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Patterns of spatial changes in demersal species in the Gulf of Cadiz and northern Alboran Sea

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Abstract

The Gulf of Cadiz (GoC) in the Atlantic Ocean and the northern Alboran Sea (AS) in the Mediterranean Sea are part of an extremely important oceanographic complex in terms of water exchange between the Atlantic and the Mediterranean through the Strait of Gibraltar. Besides its significant role as an ecological transition system, it is unknown whether regional and local environmental drivers affect similarly species inhabiting these two adjacent and connected ecosystems. This study analyses the spatial shifts of representative demersal species and their response to the environmental and demographic drivers in these two regions, using information from two trawl surveys carried out in the GoC and in the AS from 1994 to 2015. Species distribution trends were observed in both basins. However, they were more evident in the GoC, where six out of eleven species presented temporal trends, than in the AS, where only two species displayed significant distribution changes. In both basins, these species showed geographic displacements towards the Strait of Gibraltar. Also, a high percentage of species presented significant differences in mean depth distribution on the two sides of the Strait of Gibraltar. Our study shows a general heterogeneity and independence in the drivers influencing species distributions in the two areas. GoC was highly influenced by both large- and regional-scale climate factors, which affected several species, while in AS the diversity of drivers was greater, with species density being the most common. This study provides a scientific basis for improving ecosystem-based management measures in these important transitional ecosystems.

Keywords: Demersal species; species distribution; centre of gravity; Gulf of Cadiz; Alboran Sea; climate effects.

Introduction

The Gulf of Cadiz (GoC) and the Alboran Sea (AS) are part of an extremely important oceanographic complex in terms of water exchange between the Atlantic Ocean and the Mediterranean Sea, which can affect the dynamics of these boundary ecosystems. Water is exchanged with the open ocean through the Strait of Gibraltar, with a flow intensity that is controlled by a wide range of both seasonal and non-seasonal factors (Parrilla, 1984). This narrow pass is the only connection between the Mediterranean Sea and the Atlantic Ocean, with the GoC and AS being the ecosystems on either side. On both the Atlantic and Western Mediterranean sides, the water column is composed of low-salinity Atlantic surface waters and dense (highly saline) Mediterranean deep waters. These masses interact together, giving rise to a specific hydrodynamic regime in the area (Ambar & Howe, 1979). While the AS is characterised by large anticyclonic gyres, some important rivers, including the Guadalquivir, discharge into the coastal areas of the GoC. The ecological connectivity between these two large ecosystems has been an important element of research from the oceanographic and ecological perspective considering the lack of knowledge on the diversity of processes that take place in the Strait of Gibraltar (Pires *et al.,* 2015). However, despite the importance of the Atlantic-Mediterranean connection for species exchange and ecosystem separation, few studies have focused on the connectivity processes at species level, having mostly examined early life stage dispersal (Pires *et al.,* 2015; Pires *et al.,* 2018). An integrative understanding of the ecological interactions between these boundary ecosystems requires an understanding of the global, regional and local drivers affecting the geographical distribution of the main community species, as this is one of the most important aspects when developing and implementing an Ecosystem Approach to Fisheries Management (EAF) in the northern AS and GoC.

Density-independent (i.e., environmental) and density-dependent (i.e., demographic) variables are both known to affect the spatial distribution of species. For example, species are often distributed according to their environmental preferences, to optimise the use of spatially heterogeneous resources or over space, in relation to their own abundance, to reduce intraspecific competition (Cianelli *et al.,* 2012; Cianelli *et al.,* 2013). For marine species, determining the relationships between species distribution and environmental and demographic factors are essential for comprehending many aspects of their ecology and allowing effective and adaptive conservation and management, as well as enabling an assessment of possible impact from anthropogenic activities (Holsman *et al.,* 2019). Species distribution models are a common approach to describing species space-use and spatially-explicit abundance. However, to better track mean temporal changes in species distributions in response to local and regional climate, metrics describing the mean population distribution, i.e., the centre of gravity (CG) (Daget, 1976), are increasingly being used (Stefanescu *et al.,* 1992; Perry *et al.,* 2005; Spedicato *et al*., 2007; Cartes *et al*., 2009; Thorson *et al.,* 2017; Delgado *et al.,* 2018). The CG model allows to calculate and precisely locate the centre of a species' distribution by means of a descriptor (e.g., longitude, latitude, or depth) weighted by the relative species abundance (Stefanescu *et al.,* 1992).

Our objective was to analyse the inter-annual changes in spatial distribution of a group of representative demersal species from the GoC and AS. In addition, we also aimed to investigate the effect certain environmental and demographic variables have on this distribution and, eventually, assess potential synchrony, coherence or similarity between the species dynamics and the influence of the environmental and demographic drivers in each area. For this goal, CG in longitude, latitude, and depth were calculated and analysed over a historical series of 22 years of research surveys (ARSA and MEDITS) from 1994 to 2015. Additionally, the relationships of the CG with local environmental variables (sea surface temperature, sea surface salinity, sea surface chlorophyll-*a* concentration, winds and sea currents), regional and global climate drivers [North Atlantic Oscillation (NAO) and a local climate index (LCI)] and demographic variables (species density) were all considered.

Materials and Methods

Study area

The study area (Fig. 1) is located in southern Spain and includes the Gulf of Cadiz (GoC) and northern Alboran Sea (AS). The GoC covers waters from the mouth of the Guadiana River, which borders Portugal in Ayamonte (Huelva), to the Cape of Tarifa (Cadiz). The AS encompasses the area from the Strait of Gibraltar to the Cape of Gata (Almeria). These two areas are very different in terms of their hydrological and biological characteristics, but they are, also, tightly connected to one another by the narrow Strait of Gibraltar (Macías *et al.,* 2014). In the GoC, the oceanic surface circulation is anticyclonic, with short-term meteorologically induced variability that changes the geostrophic stream lines and volume transport, while a counter-current flows along the inner shelf (Criado-Aldeanueva *et al.,* 2006). The region is a mesotidal basin with a wide continental shelf and it is influenced by freshwater runoff from the Guadalquivir and Guadiana rivers. The GoC presents medium primary productivity levels (e.g., Echevarría *et al.,* 2009) mainly associated with the coastal zone, frontal regions, and the discharges of the main river, the Guadalquivir (Navarro & Ruiz, 2006; Garcia-Lafuente & Ruiz, 2007; Prieto *et al.,* 2009; Macías *et al.,* 2014). Atlantic waters enter the Mediterranean surficially. This current flows towards the northeast after leaving the Strait, then turns to the southeast describing a large anticyclonic gyre which occupies the western sub-basin of the AS. The Atlantic Water impinges on the African coast and finally describes a new anticyclonic gyre in the eastern sub-basin of the AS. Likewise, colder and more saline Mediterranean waters flow below the Atlantic waters (Parrilla, 1984; Vargas *et al.,* 2019). The northwestern AS is a highly dynamic system which exhibits large variations in bio-physiochemical parameters, on a range of spatial and temporal scales due to the presence of a number of hydrographic structures, including fronts, cyclonic and anticyclonic gyres, and coastal upwelling (Minas *et al.,* 1987; Tintoré *et al.,*

