



Response of a temperate demersal fish community to global warming



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ABSTRACT

Changes in the distribution of the demersal fish species have been identified in north-European Atlantic waters. The consequence of these changes has been a northward shift of the distribution limits and changes in richness. In this study a notable increase in demersal fish species richness per sampling station was detected in the southern Bay of Biscay. This rise was due to an increase in frequency of occurrence and abundance of the majority of fish species in the area (53% from the total species). A fisheries relate explanation was discarded because the mismatch between the changes in the fishing effort and the augment in frequency of occurrence and abundance. On the contrary, these changes are in agreement with expected response under the increasing temperature of the sea observed over the last three decades, associated to global warming. These changes were positively correlated with an increase in temperature of intermediate waters in the study area. In addition, some of these species showed a notable western displacements of the Centre of Gravity in the study area, which would be expected if temperate water species would be favoured by an increase in water temperature. Our results are consistent with studies in the North Sea, where many of these species showing widened distribution limits towards north. The analysis of the results shows that the studied ecosystem, the Bay of Biscay is under a meridionalization process. On the other hand, only one tropicalization event (*Lepidotrigla dieuzeidei*), was recorded, maybe due to the conservative restrictions applied in species selection.

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1. Introduction

Fish population dynamics are intimately associated with climatic and oceanographic processes which determine species distributions, migrations, abundance and interactions (Lees et al., 2006). Hence, this interaction between temperature and fish dynamics occurs at all levels of biological organization, from individuals to habitats (Hoegh-Guldberg and Bruno, 2010; Simpson et al., 2011). Indeed, changes in temperature can affect thermodynamic processes such as metabolism, which may in turn alter ecological processes such as predator–prey interactions (Hoegh-Guldberg and Bruno, 2010). For instance, the North-Atlantic Oscillation (NAO) has been found to be the parameter which best explains fish community composition, as well as species abundance and juvenile growth patterns during the estuarine phase (Attrill and Power, 2002). Similarly, changes in the intensity of the Poleward Current or in upwelling indices affect recruitment processes and the structural stability of the fish communities of the Bay of Biscay (Sánchez and Gil, 2000; Sánchez and Serrano, 2003).

Climate change affects current and future environmental conditions substantially (Levitus et al., 2000), thus having important consequences for fish populations. However, the size and complexity of marine

ecosystems, coupled with the inherent difficulty in data compilation complicates identification and evaluation of these effects or those caused by increases in sea water temperature (Hoegh-Guldberg and Bruno, 2010). Despite this, increasing evidences point at climate change as the mechanism responsible for these effects (Parmesan and Yohe, 2003; Walther, 2010), such as growth, survival and reproduction of species (Hoegh-Guldberg and Bruno, 2010), in species distributions and range shifts (Walther et al., 2002), in richness and biodiversity (Cheung et al., 2009; Hofstede, et al., 2010), in the distribution of non-indigenous species (Occhipinti-Ambrogi and Galil, 2010), as well as of modifications in community and ecosystem structure (Hays et al., 2005), or habitat destruction by the disappearance of structural species (Hoegh-Guldberg and Bruno, 2010).

The Northeast Atlantic Ocean is no exception and evidences of climate change have been identified in many areas, for instance the Southern Bay of Biscay. Tasker (2008) compared the mean surface water temperature of the Southern Bay of Biscay over the periods 1978–1982, and 2003–2007 and found an increase of between 0.8 to 1 °C. The south-eastern corner of the Bay has shown an increase in intermediate water temperature and salinity modifications during the period 1992–2003 (González-Pola et al., 2005). Moreover, the characteristic upwelling phenomena have been weakening in the north-eastern part of the Iberian Peninsula (Bode et al., 2009), which may explain the changes observed in the planktonic ecosystem (Llope et al., 2006;

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Bode et al., 2009). However, this trend has been compromised in recent years after several strong upwelling seasons [data available at www.indicedeafloramiento.ieo.es].

From a historical perspective, notwithstanding environmental variability, warming of waters due to climate change has shown a constant increasing trend over the past decades (IPCC, 2014). However, the identification of its effects at a regional scale is challenging (Tasker, 2008; Azzurro et al. 2011). In fact, most studies conducted in the Northeast Atlantic at a regional scale have been carried out at northern latitudes, where many species have their distribution limits and range shifts or changes in species richness due to disappearances or incorporations are more easier to identified (Hiddink and Hofstede, 2008; Perry et al., 2005).

The Southern Bay of Biscay is located in the middle of the northern temperate province and is a transition area to the southern temperate province, with a mixture of fauna representative of the northern and southern areas (Lavín et al., 2006). This is reflected in the high rates of biodiversity existing in this area compared with adjacent ones. In fact, many of the species are of commercial interest resulting in an important and varied fishing activity targeting demersal species in the area (Punzón et al., 2011). One of the main problems when evaluating changes in the abundance and distribution of populations or communities is the identification of whether they synchronously respond to environmental variations (climatic and oceanographic dynamics), human activities or both (Quetglas et al., 2013).

Therefore, we are at a scenario where climate change and other anthropogenic pressures mingle with the oceanographic variability characteristic of the area. Using species abundance data gathered annually over the past 30 years in the southern waters of the Bay of Biscay we will analyse the changes in the demersal ecosystem. This analysis seeks to detect temporal trends in ecological indices and the vectors controlling the long-term changes in the ecosystem, aiding to identify how the Atlantic temperate ecosystems are adapting to global change.

2. Material and methods

2.1. Data sources

The study area encompasses the Spanish shelf in the Bay of Biscay, between the mouths of the Miño (41° 52' N–8° 52') and the Bidasoa

(43° 22' °N–1° 47' W) rivers (Fig. 1). Bottom trawl surveys have been conducted every autumn (September–October) since 1983 (only interrupted in 1987) by the Instituto Español de Oceanografía (IEO) using a standardized methodology. These surveys follow a stratified random sampling scheme with five depth strata (<70, 70–120, 121–200, 201–500, >500 m) and five geographical sectors delimited by the main geographic features (Fig. 1). The study area is divided into sampling rectangles of 5 × 5 nautical miles from which the sampling stations are selected randomly each year. The number of hauls per stratum is proportional to its trawlable surface, the sampling unit consisting of 30-min hauls at a speed of 3.0 knots, using a boca 44/60 otter trawl gear. The trawl has a mean horizontal opening of 18.9 m and a vertical opening of 2.0 m. During operation, the otter trawl is systematically monitored using a Scanmar net control system. Our analyses included only those rectangles which had been sampled at least five times during the 30 years of study, which added up to 193 rectangles.

Given that species identification may have improved along the time series (1983 to 2010), and to avoid overestimations of richness and diversity, only those species which were identified at least in 30 samples were considered. Under this threshold occurrence data were too scarce and scattered to identify any pattern and the probability of taxonomic errors increased. Thus, only the species better represented in our sampling scheme were considered, avoiding those which appeared occasionally. Species from the family Gobiidae and Myctophidae, for which doubts regarding their identification during the time series exist, were also removed from the analysis.

