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Research article

Long-term changes in taxonomic and functional composition of European marine fish communities

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Evidence of large-scale biodiversity degradation in marine ecosystems has been reported worldwide, yet most research has focused on few species of interest or on limited spatiotemporal scales. Here we assessed the spatial and temporal changes in the taxonomic and functional composition of fish communities in European seas over the last 25 years (1994–2019). We then explored how these community changes were linked to environmental gradients and fishing pressure. We show that the spatial variation in fish species composition is more than two times higher than the temporal variation, with a marked spatial continuum in taxonomic composition and a more homogenous pattern in functional composition. The regions warming the fastest are experiencing an increasing dominance and total abundance of r-strategy fish species (lower age of maturity). Conversely, regions warming more slowly show an increasing dominance and total abundance of K-strategy species (high trophic level and late reproduction). Among the considered environmental variables, sea surface temperature, surface salinity and chlorophyll-a most consistently influenced communities' spatial patterns, while bottom temperature and oxygen had the most consistent influence on temporal patterns. Changes in communities' functional composition were more closely related to environmental conditions than taxonomic changes. Our study demonstrates the importance of integrating community-level species traits across multi-decadal scales

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and across a large region to better capture and understand ecosystem-wide responses and provides a different lens on community dynamics that could be used to support sustainable fisheries management.

Keywords: biodiversity, bottom trawl surveys, climate change, European seas, fisheries, trait-based approach

Introduction

Biodiversity is undergoing rapid and widespread changes (Barnosky et al. 2011, Ceballos et al. 2015, Finn et al. 2023), a phenomenon often referred to the '6th mass extinction' that is expected to increase in the coming decades (Molinos et al. 2016, Worm and Lotze 2016). Human activities, such as habitat degradation, pollution, and fishing are identified as key drivers of marine biodiversity loss (Diaz et al. 2019, Jaureguiberry et al. 2022). Further, climate change is leading to major shifts in species' spatial distributions and population abundances (Cheung et al. 2009, Pecl et al. 2017, Hillebrand et al. 2018, Edgar et al. 2023). Understanding the impact of changes at the community scale is necessary to estimate consequences on ecosystem functioning and essential to implement ecosystem-based management within fisheries management and marine conservation frameworks (Donovan et al. 2023). However, while the effects of short-term environmental variability and long-term climate change are widely studied for fish at the species level (Albouy et al. 2012, 2013, Maltby et al. 2020, Martins et al. 2021, Scales et al. 2023), these effects are less understood at the community scale (Biswas et al. 2017, Moullec et al. 2022).

Beyond species richness, metrics related to the functional structure (i.e. species traits) of communities are increasingly recognized to provide a better understanding of the potential impacts of environmental conditions and human activities on ecosystem functioning (Cadotte et al. 2011, Carlucci et al. 2020). Traits can be defined as measurable species characteristics that influence the fitness of organisms through feeding, reproduction and survival (Violle et al. 2007). In recent years, there has been evidence supporting the effectiveness of trait-based approaches in disentangling the different mechanisms structuring communities (Martins et al. 2023). Consequently, these approaches offer valuable insights to enhance our understanding of ecosystem functioning and community responses to environmental fluctuations (Mouillot et al. 2013, Pecuchet et al. 2017, Dencker et al. 2017, McLean et al. 2018a). In addition, recent studies have shown that taxonomic and functional diversity vary temporally and spatially (Stuart-Smith et al. 2013, McLean et al. 2019a, Gaüzère et al. 2022). Changes in species composition are not necessarily linked to changes in trait diversity, as different species can have similar traits (i.e. functional redundancy; Fukami et al. 2005). Therefore, taxonomic and functional diversity components can respond differently to changing environmental conditions and human pressures (Villéger et al. 2010), with stronger links between climate and traits, compared to species, as traits are directly influenced by environmental conditions (Winemiller et al. 2015, Delalandre et al. 2023). For example, climate-induced

warming acts on species traits related to growth, maturation and lifespan, thus leading to more homogenous communities adapted to novel conditions (Fukami et al. 2005, Winemiller et al. 2015, McLean et al. 2019a, Beukhof et al. 2019c, Coghlan et al. 2024a, b). For fish, using life-history traits, such as the age and size at maturity or the parental care, allows characterizing species in two life-history theory groups: r-strategy species (e.g. low age and size at maturity, low trophic level) and K-strategy species (e.g. high size and age at maturity, few large offspring, high parental care). Species adopting an r-strategy typically thrive in naturally-variable or impacted environments and present strong and rapid responses to environmental fluctuations like warming, in contrast to K-strategy species predominantly have an advantage in stable environments (Graham et al. 2011, Lynam et al. 2017, McLean et al. 2018a).

Among the large marine ecosystems (LMEs) worldwide, some of the largest changes in environmental conditions have already been observed in European continental shelf seas over the last 25 years, including some of the highest sea surface temperature (SST) warming rates reported across the ocean (Belkin 2009). Furthermore, these marine ecosystems have been subjected to centuries of intense fishing activities (Smith 1994, Fernandes et al. 2017). These anthropic pressures have impacted the spatial and temporal dynamics of taxonomic and functional diversity. Yet, in European continental shelf seas, these dynamics are studied at the regional scale, e.g. in the Baltic (Pecuchet et al. 2016), Celtic Sea (Moyes et al. 2023), North Sea (McLean et al. 2019a), Bay of Biscay (Eme et al. 2022) and the Mediterranean Sea (Veloy et al. 2022). Studies at larger spatial scales, covering several ecoregions are still scarce (Pecuchet et al. 2017, Martins et al. 2021, Rutterford et al. 2023), while many species distributions are shifting both within and between management areas (Baudron et al. 2020). This lack of larger scale studies on fish community composition, including temporal variability, limits our understanding of fish biodiversity dynamics, particularly functional diversity, raising concerns that some conservation policies may not account for regions with unique functional compositions.

Here, we combined a large data set from 21 fishery independent bottom trawl surveys covering almost all European continental shelf seas to examine how fish communities have changed over the last 26 years in terms of both taxonomic and trait compositions, and to identify the main drivers involved. Specifically, we expect that functional composition exhibits weaker spatial changes compared to taxonomic composition, because distinct species can share similar traits and respond similarly to local environments (McLean et al. 2021). We also expect that r- and K-strategy species would undergo distinct dynamics across different spatial regions, contingent upon the

rate of warming. More specifically, we assume that regions experiencing the most significant temperature rise, would tend to favor smaller species, based on temperature–size relationships (i.e. Bergmann’s rule, James’ rule and temperature–size rule) (Daufresne et al. 2009). Indeed, smaller species are usually found in warmer places, whereas larger body-sized species are usually found in colder environments (Angilletta and Dunham 2003). In addition to temperature directly driving changes in fish body sizes, feeding modes and associated physiological adaptations can also influence the relationship between community structure and temperature (Scharf et al. 2000). Coghlan et al. (2024a, b) recently showed that herbivores, invertivores and planktivores become smaller in warmer temperatures, while piscivores slightly increase in body size with temperature. These opposite trends may deeply modify the functional structure of fish communities along temperature gradients across space or time.

