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Original Article

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Abstract

The Baltic Sea ecosystem is highly impacted by multiple human induced pressures and climate change. Despite this, restoration actions are often directed towards individual measures, ignoring trade-offs and synergies that may affect multiple ecosystem processes and services. Due to the bathymetry of the Baltic Sea, sub-basins may be differently impacted by pressures, making it challenging to observe common patterns and co-occurring processes. Here, we provide the first comprehensive analysis of systemic spatiotemporal changes of food webs across seven Baltic Sea sub-basins. Our analyses cover 26–46 years of harmonized data collection and apply integrated trend analysis in seven sub-basins. We compare temporal trends of key structural food web components, focusing on relative changes between trophic guilds, and interpret these changes in relation to variations in key environmental factors and human pressures. We found shifts in trophic-guild balance and ecosystem reorganization in all sub-basins, which were associated with regional changes in human induced pressures. According to the EU Marine Strategy Framework criteria, this indicates poor food web status across all sub-basins. In some cases, the altered food web regimes have remained despite reductions in the pressures that contributed to the initial shift. Climate warming has played a role, in some cases exacerbating the effects of other human induced pressures. Our results underscore that coordinated actions to reduce pressures such as fishing and nutrient loading are needed to improve food web status in the Baltic Sea.

Keywords integrated ecosystem analysis, fisheries, eutrophication, ecosystem-based management, good environmental status, climate change

Introduction

Marine ecosystems are subject to multiple human induced pressures, with impacts on population dynamics, species distributions and food web properties (Korpinen et al. 2021, Viitasalo and Bonsdorff 2022). These impacts are amplified by the increasing effects of climate change and are predicted to more than double by mid-century (Meier et al. 2022, Halpern et al. 2025). The responses of ecosystems to multiple drivers are often complex and challenging to unravel, as they involve interactions between many species at different spatial and temporal scales (Tomczak et al. 2022, Frelat et al. 2022), as well as interactive effects of drivers on species and species interactions (Beauchesne et al. 2021). Despite this, management is often directed towards individual species or pressures (ICES 2024a), ignoring trade-offs and synergies between management measures that may affect multiple ecosystem processes and services. To ensure effective and sustainable resource use, there is a need to better understand how ecosystems and food webs respond to external pressures.

Such a holistic understanding of ecosystem change supports ecosystem-based management (EBM) and enables the joint efforts across marine sectors to more effectively manage, conserve, and

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restore marine ecosystems (Long et al. 2015, Levin and Möllman 2015). However, to achieve this goal, analytical tools are required to systematically evaluate the status of ecosystems and help determine how species and food webs respond to different pressures (Palumbi et al. 2009, Tam et al. 2017, Eero et al. 2021). Integrated Ecosystem Assessment (IEA) frameworks (Levin et al. 2009) are increasingly developed to support both sectoral management, such as fisheries, and integrated strategies for marine regions, where there is a need to address the complex interplay between management options (Harvey et al. 2020). Furthermore, IEA frameworks can help develop more coherent monitoring databases (Tam et al. 2017), and clarify issues related to differences in responses across various ecological settings, spatially and over time (Pecuchet et al. 2020).

A global concern for EBM implementation is assessing how food webs have changed over time and whether these changes are desirable from different perspectives (Heymans et al. 2014, Maureaud et al. 2017). This can help resolve other challenges, such as shifting baselines, data gaps, and ecosystem complexity (Pinnegar and Engelhard 2008, Tam et al. 2017, Frelat et al. 2022). In the European Union (EU), EBM is underpinned by the Marine Strategy Framework Directive (MSFD), which aims to "protect the marine ecosystem and biodiversity upon which our health and marine-related economic and social activities depend" (EC 2022). The MSFD covers EU marine systems based on eleven descriptors. By this, it is one of the few multinational initiatives to provide coherent assessment across different sea areas that can guide coordinated policy and management at national and international levels (Heymans et al. 2014, Maureaud et al. 2017). Food webs are included as one of the MSFD descriptors (D4), and the two main criteria for Good Environmental Status (GES) of food webs are based on determining if the diversity within key trophic guilds and the balance between trophic guilds are affected adversely by human induced pressures (EC 2022). However, EU countries' reporting for food webs has so far been inconsistent, with differing conceptual basis, data availability, and analysis (Boschetti et al. 2021), showing a clear need to better align the assessment of food web status across national boundaries.

In the Baltic Sea, spatiotemporal food web dynamics occur over a marine region shared by nine countries, all of which but Russia are EU member states. Food web dynamics are shaped by natural factors (e.g. gradients in abiotic and biotic factors) but also by variation in human induced pressures such as fishing mortality and nutrient concentrations (HELCOM 2023a, Korpinen et al. 2021). The most characteristic feature of the Baltic Sea is a stable gradient of decreasing salinity from its connection to the North Sea towards the inner parts, with parallel changes in biogeochemistry and species composition (HELCOM 2023a). Depending on the differences in prevailing hydrological and biogeochemical conditions food webs may respond differently to perturbations, e.g. background nutrient levels can influence food web responses to climate change or increased nutrient availability in terms of basal energy production and energy transfer to higher trophic levels (Savchuk 2018, Kahru et al. 2020), increasing the assessment challenge. Still, effects of long-term human induced pressures in combination with slow water exchange have been associated with large-scale changes in food webs in several sub-basins of the Baltic Sea and increasing ecological novelty across time and space (HELCOM 2023a, Pecuchet et al. 2020, Ammar et al. 2021).

Key pressures on Baltic Sea food webs are excess nutrient inputs leading to eutrophication, which has contributed to the occurrence of vast hypoxic areas (Hansson and Viktorsson 2025), the prevalence of algal blooms, and low-oxygen tolerant benthic species (Karlson et al. 2002, Kahru et al. 2020). Additionally, overfishing strongly modifies food web interactions, by reducing predation pressure or competition with fished species (Scotti et al. 2022, Eero et al. 2023), and climate change, which is expected to have an increasing impact on ecosystems through changes in, e.g. temperature, oxygen conditions, seasonality, and ice cover, affecting spring bloom timing, growth rates and favour warm-adapted species (Viitasalo and Bonsdorff 2022, Meier et al. 2022). Historically, contaminants have had widespread effects on the population sizes of apex predators such as grey seals and sea eagles through reduced reproduction potential (HELCOM 2023a). This risk is now diminishing because of strict management measures, although the introduction of new substances remains a problem, along with increasing concerns for the spread and establishment of non-indigenous species (HELCOM 2023a). Still, commercial fish stock quotas have been declining over time in nearly all Baltic sub-basins, and cod (*Gadus morhua*) is currently under severe catch restrictions due to poor status (ICES 2024b), and forgone benefits for the recreation sector are estimated at billions of Euros per year (HELCOM 2023a), highlighting that food webs are performing poorly.

These developments showcase the importance of including adequate and updated information on ecosystem structure and function into management decisions. However, a systematic analysis across all Baltic Sea sub-basins, encompassing abiotic factors, human induced pressures, and trophic guilds, has so far not been conducted, due to the challenge of achieving coordinated data assembly and analysis (HELCOM 2023a, ICES 2024b). In this study, we provide the first comprehensive analysis of potential systemic spatiotemporal changes in open-sea systems in seven Baltic Sea sub-basins (Fig. 1) based on harmonized data collection and analysis, which builds on previously developed frameworks for the integrated assessment of ecosystem trends (Diekmann et al. 2012, Tomczak et al. 2022). Our objectives are to (i) compare temporal trends of key structural food web components in different basins, focusing on relative changes between trophic guilds; (ii) analyse observed changes in relation to variations in key environmental factors (e.g. temperature, pH, silicate, oxygen, North Atlantic Oscillation) and human induced pressures (e.g. fishing mortality, nutrients, anoxic area); and (iii) assess whether the relative abundance of trophic guilds has changed in response to human pressures. Based on previous studies of food webs in some Baltic Sea basins (Pekcan-Hekim et al. 2016, Tomczak et al. 2022, Faithfull and Bergström 2025), we expect that the relative abundance of trophic guilds has changed across sub-basins over time and that in each sub-basin the response will be related to pressure showing the highest magnitude of change over time. The results of the study can inform the development of assessments to evaluate and manage marine food webs as well as ecosystem-based approaches to Baltic Sea management.