2.2. Spatio-temporal analysis of ecological indices

With the aim to analyse spatio-temporal changes in fish richness, a nested General Linear Model (GLM) was performed to obtain the annual trend of richness (species number) by sampling rectangle (McCullagh and Nelder, 1989). We have included year nested inside sampling rectangle, obtaining a specific coefficient (and p-value) for each level of the variable sampling rectangle. Sampling rectangle has been kept as a fixed factor since, as established Underwood (1997), a variable can be considered as fixed factor if all the relevant levels are included in the analysis. Since the distribution of the response variables was normal, we assumed a normal distribution of residuals and “identity” as the function link. The proportion of variability explained by the final model was

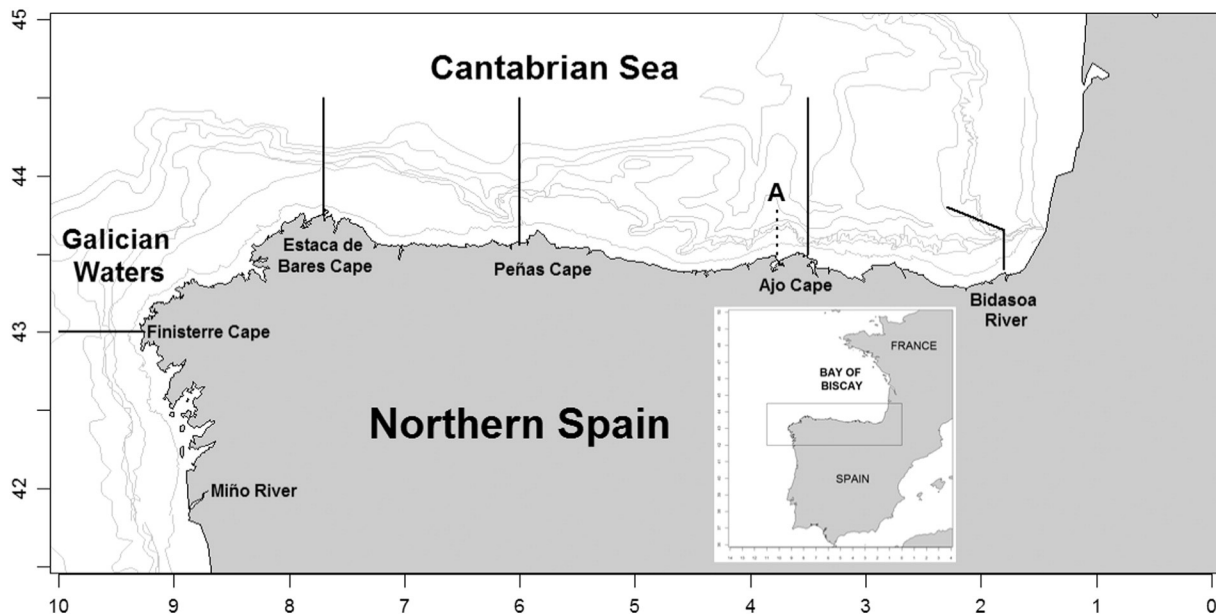


Fig. 1. Study Area (A: Santander section, where CTD measurements were taken).

Table 1

Summary of frequency of occurrence data: biogeographic guilds (Ellis et al. 2008a and 2008b); trends in the frequency of occurrence and annual increment in FO using linear model; correlation and significance between frequency and abundance; and correlation between annual FO and the temperature of intermediate waters at the 300–600 and 600–950 depth strata. Significance codes: 0 ****; 0.001 ***; 0.01 **; 0.05 *; 0.1.