Material and methods

Bottom trawl data

The data sets used in this study cover most of the continental shelf seas in Europe, including the Baltic Sea, North Sea, Celtic Sea, Bay of Biscay and Iberian Coast, western Mediterranean Sea, the Adriatic Sea, Ionian Sea and central

Mediterranean Seas, and Aegean–Levantine Sea (i.e. ICES ecoregions, Fig. 1). The total surface of the study area (i.e. the summed surface of the ICES 1° longitude × 0.5° latitude spatial cells) exceeds 4 800 000 km². Abundance data were obtained from 21 scientific bottom trawl surveys conducted in the north-east Atlantic and the Mediterranean Sea from 1983 to 2020 (Supporting information). We extracted these data from the DATRAS International Council for Exploitation of the Sea (ICES) database (ICES 2023), and the MEDITS database for the Atlantic and the Mediterranean surveys, respectively (Bertrand et al. 2002, Spedicato et al. 2019). While all the data were obtained from bottom trawls, the gear, vessels, protocols (<https://www.ices.dk/data/data-portals/Pages/DATRAS-Docs.aspx>) as well as the species identification methods varied among the surveys (Supporting information). To account for differences in sampling effort between hauls, we standardized and log₁₀-transformed the species abundances by haul duration (no. ind. h⁻¹). We considered only taxa identified to the species level and corrected their taxonomy when necessary by referring to the World Register of Marine Species (WoRMS Editorial Board 2023). The final data set contained 615 species.

Variability in sampling effort across surveys

To cover the considered study area, we expanded the ICES grid usually used for survey and management purposes to encompass the Mediterranean Sea. Subsequently we assigned

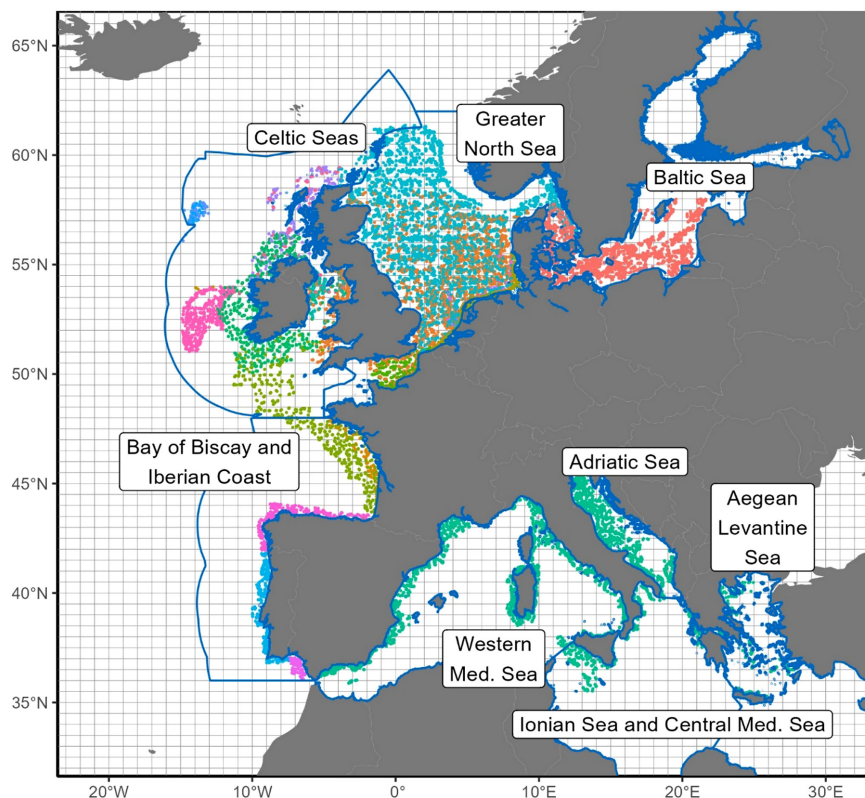


Figure 1. Map of the remaining hauls after the subsampling process. Each colored point represents one haul with colors corresponding to the 21 surveys. The borders of the eight ecoregions are highlighted in blue while the ICES grid (1° longitude × 0.5° latitude) is represented in light grey.

each haul to a specific grid cell identifier (Fig. 1). The complete data set has 107 953 hauls performed from 1983 to 2020, covering 797 grid cells.

Sampling effort varied within and across ecoregions, and through time (Supporting information). To mitigate the potential effects of incomplete survey coverage, we included only data from 1994 to 2019. We also retained cells with time series beginning before 2005 and that have at least 10 years of data coverage (Supporting information). We further subset the data to keep cells with at least two hauls in each quarter within a year. For a given ecoregion, the number of quarters included varied between one and three. Yet, we resampled the data to keep a constant number of sampled quarters along the studied period in each ecoregion. We randomly selected two hauls per cell in each year and quarter. Finally, to ensure that significant temporal changes found at the scale of the ecoregion are independent of sampling effort, we removed years from the time series to have a constant sampled haul number (defined in each ecoregion/quarter as the mean number of sampled haul more or less the SD). This step was done to keep a constant spatial footprint in ecoregion through time. To ensure the results were robust, the random selection was done 10 times and the spatial distribution of the communities were compared. The random selection of two hauls per cell grid, year and quarter did not change the results (Supporting information). Moreover, as the final data set was composed of two type of gears (i.e. bottom trawl and beam trawl, Supporting information), we ensured the independence of results from the gear type. For this, we removed one gear type after the other in the regions where the two gear types were used simultaneously, and compared the results to the results based on the full dataset (correlation higher than 0.9 in 19 cases over 24) (Supporting information).

The final data set has 513 species from 29 665 hauls in 557 unique grid cells (Fig. 1). The extent of the sampled study area was similar to the full data set (Supporting information compared to Fig. 1), with relatively consistent spatial coverage over time (Supporting information).

Species traits

Traits are useful to predict community responses to disturbances (Capdevila et al. 2022, Coghlan et al. 2024a, b), and we assumed that traits were more closely associated with environmental conditions than the species themselves. Traits summarize each species in terms of life history, habitat and trophic ecology (Supporting information), and are assumed to influence how a species responds to environmental change (Pecuchet et al. 2018, McLean et al. 2018b, 2019a, Beukhof et al. 2019b). The species traits included in this study were: length and age at sexual maturity, Von Bertalanffy K growth coefficient, trophic level (quantitative traits), spawning type, vertical habitat, and feeding mode (categorical traits). Among the 4305 trait values (615 species \times 7 traits), we extracted 3262 trait values from the North Atlantic and Northeast Pacific continental shelf seas data set collated by Beukhof et al. (2019a), and 1043 were missing. We added 59 missing traits values using Fishbase

(Froese and Pauly 2019), and the 984 other missing values were inferred from a multivariate Bayesian model based on the known trait values of the phylogenetic neighbors using the methodology and package developed by Thorson et al. (2017). The quantitative traits values were \log_{10} -transformed and standardized to mean 0, SD 1 prior to analyses.

