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Original Article

Community-level modelling of pelagic fish assemblages in the Baltic Sea reveals temporal shifts and effects of environmental drivers

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Abstract

The Baltic Sea is characterised by strong environmental gradients that shape its biodiversity and community structure. Despite a well-established body of work on individual fish species' responses to these gradients, basin-wide, multi-species assessments of pelagic fish community patterns remain scarce. Using 17 years of standardised autumn data (2007–2023) from the Baltic International Acoustic Survey (BIAS)—a fishery-independent survey primarily targeting herring and sprat that consistently samples the broader pelagic fish assemblage—we fitted species distribution models for 45 fish taxa. Predicted occurrence probabilities were used to estimate species richness and to delineate regions of common profile (RCPs), characterising the spatial structure and temporal dynamics of the clupeid-associated pelagic fish community across most of the Baltic basin. Salinity emerged as the dominant environmental driver, influencing 31 species. Seven distinct RCPs broadly tracked the southwest–northeast salinity gradient, from the saline Kattegat to the brackish northern basins, while 10 species clusters reflected corresponding ecological affinities. Modelled species richness peaked in the Kattegat and increased over the study period, particularly in the Gulf of Finland, Åland Sea, and Bothnian Sea. Between 2007 and 2023, RCP spatial extents shifted: marine-associated communities retracted westward while brackish and low-salinity assemblages expanded northward and eastward, consistent with projected climate-driven salinity reductions. Our findings provide a spatially explicit, basin-wide quantification of how environmental gradients structure the pelagic fish community and document ongoing reorganisation that has direct implications for biodiversity assessment and ecosystem-based management in the Baltic Sea.

Keywords Baltic Sea, fish community, acoustic and trawl survey, species distribution modelling, temporal trends, spatial community patterns

Introduction

The Baltic Sea is a semi-enclosed, brackish basin characterised by strong horizontal and vertical environmental gradients, particularly in salinity and temperature (Snoeijs-Leijonmalm and Andrén 2017). These gradients, along with oxygen availability and other hydrographic conditions, contribute to the Baltic Sea's distinct ecological structure. Extensive research has been carried out on individual species' responses to environmental gradients, particularly on commercial fish species. Several studies also include non-commercial species, often focusing on coastal areas (Olsson et al. 2012, Törnroos et al. 2019, Koehler et al. 2022), relying on bottom trawl surveys (Pecuchet et al. 2016, Ammar et al. 2021), or concentrating on one major non-commercial species like three-spine stickleback (Bergström et al. 2015, Olsson et al. 2019).

Beyond individual fish responses to environmental conditions, fish biodiversity and community composition have also received attention (Ojaveer et al. 2010, Törnroos et al. 2019). At the same time, most existing works on Baltic Sea fish biodiversity and community structure have been based on survey observations from specific regions or habitat types (Olsson et al. 2012, Pecuchet et al. 2016, Frelat et al. 2018). Basin-wide assessments of pelagic fish community patterns that integrate multiple species within a consistent predictive framework remain comparatively scarce.

The Baltic Sea ecosystem has experienced more pronounced temperature increases, and other anthropogenic pressures, compared to other large marine basins (Belkin 2009, Philippart et al. 2011, Reusch et al. 2018). Climate change has also altered precipitation regimes which, in turn, affect salinity and other key hydrological variables (Meier et al. 2006, BACC II Author Team 2015),

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leading to significant shifts in marine ecosystems (Möllmann et al. 2009, Olsson et al. 2012). Water hypoxia, which characterises the deeper basins, has intensified over the past century (Carstersen et al. 2014) and is expected to worsen with continued warming. Future climate projections indicate further increases in sea surface temperature, reduced sea-ice cover, increased river runoff, and declining salinity (Graham 2004, Meier et al. 2004, BACC Author Team 2008).

The environmental changes impact also the Baltic Sea fish communities, which comprise marine, freshwater, and anadromous species, many of which exist at the physiological limits of their environmental tolerance (Nielsen et al. 2001, Jørgensen et al. 2005, Bonsdorff 2006). Salinity constrains the distribution of several species, such as flatfish populations in the northern Baltic Sea (Bagge 1981), while freshwater species occur mainly in coastal and northern areas (Voipio 1981, Ojaveer 2002). Temperature also plays a critical role in species distributions in the Baltic and environmental conditions also influence reproduction, recruitment, feeding, and population dynamics. Baltic cod, for example, spawns at salinities above 11 PSU (Nissling and Westin 1997), while sprat distribution and reproduction are temperature-limited (Muus and Nielsen 1999, MacKenzie and Köster 2004), as is the recruitment of pike perch and perch (Heikinheimo et al. 2014, Kokkonen et al. 2019). Fish populations in the Baltic Sea have also been impacted by large environmental variability, leading to changes in growth, survival, and production rates (Viitasalo and Bonsdorff 2022, Rosciszewski-Dodgson and Cirella 2024). Several species have experienced declines over recent decades, including flounder and cod, which have decreased drastically since the 1980s due to eutrophication and climate change (Jokinen et al. 2015, Casini et al. 2019, ICES 2025). Hypoxia has further contributed to the decline of cod (Eero et al. 2015, Casini et al. 2016) while populations of some flatfish species, like plaice, have been increasing in the most recent years (ICES 2024), and temperate marine pelagic species, like anchovy, have been increasingly present in the southwestern basin (Petitgas et al. 2012).

While species-specific responses to environmental variables and regional or coastal biodiversity patterns are well understood (Koehler et al. 2022), integrative assessment of pelagic fish communities that link environmental drivers to multi-species distribution patterns across the entire Baltic Sea remain limited (Peltonen and Weigel 2022). In particular, community-level patterns of non-commercial species emerging from their combined spatial distribution have rarely been examined consistently across space, and time. Recent findings by Peltonen and Weigel (2022) suggest that marine species are impacted by habitat contractions, while freshwater species are benefitting from an expansion of suitable habitats, in Finnish coastal areas. However, pelagic community assemblage patterns, and changes in them, have not yet been explored across the entire Baltic basin using fishery-independent information from pelagic acoustic and trawl surveys.