Species	Biogeographic Guild	FO Trend				FO vs Abundance.		FO vs Intermediate T ^a			
		Slope	r ²	Sig.	Δ FO	r ²	Sig.	T ^a 300–600 m		T ^a 600–950 m	
								r ²	Sig.	r ²	Sig.
<i>Acantholabrus palloni</i>	Lusitanian	0	0.03	–	–	0.688	***	0.471	.	0.348	–
<i>Argentina sphyraena</i>	Lusitanian	0.005	0.3	**	14.14	0.497	**	0.139	–	0.234	–
<i>Argyropelecus hemigymnus</i>	Atlantic	0.001	0.14	.	1.664	0.739	***	0.695	**	0.653	**
<i>Arnoglossus imperialis</i>	Lusitanian	0.003	0.16	*	6.5	0.535	**	0.667	**	0.701	**
<i>Arnoglossus laterna</i>	Lusitanian	0.003	0.09	–	–	0.482	*	–0.258	–	–0.116	–
<i>Aspitrigla cuculus</i>	Lusitanian	0.006	0.41	***	15.76	0.672	***	0.295	–	0.142	–
<i>Bathysolea profundicola</i>	Lusitanian	0.001	0.09	–	–	0.663	***	0.185	–	0.067	–
<i>Blennius ocellaris</i>	Lusitanian	0.008	0.41	***	21.74	0.827	***	0.08	–	–0.045	–
<i>Boops boops</i>	Lusitanian	0.007	0.38	***	19.19	0.871	***	0.439	.	0.409	–
<i>Buglossidium luteum</i>	Lusitanian	0	0	–	–	0.561	**	–0.45	.	–0.229	–
<i>Callionymus lyra</i>	Lusitanian	0.005	0.31	**	13.44	0.406	*	0.604	**	0.616	*
<i>Callionymus maculatus</i>	Lusitanian	–0	0.07	–	–	0.64	***	–0.21	–	0.081	–
<i>Capros aper</i>	Lusitanian	0.007	0.37	***	18.02	0.403	*	0.173	–	0.064	–
<i>Cepola rubescens</i>	Lusitanian	0.002	0.06	–	–	0.712	***	–0.477	.	–0.444	.
<i>Chelidonichthys gurnardus</i>	Lusitanian	0.011	0.44	***	28.21	0.788	***	0.091	–	0.202	–
<i>Chelidonichthys lucernus</i>	Lusitanian	0.004	0.26	**	9.282	0.81	***	0.109	–	0.253	–
<i>Chelidonichthys obscurus</i>	Lusitanian	0.001	0.02	–	–	0.524	**	–0.209	–	–0.053	–
<i>Chimaera monstrosa</i>	Atlantic	0.001	0.22	*	3.588	0.259	–	0.574	*	0.532	*
<i>Chlorophthalmus agassizii</i>	Atlantic	–0	0.25	**	–1.77	0.674	***	–0.424	.	–0.548	*
<i>Coelorhynchus coelorhynchus</i>	Atlantic	0.002	0.34	**	6.084	0.876	***	0.759	***	0.727	**
<i>Conger conger</i>	Lusitanian	0.008	0.58	***	19.94	0.833	***	0.681	**	0.681	**
<i>Echiodon dentatus</i>	Mediterranean	–0	0.04	–	–	0.708	***	–0.325	–	–0.12	–
<i>Etmopterus spinax</i>	Atlantic	0.001	0.38	***	2.834	0.528	**	0.752	***	0.728	**
<i>Gadiculus argenteus</i>	Lusitanian	–0.01	0.41	***	–19.1	0.354	–	–0.269	–	–0.098	–
<i>Gaidropsarus macrophthalmus</i>	Lusitanian	–0.01	0.18	*	–21.1	0.786	***	–0.754	***	–0.677	**
<i>Gaidropsarus vulgaris</i>	Lusitanian	0	0	–	–	0.838	***	0.243	–	0.128	–
<i>Galeus sp</i>	Lusitanian	0.003	0.33	**	7.02	0.681	***	0.731	***	0.689	**
<i>Helicolenus dactylopterus</i>	Atlantic	0.011	0.41	***	29.61	0.794	***	0.719	***	0.752	***
<i>Hexanchus griseus</i>	Atlantic	–0	0.14	.	–1.59	0.825	***	–0.398	–	–0.162	–
<i>Labrus bimaculatus</i>	Lusitanian	0.001	0.3	**	2.47	0.621	***	0.272	–	0.343	–
<i>Lampanyctus crocodilus</i>	Atlantic	0	0.01	–	–	0.578	**	–0.154	–	–0.257	–
<i>Lepidopus caudatus</i>	Atlantic	0	0	–	–	0.179	–	0.315	–	0.493	.
<i>Lepidorhombus boscii</i>	Lusitanian	0.004	0.55	***	11.08	0.796	***	0.62	**	0.579	*
<i>Lepidorhombus whiffiagonis</i>	Lusitanian	–0.01	0.5	***	–23.7	0.625	***	–0.553	*	–0.559	*
<i>Lepidotrigla dieuzeidei</i>	African	0.008	0.69	***	20.67	0.712	***	0.831	***	0.744	***
<i>Leucoraja naevus</i>	Lusitanian	0.003	0.52	***	8.19	0.813	***	0.522	*	0.481	.
<i>Lophius budegassa</i>	Lusitanian	–0.01	0.35	**	–23.9	0.814	***	–0.466	.	–0.376	–
<i>Lophius piscatorius</i>	Lusitanian	0	0	–	–	0.562	**	0.447	.	0.583	*
<i>Macroramphosus scolopax</i>	Lusitanian	–0	0.03	–	–	0.442	*	–0.843	***	–0.851	***
<i>Malacocephalus laevis</i>	Atlantic	0	0	–	–	0.716	***	–0.055	–	–0.189	–
<i>Maurollicus muelleri</i>	Atlantic	0.011	0.54	***	27.95	0.817	***	0.743	***	0.722	**
<i>Merluccius merluccius</i>	Lusitanian	0	0.01	–	–	0.528	**	0.187	–	0.242	–
<i>Microchirus variegatus</i>	Lusitanian	0.005	0.56	***	12.74	0.737	***	0.711	***	0.737	**
<i>Micromesistius poutassou</i>	Atlantic	–0.01	0.42	***	–16.3	0.468	*	–0.531	*	–0.403	–
<i>Molva macrophthalma</i>	Lusitanian	0.01	0.43	***	26.34	0.851	***	0.756	***	0.744	***
<i>Mullus surmuletus</i>	Lusitanian	0.005	0.42	***	13.75	0.635	***	0.847	***	0.86	***
<i>Pagellus acarne</i>	Lusitanian	0.004	0.4	***	10.95	0.527	**	0.694	**	0.697	**
<i>Pagellus bogaraveo</i>	Lusitanian	–0	0.08	–	–	0.836	***	0.294	–	0.291	–
<i>Pagellus erythrinus</i>	Lusitanian	0	0.02	–	–	0.535	**	–0.048	–	0.167	–
<i>Phycis blennoides</i>	Lusitanian	0.005	0.06	–	–	0.601	***	0.427	.	0.601	*
<i>Raja clavata</i>	Lusitanian	0.008	0.71	***	21.24	0.806	***	0.883	***	0.869	***
<i>Raja montagui</i>	Lusitanian	0.004	0.61	***	10.56	0.545	**	0.551	*	0.739	**
<i>Sardina pilchardus</i>	Lusitanian	–0	0.12	.	–6.29	0.83	***	0.117	–	0.141	–
<i>Scomber japonicus</i>	Lusitanian	0.002	0.2	*	5.2	0.939	***	0.154	–	0.146	–
<i>Scomber scombrus</i>	Atlantic	0.007	0.14	.	17.68	0.526	**	0.29	–	0.255	–
<i>Scorpaena loppei</i>	Lusitanian	0.001	0.15	*	2.886	0.691	***	–0.153	–	–0.215	–
<i>Scorpaena notata</i>	Lusitanian	0	0.01	–	–	0.655	***	–0.094	–	–0.16	–
<i>Scorpaena scrofa</i>	Lusitanian	0.001	0.14	.	2.262	0.599	***	0.823	***	0.791	***
<i>Scyliorhinus canicula</i>	Lusitanian	0.007	0.48	***	18.1	0.772	***	0.708	***	0.688	**
<i>Scyliorhinus stellaris</i>	Lusitanian	0.001	0.12	.	2.418	0.813	***	–0.094	–	0.128	–
<i>Serranus cabrilla</i>	Lusitanian	0.003	0.51	***	8.996	0.724	***	0.277	–	0.147	–
<i>Solea solea</i>	Lusitanian	0.003	0.38	***	7.384	0.687	***	0.507	*	0.524	*
<i>Spondyliosoma cantharus</i>	Lusitanian	0.002	0.47	***	4.602	0.788	***	0.64	**	0.606	*
<i>Trachinus draco</i>	Lusitanian	0.002	0.45	***	5.772	0.661	***	0.328	–	0.445	.
<i>Trachurus mediterraneus</i>	Lusitanian	0.002	0.15	*	5.824	0.081	–	0.26	–	0.357	–
<i>Trachurus trachurus</i>	Lusitanian	0	0	–	–	0.124	–	0.16	–	0.156	–
<i>Trigla lyra</i>	Lusitanian	0.005	0.22	*	12.17	0.351	–	–0.093	–	–0.027	–
<i>Trisopterus luscus</i>	Lusitanian	0.003	0.1	–	–	0.477	*	–0.114	–	–0.312	–
<i>Trisopterus minutus</i>	Lusitanian	0.005	0.22	*	13.1	0.481	*	0.387	–	0.545	*
<i>Zeus faber</i>	Lusitanian	0.009	0.33	**	23.97	0.553	**	0.065	–	–0.204	–