External drivers

To understand whether environmental drivers influence the temporal and spatial distribution of the taxonomic and functional composition of fish communities, we selected parameters based on published literature including bottom and surface temperature, bottom oxygen, surface chlorophyll-a concentration, surface salinity, bottom current strength, and mixed layer depth (Receveur et al. 2019, 2022, Cresson et al. 2020, Gislason et al. 2020, Ammar et al. 2021, Duncan et al. 2022, Rutterford et al. 2023). All environmental variables were available on a 0.25° spatial grid with a monthly-averaged resolution from 1993 to 2019. We extracted the physical variables (temperature, currents, salinity, and mixed layer depth) from the ARMOR3D reanalysis (European Union-Copernicus Marine Service 2020) while the biogeochemical variables (i.e. chlorophyll-a and oxygen concentration) were extracted from a NEMO-PISCES biogeochemical model simulation. NEMO-PISCES simulation was forced by reanalysis data (GLORYS2V4-FREE and ERA-Interim for the oceanic and the atmospheric conditions respectively) and was validated by comparison with observed data (European Union-Copernicus Marine Service 2018). The seven variables were averaged on the ICES spatial grid ($0.5^\circ \times 1^\circ$) to match the spatial resolution of biological data. The seven variables were averaged by quarter to align to the season of bottom trawl sampling, and the yearly and quarterly mean and the SD values were considered in the analysis.

For each $0.5^\circ \times 1^\circ$ grid cell, we extracted the Bottom depth from the General Bathymetric Chart of the Oceans database (GEBCO 2022) and then computed the depth span (max depth-min depth).

Commercial fishing effort data [hours of fishing detected with Automatic Identification System (AIS) data] were available from 2012 to 2019 for the whole studied region on a daily basis and on a 0.1° spatial grid, from the version 2.0 of the Global Fishing Watch data (Kroodsma et al. 2018). The hours of fishing were summed by year and quarter and by $0.5^\circ \times 1^\circ$ (ICES grid) grid cell, and then averaged over the 2012–2019 period. All fishing gears may impact demersal species, both directly (i.e. by removing the targeted species biomass) or indirectly (e.g. by removing non-targeted species but which are connected through trophic interactions). Therefore, in the initial analysis, all types of fishing gear were considered. As direct biomass removal must be more impacting, the analysis was repeated using only trawlers (pelagic and bottom), and lead to the same results.

All variables described above were standardized to mean 0, SD 1 prior to the analysis, so that resulting statistical outputs would be directly comparable.

Data analyses

Taxonomic and functional data processing

For the taxonomic community analysis, the matrix of \log_{10} -transformed species abundances (29 665 hauls \times 513 species) was transformed using a Hellinger transformation ($y'_{ij} = \sqrt{\frac{y_{ij}}{y_{i+}}}$, where j indexes the species, i the haul, and $i+$ is the row sum for the i th sample). The Hellinger transformation is useful to avoid the influence of double-zero in the principal component analysis (PCA) based on Euclidean distances. PCA was then applied with the hauls as individual observations and species as variables, to quantify and characterize the spatio-temporal dynamics of taxonomic composition. To ensure that the results were not only driven by the most abundant species, we also used the Bray–Curtis index which quantifies the level of dissimilarity in species composition based on their relative abundances (Legendre and Legendre 2012). We then applied a principal coordinate analysis (PCoA) to the Bray–Curtis dissimilarity matrix after square root transformation, to avoid negative eigenvalues (Legendre and Legendre 2012). The spatial distribution patterns of the taxonomic communities and the position of ecoregions in the taxonomic space were very similar whether the analyses were conducted using the Bray–Curtis/PCoA or the Hellinger/PCA framework (Supporting information).

In the functional community analysis, we computed the community-weighted mean (CWM) trait values for each trait within every haul. For a given trait, CWM values correspond to the averaged trait values of the species present in each haul, weighted by their log-abundances. This results in single numeric values for quantitative traits and proportions for categorical traits. A multiple factor analysis (MFA) was then undertaken using the CWMs data [29 665 trawls \times 18 mean trait values (4 quantitative traits and 3 categorical traits with 3, 6 and 5 categories each, Supporting information)].

Spatio-temporal patterns

To facilitate analysis at different spatial and temporal scales, we summarized the first three principal components scores (PC1, PC2 and PC3; taxonomic composition) and MFA scores (MF1, MF2 and MF3; functional composition) in two ways: through space (one mean value per ICES grid cell for the entire time series), and through time and ecoregions (one mean value per year in each ecoregion; Supporting information). For the latter aggregation, we used a linear model with the mean PC/MF value as the response variable and year as the explanatory variable to assess the significance of yearly linear changes. To ensure the results were representative of the ecoregion, the analysis was repeated at the grid cell scale.

To quantify the relative importance of space versus time in explaining the variability in taxonomic and functional communities composition, we used the STATIS approach (Lavit et al. 1994). This method is based on Euclidean distances between configurations of the same observations obtained in K different states. The different states used here were the years and the grid cells. We then calculated the Rho-vector coefficients (RV) across all years and all potential grid cell combinations

(Robert and Escoufier 1976). We finally averaged all grid cells RV values and all years RV values to quantify the spatial and the temporal variability respectively (e.g. a high mean spatial RV value meaning high spatial homogeneity).

Assessing external drivers influence on fish communities

We used a generalized least square (GLS) model to estimate the influence of environmental variables on the spatial and temporal variability of the taxonomic and functional composition of communities.

To assess spatial variability, we used the mean spatial PC/MF scores (one mean value per grid cell for the entire time series) as response variables in the GLS models. A Gaussian spatial autocorrelation factor was included in these models using the centroid latitude and longitude of the grid cells as random variables. For the GLS models, mean environmental parameters and their variability coefficients (i.e. the SD) were used as explanatory variables. In addition to the environmental parameters, fishing effort was also considered in the GLS models through the average annual fishing effort within each grid cell from 2012 to 2020.

For the temporal aspect, the mean temporal PC/MF scores of each ecoregion with significant yearly-trend (based on the linear model results, with 5% significance level) were used as response variables in the GLS model (one mean value per year and ecoregion). One model was fitted by ecoregion. Gaussian temporal autocorrelation structure was included in these models using the year as a random variable.

All possible additive GLS models were tested (i.e. all models with one variable, then with all possible combinations with two variables, until the full model with all variables), including intercept only models. We retained the model with the lowest Akaike's information criterion (using the correction for small sample size AICc). From the model with the lowest AICc score, only variables that had p-values < 0.05 are discussed in the paper (the Supporting information provide the results for the models with the five lowest AICc scores for each analysis undertaken).

All statistical analyses were performed using R ver. 4.2.1 (www.r-project.org). The species traits were estimated with the function `Plot_taxa` from the 'FishLife' package (Thorson et al. 2023). The PCA used the function `PCA` and the MFA used the function `MFA`, both from the 'FactoMineR' package (Lê et al. 2008). The STATIS analysis used the `statist` function from the 'ade4' package (Dray and Dufour 2007), and the GLS models used the `gls` function from the 'nlme' package (Pinheiro and Bates 2000).