Here, we analyse long-term data from the Baltic International Acoustic Survey (BIAS), a fishery-independent survey primarily targeting the clupeid herring and sprat but consistently sampling the broader pelagic fish assemblage across the Baltic Sea. By modelling their spatial patterns, we seek to improve our understanding of how environmental changes influence clupeid-associated fish communities' distribution. The comprehensive spatial coverage, temporal extent, and taxonomic resolution of the BIAS dataset, combined with a consistent modelling framework, allow for a detailed exploration of fish community-level patterns, and changes in them, across the entire Baltic Sea, that complements and extends previous studies.

Materials and methods

Study area

The study area encompasses most of the Baltic Sea sub-basins, including the Kattegat, Baltic Proper, Bothnian Sea, and Gulf of Finland (Fig. 1). The inclusion of the Kattegat, not part of the Baltic Sea *stricto sensu*, aligns with the design of the BIAS survey and with the definition of the Baltic Sea Area according to the Baltic Marine Environment Protection Commission (HELCOM). Geographically, the study region is bounded by the coordinates 9.5°E to 30.3°E (west to east), and 53.5°N to 63.5°N (south to north) and is restricted to at most 30 km away from the closest BIAS trawl location. To avoid extrapolating our findings from offshore data to very distinct environmental conditions and species composition, in coastal areas, the study area was limited further by removing coastal areas (distance to shore $<$ 3 km for ICES subdivisions 22 and 23; $<$ 6 km for subdivisions 21 and 24; and $<$ 10 km for other subdivisions).

Fish data

The BIAS surveys are conducted annually in September and October, and they follow internationally recognized protocols of active acoustics and scientific fishing—by pelagic trawl—for providing abundance indices of Baltic small pelagic fish stocks to be used in stock assessment (ICES 2017). Although BIAS targets particularly herring and sprat, all other fish species captured in the hauls are also recorded during the surveys, offering a unique opportunity to gather comprehensive data on fish biodiversity associated to herring and sprat. Each survey comprises approximately 200 haul stations, with at least two hauls performed per ICES statistical rectangle, each measuring 30 min of latitude by 1 degree of longitude.

We retrieved information on $N = 2535$ hauls (41 invalid hauls and 18 hauls from the Gulf of Riga were excluded from the original dataset) collected in the years 2007–2023 by eight countries (Estonia, Finland, Germany, Latvia, Lithuania, Poland, Russia, and Sweden; Fig. 1). Among the included hauls, $N = 119$ were located in coastal areas, i.e. outside of the study area. Haul-specific data, such as the start coordinates, trawl duration, as well as the trawl minimum and maximum depths, were available for all the hauls. We appended these data to environmental covariates corresponding to the start location of the trawls (see the *Environmental data* section). In the analysed hauls, a total of $N = 96$ unique taxon codes (AphiaID) were recorded, of which the most common $N = 45$ ish taxa (to be called species hereafter; Table S1) were included in the analyses (see Supplementary Material S1).

Environmental data

The environmental variables selected as explanatory variables to the analyses encompassed water physics, water chemistry, and topography (Table 1). Environmental predictors covered the same geographic area and time span as the survey data (mid-September