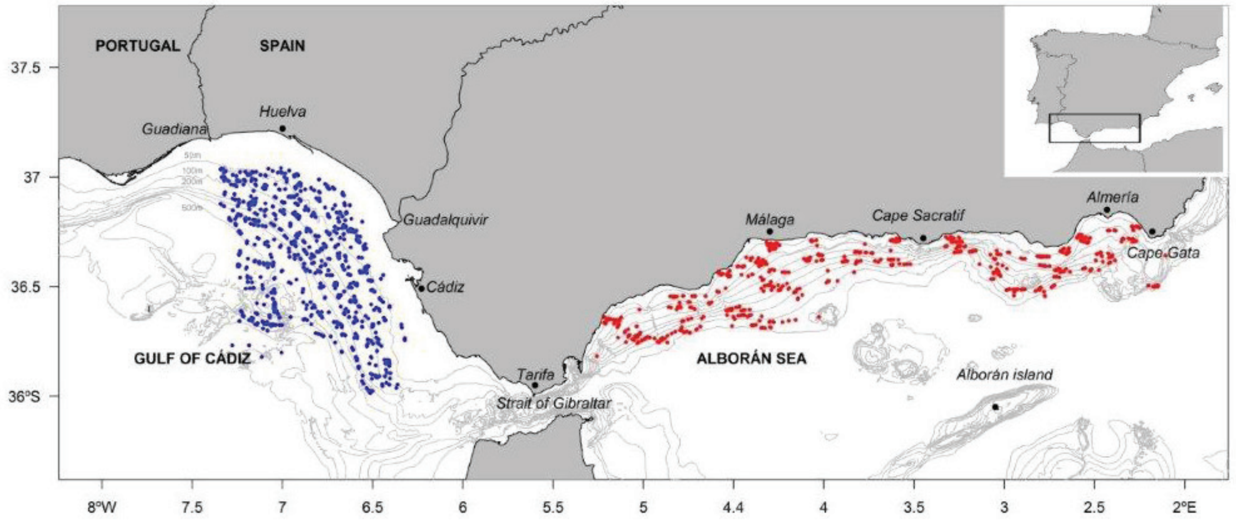

Fig. 1: Iberian Peninsula and the study area of the Gulf of Cadiz and northern Alboran Sea. The locations of hauls during ARSA surveys (blue points) and MEDITS surveys (red points) from 1994 to 2015 are shown.

1991; Gleizon *et al.,* 1996; Viúdez *et al.,* 1996; Gomís *et al.,* 1997; Rodríguez *et al.,* 1998). In the AS, in contrast with GoC, the continental shelf is very narrow, there is no important river discharge, the tidal influence is much lower, and one of the main drivers of primary productivity in the region is the inflow of Atlantic waters through the Strait of Gibraltar (Macías *et al.,* 2007). Local wind-driven upwelling can also occur in the northern AS, depending on the angle of the Atlantic Jet and the speed nutrients are injected into the system.

Samples

The species abundance data from 1994 to 2015 came from two bottom trawl surveys carried out in the GoC (ARSA; Sobrino *et al.,* 1994) and northern AS (MEDITS; Bertrand *et al.,* 2002; Spedicato *et al.,* 2019). The two surveys were carried out during day-light hours with the stations being distributed according to a stratified sampling scheme where depth was the stratification parameter adopted. The number of hauls per stratum was proportional to the surface area available for trawling within each stratum. A 20 mm codend mesh size was used. The ARSA surveys were conducted in winter-spring (February-March), and the MEDITS surveys were undertaken in the spring (April-May). Each individual caught was identified to the lowest taxon possible, weighed and counted. For each haul, individuals of each species were standardised to number of individuals per km^2. In order to obtain these values, the swept area from each haul was estimated from the monitoring of the horizontal opening of the gear and the distance covered during the haul. A total of 11 species were selected for the study according to the following criteria (Delgado *et al.,* 2018): high catchability, and those species most representative in terms of abundance, commercial or conservation interest (Table 1).

Descriptors of spatial location

To analyse the movements of the species in regard to latitude, longitude and depth over long-term time series, centres of gravity of selected species have been calculated per year (CG; Daget, 1976; Stefanescu *et al.,* 1992). The CG indicates the optimal habitat of a species, which is often located where the species also reaches its maximum density (Cartes *et al.,* 2011); it is calculated as follows:

$$CG = \frac{\sum_{i=1}^{N} x_i s_i z_i}{\sum_{i=1}^{N} s_i z_i}$$

where z_i are density values (N.·km^{-2}) at locations x_i, and s_i are the areas of influence for CG longitude and latitude. 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) (ICES 2010; Woillez *et al.,* 2009; RGeostast package (Renard *et al.,* 2014)). The CG is unaffected by zero population density values. The outer border of the domain can be a known or supposed boundary of the sample population (Woillez *et al.,* 2009; Delgado *et al.,* 2018).

Table 1. Representative species selected of Gulf of Cadiz and northern Alboran Sea by depth strata and taxonomic group, showing the mean density of species (N/km^2) in the two surveys.

		GULF OF CADIZ		ALBORAN SEA		
Depth strata	**Group**	**Species**	**Mean (Ind/km^2)**	**Species**	**Mean (Ind/km^2)**	**Abbreviation**
<100 m	Fish	*Mullus barbatus*	100.37	*Mullus barbatus*	1324.77	Mbar
Shallow shelf Shelf		*Pagellus acarne*	369.65	*Pagellus acarne*	4013.08	Paca
		Boops boops	200.94	*Boops boops*	2559.09	Bboo
	Molluscs	*Octopus vulgaris*	92.86	*Octopus vulgaris*	248.11	Ovul
100-200 m	Fish	*Merluccius merluccius*	927.66	*Merluccius merluccius*	567.10	Mmer
Deep Shelf	Crustaceans	*Parapenaeus longirostris*	5323.35			Plon
		Plesionika heterocarpus	14960.65			Phet
	Molluscs			*Eledone cirrhosa*	87.66	Ecir
200-500 m	Fish	*Phycis blennoides*	78.73	*Phycis blennoides*	239.29	Pble
Upper Slope	Crustaceans			*Parapenaeus longirostris*	615.67	Plon
				Plesionika heterocarpus	15211.01	Phet
	Molluscs	*Eledone cirrhosa*	89.27			Ecir
>500 m	Fish	*Galeus melastomus*	801.94	*Galeus melastomus*	2540.69	Gmel
Midle Slope		*Etmopterus spinax*	765.27	*Etmopterus spinax*	288.51	Espi