Results

Spatial patterns of fish communities

The fish taxonomic community composition varied between ecoregions, however, we found that the four Mediterranean ecoregions had similar fish taxonomic composition (Fig. 2A). The fish community along the Bay of Biscay and the Iberian coast showed greater similarity to

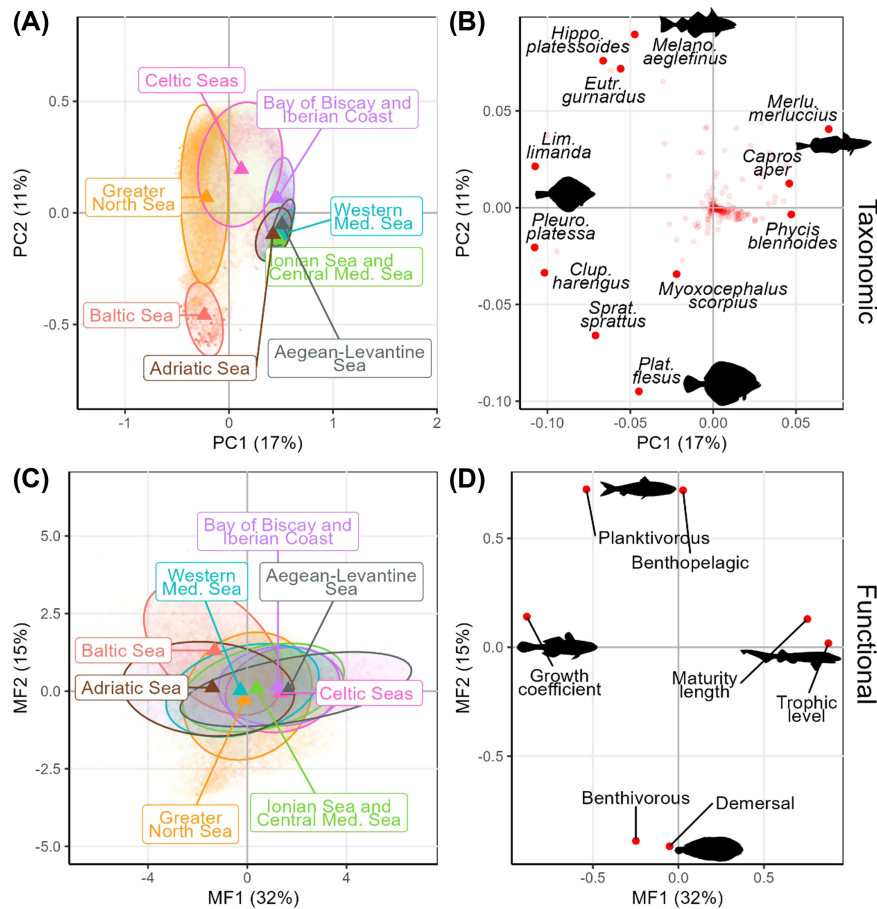


Figure 2. (B) Taxonomic and (D) functional spaces from the PCA and MFA, respectively with only species/traits with coordinates higher than the 95% percentile of each dimension; position of the fish assemblages on the 1st principal component (PC1/MF1; x-axis) and 2nd principal component (PC2/MF2; y-axis) in the (A) taxonomic and (C) functional spaces. The colors on (A) and (C) show the ecoregions (Fig.). The variance explained by each dimension is given on the corresponding axis. *Clup. harengus*: *Clupea harengus*; *Hippo. platessoides*: *Hippoglossoides platessoides*; *Lim. limanda*: *Limanda limanda*; *Melano. aeglefinus*: *Melanogrammus aeglefinus*; *Merlu. merluccius*: *Merluccius merluccius*; *Micro. poutassou*: *Micromesistius poutassou*; *Plat. flesus*: *Platichthys flesus*; *Pleuro. platessa*: *Pleuronectes platessa*; *Sprat. sprattus*: *Sprattus sprattus*; *Trach. trachurus*: *Trachurus trachurus*; *Triso. esmarkii*: *Trisopterus esmarkii*; *Merlan. merlangus*: *Merlangius merlangus*.

the fish community found in the Mediterranean Sea than to the North Sea, despite its closer geographic proximity to the North Sea (Supporting information). When considering the first component of the PCA (17% of the variance), the Baltic Sea and the North Sea fish communities exhibited a high level of similarity, but when considering the second component (11% of the variance), we observed a greater divergence in the fish communities between these two areas (Supporting information). The fish community in the North Sea was mostly dominated by common dab *Limanda limanda*, whiting *Merlangius merlangus*, European plaice *Pleuronectes platessa* and Atlantic herring *Clupea harengus*; Fig. 2B). In contrast, the Baltic Sea fish community was mainly characterized by European sprat *Sprattus sprattus* while the Bay of Biscay, Iberian coast and Mediterranean Sea, by hake *Merluccius merluccius* and boarfish *Capros aper*. The third dimension (PC3) explained 9% of the variance (Supporting information).

The taxonomic composition of fish communities showed a stronger spatial variability than the functional composition

(Fig. 2C). However, the spatial distribution of MF1 (32% of the variance) differed between the north and the south of the North Sea, and a portion east of the Celtic Sea (Supporting information). The Baltic Sea was similar in functional composition to the southern part of the North Sea for MF1, but similar to the northern part of the North Sea for MF2 (15% of the variance, Supporting information). MF3 explained 11% of the variance (Supporting information).

The Baltic Sea and Adriatic Sea were characterized by fast-growing and planktivorous species (Fig. 2D). The North Sea exhibited a north/south gradient; the northern part dominated by generalist, and late-reproducing species, while the southern part by benthivorous species (Fig. 2D). The Bay of Biscay and Iberian Coast, Celtic Sea and Aegean-Levantine Sea were characterized by generalist, high trophic level, and late reproduction strategy species with the exception of the Atlantic Horse mackerel. The northern regions (Baltic Sea, North Sea, Celtic Sea) were characterized by non-guarder species, while the four Mediterranean regions by bearer and guarder species (Supporting information).

Temporal dynamics of fish communities

Taxonomic community composition was almost two times more variable in space ($RV=0.51$; $SD=0.23$) than in time ($RV=0.90$; $SD=0.13$). The ratio was very similar for functional community composition between spatial variability ($RV=0.61$; $SD=0.18$) and temporal variability ($RV=0.96$; $SD=0.033$). Due to the strong spatial heterogeneity, we partitioned the entire study area into distinct ecoregions, and focused on the temporal trends within each ecoregion.