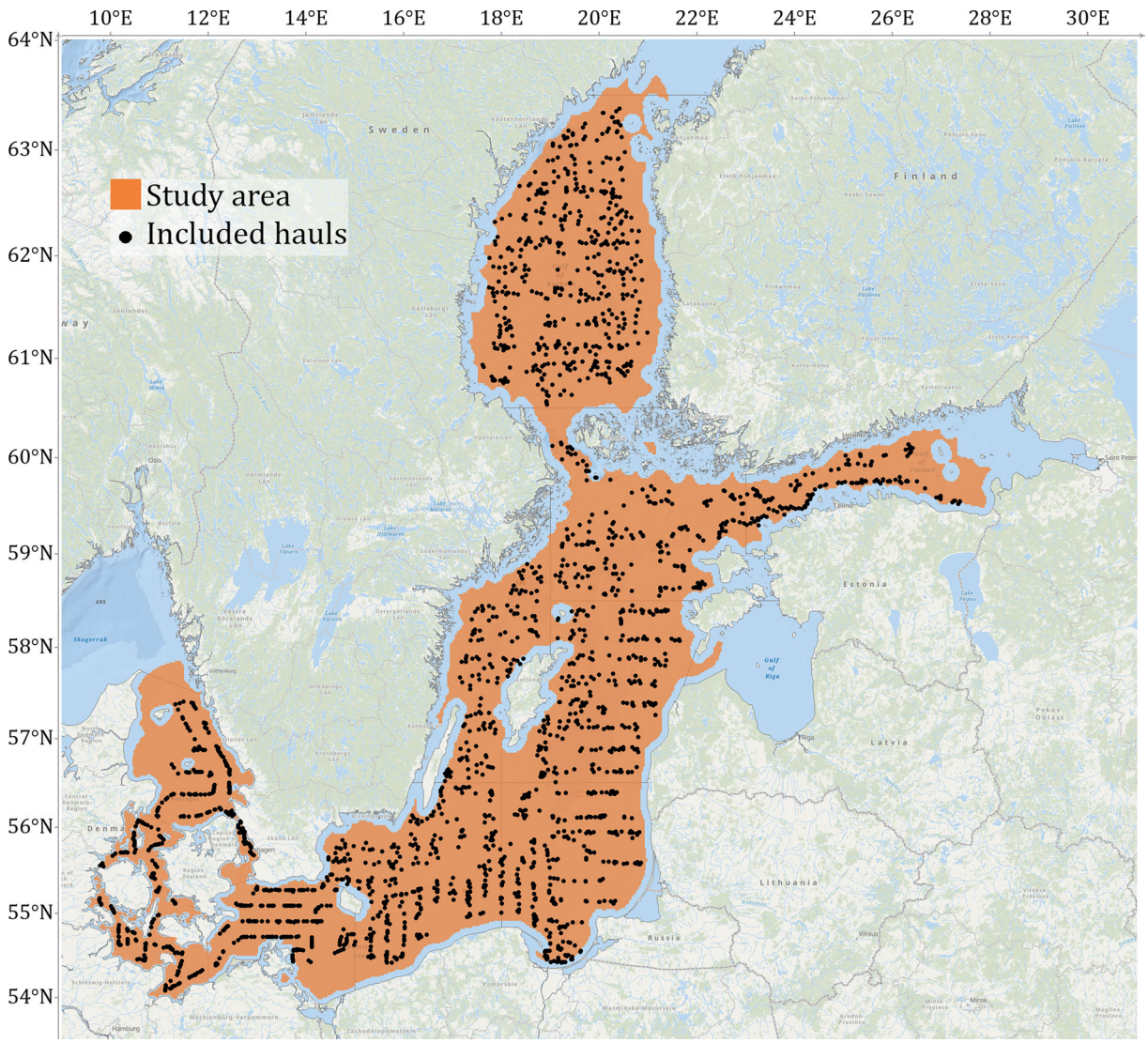

Figure 1 The study area (orange) in the Baltic Sea and the trawl hauls' locations (black dots).

Table 1. Water quality and topography variables, units, water layer, and season from which the samples were included.

Variable	Unit	Water layer	Season	Data source
Bathymetry	m	–	Static value	GEBCO
Distance to shore	km	–	Static value	Calculated from coastline
Distance from bottom	m	–	–	Calculated from bathymetry and depth
Depth	m	–	–	BIAS metadata
Salinity	PSU	0–103 m	September-October	CMEMS
Water transparency	m	0 to maximum Secchi depth	September-October	CMEMS
Temperature	°C	0–103 m	September-October	CMEMS
Dissolved bottom oxygen	mmol m^{-3}	Largest depth sampled	September-October	CMEMS

CMEMS, Copernicus Marine Environment Monitoring Service; GEBCO, General Bathymetric Chart of the Oceans.

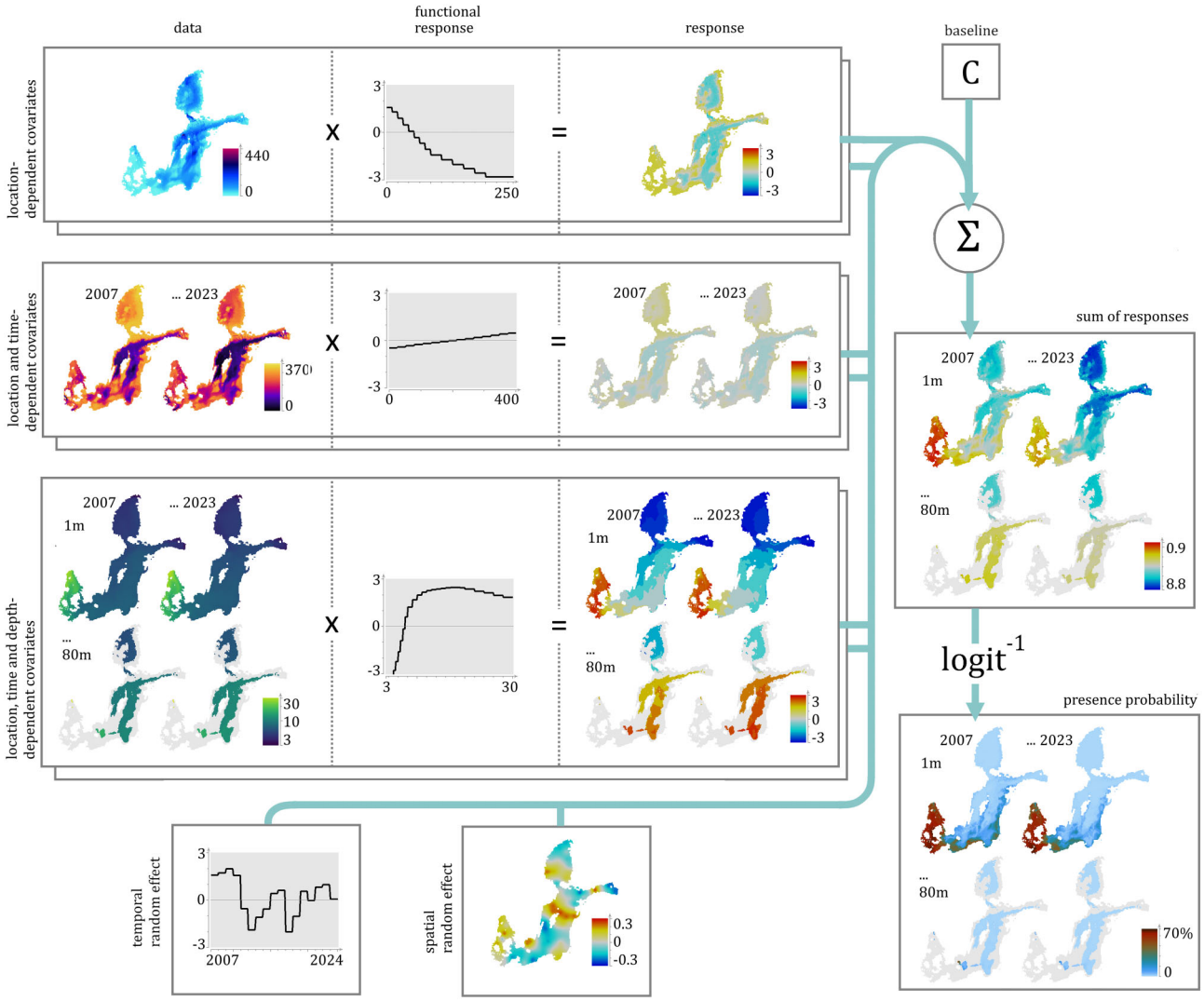

Figure 2 Conceptual illustration of the modelling workflow.

to end October) in 4 km^2 grid cells (Figs S2–S8). Salinity, temperature, water transparency and dissolved bottom oxygen data were sourced from the Copernicus Marine Service (CMEMS) with daily averages for the survey period of each year. Temperature and salinity were obtained from the CMEMS vertical grid, which consists of layers with exponentially increasing thickness—ranging from 0.5 m near the surface (e.g. 0–0.5 and 0.5–1.52 m) to over 10 m at depth (e.g. 70–80, 80–91, 91–103 m)—spanning the full water column. For each haul, the temperature and salinity value from the layer corresponding to the haul depth was used. Bathymetry data were sourced from the General Bathymetric Chart of the Oceans (GEBCO; Fig. S2). Trawl depth (hereafter 'depth') and time of the day were obtained from the BIAS survey dataset. Distance to shore was calculated as the geodesic (haversine) distance to the nearest coastline point (Fig. S3).

