). Several studies have demonstrated how each water mass is differentially affected by the NAO. For instance, on the shelf, the concurrence of local wind component (easterlies; negative LCI) and negative NAO index reinforces an open-sea flow reversal and the subsequent eastward current in



autumn–winter months in the Gulf of Cádiz area of the southern Iberian coastal LME (Criado-Aldeanueva et al. 2009 and references therein). This type of linkage between local climate variability and large-scale climate patterns has already been observed in other geographical areas (Atlantic, Beaugrand & Reid 2003; northwestern Mediterranean, Molinero et al. 2005). Regarding the deep shelf, the ENACW is affected by the interannual to interdecadal variability in the intensity of the North Atlantic gyre circulation, also related to NAO fluctuations (Volkov & Fu 2011). Finally, regarding the possible linkage between deep-water mass variations and the NAO, several indications suggest the inclusion of this climate index as a potential driver of bathymetric and geographic changes in deep distributed species. The dynamics of the MOW (or the MOW reservoir variability) has also been suggested to be influenced by the NAO (Lozier & Stewart 2008, Bozec et al. 2011). Furthermore, Tsimplis et al. (2013) have suggested that although the NAO influence on the Mediterranean Sea level is primarily expressed by local atmospheric pressure effects and the effects of winds over the basin, there is also a third contributing mechanism linked with the NAO due to a change in the oceanic baroclinic circulation driven by the wind in the Atlantic Ocean. In connection with this, several indications regarding the effect of climate indices on MOW variability in the eastern part of the Gulf of Cádiz area of the southern Iberian coastal LME are becoming the subject of research as a new study line (M. J. Bellanco et al. unpubl. data).

In the case of the deep species such as the elasmobranch *Raja clavata*, none of the explanatory covariates explained the eastward trend, which also involved depth changes. This bathymetric stratum is less influenced by the environmental drivers affecting the upper water column that are included in our analyses. The spatiotemporal variability of deeper species might probably be related to other hydrographic characteristics of deep water masses, such as subsurface temperature, although there is very scarce information. These movements could be consistent with the thermohaline anomaly observed in the western Mediterranean Deep Water from 2005 (López-Jurado et al. 2005, Balbín et al. 2016, Schröder et al. 2016) or with a recent cooling of water masses at 200 m detected in the Gulf of Cádiz area of the southern Iberian coastal LME (M. J. Bellanco & R. Sánchez-Leal unpubl. data). In the case of the elasmobranch with a shallower distribution range, *S. canicula*, the combined influence of climatic and oceanographic factors may explain the observed

geographical shifts. It is also known that deeper species can be highly influenced by surface environmental variability that affects the dynamics of pelagic subsidies and the transfer of organic matter to the bottom through the seasonal sinking of phytodetritus (Smith et al. 2013, Hidalgo et al. 2015). These processes could also explain the influence of the NAO on *Nephrops norvegicus* given the dependence of this species on organic matter and thus on pelagic subsidies.

To conclude, there is clear evidence of a climate-induced geographical shift of the demersal community in the eastern Gulf of Cádiz area of the southern Iberian coastal LME towards the Strait of Gibraltar throughout the study period. This was particularly evident for species occupying the shallow shelf and with a mean location situated south of the Guadalquivir River mouth. Our results also show how hydroclimatic factors modulated this segregated behavior by depth strata. In general, the shallow water shelf of the southern Iberian coastal LME was strongly influenced by climate variations at the regional scale (LCI index) and at the species-specific level (NAO influence), while uncertain oceanographic processes could be responsible for changes in deeper strata, and call for further research. The present study revealed that this transitional Atlantic–Mediterranean water occupying the southern Iberian coastal LME and, particularly, many species of the demersal community with contrasting life history (from Sparidae to Elasmobranchs) are sensitive to climate variations. These findings together with previous information (Ruiz et al. 2006, Vargas et al. 2010) provides a scientific basis to design future studies and modeling frameworks that could advise on projections of changes at a regional scale, as has been shown in the Mediterranean at a larger spatial scale (Albouy et al. 2013).

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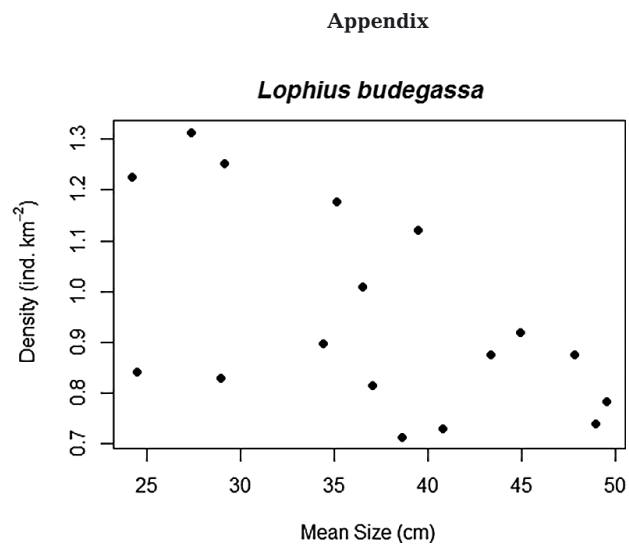


Fig. A1. Number of ind. km<sup>-2</sup> versus mean size (cm; weighted by number of individuals) of *Lophius budegassa*. Pearson correlation coefficient:  $-0.5$ ,  $p < 0.05$

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