Changes in the taxonomic composition differed across the ecoregions. For example, the dominance of European plaice *Pleuronectes platessa* increased over the last decades in the Baltic Sea (PC1 slope = -0.0016 ; p -value < 0.05) and in the Celtic Sea (PC1 slope = -0.0019 ; p -value < 0.05), while the dominance of common dragonet *Callionymus lyra* increased in the Baltic Sea (PC3 slope = -0.0036 ; p -value < 0.05), North Sea (PC3 slope = -0.002 ; p -value < 0.05), and Celtic Sea (PC3 slope = -0.002 ; p -value < 0.05 ; Fig. 3, Supporting information). We observed that these species dominance increases were almost all associated

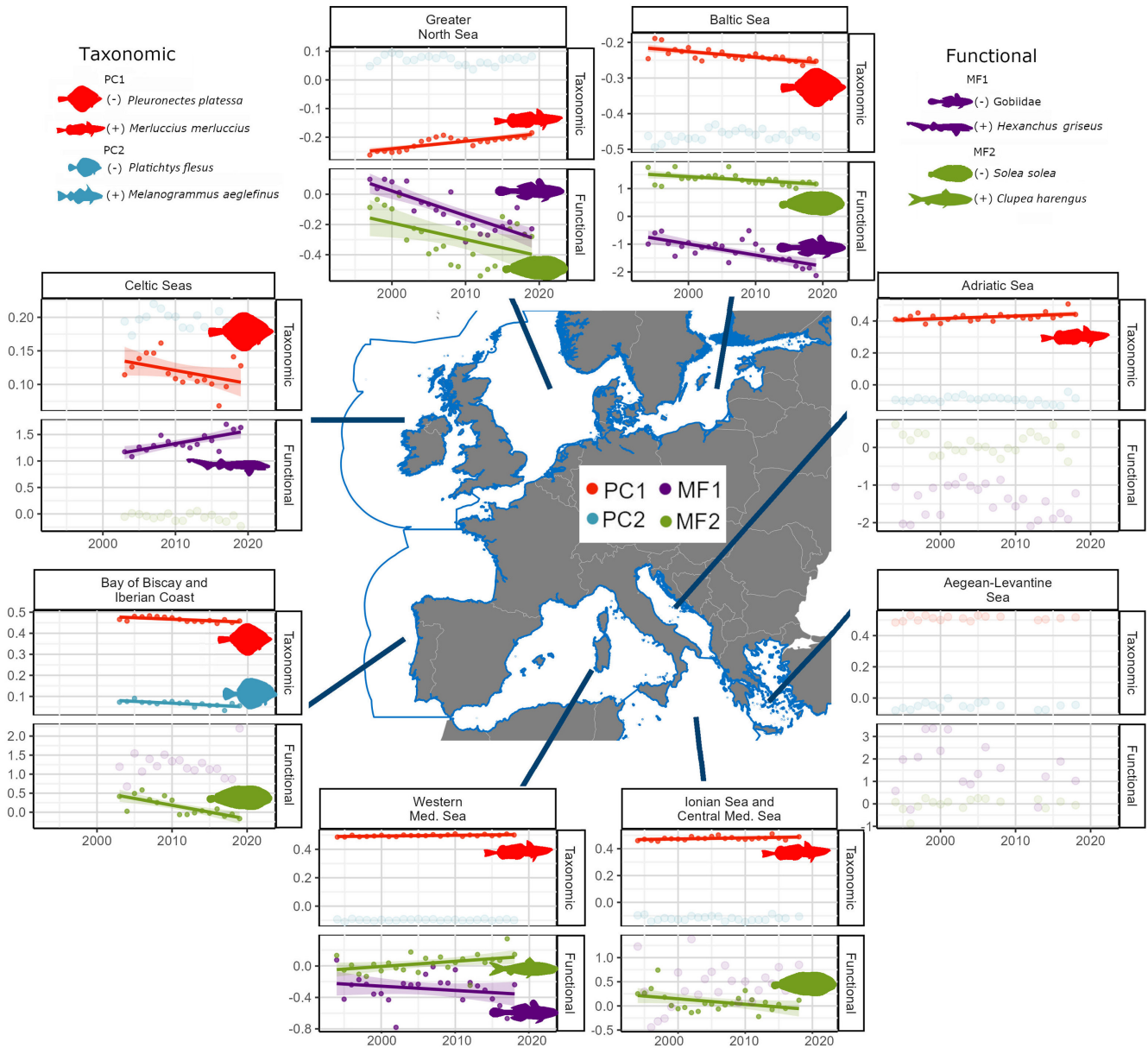


Figure 3. Mean values of taxonomic PC1 (1st principal component, red), and PC2 (blue; first row), and functional MF1 (1st multiple factor component, purple), and MF2 (green; second row) by year (x-axis) by ecoregion (panels). The regression lines show significant temporal trends, with the corresponding confidence interval shaded. The species silhouettes in each panel show the most driving species (extracted from Fig. 2) and traits (representing by specific species identical as on Fig. 2) for each dimension. The symbols (+) and (-) indicate positive and negative trends respectively for PC1/PC2/MF1/MF2.

with temporal increases in the absolute abundance of these species (Supporting information). The dominance of hake *M. merluccius* increased in the assemblages in three of the Mediterranean ecoregions [western Mediterranean Sea (PC1 slope=0.0005; p-value < 0.05), Ionian Sea and the central Mediterranean Sea (PC1 slope=0.0008; p-value < 0.05), and the Adriatic Sea (PC1 slope=0.002; p-value < 0.05; Fig. 3), however, these changes in hake dominance were not associated with changes in mean abundance (Supporting information). Finally, European flounder *Platichthys flesus* increased in dominance in the Bay of Biscay and Iberian coast (PC2 slope = -0.0002; p-value < 0.05, Fig. 3).

We detected significant temporal changes in the functional composition between ecoregions (Fig. 3). Both the Baltic and North Sea's communities became dominated by fast-growing species like those in the family Gobidae (Baltic Sea MF1 slope = -0.04, p-value < 0.05; North Sea MF1 slope = -0.02, p-value < 0.05), demersal species (Baltic Sea MF2 slope = -0.02, p-value < 0.05; North Sea MF2 slope = -0.01, p-value < 0.05), and bathypelagic species (Baltic Sea MF3 slope = 0.03, p-value < 0.05; North Sea MF3 slope = 0.009, p-value < 0.05; Fig. 3, Supporting information). In the Celtic Sea, species that reproduce late and with a high trophic level like megrim *Lepidorhombus whiffiagonis* (trophic level = 4.34), John Dory *Zeus faber* (trophic level = 4.5), or blackmouth catshark *Galeus melastomus* (age at maturity = 3.8 years) were increasingly dominant (MF1 slope = 0.024, p-value < 0.05) and the proportion of non-guarder species increased (MF3 slope = -0.03, p-value < 0.05). In the Bay of Biscay and Iberian coast, demersal species increased (MF2 slope = -0.04, p-value < 0.05). In the western Mediterranean Sea, fast-growing species (MF1 slope = -0.007, p-value < 0.05), planktivorous species (MF2 slope = 0.007, p-value < 0.05) and non-guarder species (MF3 slope = -0.01, p-value < 0.05) became more dominant. The changes described above were usually associated with changes in absolute abundance of the species groups (Supporting information). Among all European ecoregions, the Mediterranean Sea was stable in its functional composition over the last three decades, with no significant changes for two of the four Mediterranean ecoregions, and only one dimension (MF2) for the Ionian Sea and central Mediterranean Sea (Fig. 3, Supporting information).