Environmental and demographic variables

To analyse the environmental drivers affecting the CG of species in terms of latitude, longitude and depth, several oceanographic parameters were examined for each area. The sea surface temperature (SST), sea surface salinity (SSS), water current speed U and V component (U and V water), wind speed at 10 m, U and V component (U and V 10 m), and the first empirical orthogonal function (EOF; 54.7% variance explained) of the wind spatial pattern (W1) were retrieved for 1994 to 2015; the chlorophyll-*a* concentration (Chl-*a*) was obtained from 1998 to 2015. Information on these variables was gathered from the Copernicus Marine Service (https://marine.copernicus.eu). The North Atlantic Oscillation climate index (NAO) was obtained from https://climate-dataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-pc-based. A local climate index (LCI) was also calculated for each area. The LCI summarises the monthly anomaly fields according to the variables on the first axis of the principal component analysis (PCA) (Molinero *et al.,* 2005): surface air temperature (SST), atmospheric sea level pressure, 500 hPa geopotential height, and precipitation records, obtained from the NCEP-DOE Reanalysis 2 fields provided by the NOAA (Kanamitsu *et al.,* 2002). For each area analysed, two series of monthly records of environmental variables were used, i.e., data contemporary to the survey (winter-spring: December, January, February, March for the GoC; spring: March, April, May for the AS), as well as data from the season preceding the survey (autumn: September, October, November for the GoC; winter: December, January, February for the AS) in order to account for delayed responses.

As demographic information we used the mean species abundance (density; N.·km^{-2}).

Data analysis

To analyse temporal trends in CG longitude, latitude and depth time series, linear models (LM) were fitted for each species. LM have been also used with CG to estimate the rate of change and average shifts in CG over time (Pinsky *et al.,* 2013). In order to compare CG depth from the two basins we used a t-test at a minimum significance level of $p<0.05$. Shapiro-Wilk's test was used to assess normality. Bartlett's test was used to check the homogeneity of variances. The Mann-Whitney test was used when the homogeneity of variances could not be ensured. The effect of environmental and demographic factors in CG in latitude, longitude and depth at species level was also investigated using LM. Prior to the analyses, correlation matrices and variance inflation factor (VIF) were used to detect collinearity among the explanatory variables. A VIF cut-off of 5 was applied to drop collinear variables and attain the final set of covariates included in the statistical analyses (Zuur *et al.,* 2010). The best model was the one where the significant covariates had the lowest Akaike information criterion (AIC) value. The model analyses were performed using the stats library in the R software environment (R Core Team, 2015).

Results

Species CG time trends

Distributional time trends were observed in both basins (GoC and AS). However, a higher number of species showed significant spatial displacements along the time series in the GoC compared to the AS (Fig. 2; Fig. 3). In the AS, two species displayed significant spatial trends in their CG: *Boops boops*, located on the shallow shelf, in terms of longitude ($r^2=0.405$; $p<0.01$) and latitude ($r^2=0.231$; $p<0.05$); and *Etmopterus spinax,* located on the middle slope, in terms of longitude ($r^2=0.290$; $p<0.001$) and latitude ($r^2=0.330$; $p<0.01$). For both of these, the significant time trends ran from east to west, parallel to the coast. No species presented significant depth displacements in the AS basin.

In the GoC, in contrast, six of the eleven selected species showed significant time trends in their CG, with all geographical movements being parallel to the coast and towards the Strait of Gibraltar: *Pagellus acarne, B. boops, Mullus barbatus* on the shallow shelf, *Parapenaeus longirostris* on the deep shelf, and *E. spinax* and *Galeus melastomus* on the middle slope. Of these, significant time trends were observed in terms of longitude for *B. boops* ($r^2=0.401$; $p<0.001$) and *G. melastomus* ($r^2=0.421$; $p<0.01$), latitude for *E. spinax* ($r^2=337$; $p<0.01$), and depth for *P. longirostris* ($r^2=0.171$, $p<0.05$); *P. acarne* displayed changes in both longitude and latitude ($r^2=0.667$, $p<0.001$ and $r^2=0.572$, $p<0.001$, respectively)*;* and *M. barbatus* presented changes in longitude, latitude and depth ($r^2=0.228$, $p<0.05$; $r^2=0.298$, $p<0.05$ and $r^2=0.3283$, $p<0.01$, respectively).

Differences in CG depth between the two basins

Comparatively significant differences in the CG depth of species on the two sides of the Strait of Gibraltar are worth mentioning (Fig. 4). For the shelf strata, a high percentage of species from the shallow shelf and deep shelf in the AS displayed a shallower distribution than in the GoC (*P. acarne*, *Octopus vulgaris,* and *Eledone cirrhosa*). These significant bathymetric differences were slight for all species, except for *E. cirrhosa* that exhibited depth differences of around 100 m between the basins. In contrast, in the deeper strata, crustaceans and elasmobranchs showed a shallower distribution in the GoC than the AS, with depth differences of around 100 m. For example, the mean CG for *P. longirostris* was ca. 170 m in the GoC (172.5 ± 44.01 m) and ca. 260 m in the AS (264.52 ± 25.15 m). In the case of elasmobranchs, a mean CG of around 600 m was observed in the AS (*E. spinax*: 601.78 ± 59.94 m and *G. melastomus*: 601.14 ± 24.67 m) and around 510 m in the GoC (*E. spinax*: 507.53 ± 58.29 m and *G. melastomus*: 516.46 ± 48.42).