Statistical Analysis

Species distribution models

The species distribution modelling process is illustrated in conceptual Fig. 2. For each of the $N = 45$ species, we fitted a species distribution model

$$p(Y_j|X,\ \theta_j) = \prod_i \text{Bernoulli}\left(Y_{ij}|\ \pi_j\left(X_i, \theta_j\right)\right),$$

where $D_j = \{Y_{ji}, X_i\}_{i=1}^n$ is the data collected in the BIAS survey about the presence of species j, with i being an index of the observation, Y_{ij} is the presence indicator of the species j in the i^{th} observation, X_i is the vector of covariates related to this observation, and $\pi_j(X_i, \theta_j)$ denotes the probability of observing the species j in the trawl with the covariates X_i. We modelled it as

$$\pi_j\left(X, \theta_j\right) = \text{logit}^{-1}\left(C_j + \sum_{k=1}^{11} f_{jk}\left(X^{(k)}\right)\right)$$

$$= \text{logit}^{-1}\left(C_j + \underbrace{\sum_{k=1}^{8} f_{jk}\left(X^{(k)}\right)}_{\text{Environmental responses}} + \underbrace{\sum_{k=9}^{10} f_{jk}\left(X^{(k)}\right)}_{\text{Random effects}} + \underbrace{f_{j11}\left(X^{(11)}\right)}_{\text{Sampling effort}}\right),$$

where C_j is the baseline logit probability of species j presence and $f_{jk}(\cdot)$ denotes functional response to the k^{th} covariate group $X^{(k)}$. Among these, the trawl duration acts as an offset accounting for sampling effort ($k = 11$). The response to the coordinates

($k = 10$) and year ($k = 9$) represent spatial and temporal random effects, which account for the excess variation not explained by the environmental covariates ($k \in \{1, \ldots 8\}$). Functional responses to depth and distance to bottom account for a fish's preferred depth layer in the water columns. Since this preference may change with time of day, these two functional responses were constructed to vary with time of day (that is, joint effect with a time of day; see Supplementary Material S1).

Posterior predictive analyses

After calibrating the model, we estimated the species' probability of presence for the whole study area and period. Let $\tilde{i}$ denote the particular spatio-temporal location specified with year, longitude, latitude, and a specific depth. We denote the posterior probability of observing species j in this locus with

$$\tilde{\pi}_j\left(X_{\tilde{i}}\right) = \int \pi_j\left(X_{\tilde{i}}, \theta_j\right) p\left(\theta_j | D_j\right) d\theta_j$$

where $p(\theta_j|D_j)$ denotes the (Bayesian) posterior distribution of all parameters for π_j. We estimated $\tilde{\pi}_j$ for all grid cells (approximately 1×1 nautical miles in size, $n = 79\,376$) in the study area, all studied years (2007–2023, $n = 17$) and all depth layers, up to 103 meters, available at a given location (max n = 28).

We then computed the species' average probability of presence in water column at location by taking a weighted average of all available depth layers (up to 103 meters) at this location (the weight being the proportion of water in a given depth layer out of the total water column at a location):

$$\tilde{\pi}_j\,(\text{year, long, lat}) = \sum_{\tilde{i} \in \mathrm{I}_{\text{long,lat}}} \frac{[\text{depth layer height}]_{\tilde{i}}}{\max\left(\text{bathymetry}_{\text{long,lat}}, 103\right)} \tilde{\pi}_j\left(X_{\tilde{i}}\right)$$

where $\mathrm{I}_{\text{lat, long}}$ collects the indexes for all depth layers at a particular spatial location (long, lat).

We additionally calculated expected species richness (in one trawl haul) for each spatiotemporal location (year, longitude, latitude, and depth) by summing the species-specific occurrence probabilities. We then calculated the average species richness in water column similarly to species' average probability of presence in water column. See Supplementary Material S1 for a detailed description of the model and covariates.

To assess whether the covariate effects were statistically significant, we computed their posterior predictive credible envelopes and checked whether these envelopes contained zero. This is analogous to checking whether zero is included in the posterior credible interval of fixed effects in linear models. Moreover, to assess the relative role of the different environmental drivers in explaining spatiotemporal variability in species occurrences, we applied the predictive variance partition approach of Schulz et al. (2025) and calculated the proportion of variance in the linear predictor explained by each of the environmental covariate and random effects (see Supplementary Material S1, Section 12 for detailed explanation).

Community structure analysis

To study the spatial patterns in pelagic fish communities and temporal changes in them, we clustered the geographical locations into seven Regions of Common Profile (RCPs) based on their species-specific occurrence probabilities (Woolley et al. 2020). We applied the K-means clustering algorithm ($K = 7$) to all raster points and years. We named the clusters with Roman numerals and called the vectors of cluster-specific mean species observation probabilities 'species profiles'. For visualization purposes, we also clustered the species into groups with similar distribution maps, an approach conceptually similar to species archetype distributions (Dunstan et al. 2011). We then calculated the mean of standardised distribution maps across the species in each group for plotting (all the species-wise distribution maps are available in the Supplementary Material S2).

Results

Pelagic fish communities' structure

Seven distinct RCPs were identified, each representing a region of consistent community structure (Fig. 3, panel A). Following the HELCOM sub-basin nomenclature, RCP I corresponds to the Kattegat (salinity 12–20 PSU); RCP II to the Belt Sea, Danish Straits, and a large part of the Arkona Basin (8–20 PSU); and RCP III to the southern Bornholm and Gotland basins. The remaining RCPs reflect progressively lower-salinity environments: RCP IV covers the northern Bornholm Basin and Eastern Gotland Basin; RCP V the Western Gotland Basin and Baltic Proper; RCP VI encompasses the Gulf of Finland, the Åland Sea, and eastern Bothnian Sea; and RCP VII the Bothnian Sea.