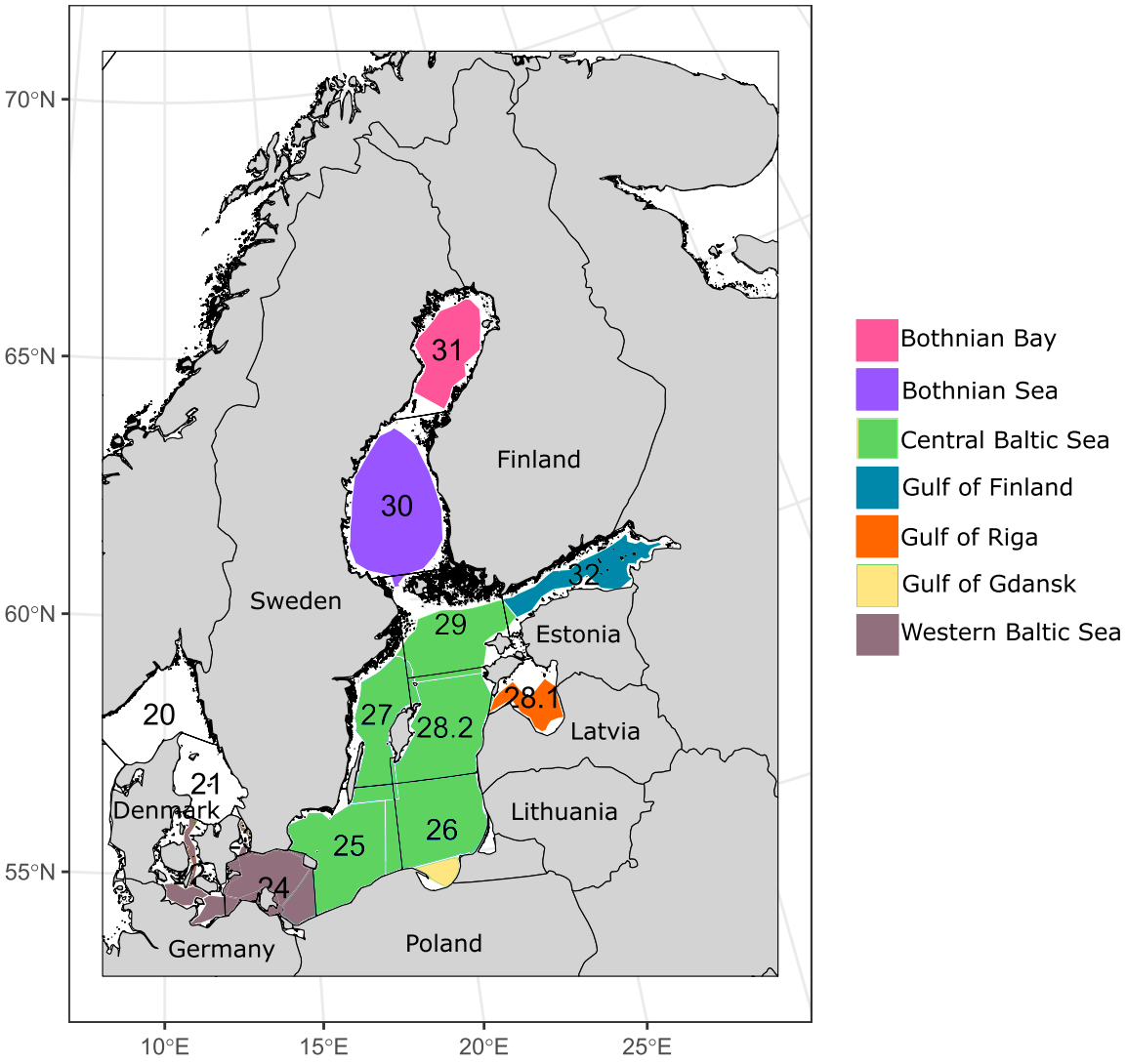

Figure 1 The seven Baltic Sea sub-basins assessed in this study. The black lines and numbers show the spatial delineation of ICES subdivisions. The current study focuses on open sea waters, as indicated by the coloured areas.

Material and methods

Study area

The Baltic Sea is a large (392 000 km^2) brackish water sea with an extensive catchment area (1 739 000 km^2), supporting a human population of 84 million, of which 24% live within 50 km of the coast (Hannerz and Destouni 2006). Salinity declines from 15 to 20 close to the entrance to the North Sea region to nearly freshwater in the innermost areas, which along with a north–south temperature gradient drives spatial variation in species composition and food web configuration (Koehler et al. 2022). Additional spatial heterogeneity arises from persistent vertical salinity stratification in the southern Baltic, seasonal sea ice cover in the north (Meier et al. 2022) and topographic sills restricting water exchange between sub-basins (Leppäranta and Myrberg 2009). Our current assessment divides the Baltic Sea into seven sub-basins, based primarily on the HELCOM offshore sub-basin division level 3 (HELCOM 2023a). To limit the number of sub-basins for analysis, we follow the BALTSEM model aggregation, combining the four Central Baltic sub-basins into one and merging the Arkona Basin, Bay of Mecklenburg, Kiel Bay, and Great Belt into a single Western Baltic Sea sub-basin (Fig. 1, Table 1, HELCOM 2024).

Data collection

We compiled environmental and biological monitoring data representing multiple trophic levels for each Baltic Sea sub-basin over the longest continuous time span available. The analysed period differed among sub-basins due to data availability for trophic groups or environmental variables: Western Baltic Sea (WB) 1997–2023, Central Baltic (CB) 1979–2021, Gulf of Gdansk (GoG) 1995–2022, Gulf of Riga (GoR) 1976–2022, Gulf of Finland (GoF) 1979–2021, Bothnian Sea (BS) 1979–2022, and Bothnian Bay (BB) 1986–2021. The primary data sources were national open-sea monitoring stations deeper than the 20 m isobath and defined according to the HELCOM open-sea spatial delineations, thereby excluding coastal waters and transition zones (Fig. 1). We obtained data from databases hosted by the Finnish Environmental Institute (SYKE), the Swedish Meteorological and Hydrological Institute (SMHI), the

Table 1. Environmental and oceanographic characteristics of the seven Baltic Sea sub-basins addressed in this study.

Basin	Abbrev.	Open sea surface area (km^2)	Mean depth (m)	Surface salinity range	Summer surface temp range (°C)	Nutrient loads 1980–2020, kton km^{-2} year^{-1} (N, P)
Western Baltic	WB	21 710	18	7.6–12.9	13.4–20.5	2.2, 0.077
Central Baltic	CB	163 172	65	6.9–8.1 (9.3–12)	6.9–19.0	3.0, 0.120
Gulf of Gdansk	GoG	3651	50	7.2–11	5.2–12.6	NA
Gulf of Riga	GoR	14 220	27	5.7–6.3	13.4–18.0	5.9, 0.21
Gulf of Finland	GoF	16 612	37	4.9–6.9	9.2–20.2	4.5, 0.29
Bothnian Sea	BS	49 577	66	5.1–6.0	12.9–17.6	1.3, 0.040
Bothnian Bay	BB	21 326	41	2.9–3.5	3.0–16.8	1.7, 0.076

Surface salinity range and summer surface temperature are taken from the yearly means in the data sets. All data is sourced from HELCOM (2023a), except for nutrient loads, which are sourced from HELCOM (2024). NA, not available.

International Council for Exploration of the Sea (ICES), the Leibniz Institute for Baltic Sea Research (IOWDB), the Latvian Institute of Aquatic Ecology (LHEI), the Institute of Food Safety, Animal Health and Environment (BIOR), the Natural Resources Institute of Finland (LUKE), and the Baltic Marine Environment Protection Commission (HELCOM). We quality controlled all datasets through expert consultation and cross-validation with verified sources. To ensure temporal consistency, we included stations with at least 10 years of observations, except for the GoG where data collected within a 3 km radius were clustered into a single site, due to the lack of long-term monitoring stations.

For biotic variables, we compiled data representing the key ecosystem components in each basin (Fig. 2, Table 2). To enable food web level analyses, we grouped the data according to trophic guilds as defined in the MSFD (EC 2022). Primary producers included Chlorophyta, Chrysophyta, Ciliophora, Cyanophyta, Bacillariophyta, Dinophyta, Cryptophyta, Haptophyta, and Euglenophyta with phytoplankton biomass measured from integrated 0–10 m samples collected between June and August. For secondary producers data corresponded to the HELCOM indicator for total zooplankton biomass, using samples collected between June and September. Zooplankton were sampled using a WP2 net (57 cm diameter, 100 μm mesh size) using vertical tows from ~5 m above the seabed to the surface at stations <30 m depth, or within predefined depth strata at deeper stations; in the Gulf of Riga, a 156 μm Juday net was used (for more details on methodology see HELCOM 2023b). We derived macrozoobenthos data from van Veen grab samples collected on soft bottoms between March and June (HELCOM 2017) and classified into the functional groups filter feeders, deposit feeders, predators (Supplementary Table S14).