Finally, within a given ecoregion, the temporal trends in a majority of spatial ICES grid cells were similar to the mean temporal trend detected at the ecoregion scale (Supporting information). At larger scale, the results were similar among the LMEs (Supporting information).

External drivers of spatio-temporal variability in fish communities

Overall, the spatial distribution of the taxonomic and functional communities composition was mainly influenced by sea surface temperature (PC1 slope = 0.25, p-value < 0.05; PC2 slope = -0.23, p-value < 0.05), surface salinity (PC1 slope = -0.056; p-value < 0.05; PC2 slope = 0.25; p-value <

0.05; MF1 slope = 0.73; p-value < 0.05; MF2 slope = -0.56; p-value < 0.05), bottom temperature variability (PC1 slope = -0.1; p-value < 0.05; MF1 slope = -0.34; p-value < 0.05; MF2 slope = -0.27; p-value < 0.05) and surface chlorophyll-a concentration (PC2 slope = -0.11, p-value < 0.05; MF1 slope = -0.54, p-value < 0.05) (steepest slopes, Fig. 4A). Spatial patterns of PC1, PC2, MF1 and MF2 were well explained by the variables, with an explained deviance of the models ranging between 48 and 74%, with higher explained deviance for the two scores of the functional community composition models (Supporting information).

The drivers of temporal taxonomic changes varied by ecoregion, bottom oxygen for the Baltic Sea (PC1 slope = -0.09, p-value < 0.05), surface temperature for the Aegean-Levantine Sea (PC2 slope = 0.02, p-value < 0.05), bottom temperature for the Celtic Sea (PC1 slope = -0.15, p-value < 0.05), and bottom oxygen for the western Mediterranean Sea (PC1 slope = -0.03, p-value < 0.05; Fig. 4B). The deviance explained by the models ranged from 14 to 43%, yet with only 5 models over 16 with significant explicative variables (Supporting information).

The temporal change in functional community composition of the different ecoregions was mostly influenced by two parameters: bottom oxygen [Celtic Sea (MF1 slope = -1.6, p-value < 0.05), Aegean-Levantine Sea (MF1 slope = -2.7, p-value < 0.05)] and bottom temperature [Celtic Sea (MF2 slope = -0.62, p-value < 0.05), Bay of Biscay and Iberian coast (MF2 slope = 1.21, p-value < 0.05), Ionian Sea and central Mediterranean (MF2 slope = 0.22, p-value < 0.05)] Monthly variability of the bottom oxygen variability (MF2 slope = 0.31, p-value < 0.05) also influenced the temporal change of functional community composition in the Adriatic Sea. The deviance explained by the models ranged from 13 to 79%, with 14 models over 16 with significant variables (Supporting information).

By summing the number of significant variables for the spatial and temporal analysis, 16 variables were significant for the taxonomic communities, against 18 for the functional communities.

Discussion

Main results

Previous studies focusing on the spatio-temporal dynamics of marine fish communities in European seas were undertaken at regional scales or considered a limited number of species at larger spatial scales. Here, we aggregated a large data set of fishes across eight ecoregions allowing us to quantify changes in taxonomic and trait-based community composition since the mid-1990s and to assess the influence of environmental and fishing drivers. We highlighted that the taxonomic composition of fish communities exhibited a relatively continuous spatial gradient. In contrast, the functional composition of these communities displays greater similarity across ecoregions (Fig. 2). Temporal changes in taxonomic composition

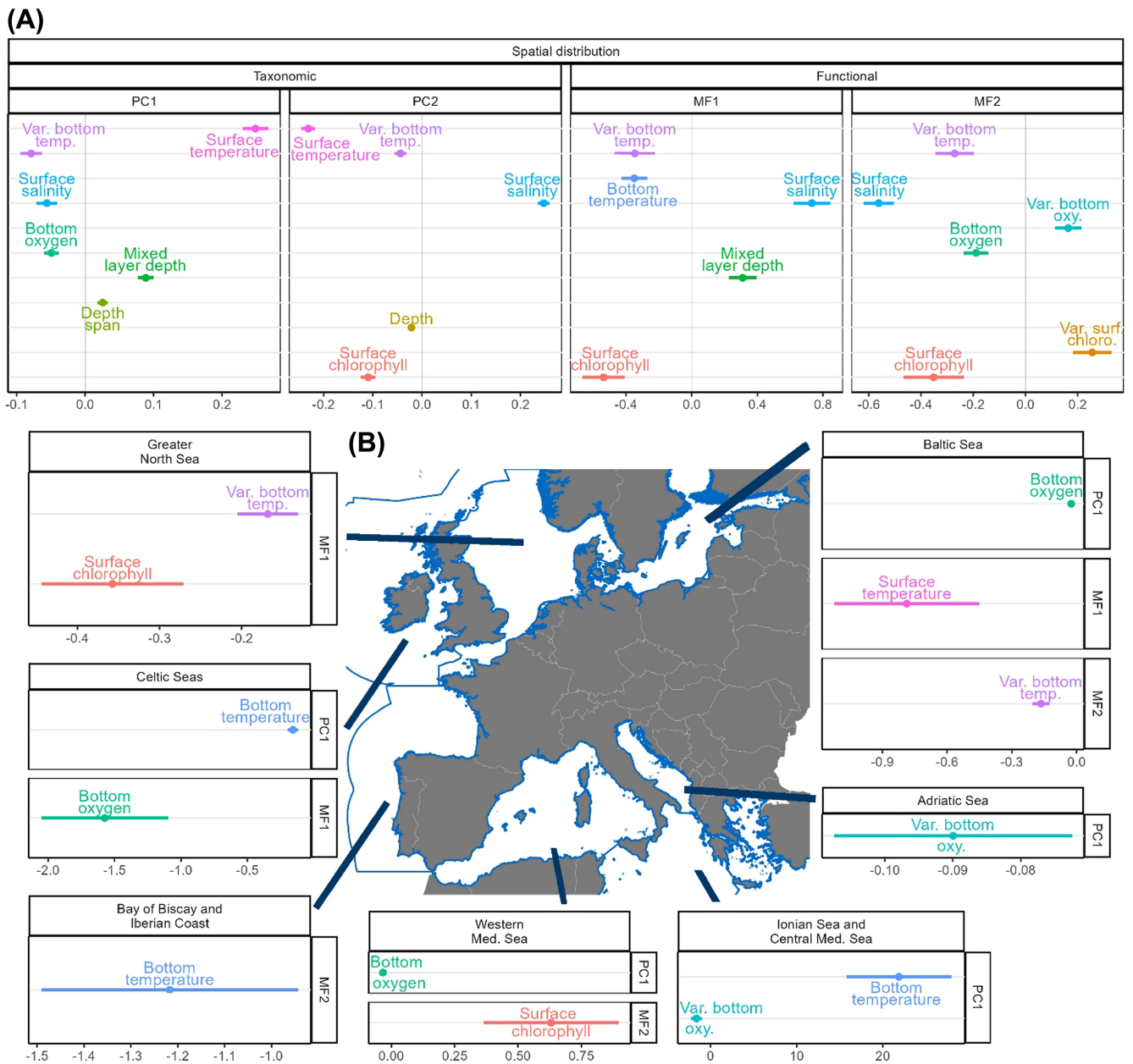


Figure 4. Significant slope values (x-axis) of the GLS models fitting the temporal mean values the spatial mean values (A) and by ecoregion (B) and function of environmental parameters (colors) for taxonomic and functional two first principal components (PC/MF; panel rows). The horizontal bars on each side of the points represent the GLS predicted SE. It is note that missing ecoregions (North Sea and western Mediterranean Sea) have no significant slope and/or no significant temporal trend (Fig. 2).