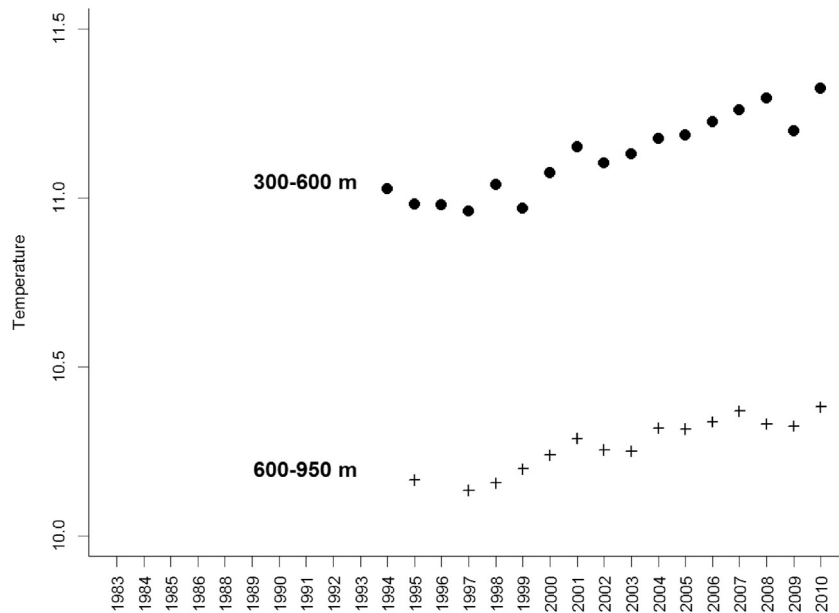


Fig. 2. Mean annual temperature of intermediate waters in the Santander station, at 300–600 m, and 600–950 m depth.

obtained using the quotient of variation in the prediction as a proportion of the total variation.

2.3. Trends in species frequency of occurrence

Frequency of occurrence (FO) is defined as the number of sampling rectangles in which a species appears one year divided by the total number of rectangles sampled that year. Trends in the annual series of species FOs were obtained by linear regression using the least squares approach. To show the temporal changes in FO, only for the species displaying significant trends, we calculated the FO increment between the initial and the final year applying the linear model.

In order to evaluate whether changes in annual FO were coupled with changes in annual stratified abundance (weight), we calculated the correlation between FO and abundances for each species (Table 1). Previously both data were standardized to z-scores. Thus, if we assume that the species catchability remains constant over time, changes in abundance should always be due to the actual availability/presence of the species.

To identify shifts (inflexion point) in the trends of FO series for each species (those with significant FO trends), we used an OLS-based CUSUM test. This test is based in the accumulated sum of standard ordinary least squares residuals (OLS) (Ploberger and Kramer, 1992). OLS residuals were obtained from assuming a constant rate change in the FO time series. This method has been applied to ecological time series in Briceno and Boyer (2008) and Reygondeau et al. (2015).

2.4. Trends in the centres of gravity overtime

To analyse the spatial inertia of the various species, we examined trends in the Centres of Gravity (CoG) of latitude, longitude and depth (Stefanescu et al., 1992) using the formula:

$$\text{CoG} = \frac{\sum x_i * z_i}{\sum x_i}$$

where x_i stands for the standardized abundance of species x in haul i , and z_i is the actual value of the variable under analysis (i.e.: depth, latitude or longitude) in that haul. Latitude and longitude were expressed in UTM coordinate system. CoG were calculated annually.

2.5. Environmental variables

Intermediate water temperature data in Cantabrian Sea were obtained from CTD measurements between 300 and 950 m depth taken at a central station in the Bay (station A in Fig. 1) from 1994 to 2010 (IEO Radiales Project) (González-Pola et al., 2005). The annual value obtained is the mean of all annual measurements (Fig. 2).

3. Results

3.1. Spatio-temporal changes in ecological indices

The variance explained in the richness model was 51.6%, and coefficients were significant in 44 sampling rectangles from 193 sampled ($p > 0.95$) (22.8%). In all of them the coefficient was positive, indicating an increase in richness per sampling rectangle overtime (Fig. 3). The distribution of the sampling rectangles with significant richness coefficient was very homogeneous throughout the study area, although most of the sampling rectangles with very high coefficients (dark blue colour) were located in the western part of the studied area.

3.2. Changes in the frequency of occurrence of species

Attending to the temporal analysis of FO (Table 1), 53% of species (37) showed an increasing trend ($p > 0.05$), 8.6% presented a decreasing trend and 38.4% showed no significant relationship. Considering changes by species ($\text{FO}_{\text{end}} - \text{FO}_{\text{ini}}$ along each species linear model) the largest increments occurred in *Helicolenus dactylopterus* (29.6%), *Chelidonichthys gurnardus* (28.2%), *Maurollicus muelleri* (27.9%), *Molva macrophthalma* (26.3%), *Zeus faber* (24%), *Blennius ocellaris* (21.7%) and *Raja clavata* (21.2%). The most important FO decreases occurred in *Lophius budegassa* (−23.9%), *Lepidorhombus whiffiagonis* (−23.7%), *Gaidropsarus macrophthalmus* (−21.11%).

A correlation between FO and abundance exist in more than 90% of the species. Only in 6 cases (*Chimaera monstrosa*, *Gadiculus argenteus*, *Lepidopus caudatus*, *Trachurus mediterraneus*, *Trachurus trachurus* and *Trigla lyra*) no significant correlation between FO and abundance was found (Table 1). And only four species among those showing significant changes in their FO overtime, showed no significant correlation between their FO and their abundance. Thus, excepting these cases, it

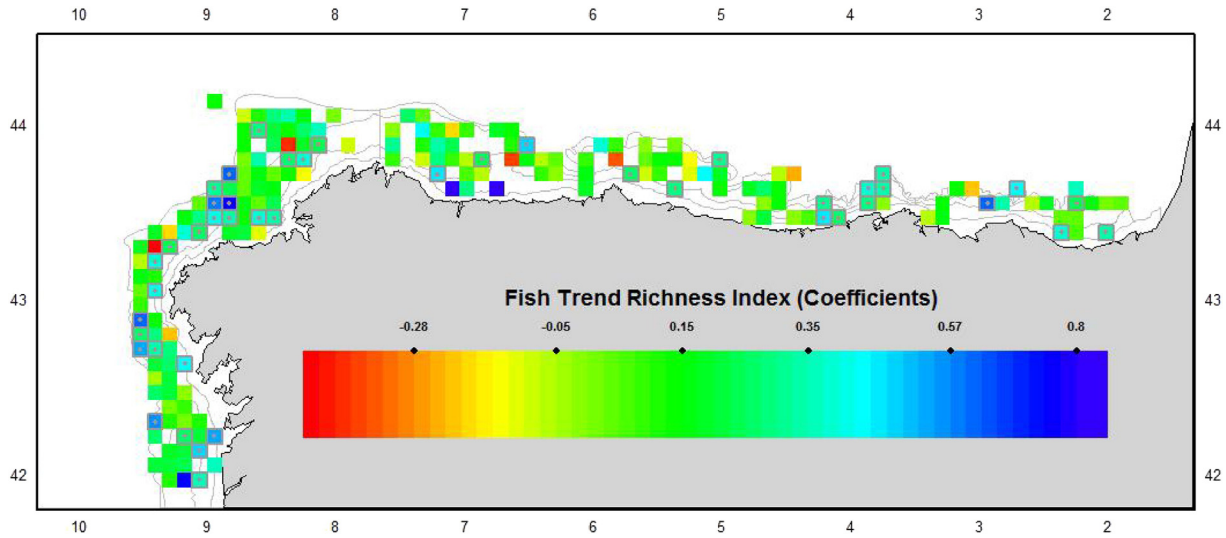


Fig. 3. Spatial distribution of coefficients of the fish richness model. Framed sampling rectangles with a grey dot are those with significant coefficients ($p > 0.95$). (For interpretation of the references to colour in this figure, the reader is referred to the web version of this article.)

can be affirmed that whenever changes in the FO were detected, these were paralleled by changes of the same sign and intensity in the abundance of the species.

