

## RESEARCH ARTICLE

# Northeast Atlantic species distribution shifts over the last two decades

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**Abstract**

Marine species are widely shifting their distributions in response to global changes and it is commonly expected they will move northward and to greater depths to reach cooler, less disturbed habitats. However, local manifestations of global changes, anthropogenic pressures, and species characteristics may lead to unanticipated and varied responses by individual species. In this regard, the Celtic-Biscay Shelf is a particularly interesting study system because it has historically been heavily fished and occurs at the interface between two distinct biogeographic provinces, its community thus comprised of species with diverse thermal preferences. In the context of rapidly warming temperatures and intense fishery exploitation, we investigated the distribution shifts of 93 taxa (65 Actinopteri, 10 Elasmobranchii, 11 Cephalopoda, 5 Malacostraca, and 2 Bivalvia), which were sampled annually from 1997 to 2020 during a scientific bottom trawl survey. We used a set of 11 complementary spatial indices to quantify taxon distribution shifts over time. Then, we explored the relative effect of taxon abundance, fishing pressure, and climatic conditions on taxon's distribution shift when a significant shift was detected. We observed that 56% of the taxa significantly shifted. Not all taxa will necessarily shift northward and to deeper areas, as it is often expected. Two opposite patterns were identified: taxa either moving deeper and to the southeast, or moving closer to the surface and to the northwest. The main explanatory factors were climate change (short- and long-term temperatures) and taxon abundance. Fishing pressure was the third, but still significant, explanatory factor of taxa of greater commercial importance. Our research highlights that taxa are displaying complex distribution shifts in response to the combined anthropogenic disturbances and underscores the need to conduct regional studies to better understand these responses at the ecosystem scale to develop more suitable management plans and policies.

**KEYWORDS**

Bay of Biscay, Celtic Sea, climate change, distribution shift, fishing pressure, functional ecology, marine taxa, spatial indices

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## 1 | INTRODUCTION

A major challenge in ecology is understanding how climate change affects population dynamics and, more broadly, ecosystem functioning and biodiversity (Auber et al., 2017). In marine ecosystems, the main effect attributed to climate change is the worldwide ocean warming with mean temperatures climbing significantly since the earliest records in 1955 (Cheung et al., 2012). Other major effects include changes in salinity; declines in sea ice extent; shifts in hydrological cycles and ocean currents; increases in sea level; acidification; and the expansion of oxygen minimum zones (Cheung et al., 2012; Doney et al., 2012). The overall result has been dramatic and led to diverse physiological, biological, and ecological responses by marine species (Assan et al., 2020; Parmesan & Yohe, 2003; Perry et al., 2005; Pinsky et al., 2013, 2020; Rijnsdorp et al., 2009; Rilov et al., 2019). Among the most common responses are distribution shifts (Cheung et al., 2012; Rubenstein et al., 2023), which have been observed in taxa ranging from phytoplankton to mammals (Pinsky et al., 2020; Poloczanska et al., 2013, 2016; Rubenstein et al., 2023). Indeed, marine species have a substantial capacity for colonizing new areas and migrating over large distances when they no longer experience optimal conditions in their current environment (Pinsky et al., 2020). In general, it is expected that species will move to higher latitudes (poleward) and/or into deeper waters (Poloczanska et al., 2016). However, the reality of species' distribution shifts is often more subtle and species will also be affected by the interplay between local biotic (e.g., changes in food web relationships; Heath, 2005) and abiotic characteristics (e.g., isotherms and other abiotic dimensions of niche space; Rubenstein et al., 2023).

In this study, we attempt to identify taxa distribution shifts and then quantify the relative importance of two main ecological processes explaining taxa distribution shifts: (1) modifications in habitat suitability due to climate change and/or (2) variation in population size due to density-dependent processes and fishing exploitation (Baudron et al., 2020; Mclean et al., 2018, 2019; Mérillet et al., 2020; Nye et al., 2009; Wang et al., 2020). We applied this framework to the Celtic-Biscay Shelf (CBS), an area particularly interesting to explore how the interplay between climate change and anthropogenic pressure such as fishing affects marine ecosystems. Indeed, this area which lies at the interface between the subtropical and boreal biogeographic provinces (OSPAR Commission, 2000), is characterized by a latitudinal temperature gradient (Désaunay et al., 2006; Koutsikopoulos et al., 1998; Planque et al., 2003), and over the past 40 years, it has experienced a mean rise in temperature that is three times faster than the global mean ( $[0.1-0.35]^{\circ}\text{C}\cdot\text{decade}^{-1}$ ; Costoya et al., 2015). Furthermore, the CBS supports numerous marine species that are heavily exploited by various European fisheries (e.g., European sardine, blue whiting, horse mackerel, mackerel, and European hake; Gascuel et al., 2016; ICES, 2022a, 2022b). It is thus one of the most exploited zones in Europe while the fishing pressure of the main targeted species decreased substantially during the last 20 years (~30% in the Celtic Sea [CS] and ~45% in the Bay of Biscay [BoB]; ICES, 2022a, 2022b). The stock sizes of emblematic pelagic,

and demersal species such as Atlantic herring, European sprat, boarfish, and European seabass have thus experienced substantial variations over the last two decades (Hervann et al., 2020). Fishing is known to affect exploited species demography (e.g., abundance and truncation in age structure), life-history traits (e.g., increase in growth rates and decrease in age-at-maturity), and population spatial heterogeneity and distribution (Perry et al., 2010; Planque et al., 2010). A simple consideration of the processes that regulate fish population dynamics suggests that all these effects may decrease population resilience to environmental variability and may have adverse effects on their capacity to buffer climate changes (Hsieh et al., 2008; Perry et al., 2010). High levels of fishing pressure within the CBS are thus expected to exacerbate the climatic sensitivity of commercially exploited species (Hermant et al., 2010; Hsieh et al., 2008; Poloczanska et al., 2016; Rijnsdorp et al., 2009), and in greater proportions on the CS populations where fishing pressure is more intense than in the BoB (ICES, 2022a, 2022b). In addition to fishing pressure, species distribution range is also strongly influenced by natural population dynamics. Indeed, the distribution of a growing population expands from optimal habitats to suboptimal habitats to ease intraspecific competition (MacCall, 1990). Within the heavily exploited CBS facing climate change, we expected that density-dependent process would not be the main driving factor of species distribution shifts. However, we considered that this natural process cannot be excluded when exploring the potential factors explaining population shifts in distribution. Studying the CBS thus presents a remarkable opportunity to examine how species distribution shifts are shaped by climatic and anthropogenic influences, as well as by natural population dynamics (Adams et al., 2018; Engelhard et al., 2014; Frank et al., 2016; Hsieh et al., 2008).

The nature of species interactions with those driving factors will also likely depend on taxon-specific characteristics (Perry et al., 2005; Sunday et al., 2015). Habitat affinities and thermal preference of species in this area have raised questions about whether its populations will respond to climate change in line with general predictions (Poloczanska et al., 2016). The biological community of the CBS comprises boreal, Lusitanian, and Atlantic biogeographic guilds, including species whose populations reach the southern (e.g., Atlantic herring, greater argentine, and common dab) or northern (e.g., surmullet, Atlantic chub mackerel, and Mediterranean horse mackerel) boundaries of their distribution ranges (Poulard & Blanchard, 2005; Whitehead et al., 1984-86). In response to climate change, we expected that within the CBS, boreal species would experience range contraction, with their trailing edge (and to the unknown extent their center of gravity [CG]) shifting northward, while Lusitanian species would experience range expansion, with their leading edge (and possibly their CG) shifting northward. We expected Atlantic taxa, which are distributed over a wider area, to be less sensitive to environmental changes because they experience a broader range of abiotic and biotic conditions (Sunday et al., 2015). As the leading and trailing edges of Atlantic taxa are outside the CBS, we expected to detect their distribution shifts mainly with the CG. Other ecological and biological traits, such as vertical distribution

(i.e., swimming ability) and taxonomic class (e.g., life cycles), may also influence species' response to changes in habitat suitability by facilitating or restricting their distribution shifts (Perry et al., 2005; Sunday et al., 2015). We expected taxa with a greater capacity to swim to have faster range extensions than taxa with low mobility (Sunday et al., 2015) and short-life cycle taxa to shift in a greater proportion than the other taxonomic classes (Perry et al., 2005).

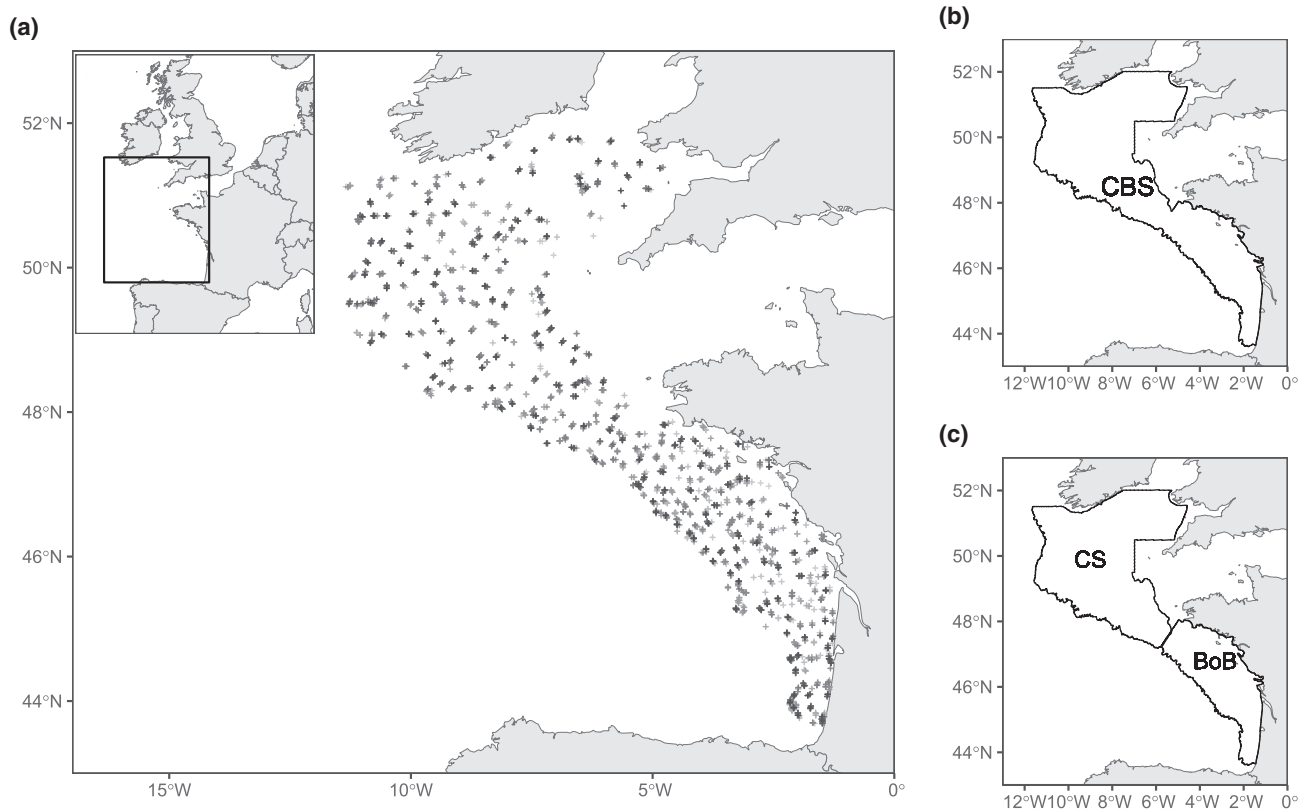
We explored these theoretical expectations by analyzing changes in the distribution patterns of diverse Northeast Atlantic taxa (65 Actinopteri, 10 Elasmobranchii, 11 Cephalopoda, 5 Malacostraca, and 2 Bivalvia) with different relative commercial importance and taxon characteristics over a 23-year period. We first characterized taxon distribution shifts using a set of spatial indices that described distribution limits, the mean spatial location of a taxon's population(s), and dispersion around this mean, which reflects the degree of distribution range expansion or contraction (Bez & Rivoirard, 2001; Woillez et al., 2007, 2009). We considered a large set of indices to capture the different dynamics of the shifts and assess the displacement in three dimensions: latitude, longitude, and depth. Species shifts consist of colonizations at the leading edge, extirpations at the trailing edge, or both (Fredston-Hermann et al., 2020), which will be reflected in a shift in the population distribution limits represented by the 0.05 and 0.95 quantiles, and in the distribution range, expansion or contraction represented by the positive area (PA) and inertia.