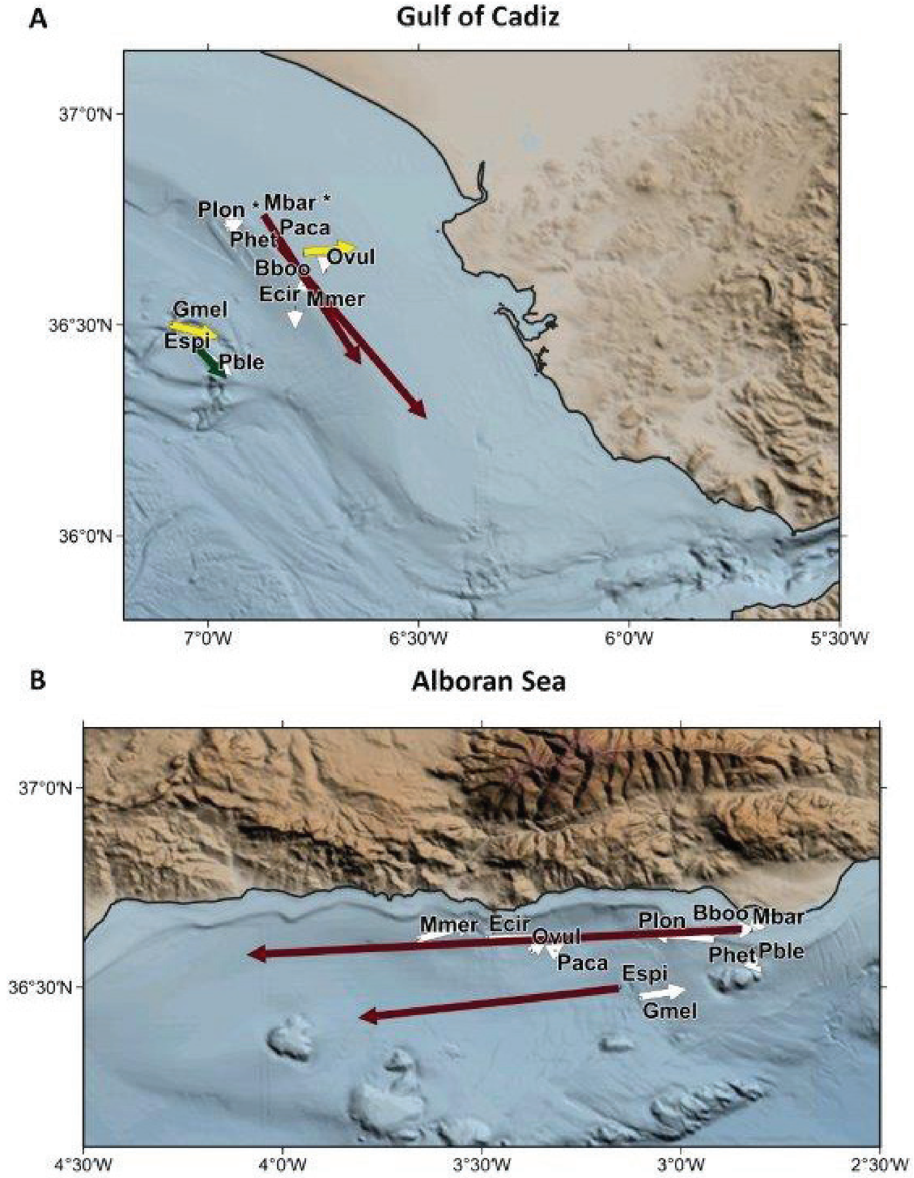

Fig. 2: Vectors showing the average shift of the centre of gravity (CG) in terms of latitude and longitude for each species examined from the Gulf of Cádiz (A) and northern Alboran Sea (B) (from linear models fitted to CG time series). Arrow colour indicates significant shifts in longitude (yellow), latitude (green), longitude and in latitude (brown), and no significant shift (white). *Significant depth shift. Species abbreviations: See Table 1.

Time trends of environmental and demographic variables

Temporal changes in the environmental and demographic variables (density) differed according to the region. The environmental variables with a significant role in the AS (Fig. 5A) showed inter-annual fluctuations with no clear trends except for Chl-*a,* which displayed an increasing trend in both spring and winter. Seasonal differences were observed in SST (spring values higher than winter), as well as Chl-*a* and LCI (winter values higher than spring). The NAO showed different trends in winter and spring with more variability in winter. SSS values were very similar in both seasons. In terms of density values, *B. boops, G. melastomus, O. vulgaris,* and *M. barbatus* (Fig. 5B) showed significant increasing trends over time. In the case of *P. acarne, B. boops, M. barbatus,* and *O. vulgaris* a similar pattern was observed, with lower densities at the beginning of the study period. Moreover, these species presented very low densities in the 1999 survey with high, notably synchronic, fluctuations as depicted by the significant positive correlations between *P. acarne-B. boops* (c=0.7, p<0.01) and *M. barbatus-O. vulgaris* (c=0.7, p<0.01). The other species displayed oscillations with no clear cyclic or temporal trends.

The time series variability of the environmental and climate variables that played a significant role on species distribution changes in the GoC is shown in Figure 6A. The SST time series displayed wide differences between autumn and winter-spring in the study area. W1 exhibited larger fluctuations in winter-spring than in autumn. Similarly, both climate indices (LCI and NAO) showed stronger variations in winter-spring. No clear trends in density were observed (Fig. 6B), except a slight increase over time for *M. barbatus* and *O. vulgaris*, and a small decrease in the latter years for *B. boops* and *P. acarne*.