The OLS-based CUSUM test identified an inflexion point for all species for which FO was significant (Fig. 4), centred in the year 2003. The other two years with more changes in the trend were 1995 and 2000.

3.3. Changes in the centres of gravity

Thirty-five percent of the species showed significant changes in their depth centre of gravity (CoG_{depth}), and in 80% of the cases these changes were towards deeper areas (Table 2). The steepest increases ($slope > 3.3$) were shown by those species which typically inhabit the continental slope such as *Chlorophthalmus agassizii*, *Galeus* spp., *C. monstrosa*, *Malacocephalus laevis* or *Phycis blennoides* (Table 2). The remaining species showing significant changes displayed more

moderate trends. Among them, *Lepidotrigla dieuzeidei*, *A. imperialis*, *L. budegassa*, and *Trisopterus luscus* moved their centres of gravity to shallower areas (Table 2).

Longitudinal and latitudinal changes in the centres of gravity were $|slope|_{LAT} \geq 218$ and $|slope|_{LON} \geq 1389$, and less frequent than those of depth, affecting 19% and 27% of the species, respectively. However, species showing changes in the latitudinal and longitudinal CoG, also modified their CoG_{depth} . With exception of *B. profundicola*, *S. cabrilla*, *Trisopterus minutus* and *Etmopterus spinax* whose CoG_{long} was displaced towards the west, and *R. clavata*, *Pagellus acarne* and *Aspitrigla cuculus*, whose CoG_{lat} was displaced towards the south. These species showed no significant displacement of the remaining CoG. In general, most latitudinal displacements occurred towards the south (84%), whilst most longitudinal ones were towards the west (88%).

3.4. Relationship with local environmental variables

As regards temperature, 60% (22 sp.) of the species showing significant increases in their FO had a significant positive correlation with the temperature of intermediate waters (300–600 or 600–950 m depth) (Table 1). Except *Leucoraja naevus* and *T. minutus*, the rest were significantly correlated with the temperature of both strata. *H. dactylopterus* and *L. naevus* also showed a positive correlation with the temperature of intermediate waters.

4. Discussion

Our results confirm a spatio-temporal increase in fish species richness in the southern Bay of Biscay. This increase appears to be a generalized phenomenon in our study area, as shown by its occurrence throughout our randomly distributed sampling stations. The analysed area is subject to intense fishing pressure, especially to trawling activities (Punzón et al., 2011), and a decrease in fishing pressure could have been responsible for the observed trends in abundance and richness of the main species (Hiddink et al., 2006). However, recent work analysing mortality due to fishing in the study area (Modica et al., 2014), shows that a significant reduction in the fishing mortality did not occur until the beginning of the 21st century, whilst changes in the trends of a great part of the species analysed here occurred before, or directly after, thus leaving a very short time to transfer the effect of effort reduction (using the cumulative fishing mortality as proxy) to fish populations. Therefore, the reduction in effort would not be enough, at least as a single event, to explain our results.

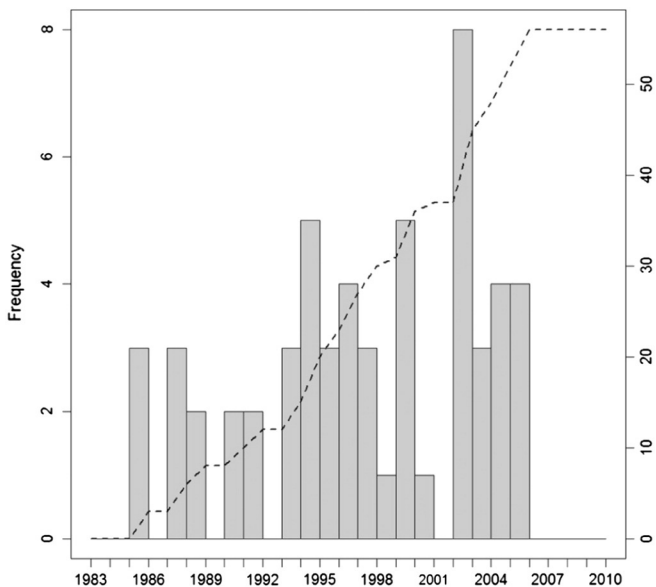


Fig. 4. Year frequency in which changes in trend in the FO occurred and accumulated frequency throughout the annual series.

Table 2
Trends in depth, latitude (UTM) and longitude (UTM) CoG by species.