We expected these shifts to be then integrated at the scale of the mean spatial location of a taxon's population(s) (i.e., CG). We then examined the relationships between the distribution shifts and driving factors, namely, climate change, fishing pressure, and taxon abundance to disentangle their influences on the observed population distribution shift. To explore the influence of taxon characteristics on their distribution shifts, our results were scrutinized according to functional traits such as population distribution zone, taxonomic class, biogeographic guild, vertical distribution guild, and relative commercial importance.

## 2 | MATERIALS AND METHODS

### 2.1 | Data collection

The scientific bottom trawl survey EVHOE (Evaluation of fishing resources of Western Europe; EVHOE cruise, R/V Thalassa, IFREMER; Laffargue et al., 1987, Laffargue et al., 2021a, 2021b) was carried out between October and December from 1997 to 2020 along the CBS. The latter occurs at the interface between the CS and the BoB (Figure 1). EVHOE relies on a stratified random sampling design in which 119–158 stations were sampled annually. At each station, specimens were collected using a 36/47 GOV bottom trawl (opening



**FIGURE 1** Area sampled during EVHOE survey. (a) Location of sampling stations between 1997 and 2020 (grayscale intensity increases with time). Geographical delineation of the distribution zones: (b) Celtic-Biscay Shelf (CBS), (c) Celtic Sea (CS), and Bay of Biscay (BoB). Map lines delineate study areas and do not necessarily depict accepted national boundaries.

width: 20 m; height: 4 m; mesh size: 20 mm) operated for 30 min at a towing speed of four knots. Once on board, species were identified to the finest possible taxonomic scale. Due to the variation in taxonomic resolution, some species were assigned to a coarser taxonomic level (Table S1), hereafter named “taxon” and “taxa.” We excluded the 2017 dataset, as an incident of boat engine failure prevented the completion of the sampling campaign. To reduce potential bias due to the sampling method, we only retained the taxa with reliable temporal and spatial coverage. We selected taxa collected during at least 80% of the studied years and at 5% or more of the sampling stations within a given year (Table S1). This selection was adapted for the analysis of temporal shifts in taxon distribution but not for the exploration of invasive species income.

## 2.2 | Taxon characteristics

Species traits are widely recognized as being more effective than phylogenetic identity in understanding and predicting the impacts of environmental changes on biodiversity (D'agata et al., 2016). To investigate which traits are better at driving shifts in taxon distribution, each taxon was characterized by its taxonomic class, population distribution zone, biogeographic guild, vertical distribution guild, and relative commercial importance. We summarized the ecological hypotheses behind the selection of these taxon characteristics and their expected responses in the CBS in Table 1. Using taxon population presence/absence data over the studied period, we attributed a distribution zone to each taxon's population: CS, BoB, or CBS (Figure 1). We used a criterion of a 1-degree latitude difference between the CS and the BoB to identify taxon with two delineated populations in the CBS. We addressed these results to scientific and stock assessment expertise for validation. Based on information from the scientific literature, FishBase, and ICES, each taxon was assigned to a biogeographic guild (Atlantic, boreal, or Lusitanian) and a vertical distribution guild (pelagic, demersal, benthic swimmer, or benthic; Table S1). Two benthic guilds were defined according to taxa swimming capacity: the benthic swimmer taxa were Actinopteri, Elasmobranchii, and Cephalopoda and the benthic taxa were Malacostraca and Bivalvia (Table S1). We calculated each taxon's relative commercial importance using ICES mean catches in FAO divisions 27.7 g,h, and 27.8 a,b, corresponding to the CS and the BoB delineated in our study, respectively, between 2006 and 2019 (ICES, 2021). Based on this information, taxa were considered to be of lesser commercial importance (mean catch for taxon <0.25 quantile of the distribution of mean catches for all taxa) or of greater commercial importance (mean catch for taxon ≥0.25 quantile of the distribution of mean catches for all taxa).

## 2.3 | Spatial indices

For each sampling year and population, we calculated the following spatial indices: CG, 0.05 and 0.95 quantiles of latitude, longitude,

and depth; inertia; and PA. We used the 0.05 and 0.95 quantiles as the annual minimum and maximum limits of latitude, longitude, and depth (Figure S1). For each taxon, the 0.05 and 0.95 quantiles were the thresholds below and above which 5% of the annual values of a given index were observed, respectively. We summarized the ecological hypotheses behind the selected indices and the expected responses of taxa within the studied area in Table 1.

The CG is the mean location of a given population (latitude CG and longitude CG) (Wuillez et al., 2007):

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

where for a given population  $i$ ,  $x_i$  is the longitude or latitude,  $s_i$  is the area of influence (square nautical mile), and  $z_i$  is the taxon density (number of individuals at a sampling station divided by the surface area sampled in square nautical miles). To account for the effects of the stratified random sampling design, the area of influence for the stations was included in the CG calculation using the Voronoi tessellation (Wuillez et al., 2007, 2009).

We calculated the population depth CG (depth\_CG) by taking the mean depth values at a given station and weighting them by taxon density at each station.

We examined the consistency of annual station-specific sampling CG and mean depth (i.e., unweighted by  $z_i$ ) over time (Wuillez et al., 2009), and we excluded the potential influence of sampling design issues on taxa displacement patterns over time.

Inertia ( $I$ ) represents the spatial dispersion of a population around its CG and is expressed in square nautical miles (Wuillez et al., 2007):

$$I = \frac{\sum_{i=1}^n (x_i - CG) 2s_i z_i}{\sum_{i=1}^n s_i z_i} \quad (2)$$

The PA describes the area occupied by the population at densities greater than zero and is also expressed in square nautical miles (Wuillez et al., 2007):

$$PA = \sum_{i=1}^n s_i [z_i > 0] \quad (3)$$

$I$  and PA are complementary indices of a population's spatial occupancy:  $I$  refers to the mean square distance between an individual and the CG of its population, and PA is the area of population presence.

## 2.4 | Analyzing spatial distribution patterns

To examine distribution shifts by the taxa's populations, we analyzed the 11 spatial indices over time using linear regression (Gaussian distribution with identity link function; Zuur et al., 2009). We determined whether a serial correlation was present in the residuals using a Durbin–Watson test (Durbin & Watson, 1950). If affirmative, we analyzed the values of that particular spatial index over time using a generalized least squares regression with a first-order autoregressive

**TABLE 1** Summary of the spatial indices, taxon characteristics, and explanatory variables with the corresponding ecological hypotheses behind each index selection and expected responses in the Celtic-Biscay Shelf.

Variable category	Index	Ecological hypothesis behind index selection	Expected response in the Celtic-Biscay Shelf
Spatial index	Latitude and longitude center of gravity (CG)	The CG of a population represents the mean location of the population (Wuillez et al., 2007) and is thus an integrated spatial index of its distribution	We expected northward and westward shifts to be the most prevailing shifts because they would transcribe shifts to cooler waters in the area (Figure S2). The leading and trailing edges of Atlantic taxa being outside the Celtic-Biscay Shelf, we expected to detect their distribution shifts mainly with the CG We expected CG to respond to change in population size induced by fishing pressure
	Latitude and longitude limits (0.05 and 0.95 quantiles)	Taxa distribution shifts consist of colonizations and/or extirpations at the trailing edge and/or leading edge (Fredston-Hermann et al., 2020). Latitude and longitude limits are thus good indices to capture taxa distribution shifts (Fredston-Hermann et al., 2020).	We would expect latitudinal and longitudinal limits to be one of the first spatial indices to show shift in distribution and thus recorded a greater percentage of distribution shifts than CG In response to climate changes in the area, taxa trailing and leading edges (southern and northern limits, respectively) are expected to shift northward and/or westward to cooler waters in the area (Figure S2). We expected leading edges to shift in greater proportions than trailing edges (Fredston-Hermann et al., 2020). Boreal taxa whose trailing edge is in the studied area are expected to shift their trailing edge in higher proportions than other taxa. Similarly, Lusitanian taxa whose leading edge is in the studied area are expected to shift their leading edge in higher proportions than other taxa We expected spatial limits to respond to change in population size induced by fishing pressure. Fishing pressure distribution is not homogenous in the area and between taxa (Eme et al., 2022, ICES, 2022a, 2022b), therefore we did not expect a general trend in space but local taxa-specific responses
	Depth CG	Depth is the third dimension in which marine species can shift and several studies highlighted the relevance of this spatial index to explore species distribution shifts (e.g., Chaikin & Belmaker, 2023). Its CG represents the mean depth of the population (Wuillez et al., 2007) and is thus an integrated spatial index of its distribution	Significant links between thermal preference and depth shifts suggest that environmental and anthropogenic pressures can drive taxa depth redistribution (Chaikin & Belmaker, 2023). We mainly expected a deepening shift of the taxa (Poloczanska et al., 2016). However, due to the particularly large size of the Celtic-Biscay continental shelf (Koutsikopoulos & Le Cann, 1996), we do not expect depth CG to be one of the main spatial indices to highlight taxa distribution shift. We do not expect fishing pressure to influence depth CG distribution
	Depth limits (0.05 and 0.95 quantiles)	In the same vein as latitude and longitude limits, depth limits are considered to be relevant in capturing taxa distribution shifts (Fredston-Hermann et al., 2020).	We expected a deepening pattern of the taxa, and especially boreal and CS taxa, to remain within favorable habitat in terms of temperature range We do not expect fishing pressure to influence depth limits distribution
	Positive area	This index reflects the surface expansion or contraction as a result of population dynamics to cope with their environment.	In response to changes in environmental conditions, we expected Lusitanian taxa and BoB populations to expand while boreal taxa and CS populations to contract their distributions. We expected to have a higher percentage of expansions than contractions; contractions appeared to be five times slower than the rate of range expansions (Poloczanska et al., 2013) Fishing is known to spatially constrain population distribution and affect its spatial variability (i.e., loss of population sub-units and contraction of the population; Perry et al., 2010; Planque et al., 2010; Wang et al., 2020). If the fishing pressure is more intense on the edge of population distribution, we would expect PA to decrease with increasing fishing pressure, and if the fishing pressure is located closest to taxa CG we expected PA to remain unchanged or to increase with increasing fishing pressure as a response of taxa extirpation of the non-suitable area
	Inertia	The spatial dispersion of the population around its CG reflects population distribution's expansion or contraction at a more integrate scale than the positive area	We expected this index to be less sensitive than the positive area. We expected Lusitanian taxa and BoB populations to expand while boreal taxa and CS populations to contract their distributions in the studied area As fishing is affecting population spatial variability (Wang et al., 2020), we would expect inertia to increase with increasing fishing pressure