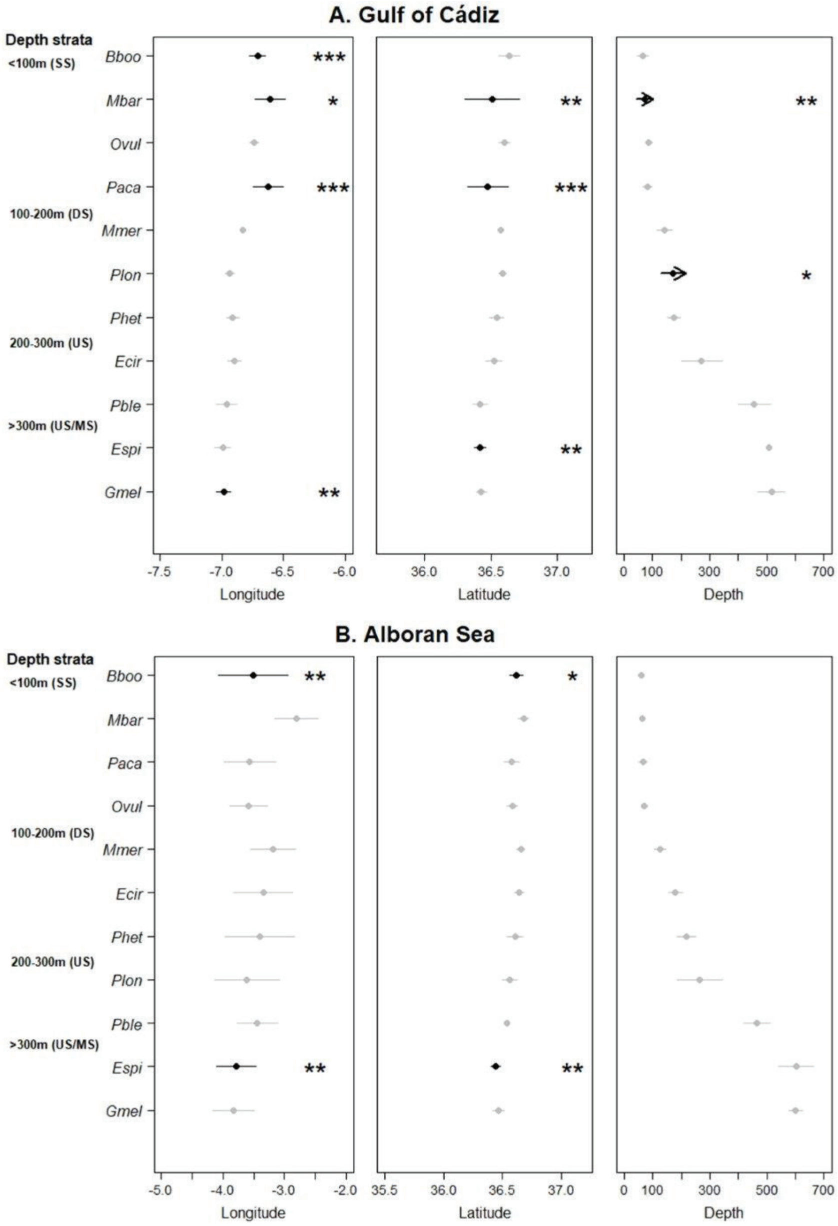

Fig. 3: Mean and standard deviation in CG in terms of longitude, latitude and depth by species and bathymetric stratum in the Gulf of Cádiz (A) and northern Alborán Sea (B). Black symbols: significant temporal trend. Arrows: direction of trends for CG depth. Level of significance: *p<0.05; **p<0.01; ***p<0.001. Species abbreviations: See Table 1.

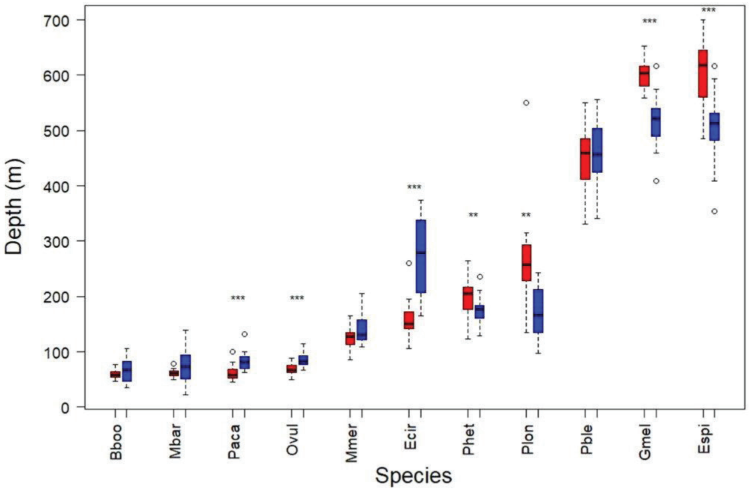

Fig. 4: Comparison of CG depth distribution by species and between basins: Gulf of Cadiz (blue boxes) and northern Alboran Sea (red boxes). Level of significance: *p<0.05; **p<0.01; ***p<0.001. Species abbreviations: See Table 1.

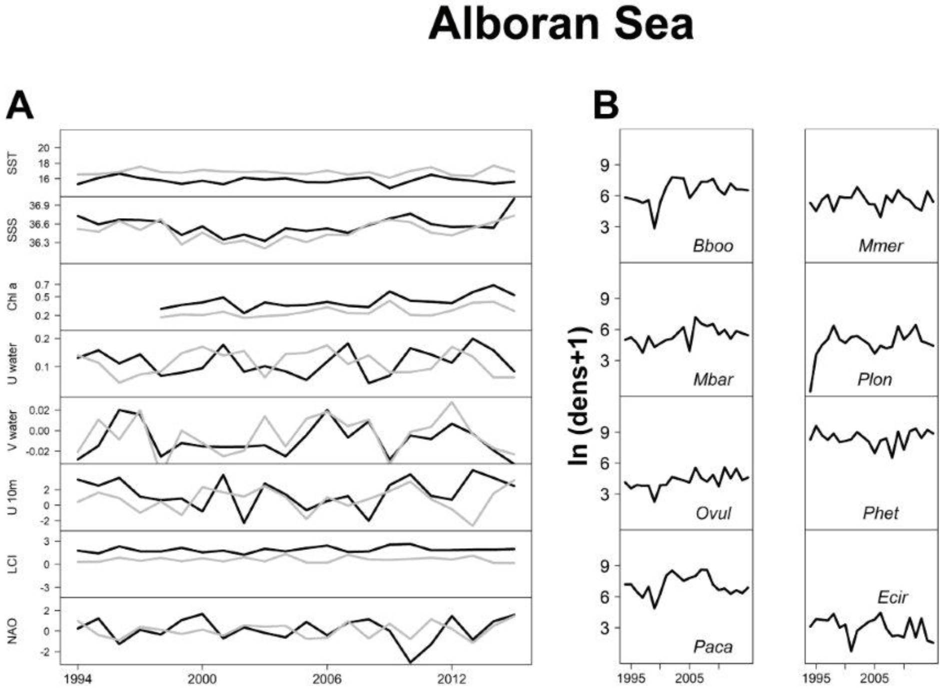

Fig. 5: Time series of environmental variables (A) with a significant role in the spatial changes of species in winter (black) and spring (grey), and species density (ln (dens+1)) (B) for the northern Alboran Sea. Sea surface temperature (SST, ºC), sea surface salinity (SSS, psu), Chlorophyll-*a* concentration (Chl-*a*, mg·l^{-1}), U water (m·s^{-1}), V water (m·s^{-1}), U 10 m (m·s^{-1}), LCI, and NAO.