We obtained fish data for the main commercial stocks from ICES (ICES 2024b or individual stock assessments), with herring (*Clupea harengus*), sprat (*Sprattus sprattus*) and vendace (*Coregonus albula*) classified as planktivores, flounder (*Platichthys flesus*), and plaice (*Pleuronectes platessa*) as demersal sub-apex predators (hereafter benthivores), and cod as predatory fish. Stock data for cod, sprat and plaice overlapped our defined basin boundaries between the CB and the GoF and GoG, being based on the ICES rectangles (ICES 2024b, Fig. 1. Supplementary information Tables S1–S14). To estimate fish stocks independently for the GoF, we used a separate 2014 herring assessment (Raateoja and Setälä 2016), while for other fish species, we estimated spawning stock biomass (SSB) by scaling total assessment values by the ratio of catch in the GoF compared to the whole assessment area. For the GoG, official landings of cod, herring, sprat, eelpout (*Zoarces viviparus*), flounder, plaice, and turbot (*Scophthalmus maximus*) were obtained from the Fisheries Monitoring Centre database, and catch per unit effort (CPUE) was calculated from scientific cruise data. We included grey (*Halichoerus grypus*) and ringed seals (*Pusa hispida botnica*) as apex predators using basin-specific abundance indices; because survey data did not cover the full study period, we used data prior to 1990 (Harding et al. 2007), combined with more recent LUKE surveys, and linearly extrapolated between 1976–1990 consistent with population growth rate estimates found in Harding et al. (2007). We estimated harbour porpoise (*Phocoena phocoena*) wet-weight density for the Western Baltic by combining empirical observations with model-based estimates for years without data. The final GAM ($k = 5$) was selected among several candidate models based on Akaike's information criterion (AIC); (Suppementary information Table S2). We excluded seabirds from the analysis due to high mobility and strong seasonal variation in abundance. We described environmental conditions and human-induced pressures using 27 variables (Table 3). Across all time series, we interpolated missing values as the mean of the two preceding and two subsequent years. We limited the influence of interpolated data by restricting analyses to variables with no more than four consecutive years of missing observations and <5% of data used in any of the analyses was interpolated (Supp.).

Analyses

The main aim of the analyses was to compare long-term temporal changes in the relative abundance between trophic guilds across Baltic Sea sub-basins in relation to environmental drivers and human induced pressures. We carried out integrated trend analysis (ITA; Diekmann et al. 2012) using a combination of univariate analyses, multivariate ordination analyses and breakpoint analyses. The strength of this analysis is that we compare trends over time, not absolute values, therefore differences in measurement units between trophic guilds or basins are unimportant, if they are consistent within basin and trophic guild, as in our collected data sets. We transformed all data [$\ln(y + 1)$] to improve normality and standardized to zero mean and unit variance to account for differing units and value ranges. For all explanatory variables, we used both same-year values and 3-year moving-average lags (e.g. F_{3-7} 3 year lag) to capture immediate and time-lagged effects on longer-lived trophic guilds.

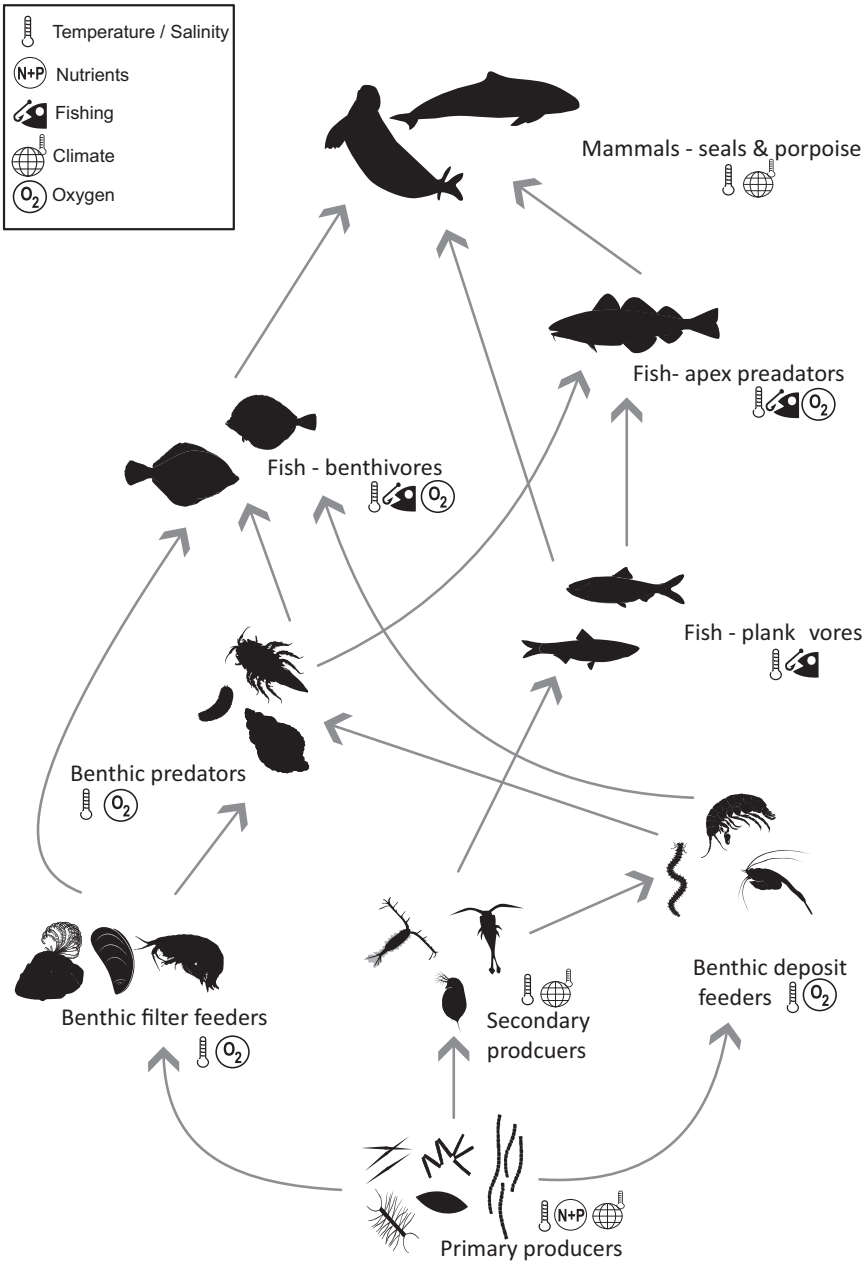

Figure 2 A simplified schematic food web diagram of the main trophic guilds considered in this study and the main environmental and human induced pressures that are expected to affect the respective trophic guilds. Note that the pressures have been simplified in the diagram to aid visualization—a full list of the explanatory variables is in Table 3.

To examine basin specific trends, we plotted all response and explanatory variables over time and applied generalized additive models (GAMs) with restricted maximum likelihood estimation and 95% confidence intervals. Prior to analysing relationships between trophic guilds and drivers, we screened explanatory variables for covariance using pairwise correlations with Pearson's correlation coefficient (Supp. Figs S3, S7, S11, S15, S19, S23, and S27). We quantified the direction and magnitude of trends in trophic guilds and selected drivers by calculating the first derivative of the fitted smooths across each time series and summarizing as the mean derivative.

To investigate changes in the biotic data in relation to the explanatory variables over time, we used a multivariate ordination method, distance based redundancy analysis (dbRDA), where response variables can be unconstrained or constrained by explanatory variables in multiple dimensions, hence summarizing the variation in the biotic variables explained by environmental or human induced pressures (Table 3). As the measure of association, we used chord distances, which are suitable for abundance and biomass data (Legendre and Anderson 1999). We analysed trends among trophic guilds separately for each basin using the capscale function (constrained dbRDA; Table 1) from the

Table 2. Brief description of the data used for the trophic guilds across the different sub-basins.

Trophic guild	Description	Months	Extent	Unit
Primary producers	Phytoplankton	Jun–Aug	0–10 m depth	mg m^{-3}
Secondary producers	Zooplankton biomass	Jun–Sept	0-sea floor	mg m^{-3}
Ben. filt	Macrozoobenthic filter feeders	Apr–Jun	Sea floor	ind m^{-2}
Ben. dep	Macrozoobenthic deposit feeders	Apr–Jun	Sea floor	ind m^{-2}
Ben. pred	Macrozoobenthic predators	Apr–Jun	Sea floor	ind m^{-2}
Planktivores	Herring, sprat, vendace spawning stock biomass (SSB)	Yearly	ICES rectangles for WB, CB, GoR, BS, BB,	tonnes
	Herring, sprat CPUE	Yearly	GoG, GoF	kg h^{-1}
Benthivores (Sub-apex demersal predators)	Flounder, plaice SSB	Yearly	ICES rectangles for WB, CB	tonnes
	Flounder, plaice, eelpout, turbot CPUE	Yearly	GoG, GoF, GoR	kg h^{-1}
Piscivores (Fish apex predators)	Cod SSB	Yearly	ICES rectangles for WB, CB	tonnes
	Cod CPUE	Yearly	GoG	kg h^{-1}
Mammals (Mammalian apex predators)	Grey seal, ringed seal, harbour seal	Yearly	All sub-basins (ringed seal only BB)	Number
	Harbour porpoise	Yearly	WB	Kg WW/Km^2

The trophic guilds comprise the taxa as indicated in the 'Description,' which differs between sub-basins as described in the 'Extent' column. See Supplementary Information for more details and data sources.

vegan package (Oksanen et al. 2020) in R (R Core Team 2021). We performed model selection with ordistep using the lowest AIC to identify the most parsimonious models and exclude non-significant variables. Initially, we included all variables that were deemed to be ecological relevant (Fig. 2), but excluded highly correlated variables during the model simplification process. Highly correlated variables had variance inflation factors > 5, which we considered collinear and removed sequentially, starting with the variable explaining the least variation based on model selection (Zuur et al. 2010).