(Continues)

TABLE 1 (Continued)

Variable category	Index	Ecological hypothesis behind index selection	Expected response in the Celtic-Biscay Shelf
Taxon characteristic	Taxonomic class	Taxonomic classes share ecological and biological traits that can facilitate the capacity of the taxa to cope with climate change	We would expect Cephalopoda, characterized by a short-live cycle to shift in a greater proportion than the other class in response to climate change and fishing pressure. We also expected Bivalvia to shift at a rate not significant over the 20 years of the study period, the capacity of displacement of these taxa and their life cycles did not allowing them to rapid shift in distribution
	Population distribution zone	Taxa with a wider distribution zone within the Celtic-Biscay Shelf, experience a broader range of abiotic and biotic conditions and may be less sensitive to environmental changes	CS and BoB populations are expected to be more sensitive to climate change, especially taxa populations which reach the southern or northern boundaries of their distribution ranges. Leading edges are best at tracking climate change than trailing edges (Fredston-Hermann et al., 2020), we thus expected to record more distribution shifts of Lusitanian taxa We expected CS population to be more affected by fishing than BoB due to higher fishing pressure in the former area (ICES, 2022a, 2022b)
	Biogeographic guild	Taxa with expanded latitudinal ranges experience a broader range of biotic and abiotic conditions, and therefore have greater ecological resilience and may exhibit less shift in distribution than taxa with more restricted distribution	We would expect boreal and Lusitanian guilds to be more sensitive to environmental and anthropogenic changes than Atlantic guild due to their more limited distributions. We expected that boreal species would experience range contraction, with their trailing edge (and to the unknown extent their CG) shifting northward, while Lusitanian species would experience range expansion, with their leading edge (and possibly their CG) shifting northward. We expected Atlantic taxa, which are distributed over a wider area, to be less sensitive to environmental changes because they experience a broader range of abiotic and biotic conditions (Sunday et al., 2015). The leading and trailing edges of Atlantic taxa being outside the Celtic-Biscay Shelf, we expected to detect their distribution shift with the CG
	Vertical distribution guild	Vertical distribution guilds are differentially affected by environmental changes due to their ability to swim and shift their distribution (Roberts et al., 2020)	We expected taxa with a greater capacity to swim have faster range extensions than taxa with low mobility (Sunday et al., 2015) Indeed, we expected highly mobile taxa, such as pelagic, and demersal, to disperse and extirpate in a higher proportion, and to larger distances than benthic swimmer and benthic species (Pinsky et al., 2020)
	Relative commercial importance	Fishing is known to affect exploited species' demography (e.g., population size, truncation in age structure) and life-history traits (e.g., increase in growth rates and decrease in age-at-maturity), as well as population spatial heterogeneity and distribution (Perry et al., 2010; Planque et al., 2010) which may affect the resilience of the taxa to cope with environmental increase in variability and change over time	We would expect taxa of greater commercial importance to be more sensitive to climate change than taxa of lesser commercial importance (Planque et al., 2010). We expected that climate and fishing pressure indices would be the main explanatory variables of their distribution shifts
Explanatory variable	Taxon abundance	Shift in taxa distribution may occur as a density-dependent response to changes in abundance within the range through time (MacCall, 1990). Besides, increased abundance may lead to lower population spatial variability, as a growing population typically expands from optimal habitats to suboptimal habitats to ease intraspecific competition (Wang et al., 2020).	Our hypothesis is that changes in taxa abundance through density-dependence can explain taxa shift in distribution (MacCall, 1990) in the three dimensions (latitude, longitude, and depth).

TABLE 1 (Continued)

Variable category	Index	Ecological hypothesis behind index selection	Expected response in the Celtic-Biscay Shelf
	Taxon fishing pressure	Shift in taxa distribution may occur as a response to fishing pressure which is known to directly or indirectly change the structure of the population by altering abundance and age structure, and by spatially constraining the population distribution (i.e., loss of population sub-units and contraction of the population) (Perry et al., 2010; Planque et al., 2010; Wang et al., 2020)	The Celtic-Biscay Shelf is one of the most exploited zones in Europe, we thus expected fishing pressure to explain a significant percentage of the distribution shifts. We expected fishing pressure to affect taxa distribution in latitude, longitude, and area (PA and I). We expected this variable to explain a great proportion of distribution shifts of taxa of greater commercial importance The combined effect of fishing and climate changes may have synergetic, dampened, or antagonist effects on populations and lead to unexpected responses (e.g., southward or eastward shifts)
	Bottom temperature anomalies	Shift in taxa distribution may occur as a change in environmental condition suitability	According to the geographical particularities of the Celtic-Biscay Shelf, we expected a decreasing percentage of climate indices explaining taxa distribution shifts from local to global. Indeed changes in species distributions have been observed to be more sensitive to local temperature than global climate scale indices (Collie et al., 2008; Engelhard et al., 2011).
	North Atlantic Oscillation (NAO)	Bottom temperature anomalies, North Atlantic Oscillation, and Atlantic	Local climate particularities may significantly influence the direction and shape of taxa distribution shifts (Rubenstein et al., 2023). We thus expected regional bottom temperature anomalies to have a great capacity to explain taxa shift in distribution followed by North Atlantic Oscillation, a good proxy for the degree of interannual ecological variability at a North Atlantic scale (Hurrell, 1995), and Atlantic Multidecadal Oscillation, which measures climate variability at the Atlantic scale and over a long time scale
	Atlantic Multidecadal Oscillation (AMO)	Multidecadal Oscillation are climate indices that expressed climate change and variability at local, regional, and global scales, respectively	

Note: The expected responses of the explanatory variables are related to the two main hypotheses tested in our study to explain the causes of taxa distribution shifts: (1) modifications in habitat suitability (e.g., increase in seawater temperatures) and/or (2) variation in population size due to density-dependent processes and fishing exploitation (Baudron et al., 2020; Mclean et al., 2018, 2019; Méritellet et al., 2020; Nye et al., 2009; Wang et al., 2020).

fit (a model adapted to serial correlations inherent to time series; Zuur et al., 2009). *p*-values were adjusted with Benjamini–Hochberg correction for multiple tests (Benjamini & Hochberg, 1995). For each model, we extracted the corrected *p*-value and the slope coefficient as model results. We used chi-squared tests to explore whether spatial distribution patterns differed among taxon characteristics (distribution zone, taxonomic class, biogeographic guild, vertical distribution guild, and relative commercial importance).

Then, we performed a Hill–Smith analysis (Hill & Smith, 1976) on the log (*x*+1) transformed slope coefficients of all the spatial indices of taxa for which at least one spatial index was significant ( $\alpha \leq 0.05$ ) to summarize distribution shifts and identify common patterns. We ran a clustering analysis (with the *k*-means method applied to Euclidean distances) on the individual coordinates extracted from the Hill–Smith analysis to sort taxa with similar shifts in distribution patterns. We determined cluster number employing the Elbow method (Syakur et al., 2018).

## 2.5 | Factors influencing distribution shifts

When a taxon's spatial index differed significantly over time ( $\alpha \leq 0.05$ ), we examined the relationship of the pattern with taxon abundance, fishing pressure, and three indices of climate change. We summarized the ecological hypotheses behind the factors influencing

taxa distribution shifts and the expected responses of taxa within the studied area in Table 1.

We used a regional short-term climate index which expressed bottom temperature anomalies (BT\_ano), and two global long-term climate indices, the North Atlantic Oscillation (NAO) index and the Atlantic Multidecadal Oscillation (AMO) index. More specifically, BT\_ano expresses the relationship between annual differences in bottom temperatures and the mean bottom temperature over the survey period and distribution zones (CS, BoB, and CBS). The monthly aggregated bottom temperatures were provided by the Atlantic Margin Model FOAM (Forecasting Ocean Assimilation Model). The data had a horizontal resolution of 7 km ( $0.111 \times 0.067^\circ$ ) and covered the period from 1997 to 2020 (Tonani & Ascione, 2021). In accordance with a preliminary exploration of spatiotemporal heterogeneity in BT\_ano across the distribution zones (Figure S2), we calculated the annual BT\_ano for each distribution zone (CBS, CS, and BoB; Figure S3 and Table S1) using the following equation:

$$BT\_ano_{zone_i, year_j} = \frac{T_{zone_i, year_j} - \text{mean } T_{zone \text{ all years}}}{sd T_{zone \text{ all years}}} \quad (4)$$

The NAO index is defined as the pressure difference between the Azores High and the Icelandic Low. We used the mean annual winter NAO index values (December of the previous year to March of the focal year; NOAA, 2021a; Figure S3). It is a good proxy for the degree of interannual ecological variability (Hurrell, 1995), which

integrates different climatic factors, such as wind speed, wind direction, air temperature, and precipitation (Stenseth & Mysterud, 2005).

The AMO index quantifies long-term temperature cycles (with a period of ~70 years) based on the detrended Kaplan SST dataset ( $5 \times 5^\circ$  grid) from 0 to  $70^\circ$  N (Nye et al., 2009; Sutton & Hodson, 2005). It is affected by thermohaline circulation and indicates the degree of natural temperature variation once anthropogenic impacts have been removed (Nye et al., 2009; Sutton & Hodson, 2005). We used the mean annual AMO index values (NOAA, 2021b; Figure S3).

A relative abundance index (hereafter referred to as abundance) was used as a descriptor of population status (Hutchings & Baum, 2005). To account for the randomly stratified sampling design, we calculated taxon relative abundance index as the number of individuals of a given taxon elevated to the surface area (in square nautical miles) of the CS, BoB, or CBS depending on the delineation of the populations within the distribution zones (Table S1; Mahé & Poulard, 2005).