Between 2007 and 2023, the RCP spatial extents shifted, with some RCPs contracting and others expanding (Fig. 4). RCP II retracted westward, while RCP III expanded westward. Similarly, RCP IV contracted significantly southward and was replaced by RCP V. In the north, RCP VI significantly extendend its range to encompass the Åland Sea and part of the eastern Bothnian Sea, largely at the expense of RCP VII, which contracted accordingly.

The distribution of some species also exhibited changes over time between 2007 and 2023 (Fig. S13). *Engraulis encrasicolus*, for instance, displayed marked interannual variability with occurrence probabilities ranging between 5% and 20%. Other species showed more directional trends over the study period. *Scomber scombrus*'s probability of occurrence increased from 3% to 10%, similarly to *Nerophis ophidion*'s which increased from near zero to ∼9% (RCP VI-VII), *Platichthys flesus* which increased from ∼5% to ∼20%, and *Pungitius pungitius* from ∼20% to ∼35%. Conversely, *Trachurus trachurus* probability of occurrence declined from 17% to ∼7% over the 17-year period.

Environmental drivers of fish distribution

In parallel, ten distinct clusters were identified based on similarity in the species' distribution patterns over the 17-year study period (Fig. 3, panels B and C). Cluster (a) comprises the three ubiquitous species (*Clupea harengus, Sprattus sprattus*, and *Gasterosteus aculeatus*). Cluster (b) includes typical marine species associated with higher salinity and largely restricted to the Kattegat (*S. scombrus*, *T. trachurus, Sardina pilchardus*, *Merluccius merluccius*, among others). Cluster (c) consists of species associated with saline waters and commonly occurring in both the Kattegat and Belt Sea, while cluster (d) includes species occurring predominantly in the Kiel Bay and Bay of Mecklenburg, and to a lesser extent in the Kattegat and Belt Sea. Cluster (e) is formed by *Gadus morhua* and *Enchelyopus cimbrius*, occurring predominantly in the Bornholm Basin and Southern Baltic Proper. Cluster (f) contains species associated with intermediate salinity (*Cyclopterus lumpus*,

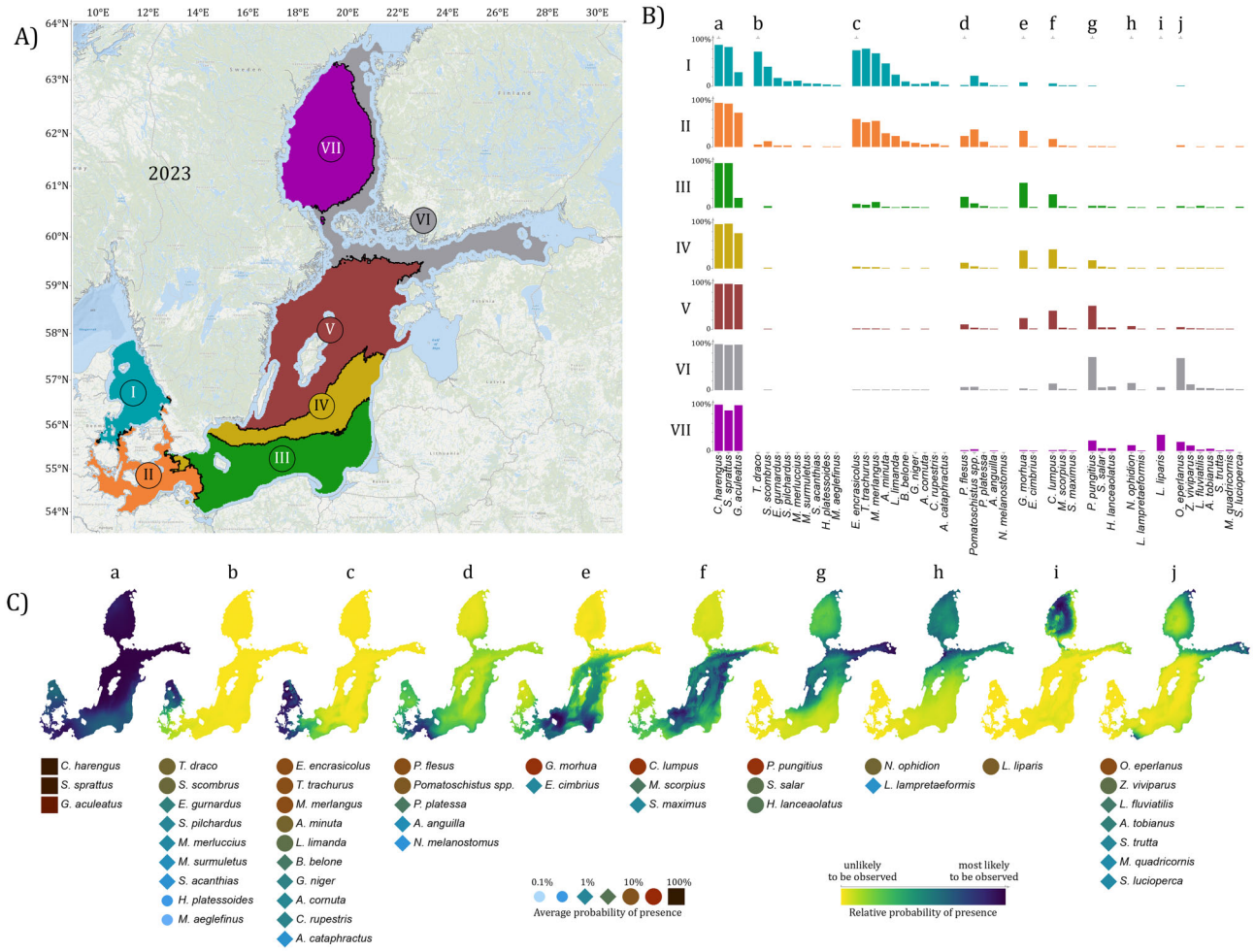

Figure 3 Cluster analysis and summary of species distribution maps. (A) Geographical regions with consistent community structures (i.e. RCPs) in 2023; (B) Species average occurrence probabilities in RCPs (i.e. species profiles); (C) The average occurrence probability maps of species clusters (i.e. species archetype distributions) and species-specific average occurrence probabilities over the study area.