As the ordination analyses only identify linear relationships between variables, we used multivariate GAMs to test for non-linear associations between explanatory variables and temporal changes in trophic guilds. GAMs regressed the first and second unconstrained (i.e. only trophic guilds) dbRDA axes scores against the explanatory variables. We constructed GAMs using the mgcv package in R (Wood 2017) with restricted maximum likelihood estimation and allowed three basis functions (k) for the smooth terms. We examined residuals for autocorrelation and used stepwise model simplification based on AIC to determine the simplest models explaining the greatest variation.

Finally, we applied breakpoint analyses to detect distinct temporal shifts in community composition. Because individual methods tend to overestimate the number of shifts (Haines et al. 2025), we applied three complementary approaches. First, we used chronological clustering to analyse multiple time series simultaneously (Brodgar, Highland statistics Ltd), generating a distance matrix in which consecutive years were clustered when sharing a defined proportion of common links (Legendre et al. 1985). We used 50% common links and an alpha of 0.01, which is conservative, to identify larger community shifts. Second, we assessed breakpoints based on the dbRDA axes scores, using sequential *t*-test analysis of regime shifts (STARS v. 4.0), which detects shifts in the time series based on the Student's *t*-test (Rodionov 2015). We did not pre-whiten data; a minimum regime length of 5 years was imposed to identify stable periods, and time series were detrended prior to analysis to avoid detecting multiple change points from gradual mean shifts (Tomczak et al. 2022). Third, we performed a breakpoint analysis on the dbRDA axes scores using the EnvCpt package in R (Killick et al. 2021). This fits up to 12 different models varying in trends, means and autocorrelation, and identifies the best model using the lowest AIC. We combined results for all the three methods by defining a 'shift' when at least two methods identified the same breakpoint within a 2-year window.

Results

Temporal trends in key food-web components differed among sub-basins (Fig. 3) but showed several common patterns (Fig. 4). Primary producers increased in most sub-basins, with declines only in the Bothnian Bay and the Gulf of Gdansk. Secondary producer biomass showed basin-specific trends, increasing in some sub-basins and decreasing in others. Among macrozoobenthos, benthic predators exhibited no consistent temporal trends, whereas filter feeders mostly declined over time and deposit feeders increased, driven by Baltic wide trends in species specific dynamics of *Monoporeia* sp. and *Marenzellaria* sp. respectively. Apex predatory fish declined in all sub-basins where assessed, while benthivorous and planktivorous fish exhibited strong but directionally variable trends across sub-basins. Among apex mammalian predators, grey and ringed seals increased in all sub-basins where present, whereas harbour porpoise abundance declined over time. When comparing trends across sub-basins in trophic guilds over time there were no clear patterns of association between sub-basins (Supp. Fig. S2).

Environmental drivers also changed through time. Dissolved inorganic phosphorus (DIP) increased in most sub-basins, while

Table 3. Main characteristics of the explanatory variables used in the analyses.

Abbrev.	Explanation	Months	Depth (m)	Unit
SAL-deep	Winter salinity of deep water	Nov–Mar	>100	PSU
SAL-win	Winter surface salinity	Nov–Mar	0–10	PSU
SST-spr	Spring sea surface temperature	Apr–Jun	0–10	°C
SST-su	Summer sea surface temperature	Jun–Sept	0–10	°C
SST-win	Winter sea surface temperature	Nov–Mar	0–10	°C
SHT-su	Summer deep water temperature	Jun–Sept	>100	°C
Ice-max	Maximal ice extent—whole Baltic	Yearly	NA	km^2
NAO	North Atlantic Oscillation	Jan–Dec	NA	NA
WBSI	Winter Baltic Climate Index—whole Baltic	Yearly	NA	
pH	pH	Nov–Mar	0–10	pH
Ox-deep	Oxygen deep layer, winter	Nov–Mar	>100	ml l^{-1}
Anoxic	Anoxic area <0 ml l^{-1} O_2	Yearly	NA	km^2
Hypoxic	Hypoxic area <2 ml l^{-1} O_2	Yearly	NA	km^2
DIN	Dissolved inorganic nitrogen surface layer winter	Nov–Mar	0–10	µmol l^{-1}
DIP	Dissolved inorganic phosphorus surface layer, winter	Nov–Mar	0–10	µmol l^{-1}
TN	Total nitrogen surface layer, winter	Nov–Mar	0–10	µmol l^{-1}
TP	Total phosphorus surface layer, winter	Nov–Mar	0–10	µmol l^{-1}
DIN-deep	Dissolved inorganic nitrogen in deep layers, winter	Nov-Mar	>100	µmol l^{-1}
DIP-deep	Dissolved inorganic phosphorus in deep layer water, winter	Nov–Mar	>100	µmol l^{-1}
TN-deep	Total nitrogen deep layer, winter	Nov–Mar	>100	µmol l^{-1}
TP-deep	Total phosphorus deep layer, winter	Nov–Mar	>100	µmo l^{-1}
TN-load	Nitrogen load (waterborne and atmospheric)	Yearly	NA	tonnes y^{-1}
TP-load	Phosphorus load (waterborne and atmospheric)s	Yearly	NA	tonnes y^{-1}
Humus	Humic matter (western Baltic only)	Jun–Aug	0–10	mg l^{-1}
Si	Silicate	Nov–Mar	0–10	µmol l^{-1}
Herr F_{3-7}	Herring fishing mortality age 3–7	Yearly	NA	ICES rectangle
Sprat F_{3-5}	Sprat fishing mortality age 3–5	Yearly	NA	ICES rectangle
Plaice F3-5	Plaice fishing mortality age 3–5	Yearly	NA	ICES rectangle
Cod F_{4-6}	Cod fishing mortality age 4–6	Yearly	NA	ICES rectangle
Vendace F_{3-5}	Vendace fishing mortality age 3–5	Yearly	NA	BB
Planktivore landings	Sum of herring and sprat total catches of commercial fleet	Yearly	NA	GoG
Benthivore landings	Flounder total catches of commercial fleet	Yearly	NA	GoG
Cod landings	Cod total catches of commercial fleet	Yearly	NA	GoG

Time series for the Winter Baltic Climate Index (WBSI), Ice-max, and North Atlantic Oscillation (NAO) are the same across all sub-basins. See Supplementary information for more details and data sources.

dissolved inorganic nitrogen (DIN) trends varied among basins. Deep-water oxygen concentrations and salinity generally declined, though not uniformly across all sub-basins. Fishing mortality of herring increased in four sub-basins and decreased in three. Sub-basin-specific relationships between trophic guilds, key taxa, and explanatory variables are described below and in Supplementary information.

Western Baltic Sea

Between 1997 and 2023, the Western Baltic experienced declining biomasses across nearly all trophic guilds, including pelagic secondary producers (zooplankton), planktivorous fish (sprat and herring), piscivores (cod), and apex mammalian predators (harbour porpoise) (Figs 3 and 4). Benthivores (i.e. plaice), benthic predators, and harbour seals (apex mammalian predators) were the only trophic guilds that increased over time (Figs 3 and 4). The physio-chemical environment of the Western Baltic Sea also changed. Phosphorus concentrations (DIP) increased between 1990 and 2005, whereas nitrogen concentrations decreased. Silicate increased, although salinity levels have been relatively stable except for an inflow period between 2000 and 2010. Winters have become less severe and spring SST is variable but increasing, warmer waters may also contribute to observed decreasing oxygen concentrations. Fishing mortality of all trophic guilds has decreased.