To quantify fishing pressure, we estimated a harvest rate as the ratio between nominal catches (ICES, 2011, 2021) and the biomass estimated during EVHOE (within the CS, BoB, and CBS). We decided against using fishing mortality (e.g., ICES analytical assessment) as a proxy for fishing pressure because both analytical stock assessments are lacking for most of the studied taxa and EVHOE's survey area did not entirely match up with ICES fish stock delineations.

For each taxon, we explored the relationship between the spatial index and the above explanatory variables (taxon abundance, fishing pressure, BT\_ano, winter\_NAO, and annual\_AMO) using generalized linear regression (Gaussian distribution with identity link function; Zuur et al., 2009). In these analyses, we employed the regional climate index for the appropriate distribution zone (BT\_ano\_CBS, BT\_ano\_CS, or BT\_ano\_BoB), and we included fishing pressure only in the models for taxa of greater commercial importance (Table S1). Explanatory variables were standardized, and years with missing data were omitted. In each model, all the possible combinations of explanatory variables were included (Table S2). We examined the multicollinearity between explanatory variables using the variance inflation factor (Zuur et al., 2010). Since multicollinearity was absent or weak ( $VIF < 4$ ), all the explanatory variables were retained in the models.

To assess whether the explanatory variables affected taxa distribution shift, we evaluated the relative importance of each explanatory variable and we determined the variables' estimates and their 80% confidence intervals (Galipaud et al., 2014; Mariton et al., 2022). The relative importance (i.e., the cumulative AICc weight) of each explanatory variable was calculated by summing Akaike weights across all models that included the explanatory variable (Table S2; Arnold, 2010; Burnham & Anderson, 2002). The variables' estimates and 80% confidence intervals were obtained by computing the average model using all the models (Arnold, 2010). According to Mariton et al. (2022), an explanatory variable should be considered to have an effect when the 80% confidence interval of its estimates does not include zero and its relative importance is above 0.5.

### 3 | RESULTS

Our study focused on 93 taxa in total: 65 Actinopteri, 10 Elasmobranchii, 11 Cephalopoda, 5 Malacostraca, and 2 Bivalvia. Most were demersal or benthic swimmers (48% and 33%, respectively) and pelagic and benthic taxa were represented to a lesser extent (11% and 8%, respectively; Figure 2 and Table S1). There was an important representation of the Lusitanian guild (62%), while the boreal and Atlantic guilds were present in lesser, equal percentages (18%; Figure 2 and Table S1). Two-thirds of the taxa were of greater commercial importance (Figure 2 and Table S1). There were 83 taxa with continuous populations within a single distribution zone (62 taxa in the CBS, 7 in the CS, and 14 in the BoB), and 10 taxa occurred in two distinct populations (Figure 2 and Table S1). Thus, we analyzed distribution shifts for 103 populations ( $83 + 20$  [i.e.,  $10 \times 2$ ]; Table S1).

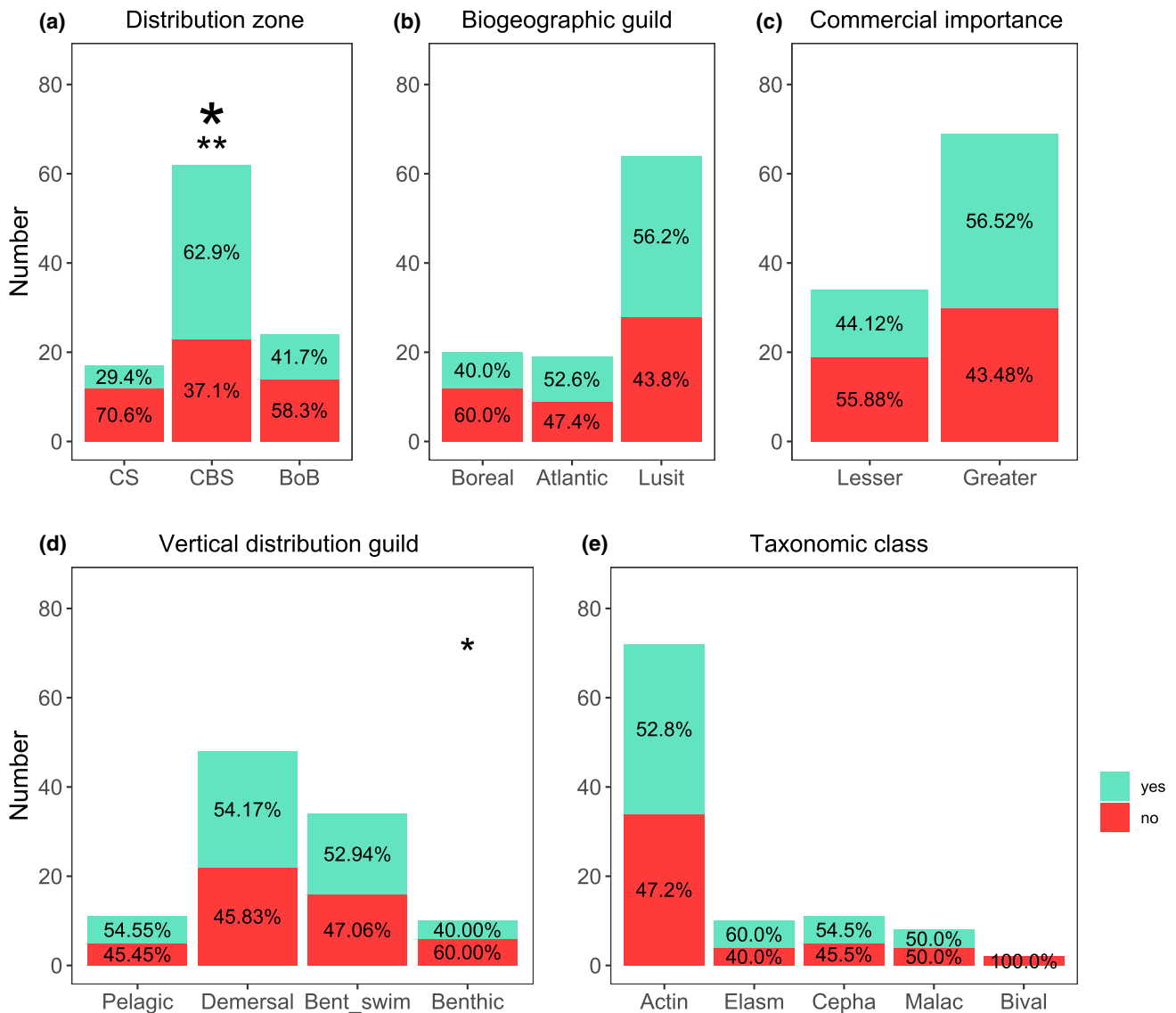
#### 3.1 | Distribution shifts

We observed that, between 1997 and 2020, 56% of the taxa (46% of the taxa's population) displayed at least one significant distribution shift. The proportions of shifting and non-shifting taxa differed significantly among the distribution zones, such that populations along the CBS shifted more commonly (Figure 2a and Table S3a) than the CS and BoB populations. Taking a closer look by the spatial index, we noted differences in the shifting proportions between the distribution zone and vertical distribution guild (Figure 2 and Table S3b,c): a greater percentage of the CBS populations shifted their upper depth limits (depth\_q 0.95 mainly upward; Figure 2a and Table S3b,c) and their PA (mainly expanding); and a greater percentage of the benthic taxa shifted their southern limits (lat\_q 0.05; Figure 2d and Table S3b,c).

The mean rate of CG shift was  $55.8 \pm 21.4 \text{ km.decade}^{-1}$ . At the community level, the mean shift of lat\_CG was northward  $13 \pm 67 \text{ km.decade}^{-1}$  (q0.05:  $-102 \pm 149 \text{ km.decade}^{-1}$  and q0.95:  $28 \pm 19 \text{ km.decade}^{-1}$ ), long\_CG was eastward  $32 \pm 39 \text{ km.decade}^{-1}$  (q0.05:  $-20 \pm 44 \text{ km.decade}^{-1}$  and q0.95:  $136 \pm 24 \text{ km.decade}^{-1}$ ), and depth\_CG was upward  $16.5 \text{ m.decade}^{-1}$  (q0.05:  $-2.4 \pm 47 \text{ m.decade}^{-1}$  and q0.95:  $1.9 \pm 39 \text{ m.decade}^{-1}$ ) with an expansion of taxa distribution areas (I mean:  $3.7 \pm 4.9 \text{ km}^2 \text{.decade}^{-1}$  and PA mean:  $11149 \pm 15,413 \text{ km}^2 \text{.decade}^{-1}$ ), resulting in expansion of the latitude, longitude, and depth limits (Table S4).

Taxa shifted northward at a mean rate of  $65 \text{ km.decade}^{-1}$  (range:  $14\text{--}156 \text{ km.decade}^{-1}$ ; Table S4), and the northernmost shifts were observed in benthic swimmer and benthic taxa (surmullet\_CBS, munitida\_CS, and lesser weever\_BoB; Figure 3a). Southward shifts took place at a mean rate of  $-89 \text{ km.decade}^{-1}$  (range:  $-333\text{--}-22 \text{ km.decade}^{-1}$ ; Table S4), and the southernmost shifts were seen in demersal, pelagic, and lesser commercial taxa (maurolicus\_CBS, greater argentine\_CBS, and hollowsnout grenadier\_CBS; Figure 3a). The same number of taxa populations shifted northward and southward