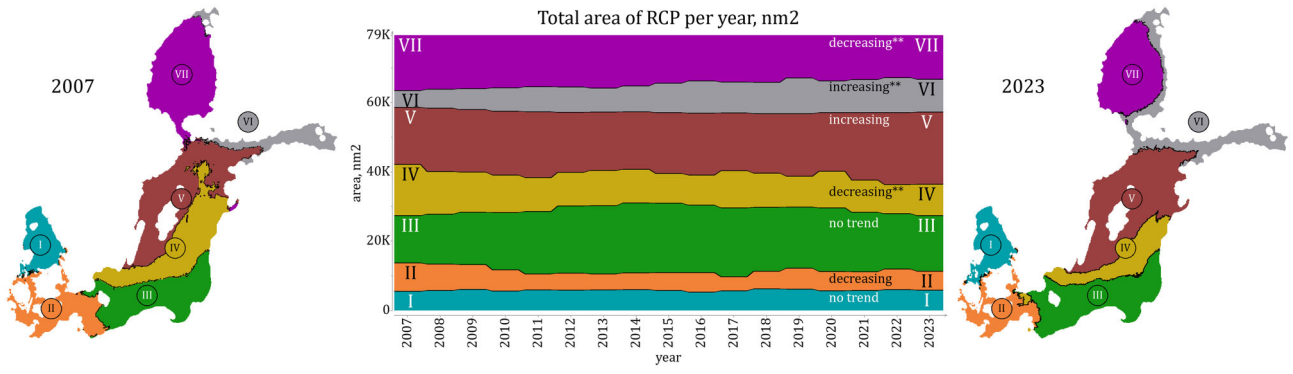

Figure 4 Change in geographical regions of common species profile (i.e. RCPs) between 2007 and 2023. Bayesian linear regression was used to access trends in RCP extends: trends whose 90% Credible interval (CrI) excluded zero were marked as increasing or decreasing. Additionally ∗ indicates 99% CrI and ∗∗ indicates CrI 99.9%.

among others) occurring predominantly in the Bornholm Basin and throughout the Baltic Proper. Cluster (g) consists of species strongly associated with the Gulf of Finland but also occurring in the Baltic Proper and Bothnian Sea. Cluster (h) is represented by *Nerophis ophidion* and *Lumpenus lampretaeformis*, restricted to the Bothnian Sea and Gulf of Finland, while cluster (i) is represented solely by *Liparis liparis*, occurring offshore in the Bothnian Sea. Finally, cluster (j) comprises the remaining species and includes a mix of freshwater and anadromous species restricted to areas closer to the coast.

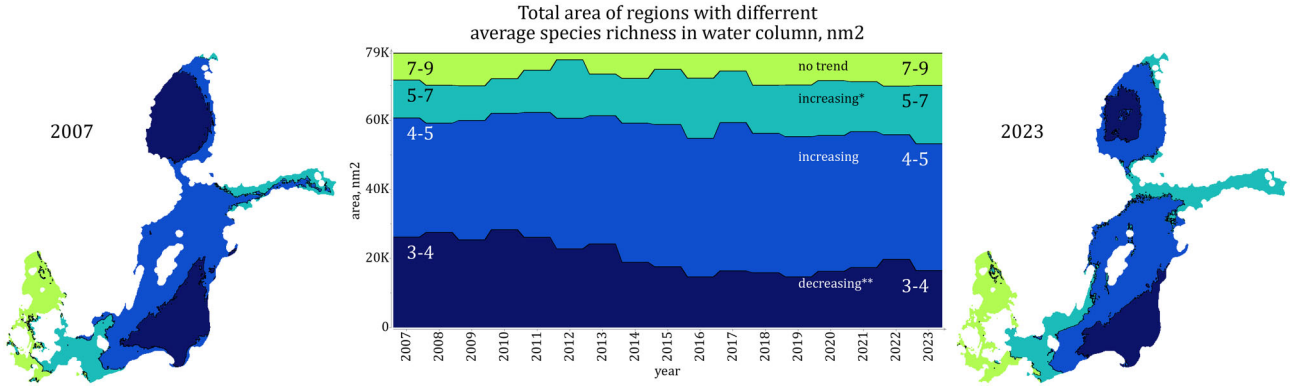

Figure 5 Predicted species richness in the study area by year, from 2007 to 2023. Bayesian linear regression was used to access trends in RCP extends: trends whose 90% Credible interval (CrI) excluded zero were marked as increasing or decreasing; Additionally $*$ indicates 99% CrI and $**$ indicates CrI 99.9%.

Salinity emerged as the primary environmental driver of species occurrence, influencing 31 species, most of which exhibited clear threshold responses (Figs. S14 and S30), and explaining the greatest share of variance in occurrence probabilities for 27 of them (Fig. S31). Of these, 22 were limited by low salinity—predominantly euryhaline and marine species absent from the fresher northern basins—while nine were constrained by higher salinity levels. These patterns are clearly mirrored by the species clusters and RCPs. However, salinity mostly explained spatial variability in species occurrences since its variance partition remained approximately constant over the years for all species (Fig. S32). Temperature influenced 12 species, split between those favouring higher and lower values (Fig. S15). Trawl depth also influenced 12 species, some of which showed different depth preferences depending on the time of day (Fig. S20). Namely, for *Limanda limanda* the probability of being found deeper in the water column diminishes at night and increases during daytime, while other species, such as *Squalus acanthias,* are more commonly found at greater depths during both night and day. Visibility influenced eight species, split between those favouring higher and lower values (Fig. S18). Bottom dissolved oxygen affected six species, all limited by lower oxygen levels (Fig. S17). Bathymetry influenced five species, two of which were negatively associated with greater seafloor depth (Fig. S16). Distance to shore influenced five species, all favouring areas closer to the coast (Fig. S19). Finally, distance from bottom influenced four species, some of which also showed time-of-day depth preferences (Fig. S21).