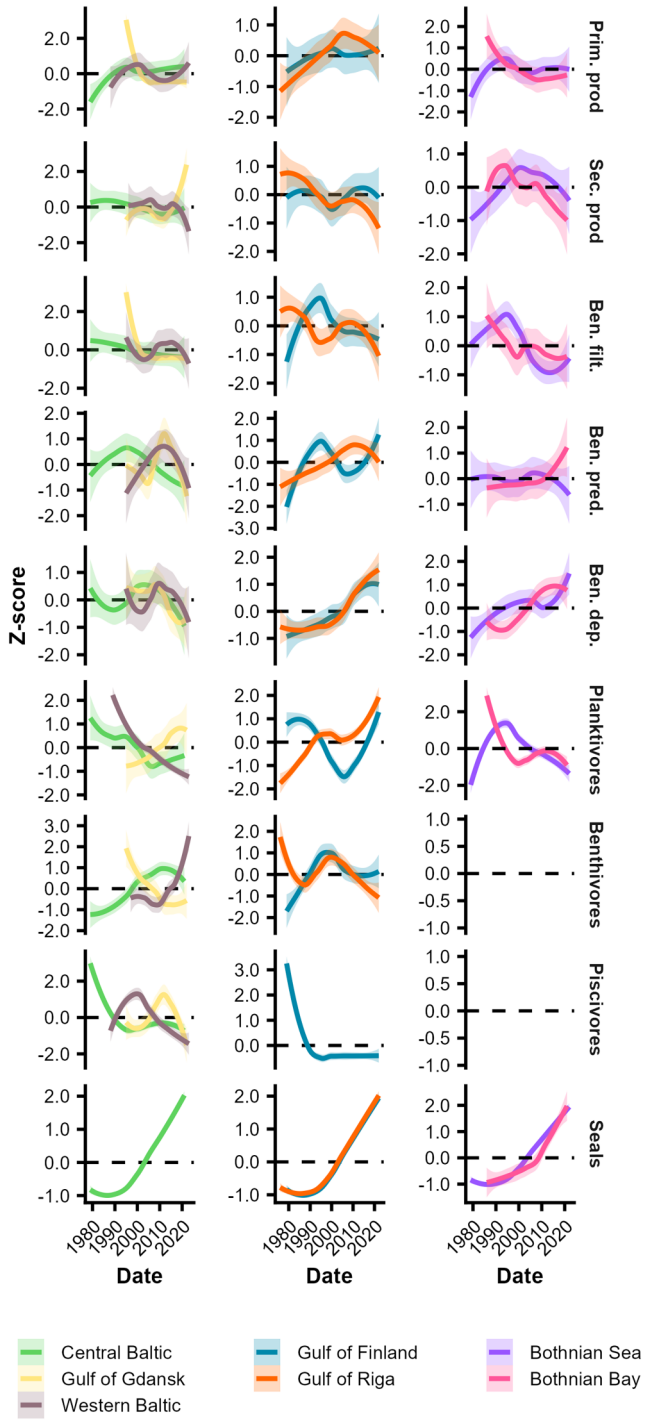

Figure 3 Smoothed trends in trophic guild abundance or biomass over time. Shaded area represents ± standard error. Note that seal trends are dominated by grey seals for all sub-basins except Bothnian Bay where ringed seal is also included.

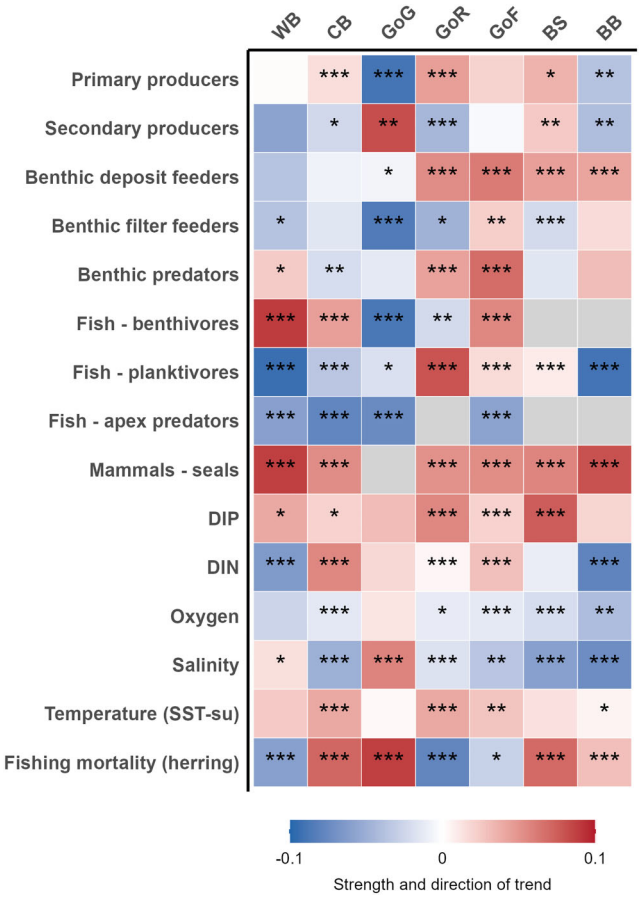

Figure 4 Overview of trends in trophic guild abundance in each basin (abbreviations in the text), together with trends in selected environmental variables representing the key drivers, nutrients, oxygen, salinity, climate, and fishing pressure. Each tile is coloured according to the mean value of the derivative of the smooth term (time) calculated using GAMs. Red indicates an increasing and blue a decreasing trend over time. A stronger colour reflects a stronger trend. Grey indicates there was not enough data available to analyse for the combination of basin and trophic guild. Harbour porpoise was excluded from the analysis as it is only present in the Western Baltic and has an opposing trend to seal abundance. The significance of the GAM models are $^{***}P < 0.001$, $^{**}P < 0.01$, $^{*}P < 0.05$, not significant.

Cod fishing mortality was the environmental driver most strongly associated with changes along the first dbRDA axis both in linear and non-linear analyses (Table 4), along with the guilds predatory fish (cod), planktivorous fish (herring and sprat) and primary producers (Fig. 5a). The second dbRDA axis was associated with decreasing plaice fishing mortality and declining Winter Baltic Climate Index (WBSI), reflecting warmer winters in the linear analysis and cod and plaice fishing mortality in the non-linear analysis (Table 4). Decreasing biomasses of apex predatory fish (cod) and planktivorous fish were associated with increasing biomasses of benthivores (plaice) and mammalian apex predators (seals) (Figs 3 and 4). A large change in the balance between trophic guilds occurred in 2003–2006, coinciding with a sharp decrease in cod (Fig. 5a). If comparing decade-averaged values ($n = 10$), the estimated spawning stock biomasses of herring and cod in the last assessed decade were only 34% and 26% of the average biomasses during the peak decade (1994–2004), respectively.

Central Baltic

Between 1979 and 2021, the relative abundance between trophic guilds changed dramatically. Seal abundance steadily increased over time. Herring and cod had high biomasses from late 1970s to the early 1980s, which corresponded with a period of colder

Table 4. GAM results, showing the two explanatory variables with the most significant correlations with the dbRDA axes for each basin.

Basin	Axis	Model	edf	Dev.Ex
Western Baltic	dbRDA1	Humus***	1.00	88.0%
		Cod $F_{4\text{-}6}$ 3 year lag***	1.00	
	dbRDA2	Cod $F_{4\text{-}6}$ 3 year lag***	1.97	74.3%
		Plaice $F_{3\text{-}5}$ 3 year lag***	1.00	
Central Baltic	dbRDA1	Anoxic area***	1.79	83.9%
		Herring $F_{3\text{-}6}$ 3 year lag***	1.91	
	dbRDA2	Anoxic area***	1.94	38.1%
		Sprat $F_{3\text{-}5}$***	1.00	
Gulf of Gdansk	dbRDA1	Cod landings***	1.92	65.9%
		Planktivore landings***	1.70	
	dbRDA2	Ice extent 3 year lag***	1.00	58.5%
		Landings flatfish*	1.77	
Gulf of Riga	dbRDA1	Ice extent 3 year lag***	1.00	60.3%
		DIN*	1.00	
	dbRDA2	Ice extent 3 year lag***	1.93	42.9%
		Herring $F_{2\text{-}6}$ 3 year lag**	1.00	
Gulf of Finland	dbRDA1	SHT-su***	1.00	60.3%
		Herring $F_{3\text{-}6}$ 3 year lag***	1.85	
	dbRDA2	TP***	1.95	52.4%
		WBSI 3 year lag***	1.92	
Bothnian Sea	dbRDA1	Herring $F_{3\text{-}7}$ 3 year lag***	1.97	75.2%
		WBSI 3 year lag*	1.20	
	dbRDA2	SAL_win***	1.78	69.1%
		Herring $F_{3\text{-}7}$ 3 year lag***	1.87	
Bothnian Bay	dbRDA1	Ox deep**	1.00	65.6%
		SAL-win**	1.00	
	dbRDA2	DIP***	1.85	29.0%
		WBSI 3 year lag***	1.78	

The significance of the GAM models are ***$P < 0.001$, **$P < 0.01$, *$P < 0.05$. Abbreviations as in the text and edf: effective degrees of freedom and Dev.Ex: percentage deviation explained by the model.

winters, higher surface salinity and relatively high oxygen concentrations at depths >100 m. However, herring and cod have declined dramatically over the last 40 years (Fig. 3), to 32% and 26% of their previous biomass, respectively (mean of years 2012–2021 compared to 1974–1983). During this period changes in environmental and human induced pressures were evident, with cod fishing pressure increasing until the early 2000s, and herring fishing mortality continuing to increase. Nutrient concentrations have increased over time along with deepwater and sea surface temperatures. Deepwater oxygen concentrations have decreased and the area of anoxic seabed has increased over time (Supp. Fig. S8).