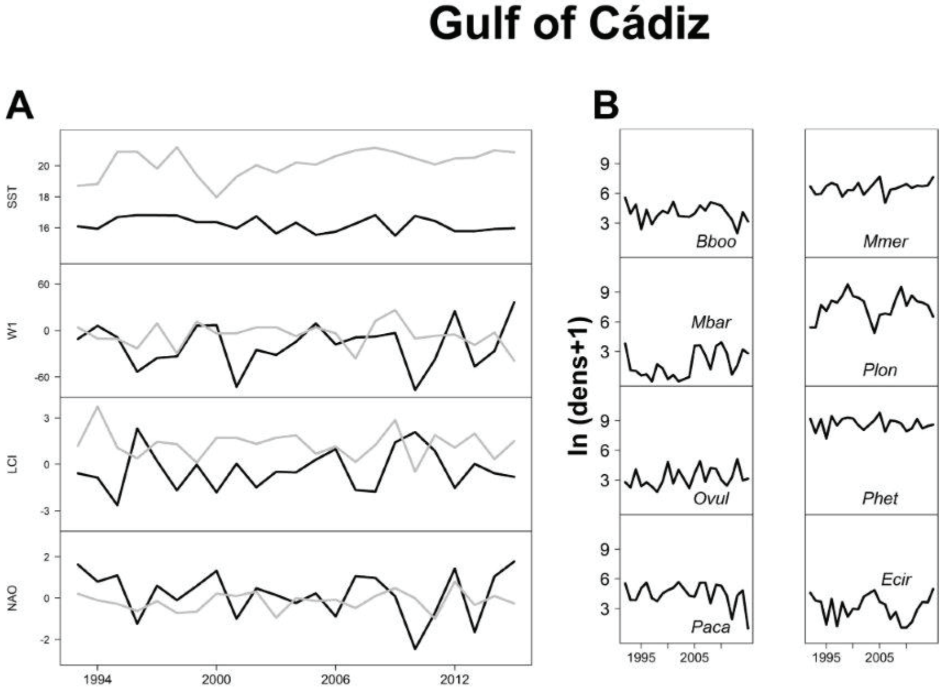

Fig. 6: Time series of environmental variables (A) with a significant role in the spatial changes of species in autumn (grey) and winter-spring (black), and species density (ln (dens+1)) (B) for the Gulf of Cadiz. Sea surface temperature (SST, ºC), first EOF wind mode (W1, m·s^{-1}), LCI, and NAO.

Environmental and Demographic effects

For each species, Table 2 shows the best LM that fit the CG for each response variable (latitude, longitude and depth), both in the GoC and AS with the statistically significant co-variates included in each model. The responses were not homogeneous, evidencing clear differences between species and regions. In general terms, a greater diversity of effects was observed in the AS, contrasting with the scenario in the GoC. In the AS, there was more significant influence of driver variables on the species in terms of depth than latitude or longitude, even though there was a lack of a temporal trend of the CG depth for any species. However, in the GoC, the effect on CG depth was only observed for two species, *M. barbatus* and *O. vulgaris*. Density dependence was the most frequent driver related to distributional CG changes in the AS, while in the GoC, this was the NAO.

Table 2. Best linear models (LM), including statistically significant covariates, for the variability in CG (longitude, latitude and depth) for each species in the Gulf of Cadiz and northern Alboran Sea. The results for those with no significant variables are not shown. Explanatory covariates: Chl-*a* (Chlorophyll-*a*); NAO (North Atlantic Oscillation); LCI (Local Climate Index); SST (sea surface temperature); SSS (sea surface salinity); U water (water current speed U component); V water (water current speed V component); U 10m (wind speed at 10 m; U component); W1 (first EOF wind); dens (density). W: winter (winter-spring in the GoC); S: spring; A: autumn; r^2: coefficient of determination. Level of significance: *p<0.05, **p<0.01, ***p<0.001. Species abbreviations: See Table 1.

GULF OF CADIZ		**Longitude**		**Latitude**		**Depth**	
Depth (strata)	**Species**	**Covariate (E)**	**r^2**	**Covariate (E)**	**r^2**	**Covariate (E)**	**r^2**
<100 m	*Mbar*	W1 A**	0.3			NAO A*	0.2
Shallow Shelf	*Paca*						
	Bboo	SST W**	0.4	LCI W*	0.25		
	Ovul			dens*	0.21	dens *	0.25
100-200 m	*Mmer*						
Deep Shelf	*Plon*			NAO A*, dens*	0.33		
	Phet			LCI W*	0.27		
200-500 m	*Ecir*			W1 A**	0.32		
Upper Slope	*Pble*	W1 A*	0.2				
>500 m	*Gmel*	SST A*	0.6				
Middle Slope	*Espi*	NAO A*, W1 A*	0.3	NAO A*, SST A*	0.33		
ALBORAN SEA							
<100 m	*Mbar*	dens*	0.2	dens*	0.22		
Shallow Shelf	*Paca*	NAO S*, NAO W*	0.4	NAO W *	0.19	SSS S**, U water S**, Uwater W*, dens*	0.6
	Bboo	V water S*	0.2				
	Ovul						
100-200 m	*Mmer*	dens*	0.3	SST S*	0.18		
Deep Shelf	*Ecir*					SSS S*, Chl-*a* S**, LCI S*	0.5
200-500 m	*Phet*					dens*	0.24
Upper Slope	*Plon*					Chl-*a* W*	0.24
	Pble					SST S*, dens***	0.6
>500 m	*Gmel*	LCI S*, U 10m S **, NAO S***, NAO W***	0.7	dens*	0.19	SST S*, NAO S*	0.4
Middle Slope	*Espi*					LCI S*, V water S**	0.4

In the AS, density-dependent significant changes on CG were observed for *M. barbatus* (longitude and latitude), *P. acarne, P. heterocarpus,* and *Phycis blennoides* (depth), *Merluccius merluccius* (longitude), and *G. melastomus* (latitude). Response to large scale climate modes (i.e., the NAO) was observed in longitudinal and latitudinal CG changes in *P. acarne,* and in longitudinal and depth CG changes in *G. melastomus*. In contrast, the LCI affected the depth CG changes of *E. cirrhosa* and *E. spinax,* and the longitude CG changes in *G. melastomus*. SSS affected depth in *P. acarne* and *E. cirrhosa,* while SST affected bathymetric CG changes in *P. blennoides* and *G. melastomus,* and Chl-*a* on *E. cirrhosa* and *P. longirostris*. *O. vulgaris* was the only species that did not respond to any of the variables investigated.

In the GoC, the NAO was found to be the most frequent driver, with a significant effect on *M. barbatus* (depth), *P. longirostris* (latitude), and *E. spinax* (latitude and longitude). LCI also affected *B. boops* (latitude) and *Plesionika heterocarpus* (latitude). W1 influenced *M. barbatus* (longitude)*, E. cirrhosa* (latitude), and *P. blennoides* (longitude), while SST affected *B. boops* (longitude) and *G. melastomus* (longitude). Density was the only variable related to changes seen in *O. vulgaris* (latitude and depth). *P. acarne* and *M. merluccius* responded to none of the co-variates included in the study in this region.

Discussion

Our study reports the spatiotemporal changes of representative demersal species and their response to the environmental and demographic drivers in two regions, the Gulf of Cadiz (GoC) and northern Alboran Sea (AS). Additionally, this study attempted to reveal potential homogeneity and coherence in these two nearby areas in the drivers affecting temporal changes in spatial distribution. However, our results reveal a clear heterogeneity in depth distribution and spatiotemporal shifts of demersal species between and within the open waters of the Atlantic Ocean (GoC) and the semi-enclosed waters of the Mediterranean Sea (AS), as well as clear differences in their response to environmental and demographic variables.