Species richness

Average species richness, derived from stacking individual species model predictions, ranged between 3 and 9 (Fig. 5). The modelled species richness reached its highest values in the Kattegat. In the sampling data, the number of species found per haul varied between 0, and 16. Overall, species richness increased significantly over the years, particularly in the Gulf of Finland, Åland Sea, and Bothnian Sea.

Discussion

By integrating systematic BIAS monitoring data with species distribution modelling and community-level clustering, this study provides a basin-wide assessment of how environmental gradients, particularly salinity, have structured pelagic fish assemblages in the Baltic Sea and how these assemblages have varied over nearly two decades. Our results reveal that community-level distributions have undergone clear reorganisation, with some taxa expanding into new areas and others contracting. These changes are consistent with the strong environmental gradients of the Baltic Sea, a semi-enclosed and brackish system that is highly sensitive to climate variability and human pressures.

Salinity as the primary structuring force

The salinity thresholds reflected in our species distribution models are consistent with experimentally established physiological limits. *G. morhua* (cod) is among the most thoroughly documented cases: eastern Baltic cod populations have adapted to brackish conditions through physiological differentiation; however, prolonged exposure to reduced salinity imposes osmotic stress on this species (Kijewska et al. 2016), thus potentially reducing energy for growth, movement, and feeding. Our results mirror this constraint and likely reflect metabolic performance in low-salinity waters, with cod occurrence declining sharply below ~9 PSU—a pattern that at the community level is captured by the restriction of Cluster e species to RCP IV, covering the Baltic Proper. At the other end of the gradient, freshwater and low-salinity-tolerant species such as *O. eperlanus* were constrained by higher salinities, reinforcing that physiological limits operate bidirectionally along the salinity gradient.

These species-level constraints scale up to organise the basin-wide community structure we identified, with the seven RCPs broadly tracking the southwest-to-northeast salinity gradient from the saline Kattegat (RCP I) to the brackish northern basins (RCPs VI–VII). This mirrors findings from Frelat et al. (2018), who identified three spatially distinct sub-assemblages of demersal fish structured along the salinity gradient from the Kattegat to the Baltic Proper. A similar pattern was described by Engelhard et al. (2011) for North Sea fish assemblages, who showed that biogeographic ecotype—reflecting species' thermal and salinity affinities—was the single most powerful predictor of community-level abundance trends, explaining more variance than trophic guild, body size, or habitat preference. In our context, salinity plays an analogous structuring role, with ecologically

coherent species clusters (e.g. Clusters b-c for marine taxa restricted to high-salinity areas; Clusters h–j for glacial relicts and freshwater taxa in low-salinity northern basins) corresponding closely to discrete RCPs. While salinity tolerances of Baltic fish are well documented in trait-based syntheses (e.g. Koehler et al. 2022, Froese and Pauly 2025), our contribution lies in providing spatially explicit, basin-wide quantification of how these constraints manifest in pelagic community structure—and, critically, how they are already shifting under ongoing environmental change, as highlighted by the retraction of marine RCP clusters and expansion of brackish and freshwater RCP clusters, in line with earlier findings and/or predictions (MacKenzie et al. 2007, Peltonen and Weigel 2022). Variance partitioning further confirmed that salinity's influence was predominantly spatial rather than temporal, with its contribution to explained variance remaining approximately constant across years (Fig. S32), consistent with the Baltic's near-permanent southwest-to-northeast salinity gradient.

Although salinity dominated community structure, other environmental factors also left traceable imprints on RCP patterns. For example, cold-adapted species such as *L. liparis* and *N. ophidion* grouped in northern, cooler RCPs (VI–VII), while marine taxa that have recently appeared in the Baltic, such as *E. encrasicolus*, were more common in southern, warmer RCPs (I–II). This suggests that temperature acts largely in synergy with the dominant salinity and geographical gradients, reinforcing but not independently structuring community boundaries.

Species-level trajectories reinforce the interpretation of community reorganisation. *E. encrasicolus's* interannual variability in the southwest Baltic (5%–20%) likely reflects occasional incursion of this species from the North Sea, which cannot form self-sustaining populations in the Baltic (Ojaveer et al. 2010). In contrast, other species displayed more directional changes over the study period. The decline of *T. trachurus* is consistent with the westward retraction of RCP II and the encroachment of more brackish-tolerant communities captured by the expanding RCP III. In contrast, *N. ophidion's* expansion suggests range extension into previously marginal habitats; however, the population dynamics of this species remain poorly understood (Ojaveer et al. 2010). The increase of *N. ophidion* in the northern basins aligns with the northward and eastward extension of RCP V and the expansion of RCP VI into the Åland Sea and eastern Bothnian Sea, consistent with a broader shift towards brackish-tolerant community composition in the north. Taken together, these species-level trajectories and the concurrent reorganisation of RCP spatial extents—with marine-associated RCPs (II and IV) contracting and brackish or low-salinity RCPs (III, V, and VI) expanding—point to an ongoing, basin-wide restructuring of pelagic fish communities that is consistent with projected reductions in Baltic salinity under continued climate change (Meier et al. 2004, Dahlke et al. 2020).

Fish diversity patterns

The Baltic Sea is one of the most species-poor marine ecosystems globally, with low fish diversity primarily driven by the low salinity levels, which create physiologically stressful conditions for both marine and freshwater species (Voipio 1981; Ojaveer and Kalejs 2005). Overall, approximately 100 fish species are established in the Baltic Sea, but when the transitional Kattegat area is included, this number rises to about 200 (Ojaveer et al. 2010). Diversity is unevenly distributed following the salinity gradient: several subbasins in the northeastern Baltic support around 70 species, while the Bothnian Sea holds fewer than 50 (HELCOM 2007; Urho and Lehtonen 2008).