were similar across the Northeast Atlantic, mostly characterized by an increase in the abundance of European plaice *P. platessa* while the North Sea and the western Mediterranean Sea were characterized by an increase of hake *Merluccius merluccius*. In terms of temporal changes in functional composition, the Baltic Sea, North Sea and western Mediterranean Sea shared similar patterns, characterized by a dominance and increase in abundance of r-strategy species, while in the Celtic Sea, changes in fish communities were marked by an increase in K-strategists. Our results suggest that surface

conditions, primarily temperature, salinity and chlorophyll-a, and the vertical water column structure, influenced the spatial distribution of both communities' aspects. Conversely, bottom conditions, particularly temperature and oxygen, exert the most significant influence on the temporal dynamics of both communities' aspects. Ultimately, a broader array of environmental parameters exerted influence on the functional community as opposed to the taxonomic community: 1) higher explained deviance for the spatial patterns of functional structure, 2) more models with significant variables

for the temporal trends of functional structure and 3) more significant variables explaining the functional than the taxonomic structure. This emphasis that species traits, rather than species identity, is more relevant to unravel how communities are shaped by their environment.

Large-scale variability

The composition of fish communities was dominated by r-strategy species in the southern North Sea, Baltic Sea and Adriatic Sea and by K-strategy species in the northern North Sea, Celtic Sea and the Bay of Biscay and Iberian Coast. Using a different methodology, Pecuchet et al. (2017) found the same large-scale spatial patterns in the functional composition of demersal fish communities. However, while they only quantified the temporal changes in the North Sea, we explored temporal changes over the entire European continental shelf. Additionally, we highlighted the increase of benthivorous and demersal species in four of the 10 ecoregions (i.e. Baltic Sea, North Sea, Bay of Biscay and Iberian Coast, western Mediterranean Sea and Ionian Sea and central Mediterranean Sea). The dominant species responsible for this change in the northeast Atlantic are flat fishes: two megrim species *L. whiffiagonis*, *Lepidorhombus boscii*, the common dab *L. limanda*, the European flounder *Platichthys flesus*, the European plaice *P. platessa*, and the turbot (*Scophthalmus maximus*; Supporting information). We make the hypothesis that this increase of benthivorous diet is driven by changes and potential increased abundance of the benthic community. Future investigations comparing the benthic and demersal communities temporal changes at the European scale would be of great interest to validate this hypothesis.

We were also able to identify a temporal and spatial decoupling in taxonomic and functional composition changes, and that this decoupling was different between the fast warming regions and the slower warming regions (Belkin 2009). An important caveat is that we ignored the seasonal variability and we combined 21 surveys using two types of trawls, making the assumption that the results are robust to seasonal variability and to gear type differences (Supporting information).

We showed that common changes can occur in different European ecoregions, as already suggested before (Bell et al. 2018). This observation suggests that using several metrics (e.g. the PC1/PC2/MF1/M2 scores), calculated at larger spatial scale than the stock, may provide information to managers that could be used in addition to classic stock indicators (e.g. spawning biomass). We show that it is important to measure and understand local species' abundance and assemblage compositions, in addition to species' presence-absence, to improve understanding of the ecological climate resilience in fish communities and identify adaptive management strategies. In particular, species presence-absence and information on range shifts alone are not enough to predict the ecological and economical effects of climate change (Simpson et al. 2011). Using such alternative metrics would improve managers' ability to measure, understand and consider the ecosystem

changes associated with fishing, and would therefore support the integration of ecosystem-based management into fisheries management (Arkema et al. 2006, Leslie and McLeod 2007). To conclude, we encourage fishery managers to more holistically consider changes in surrounding ICES management areas in addition to their focal area, to provide a better understanding of changes at the local scale, and also to anticipate responses to future disturbances.

Local-scale variability

A shift in communities around 1997 has already been linked to a phase shift in the Atlantic Multidecadal Oscillation (Auber et al. 2015), with major changes occurring in the English Channel (more demersal species) and in the southern North Sea (more pelagic species) (McLean et al. 2018b). Over the last 30-years, the North Sea fish community diverged in species composition, but converged in terms of traits (McLean et al. 2019a), with an increasing prevalence of r-selected species (Beukhof et al. 2019b). Our study confirmed the trend toward r-selected species in the North Sea. In the neighboring Baltic Sea, our results also confirmed the trend towards communities that were increasingly dominated by r-selected fish species (Beukhof et al. 2019b). Conversely, most of the temporal changes were not significant in the Mediterranean Sea, and the spatial taxonomic and functional structures were homogenous in two of the four Mediterranean ecoregions, as demonstrated before on a shorter time series (Granger et al. 2015). While Granger et al. (2015) only used morphological traits to study the spatiotemporal dynamics of functional composition, we included traits linked to life and reproduction strategies. Using these ecological traits, we illustrated an increase in the dominance and abundance of r-strategy fish species in the western Mediterranean Sea, results that cannot be drawn from morphological traits.

External drivers

Temperature is recognized as a pivotal parameter influencing fish communities (Gislason et al. 2020, van Denderen et al. 2023, Rutterford et al. 2023, Ottmann et al. 2024) and our study reveals that sea temperature emerged as the predominant environmental driver shaping community composition in European Seas. Nevertheless, our findings demonstrate that in regions experiencing the most rapid and pronounced warming (i.e. Baltic Sea, North Sea, Mediterranean Sea; Belkin 2009, Burrows et al. 2019) fish communities shifted towards a dominance of r-strategy species. These species have traits more adapted to warming conditions, e.g. short generation times, fast population turnover, and producing small and pelagic larvae with high dispersal rates (Rijnsdorp et al. 2009, Buisson et al. 2013, McLean et al. 2018b, 2019b). Thus, these species are believed to have greater resistance and recovery capabilities to long term disturbances given their fast population turnover and greater potential for rapid natural selection (Rijnsdorp et al. 2009, Capdevila et al. 2022).