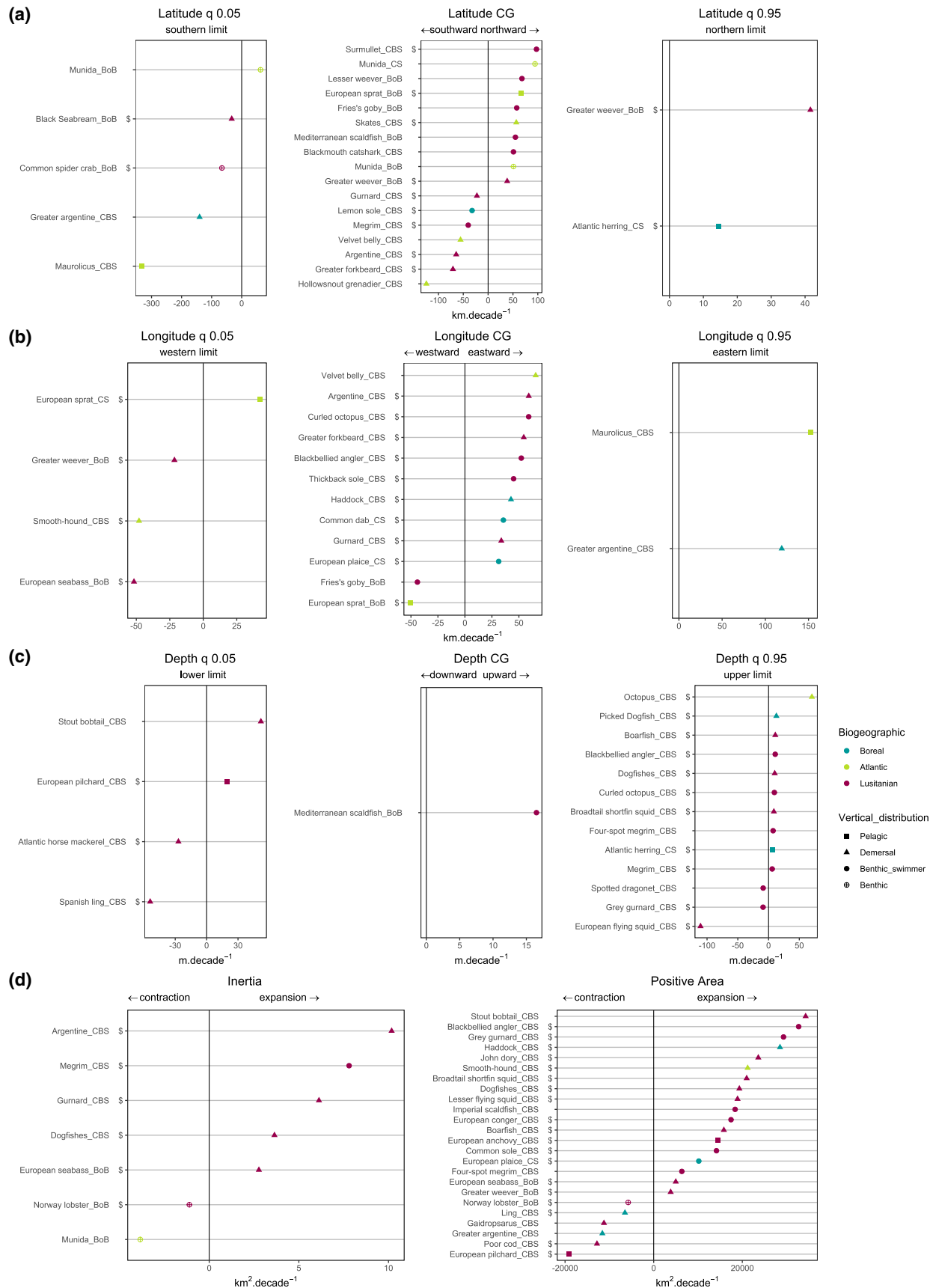




**FIGURE 2** Number of taxa and their proportion of significant (green) and non-significant (red) distribution shifts by taxon characteristics: (a) distribution zone, (b) biogeographic guild, (c) relative commercial importance, (d) vertical distribution guild, and (e) taxonomic class. Significant differences in the percentage of taxa displaying distribution shifts ( $\alpha \leq 0.05$ ) are indicated by a star on the guild demonstrating the greatest difference. Large and small stars indicate the results by taxon characteristics and spatial indices, respectively (chi-squared analysis; [Table S3](#)). Actin, Actinopteri; and Bival, Bivalvia; Bent\_swim, Benthic swimmer; BoB, Bay of Biscay; CBS, Celtic-Biscay Shelf; Cepha, Cephalopoda; CS, Celtic Sea; Elasm, Elasmobranchii; Greater, taxon of greater commercial importance; Lesser, taxon of lesser commercial importance; Lusit, Lusitanian; Malac, Malacostraca.

([Table 2](#)). Eastward shifts were undergone at a mean rate of  $61 \text{ km} \cdot \text{decade}^{-1}$  (range:  $31\text{--}152 \text{ km} \cdot \text{decade}^{-1}$ ; [Table S4](#)), and the easternmost shifts were seen in demersal, pelagic, and lesser commercial taxa (maurolicus\_CBS, greater argentine\_CBS, and velvet belly\_CBS; [Figure 3b](#)). Taxa moved westward at a mean rate of  $-43 \text{ km} \cdot \text{decade}^{-1}$  (range:  $-52 - -21 \text{ km} \cdot \text{decade}^{-1}$ ; [Table S4](#)), and the westernmost shifts were observed in demersal, pelagic, and greater commercial taxa (European seabass\_BoB, European sprat\_BoB, and smoothhound\_CBS; [Figure 3b](#)). More taxa shifted eastward than westward. In general, deepening shifts were greater (mean:  $-42 \text{ m} \cdot \text{decade}^{-1}$ ; range:  $-111 - -9 \text{ m} \cdot \text{decade}^{-1}$ ; [Table S4](#)) than did upward shifts

(mean:  $19 \text{ m} \cdot \text{decade}^{-1}$ , range:  $6\text{--}70 \text{ m} \cdot \text{decade}^{-1}$ ; [Figure 3c](#); [Table S4](#)). Only one taxon shifted in depth\_CG, the Mediterranean scaldfish, which shifted upward at a rate of  $16.5 \text{ m} \cdot \text{decade}^{-1}$ . Extreme shifts in depth were mainly seen in demersal and Lusitanian taxa (European flying squid\_CBS, Spanish ling\_CBS, octopus\_CBS, and stout bobtail\_CBS; [Figure 3c](#)). Taxa expanded their distributions at a mean rate of  $6.1 \text{ km}^2 \cdot \text{decade}^{-1}$  (I; range:  $2.7\text{--}10 \text{ km}^2 \cdot \text{decade}^{-1}$ ; [Table S4](#)) and  $18,584 \text{ km}^2 \cdot \text{decade}^{-1}$  (PA; range:  $3832\text{--}34,288 \text{ km}^2 \cdot \text{decade}^{-1}$ ; [Table S4](#)). Contractions occurred at a rate of  $-2.5 \text{ km}^2 \cdot \text{decade}^{-1}$  (I; range:  $-1.1\text{--}-3.8 \text{ km}^2 \cdot \text{decade}^{-1}$ ; [Table S4](#)) and  $-12,493 \text{ km}^2 \cdot \text{decade}^{-1}$  (PA; range:  $-19,104 - -6485 \text{ km}^2 \cdot \text{decade}^{-1}$ ; [Table S4](#)). Extreme



**FIGURE 3** Patterns of significant distribution shifts in: (a) latitude and (b) longitude (0.05 quantile, CG, and 0.95 quantile;  $\text{km}\cdot\text{decade}^{-1}$ ); (c) depth (0.05 quantile, CG, and 0.95 quantile;  $\text{m}\cdot\text{decade}^{-1}$ ); (d) inertia and positive area ( $\text{km}^2\cdot\text{decade}^{-1}$ ). Indicated for each taxon are biogeographic guild (blue: boreal, green: Atlantic, and purple: Lusitanian); vertical distribution guild (square: pelagic, triangle: demersal, filled circle: benthic swimmer, and unfilled circle: benthic); distribution zone (CS, CBS, and BoB) (Table S1); and relative commercial importance ( $\text{\$}$ : greater commercial importance; Table S1).

TABLE 2 Summary of taxon characteristics, cluster membership (Figure 3), and significant shifts in the center of gravity (CG), depth, inertia (I), and positive area (PA) between 1997 and 2020.

Common name	Scientific name	Taxonomic class	Vertical guild	Biogeographic guild	Commercial importance	Distribution zone	Cluster	CG	Depth	I	PA
Argentine	<i>Argentina sphyraena</i>	Actinopteri	Demersal	Lusitanian	Greater	CBS	2	↘			+
Atlantic herring	<i>Clupea harengus</i>	Actinopteri	Pelagic	Boreal	Greater	CS	4	↑	↑		
Atlantic horse mackerel	<i>Trachurus trachurus</i>	Actinopteri	Demersal	Lusitanian	Greater	CBS	2		↓		
Black Seabream	<i>Spondyliosoma cantharus</i>	Actinopteri	Demersal	Lusitanian	Greater	BoB	4	↓			
Blackbellied angler	<i>Lophius budegassa</i>	Actinopteri	Benthic swimmer	Lusitanian	Greater	CBS	2	→	↑		+
Blackmouth catshark	<i>Galeus melastomus</i>	Elasmobranchii	Benthic swimmer	Lusitanian	Lesser	CBS	3	↑			
Boarfish	<i>Capros aper</i>	Actinopteri	Demersal	Lusitanian	Greater	CBS	2	↑			+
Broadtail shortfin squid	<i>Illex coindetii</i>	Cephalopoda	Demersal	Lusitanian	Greater	CBS	2	↑			+
Common dab	<i>Limanda limanda</i>	Actinopteri	Benthic swimmer	Boreal	Greater	CS	4	→			
Common sole	<i>Solea solea</i>	Actinopteri	Benthic swimmer	Lusitanian	Greater	CBS	2				+
Common spider crab	<i>Maja brachydactyla</i>	Malacostraca	Benthic	Lusitanian	Greater	BoB	4	↓			
Curled octopus	<i>Eledone cirrhosa</i>	Cephalopoda	Benthic swimmer	Lusitanian	Greater	CBS	2	→	↑		
Dogfishes	<i>Scyliorhinus</i> spp.	Elasmobranchii	Demersal	Lusitanian	Greater	CBS	2		↑		+
European anchovy	<i>Engraulis encrasicollis</i>	Actinopteri	Pelagic	Lusitanian	Greater	CBS	3				+
European conger	<i>Conger conger</i>	Actinopteri	Benthic swimmer	Lusitanian	Greater	CBS	2				+
European flying squid	<i>Todarodes sagittatus</i>	Cephalopoda	Demersal	Lusitanian	Greater	CBS	1		↓		
European pilchard	<i>Sardina pilchardus</i>	Actinopteri	Pelagic	Lusitanian	Greater	CBS	4		↑		-
European plaice	<i>Pleuronectes platessa</i>	Actinopteri	Benthic swimmer	Boreal	Greater	CS	4	→			+
European seabass	<i>Dicentrarchus labrax</i>	Actinopteri	Demersal	Lusitanian	Greater	BoB	3	←			+
European sprat	<i>Sprattus sprattus</i>	Actinopteri	Pelagic	Atlantic	Greater	CS	4	→			
European sprat	<i>Sprattus sprattus</i>	Actinopteri	Pelagic	Atlantic	Greater	BoB	3	↘			
Four-spot megrim	<i>Lepidorhombus boschii</i>	Actinopteri	Benthic swimmer	Lusitanian	Lesser	CBS	2		↑		+
Fries's goby	<i>Lesueurigobius friesii</i>	Actinopteri	Benthic swimmer	Lusitanian	Lesser	BoB	4	↘			
Gaidropsarus	<i>Gaidropsarus</i> spp.	Actinopteri	Demersal	Lusitanian	Lesser	CBS	4				-
Greater argentine	<i>Argentina silus</i>	Actinopteri	Demersal	Boreal	Lesser	CBS	1	↘			-
Greater forkbeard	<i>Phycis blennoides</i>	Actinopteri	Demersal	Lusitanian	Greater	CBS	2	↘			
Greater weever	<i>Trachinus draco</i>	Actinopteri	Demersal	Lusitanian	Greater	BoB	3	↘			+
Grey gurnard	<i>Eutriga gurnardus</i>	Actinopteri	Benthic swimmer	Lusitanian	Greater	CBS	4		↓		+
Gurnard	<i>Chelidonichthys</i> spp.	Actinopteri	Demersal	Lusitanian	Greater	CBS	2	↘			+
Haddock	<i>Melanogrammus aeglefinus</i>	Actinopteri	Demersal	Boreal	Greater	CBS	2	→			+
Hollowsnout grenadier	<i>Caelorinchus caelorhincus</i>	Actinopteri	Demersal	Atlantic	Lesser	CBS	1	↓			
Imperial scaldfish	<i>Arnoglossus imperialis</i>	Actinopteri	Benthic swimmer	Lusitanian	Lesser	CBS	3				+