Given that our predicted species richness underestimates the total pelagic species richness—due to the nature of the BIAS sampling design—we focused on patterns of variation rather than absolute values. Our results reveal that, for the clupeid-associated pelagic fish community, species richness reaches its highest in the Kattegat, confirming existing literature; however, unlike the patterns described in the literature above, it does not reflect clear environmental gradients across the basin. Our study on fish diversity is integrated into a well-established body of evidence from the region, while extending the assessment to the open pelagic domain. Most previous studies of environmental drivers of Baltic fish biodiversity have focused on coastal and nearshore systems (e.g. Elliott and Dewailly 1995; Pihl and Wennhage 2002; Peltonen and Weigel 2022), or on demersal communities in the southern and western Baltic (Pecuchet et al. 2016; Smoliński and Radtke 2017; Frelat et al. 2018). Our basin-wide, pelagic perspective complements both this coastal literature and the open-sea demersal assessments, while expanding the coverage to the Gulf of Finland and the Bothnian Sea.

Although environmental factors remain the primary drivers of Baltic fish diversity and community structure, human impacts, such as overfishing of commercial species, also play substantial roles in shaping community composition (Bergström et al. 2018). These factors were not incorporated into our model but remain important considerations for biodiversity assessments.

Beyond interspecific diversity, genetic studies reported that the Baltic Sea exhibits considerable intraspecific biodiversity, with locally adapted populations of cod, herring, sprat, flounder, and turbot identified along the salinity gradient (Nielsen et al. 2003, 2004, Jørgensen et al. 2005; Hemmer-Hansen et al. 2007; Limborg et al. 2009). This indicates that some species have differentiated into different populations and genetically segregated to enhance resilience to environmental change and exploitation. However, projected climate scenarios pose a serious threat to both inter- and intraspecific diversity. The projected decrease in salinity levels, due to increased riverine input driven by higher precipitation, could further compromise biodiversity by reducing habitat suitability for species closely associated with high-salinity areas, thus exacerbating the already low diversity.

Opportunities and limitations

Our study used standardised autumn data from the BIAS. The broad taxonomic approach, covering 45 fish taxa (44 species and one genus) comprising ∼20% of fish species in the Baltic Sea (Ojaveer et al. 2010), demonstrates the value of systematically including non-commercial species in fishery-independent pelagic surveys, thereby complementing the extensive existing literature on Baltic Sea fish biodiversity with modelling-based, basin-wide insights. The sampling design of the BIAS, however, is not aimed at capturing full community diversity, which introduces biases in detectability, particularly for rare species. As a result, the species recorded in this survey are best understood as those co-occurring within clupeid-associated habitats, and our results should be interpreted accordingly—the community we characterise is not a comprehensive census of

Baltic fish biodiversity but rather a clupeid-centred assemblage. Additionally, the species richness resulting from our models' predictions is an underestimate of the true species richness at any given location.

Furthermore, the BIAS dataset is restricted to observations collected in September and October, which may not fully capture seasonal or year-long species distributions. Some species, particularly those undertaking seasonal migrations like the garpike (*Belone belone)*, might exhibit different spatial patterns at other times of the year. Therefore, our findings should be interpreted within the temporal window of the sampling period. A further consideration is whether the observed temporal changes in species distributions and community structure could reflect shifts in sampling locations over time rather than genuine biological change. Several features of our modelling framework address this concern. While the environmental covariates capture the ecological character of each sampling location, the spatial random effect accounts for residual location-specific variation beyond what the covariates explain, and the temporal random effect isolates year-to-year variation that remains after conditioning on both environmental conditions and spatial structure. Notably, the species exhibiting the clearest temporal trends show weak or diffuse spatial random effects, indicating that their temporal signals are not confounded with fixed geographic patterns. Together, these modelling choices provide reasonable confidence that the interannual changes reported here reflect genuine biological reorganisation rather than artefacts of changing sampling locations. Additionally, due to the nature of the BIAS sampling locations, we excluded the coastal areas from our model predictions. Finally, model performance was influenced by species prevalence. In general, models yielded more reliable predictions for species recorded in at least 100 sampling stations.

Conclusions

This study provides the first community-level modelling of pelagic fish species distributions across the Baltic Sea using standardised BIAS catch data. By covering 45 taxa, it highlights the potential of catch records of non-commercial species to extend biodiversity assessments beyond commercial species. Salinity emerged as the dominant driver of habitat suitability, with additional effects of temperature, trawl depth, bathymetry, and water transparency. Our results also show that, apart from a few ubiquitous species, most species are spatially restricted by environmental conditions, reflecting the strong filtering effect of the Baltic's gradients. Our findings highlight the vulnerability of marine-associated species to projected salinity declines and the relative resilience of brackish- and freshwater-adapted taxa, suggesting that climate-driven environmental change is likely to accelerate the restructuring of fish communities. These shifts have direct implications for fisheries management and conservation, as changing species distributions and associations may alter ecosystem functioning, trophic interactions, and the provision of ecosystem services.

Future studies should build on this modelling framework by extending it to benthic species, across the full Baltic Basin, to capture the full community spectrum, assessing other times of the year to account for seasonal variation, and incorporating abundance or biomass data to detect shifts in yields. Such extensions would further enhance the ability to link existing knowledge to projections of biodiversity responses under ongoing climate change, particularly in light of anticipated alterations in salinity and temperature regimes across the Baltic Sea.

Authors contribution

Valeria Mobilia and Mikhail Shubin contributed equally to this work. Valeria Mobilia (Writing—original draft [lead], Writing—review & editing [lead], Data curation [supporting], Conceptualization [equal]), Mikhail Shubin (Data curation [lead], Formal Analysis [lead], Methodology [lead], Writing—original draft [supporting], Writing—review & editing [equal]), Nicolas Goñi (Conceptualization [equal], Resources [equal], Writing—review & editing [equal]), Jarno Vanhatalo (Conceptualization [equal], Formal Analysis [equal], Funding acquisition [supporting], Project administration [equal], Supervision [lead], Writing—review & editing [equal]).

Supplementary material

Supplementary data is available at *ICES Journal of Marine Science* online.

Conflicts of interest

None declared.

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Data availability

The code is published at https://github.com/EnvStat/pelagic_fish_assemblages (https://doi.org/10.5281/zenodo.22035195). The data is published at https://doi.org/10.5281/zenodo.22027768. The results are published at https://doi.org/10.5281/zenodo.22014190. The datasets were derived from sources in the public domain: ICES Acoustic-Browse Submissions.

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