Species	Depth			Latitude			Longitude		
	Slope	r ²	Sig.	Slope	r ²	Sig.	Slope	r ²	Sig.
<i>Acantholabrus palloni</i>	-0.148	0.000	-	-380.141	0.020	-	2832.608	0.040	-
<i>Argentina sphyraena</i>	-0.270	0.040	-	-184.985	0.010	-	-40.432	0.000	-
<i>Argyropelecus hemigymnus</i>	2.109	0.040	-	270.417	0.040	-	-926.555	0.010	-
<i>Arnoglossus imperialis</i>	-0.725	0.260	**	220.773	0.010	-	1648.013	0.080	-
<i>Arnoglossus laterna</i>	0.503	0.090	-	-279.443	0.010	-	-2276.962	0.110	.
<i>Aspitrigla cuculus</i>	0.314	0.070	-	-558.426	0.320	**	1540.059	0.050	-
<i>Bathysolea profundicola</i>	3.753	0.140	.	217.289	0.010	-	-6700.493	0.250	*
<i>Blennius ocellaris</i>	0.441	0.360	***	1870.161	0.470	***	1389.620	0.290	**
<i>Boops boops</i>	0.156	0.000	-	161.584	0.050	-	10.959	0.000	-
<i>Buglossidium luteum</i>	1.535	0.430	***	266.347	0.080	-	-9030.891	0.450	***
<i>Callionymus lyra</i>	0.737	0.160	*	-711.068	0.200	*	-6595.318	0.430	***
<i>Callionymus maculatus</i>	0.238	0.020	-	-404.470	0.030	-	-1501.997	0.040	-
<i>Capros aper</i>	0.339	0.030	-	189.264	0.020	-	1229.630	0.010	-
<i>Cepola rubescens</i>	0.747	0.560	***	138.079	0.020	-	-252.020	0.000	-
<i>Chelidonicichthys gurnardus</i>	-0.133	0.000	-	563.599	0.030	-	917.227	0.010	-
<i>Chelidonicichthys lucernus</i>	0.393	0.060	-	-252.003	0.010	-	-2095.211	0.060	-
<i>Chelidonicichthys obscurus</i>	1.857	0.400	***	-126.685	0.030	-	-4016.518	0.120	.
<i>Chimaera monstrosa</i>	6.735	0.370	***	151.812	0.010	-	-4033.728	0.100	-
<i>Chlorophthalmus agassizii</i>	14.341	0.450	**	-1913.578	0.120	-	2666.430	0.020	-
<i>Coelorhynchus coelorhynchus</i>	7.305	0.130	-	-326.691	0.000	-	-2974.040	0.010	-
<i>Conger conger</i>	0.105	0.000	-	-121.134	0.020	-	-2098.919	0.110	.
<i>Echiodon dentatus</i>	2.023	0.020	-	302.120	0.000	-	3618.592	0.050	-
<i>Etmopterus spinax</i>	1.390	0.040	-	719.999	0.090	-	-10,998.384	0.520	***
<i>Gadiculus argenteus</i>	1.264	0.170	*	-348.745	0.010	-	-5301.750	0.220	*
<i>Gaidropsarus macrophthalmus</i>	2.488	0.260	**	-180.877	0.000	-	-2664.658	0.150	*
<i>Gaidropsarus vulgaris</i>	-7.139	0.230	.	2151.586	0.050	-	-4806.861	0.020	-
<i>Galeus sp</i>	8.019	0.580	***	19.088	0.000	-	-4369.857	0.160	*
<i>Helicolenus dactylopterus</i>	2.749	0.420	***	-1310.748	0.150	*	-4712.281	0.380	***
<i>Hexanchus griseus</i>	6.263	0.190	*	1065.244	0.060	-	-2849.306	0.190	*
<i>Labrus bimaculatus</i>	0.468	0.020	-	-244.820	0.000	-	2919.058	0.020	-
<i>Lampanyctus crocodilus</i>	1.033	0.010	-	-82.130	0.000	-	-1880.287	0.010	-
<i>Lepidopus caudatus</i>	1.354	0.050	-	103.883	0.000	-	-1853.234	0.010	-
<i>Lepidorhombus boscii</i>	-0.040	0.000	-	233.602	0.030	-	-1205.745	0.050	-
<i>Lepidorhombus whiffiagonis</i>	0.808	0.460	***	-235.106	0.100	-	1874.984	0.120	.
<i>Lepidotrigla dieuzeidei</i>	-3.106	0.540	***	2719.573	0.130	.	3717.276	0.150	.
<i>Leucoraja naevus</i>	0.452	0.060	-	-316.708	0.090	-	2106.880	0.080	-
<i>Lophius budegassa</i>	-0.812	0.310	**	-1599.935	0.320	**	-1541.599	0.020	-
<i>Lophius piscatorius</i>	0.322	0.010	-	-295.538	0.090	-	-1561.371	0.040	-
<i>Macroramphosus scolopax</i>	1.401	0.070	-	932.893	0.040	-	1223.110	0.010	-
<i>Malacocephalus laevis</i>	3.641	0.330	**	-2.968	0.000	-	-6470.276	0.140	.
<i>Maurollicus muelleri</i>	0.666	0.010	-	-1266.236	0.060	-	-1510.203	0.020	-
<i>Merluccius merluccius</i>	0.078	0.010	-	-213.233	0.010	-	1561.636	0.060	-
<i>Microchirus variegatus</i>	-0.037	0.000	-	343.021	0.030	-	-683.314	0.020	-
<i>Micromesistius poutassou</i>	0.909	0.070	-	33.865	0.000	-	-1625.238	0.020	-
<i>Molva macrophthalma</i>	3.334	0.140	.	704.348	0.040	-	-521.457	0.000	-
<i>Mullus surmuletus</i>	1.026	0.350	**	-218.882	0.160	*	1629.558	0.060	-
<i>Pagellus acarne</i>	0.440	0.100	-	-314.715	0.290	**	1784.842	0.040	-
<i>Pagellus bogaraveo</i>	0.460	0.010	-	210.406	0.020	-	-1052.579	0.010	-
<i>Pagellus erythrinus</i>	0.025	0.000	-	-89.023	0.090	-	334.759	0.020	-
<i>Phycis blennoides</i>	3.419	0.240	**	-296.112	0.020	-	-5220.888	0.180	*
<i>Raja clavata</i>	-0.050	0.000	-	-470.260	0.430	***	-1075.969	0.030	-
<i>Raja montagui</i>	0.985	0.400	***	-292.667	0.130	.	932.125	0.010	-
<i>Sardina pilchardus</i>	-1.152	0.080	-	-1235.152	0.190	*	8583.353	0.280	**
<i>Scomber japonicus</i>	-0.739	0.020	-	-1115.649	0.100	-	-6676.827	0.040	-
<i>Scomber scombrus</i>	-0.547	0.030	-	-1311.871	0.040	-	300.767	0.000	-
<i>Scorpaena loppei</i>	-0.445	0.060	-	221.667	0.010	-	-616.110	0.000	-
<i>Scorpaena notata</i>	-2.367	0.220	*	-1789.134	0.210	*	9866.728	0.180	*
<i>Scorpaena scrofa</i>	-6.159	0.170	.	-960.946	0.120	-	6331.641	0.100	-
<i>Scyllorhinus canicula</i>	-0.386	0.070	-	-425.990	0.300	**	-649.680	0.010	-
<i>Scyllorhinus stellaris</i>	0.149	0.000	-	90.415	0.000	-	3874.258	0.060	-
<i>Serranus cabrilla</i>	0.024	0.000	-	65.862	0.000	-	-4987.691	0.220	*
<i>Solea solea</i>	1.086	0.350	**	-683.065	0.320	**	671.232	0.010	-
<i>Spondyllosoma cantharus</i>	1.408	0.160	*	-120.652	0.010	-	-8410.137	0.170	*
<i>Trachinus draco</i>	2.165	0.460	***	613.087	0.680	***	-4737.646	0.570	***
<i>Trachurus mediterraneus</i>	-0.888	0.010	-	48.088	0.000	-	2048.606	0.010	-
<i>Trachurus trachurus</i>	-0.196	0.010	-	-676.737	0.070	-	-858.870	0.010	-
<i>Trigla lyra</i>	-0.262	0.010	-	931.913	0.040	-	7929.244	0.290	**
<i>Trisopterus luscus</i>	-0.996	0.160	*	-1276.286	0.120	.	-6050.169	0.180	*
<i>Trisopterus minutus</i>	0.527	0.080	-	-84.757	0.000	-	-4835.166	0.150	*
<i>Zeus faber</i>	0.356	0.040	-	908.132	0.120	.	1326.011	0.040	-

Significance codes: 0 '***', 0.001 '**', 0.01 '*', 0.05 '.', 0.1.