(Continues)

TABLE 2 (Continued)

Common name	Scientific name	Taxonomic class	Vertical guild	Biogeographic guild	Commercial importance	Distribution zone	Cluster	CG	Depth	I	PA
John dory	<i>Zeus faber</i>	Actinopteri	Demersal	Lusitanian	Greater	CBS	2				+
Lemon sole	<i>Microstomus kitt</i>	Actinopteri	Benthic swimmer	Boreal	Greater	CBS	2	↓			
Lesser flying squid	<i>Todaropsis eblanae</i>	Cephalopoda	Demersal	Lusitanian	Greater	CBS	2				+
Lesser weever	<i>Echiichthys vipera</i>	Actinopteri	Benthic swimmer	Lusitanian	Lesser	BoB	3	↑			
Ling	<i>Molva molva</i>	Actinopteri	Demersal	Boreal	Greater	CBS	4				-
Maurilicus	<i>Maurilicus</i> spp.	Actinopteri	Pelagic	Atlantic	Lesser	CBS	1	↘			
Mediterranean scaldfish	<i>Arnoglossus laterna</i>	Actinopteri	Benthic swimmer	Lusitanian	Lesser	BoB	4	↑			
Megrim	<i>Lepidorhombus whiffiagonis</i>	Actinopteri	Benthic swimmer	Lusitanian	Greater	CBS	2	↓	↑		+
Munida	<i>Munida</i> spp.	Malacostraca	Benthic	Atlantic	Lesser	CS	3	↑			
Munida	<i>Munida</i> spp.	Malacostraca	Benthic	Atlantic	Lesser	BoB	4	↑			-
Norway lobster	<i>Nephrops norvegicus</i>	Malacostraca	Benthic	Lusitanian	Greater	BoB	4				-
Octopus	<i>Octopus</i> spp.	Cephalopoda	Demersal	Atlantic	Greater	CBS	3		↑		
Picked Dogfish	<i>Squalus acanthias</i>	Elasmobranchii	Demersal	Boreal	Greater	CBS	4		↑		
Poor cod	<i>Trisopterus minutus</i>	Actinopteri	Demersal	Lusitanian	Greater	CBS	4				-
Skates	<i>Raja</i> spp.	Elasmobranchii	Demersal	Atlantic	Greater	CBS	3	↑			
Smooth-hound	<i>Mustelus</i> spp.	Elasmobranchii	Demersal	Atlantic	Greater	CBS	3	←			+
Spanish ling	<i>Molva macrophthalma</i>	Actinopteri	Demersal	Lusitanian	Greater	CBS	1		↓		
Spotted dragonet	<i>Callionymus maculatus</i>	Actinopteri	Benthic swimmer	Lusitanian	Lesser	CBS	2		↓		
Stout bobtail	<i>Rossia macrosoma</i>	Cephalopoda	Demersal	Lusitanian	Lesser	CBS	3		↑		+
Surmullet	<i>Mullus surmuletus</i>	Actinopteri	Benthic swimmer	Lusitanian	Greater	CBS	3	↑			
Thickback sole	<i>Microchirus variegatus</i>	Actinopteri	Benthic swimmer	Lusitanian	Greater	CBS	4	→			
Velvet belly	<i>Etmopterus spinax</i>	Elasmobranchii	Demersal	Atlantic	Lesser	CBS	2	↘			

Note: Distribution zone of taxa's populations: Celtic Sea (CS), Celtic-Biscay Shelf (CBS), and Bay of Biscay (BoB). The arrows indicate shift direction: CG, ↑ Northward, ↗ North-eastward, → Eastward, ↘ South-eastward, ↓ Southward, ↙ South-westward, ← Westward, and ↖ North-westward; depth, ↑ upward and ↓ downward. The plus sign (+) indicates range expansion, and the minus sign (-) indicates range contraction. Taxa are listed in alphabetical order (Common name) and according to their distribution zone along the north-south gradient. The summarized shifting direction of CG and depth combined the significant results of 0.05 and 0.95 quantiles and CG, respectively.

expansions were observed for Lusitanian, demersal, and benthic swimmer taxa (stout bobtail\_CBS, blackbellied angler\_CBS, argentine\_CBS, and megrim\_CBS; Figure 3d), and extreme contractions were mainly observed for Lusitanian, Atlantic and greater commercial taxa (European pilchard\_CBS, poor cod\_CBS, munida\_BoB, and Norway lobster\_BoB; Figure 3d).

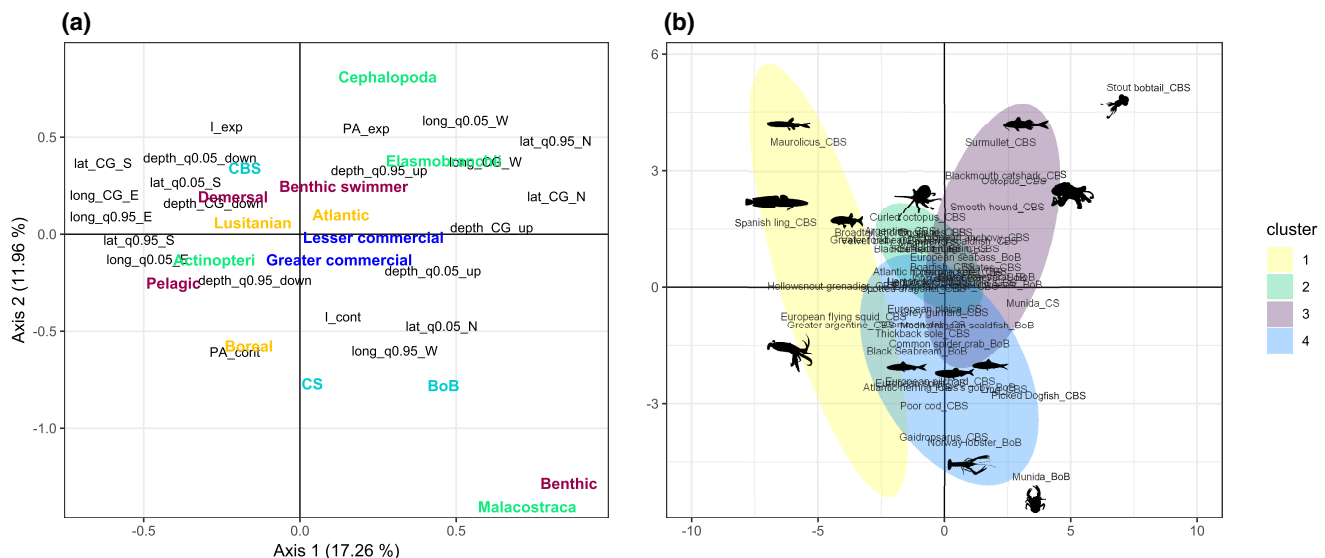
The first and second axes of the Hill–Smith accounted for 17.26% and 11.96% of the variability in distribution range shifts, respectively, resulting in 29% of the variance explained. The first axis distinguished two opposite patterns between (1) shifts southward, eastward, and into deeper waters, mostly seen in boreal, pelagic, and demersal taxa, Actinopteri, and populations along the CBS, and (2) shifts northward, westward, and into shallower waters, mostly seen in Atlantic and benthic taxa, Malacostraca, Cephalopoda, Elasmobranchii, taxa of lesser commercial importance, and populations in the BoB (Figure 4a). The second axis distinguished between population distribution contraction (seen in boreal and benthic taxa, Malacostraca, and populations in the CS and BoB) and expansion (seen in benthic swimmer and demersal taxa, Cephalopoda, Elasmobranchii, and populations along the CBS; reflected in both the PA and I; Figure 4a). The cluster analysis identified four clusters of species. Cluster 1 comprised mostly Actinopteri, demersal taxa, and CBS populations that were moving southward, eastward, and into deeper waters (Figure 4). Emblematic taxa in this cluster included maurolicus, spanish ling, and European flying squid (Figure 4b and Table 2). Cluster 4 included benthic taxa, Malacostraca, Actinopteri, taxa of greater commercial importance, and populations in the CS and BoB that were moving northward and westward and that were contracting their I and PA (Figure 4). Emblematic taxa in this cluster included Norway lobster, munida; and the pelagic European pilchard,

European sprat, and Atlantic herring (Figure 4b and Table 2). Cluster 3 included Cephalopoda, Elasmobranchii, and benthic swimmer taxa that were moving northward and westward and that were expanding their PA (Figure 4). Emblematic taxa included octopus, stout bobtail, and surmullet (Figure 4b and Table 2). Cluster 2 comprised the taxa displaying less pronounced shifts (centered in Figure 4): benthic swimmer taxa, taxa of greater commercial importance, and populations along the CBS that were expanding their distribution range (reflected in both PA and I; Figure 4) with curled octopus and argentine as emblematic taxa (Figure 4b and Table 2).

### 3.2 | Influence of global changes on distribution shifts

The results below are reported according to relative commercial importance as fishing pressure was only included in the models for taxa of greater commercial importance. Besides, the results of BT\_ano were expressed via a single index while the distribution zone-specific indices were included in the models (BT\_ano\_CBS, BT\_ano\_CS, and BT\_ano\_BoB).

A third of the significant distribution shifts could be explained by global changes (i.e., climate change and/or fishing pressure) and/or by taxonomic abundance. For taxa of greater commercial importance, climate indices were the main explanatory variable (38%; mainly winter\_NAO), followed by abundance (33%) and fishing pressure (29%) (Table 3). Shifts in latitude were exclusively explained by fishing pressure, while shifts in longitude were explained by all the variables (Table 3). Fishing pressure explained the taxa's eastward shifts in CG. BT\_ano, winter\_NAO, and taxon



**FIGURE 4** (a) Factorial map of Hill–Smith analysis looking at significant distribution shifts ( $\log [x + 1]$  transformed significant slope coefficients [ $p \leq .05$ ]) according to taxon characteristics (distribution zone, biogeographic guild, relative commercial importance, vertical distribution guild, and taxonomic class). (b) The four patterns of taxon distribution shifts identified using k-means clustering based on Euclidean distance. The taxa most representative of each cluster are highlighted (representative images next to species common name).