The change in relative abundance between trophic guilds along dbRDA axis 1 reflects a decline in piscivorous (cod) and planktivorous fish and an increase in benthivorous fish (flounder) and apex mammalian predators (grey seal). Among explanatory variables, this axis was primarily associated with increasing fishing pressure on planktivorous fish, increasing temperature, seabed anoxic area, and dissolved inorganic nutrient concentrations (Fig. 5b, Table 4). The second dbRDA axis mainly reflected changes in the macrozoobenthic guilds. This axis was linearly correlated with planktivore fishing mortality, DIP, and deepwater temperature (Fig. 5b) and non-linearly correlated with planktivore fishing mortality and anoxic area (Table 4). A shift in the balance between trophic guilds was observed around 1995, corresponding to increases in benthivore biomass following the decline of piscivorous fish and the beginning of a decline in planktivore biomass. In the early 2000s, a second shift was observed (Fig. 5b), which corresponds to planktivore fish, benthic filterers, deposit feeders and benthic predator biomasses reaching new low levels, which have held relatively constant between 2005 and 2021 (Fig. 3) and were associated with increasing nutrient concentrations and anoxic area (Table 4).

Gulf of Gdansk

Between 1994 and 2023, changes in the relative abundance between trophic guilds were characterized by increasing secondary producer and planktivore abundance, whereas the biomass of benthivores (i.e. flounder, plaice, eelpout, and turbot) and piscivorous fish (cod) decreased over time. Planktivore landings and total phosphorus were the main explanatory variables correlated with dbRDA axis 1 and ice extent and cod landings with dbRDA axis 2. Fish landings also explained most of the non-linear variation in the ordination axes (Table 4). Cod landings were positively correlated with cod abundance and planktivore landings with planktivore abundance. Large changes in the balance between trophic guilds occurred in 2003–2005 and 2014–2017. The former was associated with decreased biomass of phytoplankton and benthic

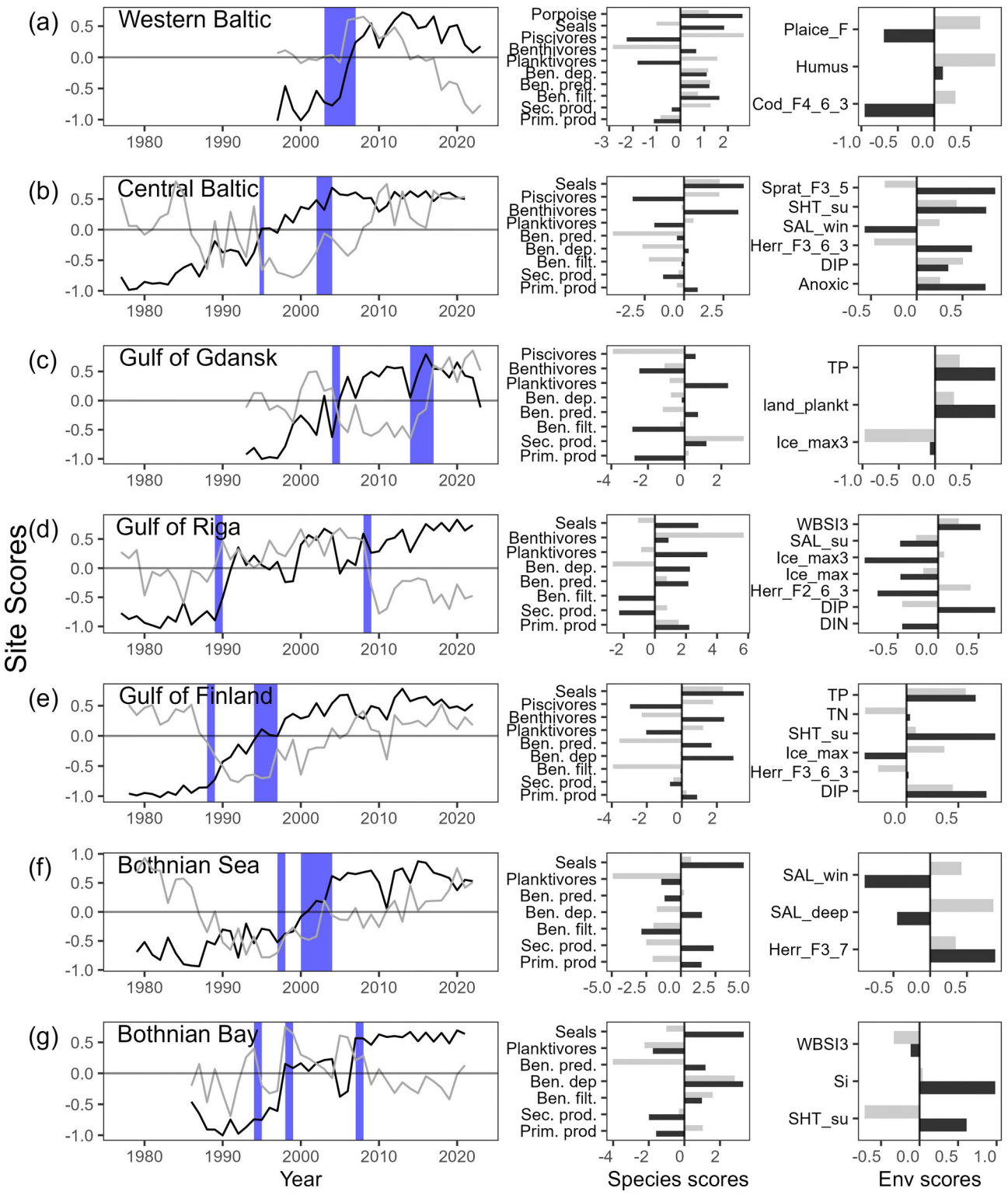

Figure 5 Ordination analysis results showing the trajectories of distance-based redundancy analysis, dbRDA axis 1 (black) and axis 2 (grey) over time (left column), with changepoints shaded. The middle column shows the species scores [how the trophic guilds are related to axis 1 (black) and axis 2 (grey)] and the right column shows the explanatory variables that were significantly related to axis 1 and axis 2.

filter feeders, primarily reflecting a sharp decline in *Mytilus* spp. and benthivorous fish, and increased abundance of planktivorous fish and cod. The latter change in 2014–2017 was associated with increased zooplankton and reduced cod biomass (Fig. 5c). Although temperature (SST-spr) has increased over time oxygen concentrations did not decrease, possibly because of enhanced inflow of oxygen-rich marine waters, as indicated by increasing salinity (Fig. 4).

Gulf of Riga

Between 1976 and 2022, changes in the relative abundance between trophic guilds were observed. Total phytoplankton biomass increased during 1980–1990 and has remained relatively stable since 2000. Total zooplankton biomass showed a decreasing trend. Benthic deposit feeders and predators increased, reflecting increases of *Macoma balthica*, *Marenzelleria* spp., and *Saduria entomon* (Fig. 3). Climate change is evident in the increase in summer SST and, similar to most other sub-basins, winter DIP continues to show an upward trend and deepwater oxygen a downward trend. In the ordination, dbRDA axis 1 increased steadily over time and was positively correlated with seal abundance, planktivore biomass, benthic predators, filter feeders, and phytoplankton biomass. DIP and the WBSI were also positively associated with dbRDA axis 1 (Fig. 5d). Explanatory variables negatively correlated with dbRDA axis 1 were herring fishing mortality and ice extent (Fig. 5d and Table 4). The pelagic food web compartment showed a large shift in 1989–1991 with increasing phytoplankton and planktivore biomass, and decreasing zooplankton, suggesting a trophic cascade. A second shift in 2008 mainly reflected a sharp decline in benthivorous fish and an increase in invertebrate benthic deposit feeders such as *Macoma balthica* and *Marenzelleria* spp.

Gulf of Finland

Between 1979 and 2022, seals, benthivorous fish and benthic deposit feeder biomass increased and piscivorous fish decreased. Cod declined dramatically in the 1980s and thereafter flounder increased. Planktivores declined in the 1990s due to a decrease in herring, but have since 2015 shown a positive trend, mostly reflecting an increase in sprat biomass. Salinity declined over time and climate effects are evident in the GoF with increasing surface and deep water temperatures (Figs 4 and 5e). In the ordination, dbRDA axis 1 increased over time and was positively correlated with increasing deepwater summer temperature (SHT-su) and DIP concentrations. Piscivore and planktivore biomasses showed a negative correlation with dbRDA axis 1, whereas seals, benthivores, and benthic filterers were positively correlated with dbRDA axis 1 (Fig. 5e). When considering non-linear correlations with dbRDA axis 1, deepwater temperature and herring fishing mortality explained most of the variation (Table 4). TN, herring fishing mortality and benthic filterers were linearly correlated with dbRDA axis 2. The balance between trophic guilds changed over time, with a large shift occurring between 1990–1996 (Fig. 5e), which was associated with the sudden decline in piscivorous and planktivorous fish biomass.