Temporal trends in species distribution

The demersal communities underwent more evident temporal trends in the displacement of their centres of gravity (CG) in the GoC than in the AS, where the species seemed to display a more stable spatial distribution. Six out of the eleven species analysed presented temporal trends in the GoC, whereas these were only seen for two species in the AS. Notwithstanding the level of high hydro-dynamism reported for the AS, the stability of the observed community is consistent with results obtained in the northwestern Mediterranean Sea (Gulf of Lion; Morfin *et al.,* 2012), while it contrasts with the geographical and depth changes of a wide set of demersal species in Atlantic areas such as the GoC (70% species, Delgado *et al.,* 2018; 54%, present study) and the Cantabrian Sea (35%, Punzón *et al.,* 2016). Although the extent of these trends and the associated mechanisms could differ, a significant common tendency seen in both basins is the movement towards the Strait of Gibraltar. This remarkable trend was mainly detected in shallow shelf species (especially Sparidae and Mullidae species) and elasmobranchs from the deeper strata. These results highlight the sensitivity of demersal species and their potential role as sentinel species of changes in these ecosystems, as recently it was reported for these areas (Delgado *et al.,* 2018).

It is especially noteworthy that only two species showed simultaneous significant time trends in both basins, *B. Boops* and *E. spinax*. Unlike other species, *B. boops* has a similar depth distribution in the two basins and it is the only Sparidae species that showed longitudinal and latitudinal trends in the AS, although in the GoC it displayed only longitudinal temporal trends. In the AS, the longitudinal gradient of *B. boops* was due to an increase of abundance from 2010 in western AS areas. The density and CG latitude and longitude temporal trends of this species correlated very closely with those of *P. acarne* up to 2010. From this year onwards, different trends were found for each of them, likely due to their different responses to the key drivers. On the other hand, *E. spinax* is the only elasmobranch species in this study that showed longitudinal movements toward the western AS. This could be related to the very high vulnerability of the species to the impact of fishing, even within the general context of high elasmobranch vulnerability (Coelho & Erzini, 2008; Guijarro *et al.,* 2012), and, in addition, to its high sensitivity to environmental changes (bottom temperature, salinity, and dissolved oxygen) (Cartes *et al.,* 2013). The latitudinal time trend detected in this shark species in the GoC in the winter-spring study contrasts with the absence of changes observed in the autumn (Delgado *et al.,* 2018). In fact, in the GoC, the present findings contrast with the higher percentage of species with significant time trends and with the southeastward and northeastward shifts marked by the Guadalquivir River plume (i.e., *P. longirostris*) in the autumn (Delgado *et al.,* 2018). This could be due to the anticyclonic oceanic surface circulation that is influenced by short-term meteorological events, a counter-current flows over the inner shelf and through two important freshwater runoffs from the Guadalquivir and Guadiana rivers (Criado-Aldeanueva *et al.,* 2006), having a strong influence in changes in species distributions in the GoC in the autumn but not in spring.

Comparison of the bathymetric distributions between the two basins

Several species displayed significant differences in their depth distribution between the basins. These were especially pronounced for the cephalopod *E. cirrhosa*, the crustaceans *P. longirostris* and *P. heterocarpus*, and the elasmobranchs, *E. spinax* and *G. melastomus*. All these differences could be consistent with the particular characteristics of the individual basins, since species are locally adapted to the hydrodynamic characteristics to ensure offspring survival and, therefore, the long-term persistence of the population. Thus, communities are locally adapted to the different hydrological conditions in each area, which results from the combination of local physical conditions and taxa adaptations to optimise survival (e.g., Patarnello *et al.,* 2007). The broader continental shelf in the GoC compared to the AS also forces species to adapt to reduced preferred habitat availability in the shallower strata of the AS. In addition, there are notable differences in the spatial distribution of water masses in the two areas that could affect species distributions (Muñoz *et al.,* 2015). The Mediterranean Water (MW) is present from 250 m depth in the GoC while in the AS it is detected from 100 m (Vargas *et al.,* 2017; Bellanco & Sánchez-Leal, 2016). Water masses distribution seems to affect the cephalopod *E. cirrhosa*, which displays a depth distribution directly related to the water masses interface between MW and Atlantic Water (AW). *E. cirrhosa* also shows appreciable differences throughout its distribution range, including both morphometric and reproductive biology perspectives (Regueira *et al.,* 2013), and its abundance and distribution vary greatly among the various areas it inhabits in the Mediterranean and Atlantic (Lefkaditou *et al.,* 2000; González & Sanchez, 2002). In the same way, *P. longirostris* is more abundant in shallower waters in the Atlantic with respect to the Mediterranean (Sobrino *et al.,* 2005), with different patterns found in the Mediterranean in terms of its geographical distribution due to a combination of environmental characteristics and different fishing pressure between the areas (Abelló *et al.,* 2002). Differences in the hydrological properties of the water masses in the studied areas could also affect the deep-dwelling middle slope species, such as *E. spinax* and *G. melastomus*. A preference for a cooler bottom temperature could be behind the deeper distribution of *E. spinax* in the AS since this species has also been found at shallower depths in Southern Portugal (around 500 m) (Coelho *et al.,* 2010) and the North Atlantic (e.g., the Celtic Sea, between 300-500 m; Ellis *et al.,* 2005).

Species demography effects

Density dependence has been reported as an important driver of changes in species distribution and habitat selection (e.g., Spencer, 2008; Bartolino *et al.,* 2011; Puerta *et al.,* 2014). In our study, the density-dependency effect was minimal in the GoC and consistent with the pattern observed in the autumn in the same ecosystem (Delgado *et al.,* 2018). However, density was the most frequent explanatory variable related to distributional changes in the AS, despite the stability of the time series trends for the CG in the majority of species. This highlights the importance of species-specific population dynamics with respect to local environmental variability in the AS, being potentially related to the narrower continental shelf and thus greater habitat competition in species less able to alter their bathymetric distribution. These density-dependent effects could be related to inter-annual variation in the strength of recruitment, habitat, or competition for food (Martín *et al.,* 2010; Bartolino *et al.,* 2011) as in the case of *M. merluccius* for which the longitudinal CG values display a significant high positive correlation with the density values, probably associated to higher recruitment events. Interannual variation in the hydrodynamic scenario could affect the retention success of early life stages, increasing the density in the nursery and recruitment grounds and triggering density-dependent changes in the distribution of hake recruits (Yaagoubi, 2019). In the GoC, density effects on spatial displacements were only observed for *O. vulgaris,* and not found at all in the autumn (Delgado *et al.,* 2018). Besides environmental and oceanographic factors, the life history of the species could determine these density dependence differences between the seasons, since *O. vulgaris* was mostly located in deeper in the winter-spring and in southern waters while in the autumn its distribution had thus shifted to shallower and northern waters in line with the recruitment (Silva *et al.,* 2002). In fact, a clear CG deviation in terms of depth and latitude was observed in this study compared with that of Delgado *et al.* (2018) (Suppl. Material Fig. S1).