**TABLE 3** Summary of the explanatory variables that significantly explained taxa shifting direction according to the relative commercial importance of the taxa. According to Mariton et al. (2022), an explanatory variable should be considered to have an effect when the 80% confidence interval (lower limit: CI0.2, upper limit: CI0.8) of its estimates does not include zero and its relative importance exceeds 0.5.

Commercial importance	Shift direction	Spatial index	Explanatory variable	Mean relative importance	Number of taxon populations	Estimates		
						Mean	CI0.2	CI0.8
Greater	Northward	lat_CG	Fishing pressure	0.7	1	0.1	NA	NA
	Southward	lat_CG	Fishing pressure	0.85	4	-0.15	-0.23	-0.08
	Eastward	long_q0.05	Abundance	0.53	1	0.1	NA	NA
	Eastward	long_q0.05	winter_NAO	0.61	1	0.14	NA	NA
	Eastward	long_q0.05	BT_ano	0.77	1	-0.19	NA	NA
	Eastward	long_CG	Fishing pressure	0.63	5	0.14	0.06	0.22
	Westward	long_CG	annual_AMO	0.64	1	0.17	NA	NA
	Westward	long_CG	Abundance	0.72	1	-0.22	NA	NA
	Upward	depth_q0.05	winter_NAO	0.85	1	5.75	NA	NA
	Upward	depth_q0.05	Abundance	0.98	1	9.07	NA	NA
	Upward	depth_q0.05	Fishing pressure	0.98	1	10.27	NA	NA
	Upward	depth_q0.95	winter_NAO	0.52	9	2.35	0.38	4.32
	Upward	depth_q0.95	Abundance	0.6	9	4.13	1.6	6.66
	Downward	depth_q0.05	Abundance	0.63	2	-8.66	-12.35	-4.97
	Downward	depth_q0.05	BT_ano	0.71	2	10.2	5.3	15.09
	Contraction	I	BT_ano	0.55	1	0.07	NA	NA
	Expansion	I	winter_NAO	0.5	5	0.16	0.12	0.21
	Expansion	I	Abundance	0.66	5	0.67	0.05	1.3
	Expansion	I	Fishing pressure	0.77	5	0.97	0.26	1.67
	Contraction	Pa	Fishing pressure	0.95	3	-1827.88	-3175.32	-480.45
	Expansion	Pa	Abundance	0.89	15	3474.74	2671.42	4278.05

TABLE 3 (Continued)

Commercial importance	Shift direction	Spatial index	Explanatory variable	Mean relative importance	Number of taxon populations	Estimates		
						Mean	CI 0.2	CI 0.8
Lesser	Northward	lat_q0.05	winter_NAO	0.58	1	0.11	NA	NA
	Southward	lat_q0.05	winter_NAO	0.51	2	-0.22	-0.23	-0.21
	Southward	lat_CG	Abundance	0.62	2	0.16	0.14	0.17
	Eastward	long_CG	Abundance	0.67	1	-0.23	NA	NA
	Eastward	long_CG	BT_ano	0.8	1	-0.33	NA	NA
	Eastward	long_q0.95	winter_NAO	0.5	2	0.22	0.09	0.35
	Upward	depth_q0.05	annual_AMO	0.53	1	-7.89	NA	NA
	Upward	depth_q0.05	Abundance	0.55	1	6.96	NA	NA
	Upward	depth_q0.05	winter_NAO	0.87	1	20.55	NA	NA
	Upward	depth_CG	Abundance	0.7	1	4.8	NA	NA
	Upward	depth_q0.95	winter_NAO	0.59	1	1.45	NA	NA
	Upward	depth_q0.95	BT_ano	0.68	1	-1.85	NA	NA
	Downward	depth_q0.95	Abundance	0.77	1	-3.25	NA	NA
	Downward	depth_q0.95	winter_NAO	0.91	1	-4.96	NA	NA
	Downward	depth_q0.95	BT_ano	0.93	1	5.39	NA	NA
	Contraction	I	winter_NAO	0.55	1	-0.17	NA	NA
	Contraction	PA	winter_NAO	0.62	2	-872.04	-1569.92	-174.16
	Contraction	PA	Abundance	0.89	2	2036.52	261.74	3811.29

Abbreviations: annual\_AMO, annual Atlantic Multidecadal Oscillation index; BT\_ano, annual bottom temperature anomalies; winter\_NAO, annual winter values of North Atlantic Oscillation index.

abundance were associated with the eastward shifts of western limits: the correlations were negative for BT\_ano and positive for winter\_NAO and taxon abundance (Table 3). Westward shifts of CG were negatively associated with taxon abundance and positively associated with annual\_AMO (Table 3). Upward shifts of both lower and upper depth limits were linked to taxon abundance and winter\_NAO, and also to fishing pressure in the case of the lower depth limits (Table 3). Downward shifts of lower depth limit were negatively correlated with taxon abundance and positively associated with BT\_ano (Table 3). Distribution range contraction (PA) was negatively tied to fishing pressure and positively (I) to BT\_ano. Distribution range expansion (PA and I) was correlated with fishing pressure, and with taxon abundance and winter\_NAO for I (Table 3).

For taxa of lesser commercial importance, distribution shifts were mainly explained by climate (67%) and taxon abundance (33%; Table 3). Among the climate indices, winter\_NAO and BT\_ano had the greatest explanatory ability (67% and 25%, respectively; Table 3). Northward shift of southern limits was positively explained by winter\_NAO (Table 3). Southward shifts of southern limits were negatively correlated with winter\_NAO and changes in CG were associated with taxon abundance (Table 3). Eastward shifts of eastern limits and CG were, respectively, positively correlated with winter\_NAO and negatively tied to taxon abundance and BT\_ano (Table 3). Upward shifts of lower depth limits were explained by taxon abundance and climate, where annual\_AMO had a negative influence and winter\_NAO had a positive influence (Table 3). Upward shift of depth\_CG was associated with taxon abundance. Upward shifts of upper depth limits were positively and negatively linked with winter\_NAO and BT\_ano, respectively (Table 3). Downward shift of upper depth limits were negatively explained by abundance and winter\_NAO and positively explained by BT\_ano (Table 3). Distribution range contraction (I and PA) was negatively correlated with winter\_NAO and positively correlated with taxon abundance (Table 3).

## 4 | DISCUSSION

This study is the first to analyze changes in the distributions of nearly 100 taxa representative of various functional traits such as thermal preference, vertical distribution, and commercial importance, in the context of rapidly warming temperatures (Costoya et al., 2015; Désaunay et al., 2006; Koutsikopoulos et al., 1998; Planque et al., 2003) and intense fishery exploitation.

It is generally expected that a significant proportion of marine species will experience distribution shifts in response to global changes. Here, we showed that 56% of the taxa shifted their distribution between 1997 and 2020 along the CBS. This shifting proportion is equivalent in magnitude to the one recorded for a demersal fish assemblage in the North Sea (58%; Perry et al., 2005) and substantially lower than the one seen in the Northeast Atlantic (72%; Simpson et al., 2011). These results are supported by Le Marchand

et al. (2020), who estimated that only 36% of species in the BoB would be unaffected by climate change, based on RCP 2.6 and RCP 8.5 projections for the periods 2041–2050 and 2091–2100; the thermal ranges of these 36% of species would likely persist in the BoB. Thus, our results join with previous works in nearby areas to underscore the sensitivity of Northeast Atlantic taxa to current and future changes in ecosystem conditions (Le Marchand et al., 2020; Perry et al., 2005; Simpson et al., 2011). We also showed that populations experienced these distribution shifts over a relatively short period (23 years) and at a relatively fast rate. We estimated that CG were shifting at a mean rate of  $55.8 \pm 21.4 \text{ km.decade}^{-1}$ , which is comparable to the rates calculated by Poloczanska et al. (2013) and by Lenoir et al. (2020) in their meta-analyses examining multiple marine species ( $54.6 \pm 11.7 \text{ km.decade}^{-1}$  and  $59.2 \pm 9.4 \text{ km.decade}^{-1}$ , respectively). We showed that in the CBS, contrary to our expectations, a greater percentage of the significant distribution shifts was recorded at the integrated scale of the CG and not at the latitude and longitude limits as expected (Fredston-Hermann et al., 2020). This finding could be related to the fact that the latitudinal limits of most of the species are outside of the survey area (Whitehead et al., 1984–86) and that the longitudinal limits are constrained by the continental slope on one side (Le Boyer et al., 2013) and the land on the other side.

Shifts in distributions were partially in line with our theoretical expectations on taxa characteristics and were mostly seen in highly mobile (pelagic) taxa, such as the Cephalopoda and Elasmobranchii, as well as in taxa distributed over a broad latitudinal range (CBS distribution zone) with greater commercial importance. In contrast, shifts were minimal for Bivalvia and Malacostraca, which are less prone to displacement. These findings emphasize that species mobility and the availability of certain environmental conditions are key factors in driving species responses to global changes (Perry et al., 2005; Pinsky et al., 2020; Sunday et al., 2015). Larval dispersal capacity, niche boundaries, and the ability to handle new biological interactions (e.g., changes in predation and competition dynamics) should also be considered carefully to appreciate species ability to extricate itself from its current habitat and colonize new areas (Doney et al., 2012). Although the differences are not statistically significant, our results tend to show an exacerbation of the climatic sensitivity of commercially exploited taxa, with the percentage of shifting being greater for taxa of greater commercial importance than for taxa of lesser commercial taxa (56% and 44%, respectively; Hsieh et al., 2008; Rijnsdorp et al., 2009; Hermant et al., 2010; Poloczanska et al., 2016). Contrary to our expectation, there was no clear difference in the impact of fishing between the CS and BoB distribution zones, while the fishing pressure in the CS was greater than that in the BoB (ICES, 2022a, 2022b).

Climate change should predominantly cause a northward and deepening shift of the species living in the temperate waters of the Northern Hemisphere (Poloczanska et al., 2016; Rubenstein et al., 2023). Our results did not fully support this expectation. Although mean latitudinal shift of CG and northern limit were northward, the same number of species were observed shifting northward



and southward. At the taxonomic level, several commercially important pelagic species have yet implemented northward shift; including the European sprat (BoB) and Atlantic herring (CS) which belong to Atlantic and boreal guilds, respectively. Numerous studies have also shown that a variety of species, have not demonstrated the expected northward shifts, or have even displayed counterintuitive shifts (e.g., equatorial shifts; Rubenstein et al., 2023). Two examples of the latter occurred in our study: the boreal lemon sole, which has shifted southward, and the Lusitanian poor cod, which has experienced distribution area contraction. Both depth limits were better at tracking taxa depth shifts than depth<sub>CG</sub> (Fredston-Hermann et al., 2020), and the CBS and CS populations showed deepening pattern but not BoB populations. The non-ubiquitous deepening of taxa facing climate change was previously demonstrated (Chaikin & Belmaker, 2023), revealing the complexity of species distribution shifts in the context of global changes.