Bothnian Sea

Over 1979–2022, there was a significant change in the relative abundance of trophic guilds, with planktivorous fish (herring) and benthic filter feeders declining and benthic deposit feeders and mammalian apex predators (grey seals) increasing. The dbRDA axis 1 showed an increasing trend over time and was primarily associated with increasing biomass of seals, but also positively correlated with primary and secondary producers and benthic deposit feeders (Fig. 5f). Explanatory variables that were correlated with dbRDA axis 1 were increasing herring mortality and decreasing salinity (Fig. 5f). The dbRDA axis 2 was associated with a decrease in planktivorous fish, zooplankton and benthic filter feeders over time. The main explanatory variables for dbRDA axis 2 were herring fishing mortality and salinity (Fig. 5f, Table 4). There was a change in the relative abundance between trophic guilds in 1998–2004, with the earlier period (1979–1997) being characterized by higher planktivore and benthic filter feeder biomass and lower nutrient concentrations, higher salinity, colder winters, and lower herring fishing mortality. The latter period (2004–2022) had higher DIN and DIP concentrations, herring fishing mortality, and benthic deposit feeders. This change was associated with the invasion of *Marenzelleria* spp., lower numbers of benthic filter feeders (including *Monoporeia*) and declining herring SSB.

Bothnian Bay

During 1986–2021, mammalian apex predators (grey and ringed seals) and benthic deposit feeders increased. However, nearly every other trophic guild has shown declining trends (Figs 3 and 4). Of the environmental variables, oxygen and salinity have decreased and silicate and deep water temperature have increased over time (Fig. 4 and Fig. S28). The dbRDA axis 1 mainly reflected increases in apex mammalian predators and benthic deposit feeders and decreasing planktivorous fish, primary producers and secondary producers. The main explanatory variables linearly associated with dbRDA axis 1 were silicate and deep water temperature, which increased over time. In the non-linear analysis, oxygen and salinity were negatively correlated with dbRDA axis 1 (Table 4, Fig. S30). The dbRDA axis 2 was negatively correlated with benthic predators, planktivorous fish, and deep water temperature and positively correlated with benthic filter and deposit feeder biomasses (Fig. 5g). The time trajectory for the dbRDA axes (Fig. 5g) showed that planktivorous fish biomass decreased until around 1996, when benthic filter feeders and apex predators (grey and ringed seal) started to increase, and planktivorous fish biomass stayed relatively constant (Fig. 3). The more recent period 2006–2022 was characterized by lower planktivore biomass, higher biomass of benthic deposit feeders (*Marenzelleria* spp.), and higher numbers of apex mammalian predators (grey and ringed seals).

Discussion

This study compares long-term changes in food web components across seven Baltic Sea sub-basins, spanning a range of hydrographic and environmental conditions from the Western Baltic to the low-salinity Bothnian Bay. Using 26–46 years of empirical data, we provide the first coherent assessment of long-term trophic guild dynamics across marine food webs and sub-basins for the region, and arguably elsewhere. Under the EU Marine Strategy Framework Directive (MSFD), achieving Good Environmental Status (GES) for food webs requires that the 'balance of total abundance between the trophic guilds is not adversely affected due to anthropogenic pressures.' Our findings show that the relative abundance of trophic guilds has been affected by human induced pressures in all sub-basins, which according to the MSFD indicates that food webs are not achieving GES in the Baltic Sea. Formal indicators to quantify GES are still lacking, and international cooperation is required to establish threshold values to define accept-

able environmental status. However, our study improves our understanding of Baltic Sea food web dynamics in seven sub-basins and highlights key data gaps and quality issues for further development of food web analyses and models.

Temporal changes in food web configurations associated with human induced pressures were evident across all sub-basins, although the most influential pressures varied with sub-basin. While some variability is expected due to natural ecosystem dynamics, relatively stable periods around a mean state can be defined as ecosystem regimes, whereas persistent and abrupt transitions affecting multiple trophic guilds constitute regime shifts (Möllmann et al. 2009, Haines et al. 2025). Our study revealed both gradual long-term trends and at least one major shift in ecosystem configuration in all studied sub-basins over the study period, of which six of these seven shifts were found between 2000 and 2010 and were related to changes in relative abundance of planktivore and benthic trophic guilds biomasses in the CB, GoG, GoR, BS, and BB sub-basins and a decrease in apex fish predators (cod) in the Western Baltic. Our findings align with previous studies documenting regime shifts across the Baltic Sea, which have also found shifts in the relative abundance of fish trophic guilds (Alheit et al. 2005, Möllman et al. 2009, Tomczak et al. 2022). Earlier basin-specific studies have linked food-web changes to climate variability, fishing pressure, and eutrophication (e.g. Casini et al. 2009, Möllmann et al. 2009, Pekcan-Hekim et al. 2016, Faithfull and Bergström 2025). Consistent with this, we found that food-web shifts were not synchronous across sub-basins but were associated with shared drivers acting at different times, including basin-specific changes in fishing pressure, nutrient levels, temperature, and oxygen conditions.

Changes in fishing pressure were linked to changes in the balance between trophic guilds across all studied sub-basins except for the Bothnian Bay. Overfishing is well known to alter marine food webs and ecosystem structure (Jennings et al. 2000), and in the Baltic Sea it has directly reduced the biomass of both target and non-target fish species and altered population size structure (ICES 2024b). Indirect effects include trophic cascades through modified predation pressure on lower trophic levels (Casini et al. 2009, Tomczak et al. 2022), as well as impacts from by-catch and seafloor disturbance (Morkunas et al. 2022, Van Denderen et al. 2022). In the Central and Western Baltic, current conditions contrast with the situation in the 1980s, when apex predatory fish (cod) biomass was high, likely due to low seal abundance and high nutrient inputs from land (Casini et al. 2009, Tomczak et al. 2022). Subsequent excessive fishing pressure reduced cod biomass and altered predator–prey interactions within the food web, including an initial increase in cod prey species such as planktivorous fish in the Central Baltic (Möllmann et al. 2009, Tomczak et al. 2022).

However, planktivorous fishes have subsequently shown clear negative trends in the Western Baltic, Central Baltic, Bothnian Sea, and Bothnian Bay sub-basins, associated with increased fishing pressure on this trophic guild (Atmore et al. 2022, ICES 2024b), and lower recruitment due to climate change and its associated effects on prey availability (Cardinale et al. 2009, Arula et al. 2022). The feeding niches of demersal sub-apex predators such as plaice and flounder partially overlap those of cod (Haase et al. 2020). This group has increased somewhat following the cod decline, potentially reflecting a combination of lower predation by cod (Orio et al. 2020) and reduced fishing mortality, since these species are removed as bycatch in the greatly reduced cod fishery (ICES 2024b). Declines in cod and herring have also had significant sociological and economic repercussions, with many small-scale coastal fishers dropping out of the fishery (Möllmann et al. 2021, Lewin et al. 2023).

The sub-basins where nutrients were a significant driver of changes in trophic guild abundance also had the highest nutrient loading per km^2, i.e. the Central Baltic, Gulf of Finland and Gulf of Riga (HELCOM 2024). Despite reduced phosphorus loading since the late 1980s, dissolved inorganic phosphorus continues to increase in most sub-basins (except Western Baltic and Gulf of Gdansk, Fig. 4, Supp. Figs S4 and S12) partly due to strong internal recycling and a long phosphorus residence time (Gustafsson et al. 2017). Elevated nutrient loads initially enhanced overall biomasses and food web productivity (Tomczak et al. 2022), but excess primary production sinks to the seafloor and consumes oxygen during decomposition (Vahtera et al. 2007). Together with rising temperatures, this has contributed to the expansion of hypoxic and anoxic areas in the Baltic (Hansson and Viktorsson 2025). In our study, increasing anoxic area was associated with shifts in several trophic guilds, including reduced biomasses of planktivorous and predatory fishes. This is consistent with previous studies linking anoxia to reduced habitat and food availability for benthic and demersal species (Karlson et al. 2002, Orio et al. 2022).

The Baltic Sea is one of the fastest warming marine regions globally (Meier et al. 2022). In the Bothnian Bay, Bothnian Sea, Gulf of Finland, Gulf of Riga, and Gulf of Gdansk, changes in trophic guild relative abundance were associated with climate-related variables, including ice cover (Ice-max), the winter Baltic Sea climate index (WBSI), and summer deep-water temperature (SHTsu). Basin size may modulate these effects; in the Central Baltic, biotic changes were not directly linked to temperature variables but instead to anoxia, which is itself driven by climate change and eutrophication (Hansson and Viktorsson 2025). The large volume of the Central Baltic may buffer climate effects over the studied timeframe (Meier et al. 2022), whereas shallower sub-basins with long coastlines such as Bothnian Bay, Gulf of Gdansk, and Gulf of Riga may be more sensitive to temperature variability and extreme events such as heatwaves (Meier et al. 2022, Viitasalo and Bonsdorff 2022). Several of the observed changes likely reflected interactions that require more detailed basin-specific studies. For instance, in the Gulf of Riga during 1977–2022, primary producers, benthic filter feeders, benthic predators, and planktivores all increased, consistent with earlier findings (Pecuchet et al. 2020). These patterns may be associated with higher DIP driving bottom-up productivity (Müller-Karulis and Aigars 2011) or an increased production due to shorter, milder winters (Ojaveer et al. 2011, Arula et al. 2022). Yet, total zooplankton biomass declined over the same period, deviating from expectations under strengthened bottom-up productivity. Notably, the Gulf of Riga analysis is based on the longest continuous time series available, derived from Juday net samples (156 μm mesh), which differs from sampling approaches used in other subbasins. In contrast, the HELCOM Mean Size Total Stock indicator (HELCOM 2023b), based on WP2 net samples (100 μm mesh), indicates an increase in total zooplankton biomass in the Gulf of Riga since 1993. This discrepancy likely reflects methodological differences, suggesting that biomass may be declining among large-bodied zooplankton captured by the Juday net, while smaller size fractions—better represented in the

HELCOM indicator data—contribute to the observed increase in total biomass.