Recent studies have associated changes in the specific composition of coastal ecosystems such as the incorporation of warm water species to cooler seas and the decrease in the abundance of typical species from these cooler areas, with climate change (Hofstede et al., 2010). Moreover, increases in water temperature have also been associated with latitudinal increases in species richness, as a positive balance between species gains and losses (Vinagre et al., 2011). In our study area, richness was modified at a local scale, while no changes in absolute richness values due to species additions or losses were detected. These changes in the Southern Bay of Biscay are a consequence of the modifications in the FO of species that were already present in the area, with the result of a local increase in richness throughout the shelf.

Considering the restrictions imposed in our species selection, and unlike Hofstede et al. (2010), we did not detect any new species addition to the system, all species being previously cited from our study area (Bañón et al., 2010). A considerable amount (81%) of the species recorded in our study correspond to the Lusitanian province, while 16% are typical of the Atlantic one, according to the biogeographical classification made by Ellis et al. (2008a, 2008b). We only identified a single species with African affinity (*L. dieuzeidei*), while none of the species had boreal affinity. Thus, the faunistic composition of fish species in the demersal assemblage in the Southern Bay of Biscay is characterised by species which are abundant in the Lusitanian area of the Iberian Peninsula, with contributions of species that are broadly distributed throughout the north eastern Atlantic Ocean and are typical of both the continental slope and deep waters (Ellis et al., 2008a). Hofstede et al. (2010) found that this fauna is expanding towards the Celtic and North seas, and causing an increase in species richness in these areas. These increases are also coherent with the correlation between species richness and temperature increase found by Macpherson and Duarte (1994) and Macpherson (2002). Our results do not indicate such an increase in richness due the incorporation of new species in the study area.

Some of the species with a significant increase in the FO in our study area (*T. minutus*, *Eutrigla gurnardus*, *Arnoglossus laterna*, *Solea solea*, and *L. naevus*), have also shown changes associated to climate change in their northern distribution limit (Perry et al., 2005). As regards the Perry et al. (2005) study there were two exceptions, *T. luscus* and *Lophius piscatorius*, that they found changes in the distribution, while in our study there were no significant changes in the FO. These simultaneous changes in various areas have already been identified for other species. For instance, *Mullus surmuletus* has shown evidences of moving towards the north of its distribution area (Brander et al., 2003), as well as increases in its occurrence and abundance in our study area. Tasker (2008) found an increased abundance of *M. surmuletus*, *Scyliorhinus canicula* and *Z. faber* in Ospar region V (central North-Atlantic), and attributed these changes in the distribution of these typical Lusitanian species to increases in water temperature. A response as that found in the Southern Bay of Biscay has already been described by Simpson et al. (2011) with Celtic and North Sea faunas, which also showed increased abundances of the majority of species with increasing temperature.

Hence, there are strong evidences of simultaneous changes in the distribution of species with Lusitanian affinities throughout their distribution area, as well as of increases in their FO and abundance in their core areas. Furthermore, the observed changes in the northern limit of their distribution respond to the hypotheses set forth by Rijnsdorp et al. (2009) and have been previously observed with fauna of other areas such as the Arctic (Simpson et al., 2011).

The only exception in the biogeographic pattern of the study area was *L. dieuzeidei* (with an African affinity), which lies in the northern limit of its distribution in the study area, where it has recently appeared coming from the Mediterranean Sea (Bañón, 2004). This species has passed from showing very low abundances to being present in 40% of the sampling stations, which indicates a clear progression of *L. dieuzeidei* in the study area. However, this displacement does not

correspond with a variation in the coordinates of its centre of gravity, as it would be expected. The latter could be due to the very short latitudinal development of the shelf compared to its broad longitudinal one in the Cantabrian Sea and the opposite in the Galician Waters. Indeed, the species' presence per sampling station in the 5 year groupings (Fig. 5), clearly indicates that its distribution limit first moved northwards and then towards the east once its north distribution limit was reached. This would imply a northward shift in its distribution limit which is equivalent to those observed in the North sea for species with Lusitanian affinities (Perry et al., 2005; Brander et al., 2003; Hofstede et al., 2010).

Brander et al. (2003) reported a similar behaviour for *Macroramphosus scolopax*, which according to these authors had its northern limit of distribution in southern Portugal in the 90's, and would have moved northwards along the Portuguese shelf. However, our results indicate that this species has been present in the Southern Bay of Biscay since the beginning of the time series (1983), first in very low amounts, then with maximum FO's in the period from 1991 to 1995, and finally (2010), with a reduction in its abundance to levels similar to those found at the beginning of the series. Even if the FO's may give the impression that there has not been any progression of the species along the southern Bay of Biscay's shelf, this result is masked by the high abundances detected during the period 1991–1996 (Fig. 5). Moreover, despite its FO dropping at the end of the time series, the species was still present all along the Cantabrian shelf. Thus, notwithstanding the northward shift of the species distribution, two other processes could be taking place simultaneously: a favourable recruitment such as that described for *H. dactylopterus* in the North Sea (Heessen et al., 1996) and/or a spatial expansion/contraction in the distribution, associated to changes in abundance (MacCall, 1990; Barange et al., 2009).

Only a small proportion of the species showing significant changes in their FO also showed changes in their CoG. Significant increases in the FO of most species showing variations in their CoG occurred towards the west and south of the study area, as well as into deeper waters. This would be expected if the Lusitanian species increased their abundance in their core distribution area (Tasker, 2008). In fact, there are two spatial variability mechanisms occurring between the east and western areas of the Bay of Biscay. On one hand, there is an upwelling phenomenon in the West and on the other a progressive warming of surface waters towards the East (Lavín et al., 2006). In both cases, there have been modifications of these phenomena associated with the climate change (Bakun, 1990; Thompson, et al., 2012), i.e.: upwelling intensity has weakened (Bode et al., 2009) and surface waters have warmed further (Llope et al., 2006). These processes have caused an increase in typically temperate zooplankton species at regional and local scale (Bode et al., 2009; Neira et al., 2014), which may have consequences both for top predators and intermediate trophic connections (Thompson et al., 2012).

Most species showing a significant trend in their depth CoG and an increase in their occurrences, augmented their abundance and presence at deeper levels. The strongest increases in depth CoG's were for species which are typical of the border of the continental slope, such as *C. monstrosa*, *C. agassizii*, *Galeus* spp., *M. laevis* or *P. blennoides*. Perry et al. (2005) associated these changes in depth to the effect of water warming, since in most cases they were paralleled by latitudinal changes in the North Sea. In their case, only changes in depth were detected, responding to climate variation with local movements. In our case, an increase in temperature of intermediate waters has been detected (González-Pola et al., 2005), which could enhance Lusitanian species increases at depths where they are normally less frequent.