The CBS is a particularly useful study system for exploring distribution shifts as it hosts both cold-affiliated boreal species and warm-affiliated Lusitanian species that reach the latitudinal limits of their distribution ranges. As would be expected from their biogeographic guilds, some Lusitanian and Atlantic taxa moved northward and/or westward (e.g., blackmouth catshark, greater weever, and European sprat) and Lusitanian taxa also mainly experienced distribution range expansion (e.g., European seabass, John dory, blackbellied angler, and broadtail shortfin squid). In the same vein, boreal taxa moved mainly eastward (e.g., common dab, European plaice, and haddock), and some experienced distribution range contraction (e.g., greater argentine and ling). Most intriguing, we observed southward shifts in the boreal guild (e.g., greater argentine and lemon sole) and distribution range contractions in Atlantic (munida) and Lusitanian (Norway lobster, European pilchard, and poor cod) taxa, which is opposite to what might be expected for these guilds in response to climate changes. According to our expectations, distribution shifts of Atlantic taxa were mainly detected by the CG index. However, boreal and Lusitanian distribution shifts were not mainly detected by shifts in their trailing and leading edge, respectively.

At the community scale, although the idiosyncrasy of taxa distribution shifts results in a low percentage of variability explained by the Hill–Smith analysis, two main opposite spatial displacement patterns arose from the multidimensional analysis. First, there were shifts northward, westward, and vertically upward by Atlantic, benthic taxa, Cephalopoda, Elasmobranchii, and Malacostraca, taxa of lesser commercial importance, and taxa with populations in the BoB. Second, there were shifts southward, eastward, and downward into deeper waters by boreal, pelagic, and demersal taxa, Actinopteri, and taxa with populations along the CBS. The association of northward and westward shifts on one side, and southward and eastward shifts, on the other side, results from the anisotropy of the CBS and associated bathymetry profile of the area (Koutsikopoulos & Le Cann, 1996). The directionality of distribution shifts is shaped by a complex combination of local or regional environmental (e.g., change in temperature and habitat fragmentation and loss) and biological (e.g., new prey or habitat competition) mechanisms (Rubenstein

et al., 2023). These dichotomic shifting patterns match with the results of regional analyses focusing on populations along the CBS (Baudron et al., 2020) and in the BoB (Le Marchand et al., 2020). Taken together, these discoveries emphasize the importance of regional analysis in clarifying and predicting fine-scale changes in taxon distribution patterns.

We then assessed how taxa shifting distributions were influenced over time by climate (via regional- and global-scale climate indices) and population dynamics (i.e., taxon abundance and fishing pressure intensity). The global and regional climate indices winter<sub>NAO</sub> and BT<sub>ano</sub> were the main explanatory variables explaining the shifts in taxa of both greater and lesser commercial importance, which highlights the dramatic influence of climate changes on taxa distribution. Along the CBS, BT<sub>ano</sub> follows a decreasing gradient from east to west, which could explain the negative relation between BT<sub>ano</sub> and eastward shifts. Westward shifts to colder areas or characterized by consistent temperatures have previously been observed in many species (Poloczanska et al., 2016) and frequently occur alongside downward shifts in depth (Dulvy et al., 2008; Perry et al., 2005). In our study area, the continental shelf has a particularly large size (Koutsikopoulos & Le Cann, 1996), which could explain why these westward shifts were not associated with downward shifts, and why southward and eastward shifts could be associated with deepening shifts. Furthermore, the border of the continental slope near the western border of the study area (400m isobath; Le Boyer et al., 2013) could also explain why there were proportionally fewer westward shifts than eastward shifts. Indeed, the habitats occupied by the studied taxa are no longer encountered after the continental slope. Thus, local and regional particularities (e.g., BT<sub>ano</sub> and habitat distributions) seem to significantly influence the direction and shape of distribution shifts (Rubenstein et al., 2023). Winter<sub>NAO</sub> is a global climate index that expresses interannual ecological variability (Hurrell, 1995). During the survey period, winter<sub>NAO</sub> was in a positive phase, which means strong wind circulation in the North Atlantic, and high atmospheric and sea temperatures in Western Europe (Ottersen et al., 2001). Winter<sub>NAO</sub> has complex impacts on species, which may result from direct changes in temperature and wind intensity (e.g., recruitment) or indirect changes cascading through the food chain (Drinkwater et al., 2003), which cannot be tested herein. Nevertheless, it remains a key index of climate change and its influence on taxon distribution patterns suggests a clear effect of the related changes in abiotic conditions on taxon's populations. This global climate index explained distribution shifts in a greater proportion than the regional BT<sub>ano</sub> for taxa of lesser commercial importance, and an equivalent proportion for taxa of greater commercial importance. This result suggests that taxa of greater commercial importance may have a greater sensitivity to a regional index than taxa of lesser commercial importance.

Taxon abundance was the second main explanatory variable affecting distribution changes in taxa of both greater and lesser commercial importance. Taxon abundance was positively correlated with distribution shifts, except for the downward and some longitudinal shifts, which suggests that the relationship was mainly positive

between taxon abundance and area occupancy. This finding has been noted in several other studies (e.g., Adams et al., 2018; Baudron et al., 2020 and in the MacCall, 1990 basin model). This density-dependent pattern of habitat occupation is illustrated by two populations that changed dramatically in taxon abundance and displayed a significant distribution shift: the European anchovy and the poor cod. The increase in abundance of the European anchovy population was combined with distribution range expansion, while the decrease in abundance of the poor cod population was combined with distribution range contraction. However, the density-dependent habitat occupation hypothesis should be applied with caution (Sheperd & Litvak, 2004). Indeed, while taxon abundance and distribution zone may covary in space and time, taxon abundance is modulated by both density-dependent and density-independent factors, such as the availability of food following a successful recruitment event (Anderson & Gregory, 2000; Fromentin et al., 2001; Sheperd & Litvak, 2004).

Fishing pressure was the third variable explaining distribution shifts for taxa of greater commercial importance. The correlation between distribution shifts and fishing pressure was mainly positive. This result suggests that fishing pressure substantially contributed to alterations in the spatial distribution of populations, as seen in the macro benthic-demersal CS community (Mérillet et al., 2020). The above patterns may be linked to the fact that, historically, the CBS has been intensively fished since the 1950s (Gascuel et al., 2016). Although the 2002 reform of the Common Fisheries Policy has reduced fishing-related mortality overall (Fernandes & Cook, 2013), our results indicate that fishing pressure remains a significant anthropogenic stressor in the area. Furthermore, we have yet to see apparent signs of recovery in biomass and ecosystem indicators (Gascuel et al., 2016). Additionally, reductions in mortality have not been homogeneous across the study area: fishing pressure was mainly localized in the eastern areas of both the CS and the BoB, and has climbed over the past 20 years in the western and northwestern parts of the CS, as well as in the eastern BoB (Eme et al., 2022). This spatial heterogeneity in fishing pressure might have led to the southward and eastward shifts of the taxa with a greater commercial importance in the CS and along the CBS. The influence of fishing on taxa can be direct by altering their population structure, demography, and life-history traits; and indirect by changing community dynamics, and food web structure and dynamics (e.g., removing long-lived species and reducing the mean trophic level; Hernvann et al., 2020; Perry et al., 2010; Planque et al., 2010).

Our models explained only 29% of the variation in distribution shifts, a result comparable to that found by Lenoir et al. (2020) (33%). Future research should therefore focus on characterizing and analyzing the effects of additional factors, such as the loss of essential habitat (e.g., nurseries), other changes in habitat quality (e.g., salinity or levels of chlorophyll A), species life-history traits (e.g., larval dispersal ability and reproduction potential), and, more importantly, the restructuring of biotic interactions, such as competition for food or predation by examining co-occurrence between predator and prey

(Selden et al., 2018). Such work is essential to improve our understanding of the ecosystem modifications occurring in the Northeast Atlantic (Eme et al., 2022; Rubenstein et al., 2023).

Our study is based on data collected during EVHOE surveys, whose standardized spatial and temporal sampling design and constant gear capturability enable the analysis of taxa distribution shifts over time. The aim of the survey is to monitor benthic-demersal fish and cephalopod populations (Laffargue et al., 2021a, 2021b) with a GOV bottom trawl specifically designed for the survey. Although it was not initially designed to sample pelagic taxa, they represent a significant percentage of the total catch weight (29% and 45% in the CS and the BoB, respectively; Laffargue et al., 2021a, 2021b), and the relative abundance indices derived from EVHOE surveys are used as tuning series in the stock assessment models of three pelagic taxa (veined squid, European squid, and Atlantic mackerel; Laffargue et al., 2021a, 2021b). Pelagic taxa included in this study are thus regularly caught which suggests a relatively good capturability for these taxa. Our results reflect the distribution of taxa sampled with a bottom trawl on sandy habitats during autumn (mainly in November), that is, just before the spawning period of the majority of the taxa at these latitudes. The same type of analysis should be performed with other sampling gears and methods (including eDNA) and over other periods of the year to increase the number of species assessed and improve our understanding of seasonal population dynamics.

Although global changes are causing widespread perturbations in the world's ecosystems, our research has underscored that we cannot ignore regional specificities, like fishing pressure and bottom temperature anomalies, as well as taxon-specific characteristics (e.g., degree of species mobility and thermal preference) when exploring population-level responses. Not all taxa will necessarily shift northward given the complex and unique mosaics of local climatic trajectories, habitat distributions, and anthropogenic pressures (Rubenstein et al., 2023). At present, many ecological management plans and policies (e.g., planning and management of protected areas or stock assessment management) continue to assume that ecosystems will stay at equilibrium over time (Pinsky et al., 2018). Understanding how organisms are dealing with climate change and anthropogenic pressures is the first step in developing successful management plans and policies for species and habitats alike, and this knowledge will be key in confronting future challenges and potential conflicts over resource and habitat use at ecosystem interfaces (Pinsky et al., 2018; Rubenstein et al., 2023).

## AUTHOR CONTRIBUTIONS

**Emilie Le Luherne:** Conceptualization; data curation; formal analysis; investigation; methodology; resources; software; validation; visualization; writing – original draft. **Lionel Pawlowski:** Conceptualization; funding acquisition; methodology; project administration; resources; supervision; writing – review and editing. **Marianne Robert:** Conceptualization; formal analysis; funding acquisition; investigation; methodology; project administration; resources; software; supervision; writing – review and editing.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in Dryad at <https://doi.org/10.5061/dryad.cc2fqz6fd>. These data were derived from the following resources available in the public domain: EVHOE survey data (<https://www.seanoe.org/data/O0688/80041/>); ICES mean catches in FAO divisions 27.7 g-h and 27.8 a-b (Eurostat/ICES compilation of catch data and statistics, ICES, 2011, 2021, Copenhagen); bottom temperatures were provided by the Atlantic Margin Model FOAM (<http://marine.copernicus.eu/>); NAO index values (<https://www.ncdc.noaa.gov/teleconnections/nao/>); and annual AMO index values (<https://psl.noaa.gov/data/timeseries/AMO/>).

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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