Climate-related changes in the catchment, such as reduced snow and ice cover, may also darken Baltic Sea waters by increasing runoff and mobilizing soil-bound organic carbon (Meier et al. 2022, Aigars et al. 2024). This can elevate dissolved organic carbon and humic substances, potentially reducing phytoplankton production and energy transfer to higher trophic levels through lower light availability or enhanced bacterial production and heterotrophy, thereby lengthening the food chain (Vähätalo et al. 2011, Wikner and Andersson 2012). In the Western Baltic, variability in humus concentration was a significant explanatory variable, likely reflecting catchment influences from human activities such as fire management and seaweed fertilization that generate humus-rich soils (Acksel et al. 2017). However, humus and water transparency (Secchi depth) were uncorrelated (Supp. Fig. S3), and incomplete time series prevented assessment of humus or dissolved organic carbon effects in other sub-basins.

Over a longer time frame, climate-driven shifts in species composition and distributions could also influence the structure and function of food webs. Globally, warming has driven poleward range shifts of marine species (Poloczanska et al. 2016, Hastings et al. 2020), but any northward species migration in the Baltic Sea is limited by the strong salinity gradient (e.g. Zettler et al. 2007). This gradient is expected to intensify with climate change due to increased freshwater runoff (Meier et al. 2022), potentially restricting the range of key marine species such as cod, herring, and several zooplankton taxa (Illing et al. 2016), while favouring low-salinity-tolerant species. Furthermore, the Baltic Sea has experienced multiple invasions of non-indigenous species, some with major consequences for local ecosystems (Ojaveer et al. 2023). Our analyses confirm that the expansion of *Marenzelleria* spp. underlies an increase in benthic deposit feeders across several sub-basins since its initial observation in the Baltic Sea in the late 1980s (Norkko et al. 1993).

In our study, salinity was an important driver in the Bothnian Sea and Bothnian Bay, where lower salinity was associated with increased biomasses of primary producers, secondary producers (zooplankton) and deposit feeders. In these basins, many abundant species belonging to these trophic guilds are of freshwater origin (Zettler et al. 2007, Rajasilta et al. 2014). Increases in freshwater taxa, such as the copepod *Limnocalanus macrurus* and cladocerans (*Bosmina* spp)., have also been associated with higher herring recruitment and weight-at-age (Rajasilta et al. 2014, Faithfull and Bergström 2025) illustrating functional links between species of various origin across different trophic levels. Previous work identified salinity as the main driver of community change in the Bothnian Bay (Pekcan-Hekim et al. 2016), whereas in our study oxygen concentrations, WBSI, salinity and silicate, were important. This may reflect changes in these environmental factors since 2013 (Supp. Fig. S28). Silicate is not a limiting nutrient in the Bothnian Bay (Andersson et al. 1996), but as salinity and silicate co-vary over time, their effects on the food web are difficult to tease apart in correlative studies such as this one. Notably, silicate concentrations have nearly doubled in the Bothnian Bay and Bothnian Sea since the mid-1990s, potentially due to increased freshwater runoff (Meier et al. 2022).

Integrated trend analyses, as applied here, are well suited to investigate ongoing changes across spatial and temporal scales, including long-term trends and regime shifts, and to evaluate whether changes occur consistently across multiple food-web compartments with implications for ecosystem structure and function (Tomczak et al. 2022). Here, we observed shifts in the balance of trophic guilds across all sub-basins, which were associated with human pressures and environmental factors. However, regime shift detection will depend on time-series length, and detection methods often overestimate the number of shifts in the time-series (Haines et al. 2025). Consequently, we applied at least two independent methods per basin to detect regime shifts, and we have not directly compared the timing of regime shifts across sub-basins.

Several ecosystem changes in the Baltic Sea have persisted despite reductions in their underlying pressures. For example, reduced cod fishing mortality in the Western and Central Baltic has not led to cod recovery, and the food web remains in a planktivore-dominated state, with flatfish becoming increasingly important (this study; Scotti et al. 2022, Eero et al. 2023). Similarly, despite ∼50% reductions in phosphorus and 30% in nitrogen inputs since the 1980s (HELCOM 2023a) anoxic areas in the Central Baltic continue to expand and dissolved phosphorus concentrations continue to increase across sub-basins (this study; Meier et al. 2022, Hansson and Viktorsson 2025). These observations support that the food web has moved to an alternative state and is unlikely to revert without major, coordinated changes in key drivers (Scheffer and Carpenter 2003). Ongoing climate change is likely to reinforce current regime shifts and further hinder recovery from eutrophication and overfishing (Meier et al. 2022), implying that substantial reductions in human pressures will be required to move food webs towards alternative regimes (Scheffer and Carpenter 2003).

The analyses presented here require standardized, open access long term data assessed at the proper scale and in the appropriate ecological context. While the Baltic Sea has relatively simple food webs compared to nearby marine ecosystems (e.g. North Sea), strong spatial environmental gradients require data at sufficient resolution. Spatial connectivity is an inherent characteristic of the Baltic Sea sub-basins, which influence each other through linkages at different levels of the food web, e.g. nutrient flows and predator migration. Despite the importance of this connectedness and the influence of coastal waters, we focused on open-sea data to determine the temporal trends of key structural food web components in different sub-basins, in relation to variations in key environmental factors to reduce fine-scale spatial heterogeneity caused by highly spatially variable inputs of nutrients and carbon from land-based sources (Vähätalo et al. 2011, Kiljunen et al. 2020). Nonetheless, offshore and coastal areas are irrefutably connected with many species migrating between different systems on a yearly or life-cycle basis (i.e. herring and stickleback). For example, declines in cod and herring associated with increased fishing pressure have been coupled to an increase in stickleback biomass (Olin et al. 2022, Faithfull and Bergström 2025), which negatively impact coastal fish populations through predation on eggs and larvae (Bergström et al. 2015, Olin et al. 2022).

Our study focused on changes in trophic guild abundance, in accordance with MSFD D4C2 criteria for food web status. However, initial broader examination shows considerable shifts in species composition within trophic guilds, which can have large ecological and economic consequences due to differing commercial values of species (e.g. herring and vendace) or negative effects on ecosystem services, e.g. cyanobacterial blooms impairing water quality or *Marenzelleria* spp. causing nutrient release from sed-

iments (Kahru et al. 2020, Ojaveer et al. 2023). Further work is needed to examine how the changes in species abundance within trophic guilds across basins are affected by human pressures as per MSFD criterion D4C1.

Conclusion

Our analysis shows that changes in trophic-guild balance and ecosystem reorganization in seven Baltic Sea sub-basins are clearly associated with changes in human-induced pressures at the sub-basin scale. Altered food web regimes have persisted despite reductions in the pressures that contributed to the initial shift. Climate warming has also played a role in shifting food web regimes in several sub-basins, in some cases exacerbating the effects of other pressures. While global action is needed to reduce warming, two local human induced pressures, overfishing and excessive nutrient concentrations, emerge as dominant, highlighting that regional management decisions can substantially influence food web status despite climate change. Healthy food webs support biodiversity and ecosystem services, including fisheries, carbon sequestration and recreation (Viitasalo and Bonsdorff 2022, Scotti et al. 2022). Achieving GES in the Baltic Sea by 2040 is valued at €5.6 billion annually, while poor ecosystem status costs an estimated €9 billion per year in lost recreational opportunities alone (HELCOM 2023a). Our results underscore that strong, coordinated, basin-wide actions to reduce fishing pressure and nutrient inputs, including internal loading (i.e as outlined in the Baltic Sea Action Plan; HELCOM 2021) are essential to restore fully functional food webs in the Baltic Sea.

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Author contributions

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Supplementary material

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

Supplementary material: Basin specific background information, meta-data tables and supplementary results and classification of benthic taxa into trophic guilds as a link to an online resource.

Conflicts of interest

None to declare.

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Data availability

The data underlying this article is available at https://doi.org/10.5281/zenodo.20321614.

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