However, our results also showed that a warming environment may induce an increase of K-strategy species, a trend which echoes a recent publication showing that piscivores are the only trophic guild benefiting from temperature increase on shallow reefs (1% per 1°C; Coghlan et al. 2024a, b), as opposed to some other studies (McLean et al. 2019a, b). This positive trend of K-strategy species with temperature might be explained, at least partly, by the metabolic theory with active ectothermic predators having a decreased foraging efficiency at lower temperature (Grady et al. 2019). An alternative explanation is that close spatial connection to the southern Atlantic regions, as well as the efficient dispersal ability of K-strategy species, may contribute to the increase of K-strategy species in the Bay of Biscay and Iberian Coast. The increase of K-strategy species may be finally linked to the decrease of fishing effort during the last decades (Ravard et al. 2014), as showed in the North Sea with a rebound of rare species, mostly with a K-strategy (Murgier et al. 2021).

Chlorophyll-a surface concentration and bottom oxygen content were also identified as important drivers of taxonomic and functional composition. Through bottom-up control, chlorophyll-a concentration influences the productivity of the whole food web. In the Bay of Biscay and Celtic Sea, the spatiotemporal dynamics of demersal fish communities were more closely linked to the diversity and abundance of small pelagic species than to temperature (Eme et al. 2022). More specifically, the high pelagic primary production in the Bay of Biscay (Cresson et al. 2020) is partly related to the high abundance of small pelagic species, and finally to the high abundance of demersal species. In the Bay of Biscay, the lowest trophic levels (i.e. plankton) had a major structuring role on this food web and the structure of fish assemblages (Lassalle et al. 2011, Cresson et al. 2020). Under the same bottom-up process, areas of high productivity have been hypothesized to concentrate higher species richness as they harbor more individuals and thus maintain a higher number of viable species' populations (Gislason et al. 2020). Our results validate the importance of bottom-up control by illustrating the structuring role of chlorophyll-a in the spatial distribution of taxonomic and functional composition of fish assemblages. Yet, for future studies, it would be important to add zooplankton, an intermediate trophic component linked to phytoplankton, to understand the role of each component in the structure of demersal fish assemblages (van Denderen et al. 2023).

The role of bottom oxygen is more challenging to interpret. Oxygen had been shown to be a major stressor for fishes in regions with specific conditions, mostly when hypoxic conditions occur (i.e. dissolved oxygen concentration below 2 mg l⁻¹; Pihl 1994, Receveur et al. 2022), but analyses of the oxygen role at a larger scale are scarce. However, around 340 000 km² of shelf bottom waters of the Northeast Atlantic were shown vulnerable to oxygen deficiency in the years 1998–2009 (cf. Fig. 10 in Ciavatta et al. 2016). It is possible that these shelf bottom waters with low oxygen concentration had a negative impact on the demersal community. In the Baltic Sea, hypoxic conditions create a physical

barrier, potentially limiting fish ability to reach their prey in these areas (Receveur et al. 2022).

Fishing effort had minimal influence on the spatial distribution of functional community composition compared to environmental variables between 2012 and 2019. We only had data for a few years of fishing in this analysis while intense fishing has been taking place in this region for centuries (Bell et al. 2018). Moreover, we used specific multivariate indicators (PC and MF scores) to study the impact of fishing pressure on fish community structure. Other indicators (i.e. the mean length of the assemblages, mean biomass) would likely result in a different conclusion particularly since fishing tends to remove the largest fish first (Bell et al. 2018) and therefore reduces biomass (van Denderen et al. 2023). It remains challenging for any analysis such as this one to identify how fisheries may impact an ecosystem unless significant changes in the management of the fisheries occur during the study period. At a minimum, longer time series of fishing data are needed to start quantifying the potential consequences of fishing on the whole ecosystem (Daan et al. 2005). Moreover, the type of trawler (bottom or pelagic) was not available in the database and the fishing effort proxy that we used (number of fishing hours based on fishing vessels AIS) was not a comprehensive representation of all fishing behavior since some vessels are missing or untracked (Paolo et al. 2024) with unknown catches and efforts. Developing fishing databases at regional and larger spatial scales is necessary to better understand the impact of fishing on marine communities.

To keep the results understandable, we only considered significant trends and we did not include temporal lags between the biological changes and the environmental variables and fishing effort variability. We may thus overlook certain community responses (including non-linear responses) due to this choice.

We found stronger links between environmental conditions and functional composition than with taxonomic composition (explained deviance for the spatial aspect, number of models with significant variables for the temporal aspect, total number of significant variables). This result confirms our hypothesis that species traits are linked to the environment more strongly than taxonomy, as they are proxies of species ecology through their life history, including favorable habitat and diet (McWilliam et al. 2023).

Perspectives

In the present study we considered two biodiversity components, but not the phylogenetic component. Phylogenetic diversity has proven to be important in numerous studies, especially for conserving evolutionarily distinct species (Winter et al. 2013, Albouy et al. 2015, Loiseau et al. 2020), and should be further investigated in future research efforts. Similarly, we have not explicitly explored the trophic interactions between species, a component of functional diversity that tends to be independent of taxonomic and phylogenetic components (Gauzère et al. 2022). Collecting a comprehensive network of trophic interactions spanning the entire Mediterranean

Sea and the North European Atlantic Ocean poses a challenge, requiring concerted modeling efforts (Albouy et al. 2019). Nevertheless, innovative methodologies, including environmental DNA metabarcoding for the detection of rare species, as well as metabarcoding of gut content (Casey et al. 2019), may unveil unknown interactions, in conjunction with established techniques such as stomach content analyses and stable isotopes. These techniques hold promise for advancing our understanding and enhancing the characterization of trophic diversity in these ecosystems (Pereira et al. 2023).

Concluding remarks

We showed that the taxonomic and functional composition of fish communities in European seas varies temporally and spatially, responding to different environmental gradients. Beyond species identity to describe an ecological community, our results provided evidence that considering species traits can improve our understanding of community response to environmental changes. Specifically, this approach enables better prediction of fish community responses to environmental drivers across different regions. Our findings also emphasized the importance of examining and monitoring biodiversity over large spatial scales and extended periods for conservation and ecosystem-based management purposes.

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Author contributions

Camille Albouy and **Arnaud Auber** share last authorship. Conceptualization: AR, FL, KE, DK, KMK, MM, BM, KEM, DM, MR, ITS, GVH, CA, AA. Data curation: AR, BM, CA, AA. Formal analysis: AR, FL, DM, CA, AA. Funding acquisition: CA, AA. Investigation: AR, FL, DM, CA, AA. Methodology: AR, FL, DM, CA, AA. Project administration: CA, AA, AR. Resources: CA, AA. Software: AR. Supervision: CA, AA, FL. Validation: AR, FL, KE, DK, KMK, MM, BM, KEM, DM, MR, ITS, GVH, CA, AA. Visualization: AR, FL, DM, CA, AA. Writing – original draft: AR. Writing – review & editing: AR, FL, KE, DK, KMK, MM, BM, KEM, DM, MR, ITS, GVH, CA, AA.

Transparent peer review

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Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.x69p8czsj> (Receveur et al. 2024).

The R code of the analysis is available on GitHub : https://github.com/auroreRECE/European_demersal_fish_assemblages

Supporting information

The Supporting information associated with this article is available with the online version.

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