In general, two different biogeographic phenomena associated with climate change have been detected in temperate seas, meridionalization, when an increase in the abundance of native fauna with southern affinities occurs (CIESM, 2008), and tropicalization when an increase in the abundance of non-native species with tropical or sub-tropical affinities takes place (CIESM, 2008). The mechanisms through which climate

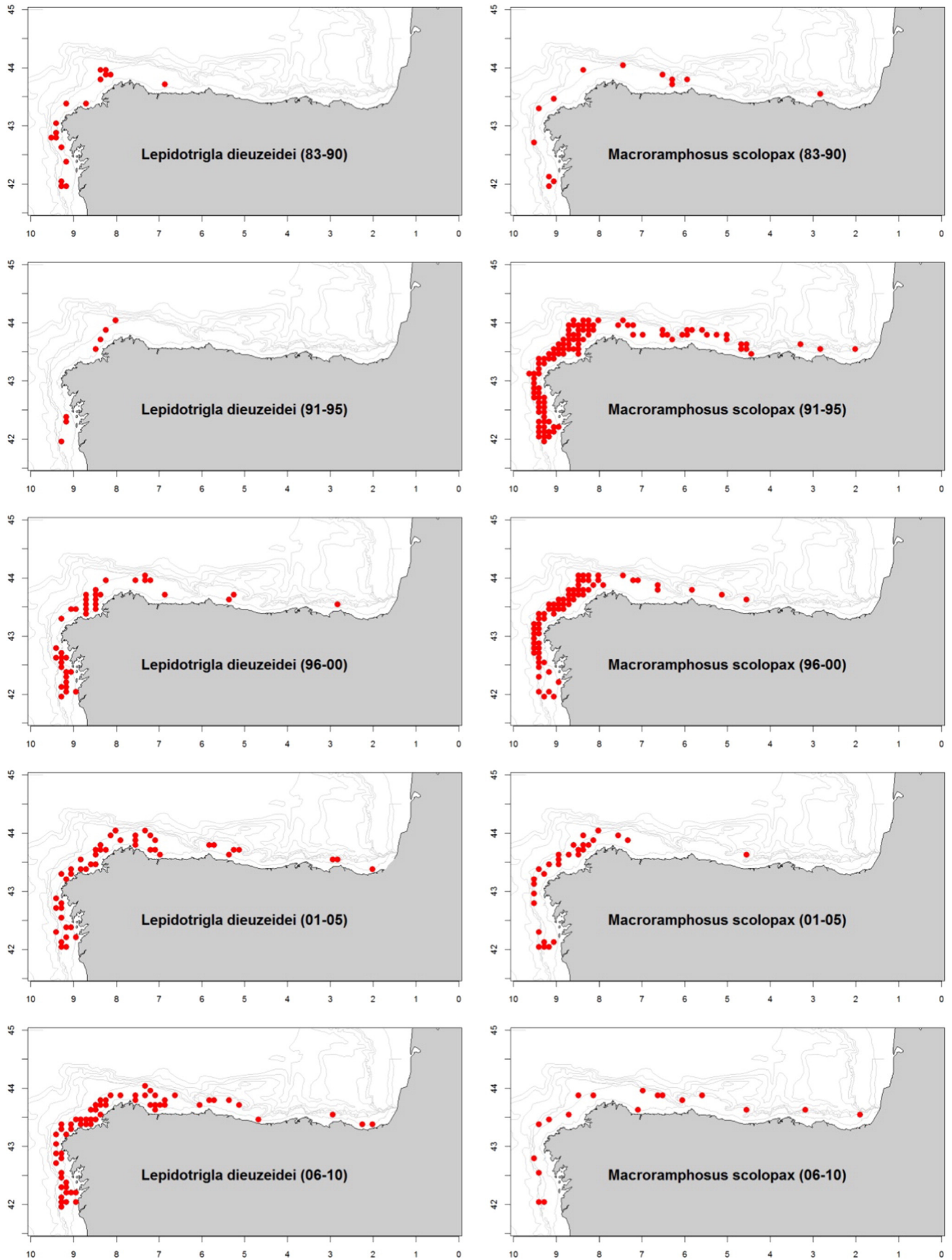


Fig. 5. Evolution in the spatial distribution of *Lepidotrigla dieuzeidei* and *Macroramphosus scolopax* in five-year grouping periods.

change may be causing these changes are very diverse and can affect different life-stages and different levels of biological organization successively and in different ways (Rijnsdorp et al., 2009). Specifically for temperate species, a direct relationship has been found between increases in water temperature and increases in metabolic rates, as well as a better adaptation of temperate species that cold water to increases in the diversity of diseases (Crozier and Hutchings, 2014). In addition temperate species (in our study, species with lusitanian and african affinities) are able to acclimate and adapt their thermal window by e.g. changing their mitochondrial density, among other physiological adjustments (Pörtner and Knust, 2007). Also it has identified a positive relationship between temperature and the recruitment of species with a Lusitanian affinity (Rijndorp et al., 2009). Therefore mechanisms exist that justify the results herein described, although it is necessary to find which ones are acting in this case.

In our case, tropicalization could only be detected through the progression of *L. dieuzeidei*. While we acknowledged this single case, the process could be more extended in the study area (Bañón et al., 2010), since our methodological approach eliminated those species which were uncommon in our samples (i.e. *Sphoeroides pachygaster*, *Symphurus nigrescens* and *Microchirus azevia*, all with African affinities, and two other species with one only record). Moreover, tropical species may find added obstacles for their northward shift in the narrow shelf or the numerous deep canyons which are common in the southern Bay of Biscay (Lloret et al., 2015).

Increasing evidence seems to point to a meridionalization of the demersal ecosystem of the southern Bay of Biscay caused by water warming (González-Pola et al., 2005, Llope et al., 2006). This phenomenon has already been described in the Mediterranean (CIESM, 2008; Azzurro et al., 2011), although not involving the high amount of species reported here. Tasker et al. (2008) identified it as one of the possible consequences of climate change. Similarly, shifts in the distributions and abundance, in the pelagic fish ecosystem have been detected elsewhere (Cheung et al., 2009). These changes, together with alterations in predator–prey interactions caused by warming (Sanford, 1999), increase predator species abundance and reduce availability of forage fish as described by Preciado et al. (2008), with paramount implications as readjustment of the food web of southern Bay of Biscay.

5. Conclusions

Our analyses of the demersal ecosystem of the Southern Bay of Biscay over 30 years show a generalized increase in the occurrence and the abundance of species with Lusitanian affinities in the last decades. Changes were detected from the beginning of the time series and are particularly apparent during the last years. Their persistence throughout the time-series indicates that they cannot be attributed only to recent reductions in fishing effort intensity. In fact, our results evidence an increase of thermophilic demersal fish species in the southern Bay of Biscay and point at climate change as the most plausible explanation. Among the most evident signs of this “meridionalization” are the high correlations found between changes in the FO and the abundance of species, and environmental variables related with climate change; the northward and deeper orientated movements of the CoG of the distribution of demersal species; and the northerly progression of the only species with an African affinity included in our analysis. All these variations are in agreement with the responses which could be expected under a climate change scenario.

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