Effects of local environmental drivers

The high level of heterogeneity observed in terms of environmental influence was certainly expected given the diversity in species-specific responses within the studied communities, as previously was observed (Delgado *et al.,* 2018; Puerta *et al.,* 2014; Puerta *et al.,* 2015). There was a greater diversity of effects in the AS, in contrast with the scenario observed in the GoC. This could be explained by the high environmental heterogeneity and dynamism in the AS (Muñoz *et al.,* 2015) but also by the greater capacity of the climate oscillations in the GoC to spatially and temporally capitalise on the influence of regional and local environmental variability (Stenseth & Mysterud *et al.,* 2005; Delgado *et al.,* 2018; see below). Within the diversity of environmental influence in the AS, surface temperature, Chl-*a*, and current strength were the most relevant. Taking into account the increased temperature of the water masses at different depths in the Mediterranean (Vargas *et al.,* 2019), geographic and bathymetric changes in shelf and deep species with greater temperature affinity could be expected as it has been observed in *G. melastomus*, *P. blennoides* and *M. merluccius,* with the effect in *G. melastomus* being consistently observed in the GoC. Species with thermal affinities to lower temperatures are known to be one of the main ‘losers’ in areas with high rates of increasing temperature like the Mediterranean Sea (e.g., Vasilakopoulos *et al.,* 2017). With regard to Chl-*a*, the AS is one of the Western Mediterranean areas with the highest levels of primary production (Vargas *et al.,* 2010). Recent studies also suggest that the demersal community in the AS is very sensitive to changes in the Chl-*a* concentration, which has also been observed at species level (M. Hidalgo, pers. comm.). In this study, the productivity regime was an explanatory variable for the variability in CG depth for *P. longirostris* and *E. cirrhosa*, two short-lived species with a size-related bathymetric distribution whose fluctuations have been linked to oceanographic processes (Abelló *et al.,* 2002; Lloret *et al.,* 2001). Years with high production could explain the strength of the recruitment pulses, influencing the bathymetric changes in the CG of species. Beyond potential effects in the early life stages of fish that could affect their distribution as juveniles (El Yaagoubi, 2019), the Atlantic water body dominates the dynamics of the Alboran area, providing nutrients (Muñoz *et al.,* 2015) and shaping local-scale productivity and the availability of trophic resources in deeper layers, with a consequent likely impact on the distribution changes of deeper species (Fanelli *et al.,* 2013; Smith *et al.,* 2013). In the GoC, the first component of the wind field is also related to geographical changes in some species, including *M. barbatus*, *E. cirrhosa*, and *P. blennoides*. The general circulation in the GoC is largely influenced by the wind (García-Lafuente *et al.,* 2007), and thus wind-induced larval transport and the consequent recruitment success could explain these displacements, as described for other species in this area (Ruiz *et al.,* 2006).

Global and local climate effects

The global climate, illustrated in this study by the NAO index, was the most repeated driver in terms of species displaying geographical shifts in the GoC. The NAO is known to be an important driver in the middle and high latitudes of the Northern Hemisphere (Hurrell *et al.,* 2003, Stenseth *et al.,* 2002), besides the Atlantic Multidecadal Oscillation has increased more attention in the last years (Zimmermann *et al.,* 2019). Previous studies report that the mid-latitude and eastern Atlantic location of the GoC makes this basin very sensitive to the NAO (ICES, 2016). The variations in environmental parameters linked to the NAO may act on biological organisms at different levels (individual and population) through physiology (metabolic and reproductive processes) or trophic relationships, including ecological cascade effects (Stenseth *et al.,* 2002; Punzón *et al.,* 2016). However, the effects of the NAO differ in strength, direction and season depending on the species and region (Stige *et al.,* 2006). Delgado et al. (2018) analysed changes in species distribution in the GoC in the autumn and evidenced a generalised NAO effect in the summer. In contrast, in the present study analysing winter-spring distributions, NAO in autumn was the most recurrent effect suggesting a generalized effect of the climatic conditions in the season prior to the survey. Previous studies evidence the fact that the NAO is not specifically associated with any local variables, as in other regions (Ottersen *et al.,* 2001; Stenseth & Mysterud *et al.,* 2005), highlighting the multiscale and multifaceted influence of the NAO in the GoC. In this ecosystem, the NAO integrates several mechanisms at multiple spatial scales beyond the study area through which this climate index often outperforms local weather variables when explaining climate-related influence on life history traits or abundance (Delgado *et al.,* 2018). Of the species affected by the NAO in the GoC, the effect on *M. barbatus* (depth) and *P. longirostris* (latitude) has been observed in the previous study in the autumn, while the effect is new for *E. spinax*. While in the AS, the effect of NAO was comparatively lower compared to the diversity of local environmental influence, two species seemed consistently affected by the combination of the NAO in the winter and summer (*P. acarne* and *G. melastomus*), suggesting that these species may have a larger distribution and are affected by an integration of processes over different seasons and over a larger geographical area, beyond the study system.

In summary, this study provides information about species distribution displacements and their associations with environmental and demographic drivers in two adjacent areas, the GoC (Atlantic Ocean) and the AS (Mediterranean Sea), connected to each other through the Strait of Gibraltar. The analysis shows that in the GoC, demersal species displacements showed more evident temporal trends than in the AS, where the species seem to be more spatially stable. The stability of the community observed in the AS is consistent with other results from the Mediterranean (Morfin *et al.,*2012) and contrasts with the changes found for demersal species in Atlantic areas (this study; Delgado *et al.,* 2018; Punzón *et al.,* 2016). GoC showed a high influence of large scale and regional climate. In the AS, there was a high diversity of environmental effects. This could be explained by the high environmental heterogeneity and dynamism in the AS and the higher capacity of the climate oscillations in the GoC to capitalise on the influence of local environmental variability.

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Supplementary Data

The following supplementary information is available online for the article:

Fig. S1: Time series for the CG of *Octopus vulgaris* in the Gulf of Cádiz in autumn (Delgado *et al.*, 2018; black line) and winter-spring (present study; grey line).