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Original Article

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Temporal changes in the Bothnian Sea food web reveal a deterioration linked to fishing pressure and recent eutrophication

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Abstract

Changes in food web dynamics can have large and irreversible effects for many species, due to natural, climate-related, or anthropogenic factors. In the Bothnian Sea, changes in key drivers, including climate change and fisheries, raise concerns that food web dynamics are deteriorating. However, no method exists for evaluating food web status for the region. We examine how the Bothnian Sea open sea food web has changed over time (1979–2021) using the EU Marine Strategy Framework Directive criteria for food web status. To analyse food web components and potential key drivers, we apply integrated multivariate analysis and generalized additive models. Results indicate changes in the MSFD criterion 'balance between trophic guilds', mainly associated with changes in herring fishing mortality, dissolved inorganic phosphorus, and salinity. Changes in the 'balance of species within trophic guilds' mainly reflected increased cyanobacteria in the phytoplankton biomass, increased stickleback abundance within the planktivorous fish guild, and declining *Monoporeia affinis* among benthic deposit feeders. The results corroborate a worsening food web status of the Bothnian Sea food web and that measures such as lowering phosphorus loading and fishing mortality would prevent further depreciation. This study contributes to development of management objectives for food webs in the region.

Keywords: food webs; Bothnian Sea; herring; trophic guilds; assessment; MSFD

Introduction

Deterioration of aquatic food webs is of global concern due to impacts from a wide range of human pressures, where the effects of overfishing, nutrient enrichment, and climate change are often central (Pauly 1995, Vasas et al. 2007, Du Pontavice et al. 2020). These pressures primarily have impacts on species and populations, but can lead to effects on food web structure and function via species interactions. Large perturbations to the structure and function of food webs can cause large and irreversible changes in the ecosystem, such as decreased productivity, food provision, resilience, or regulatory capacity (Brown et al. 2010, Pitcher and Cheung 2013, Gomes et al. 2024). Conversely, healthy food webs can vary in space and time, while maintaining ecosystem productivity and resilience, offering a buffer against various pressures and disturbances (Mccann and Rooney 2009, Lewis et al. 2022).

Safeguarding the status of food webs is included as a management objective when aiming for good environmental status of Europe's seas, e.g. in the European Union (EU) Marine Strategy Framework Directive (MSFD) (Directive 2008/56/EC, Decision 2017/848) and in recommendations on best practices for ecosystem-based management (Thrush and Dayton 2010, Tam et al. 2017). However, evaluating the status of marine food webs is difficult due to their complexity. A range of potential food web indicators have been identified (Tam et al. 2017, Otto et al. 2018, Ojaveer et al. 2020), but there is still a lack of internationally agreed approaches for systematically assessing the status of food webs in relation to marine management objectives (Boschetti et al. 2021). Furthermore, most existing indicators address food web aspects only partially, i.e. they only address a few trophic guilds or do not evaluate the balance between guilds (Korpinen et al. 2022). In a review of EU countries' reporting on food web status for the 2011–2016 MSFD cycle, a range of issues were identified, such as inconsistent trophic guild definitions, gaps in data, lack of threshold values and quantitative analyses, inconsistent assessment periods between countries, inconsistent targets, and targets that were not directly relevant to food webs (Boschetti et al. 2021). These issues reflect that there are several technical and conceptual challenges in developing an assessment that is relevant for reflecting changes in the status of food webs while balancing the limited available data.

The Baltic Sea is the northernmost of the marine regions encompassed by the MSFD. The sea is semi-enclosed with brackish conditions, strong seasonality and a climatic gradient. Of the nine bordering countries, all but Russia belong to the EU. For these, MSFD reporting is regionally coordinated by the Baltic Sea environment protection commission (HELCOM), where the assessments also follow up on progress in relation to the Baltic Sea Action Plan, which describes regionally agreed measures for the Baltic Sea environment (HELCOM 2021). However, the status of food webs has so far only been evaluated qualitatively, due to the lack of regionally coherent quantitative approaches (HELCOM 2023a). This represents a significant gap for meeting current management issues in the Baltic Sea, where several ecosystem components are not in good environmental status, implicating significant impacts

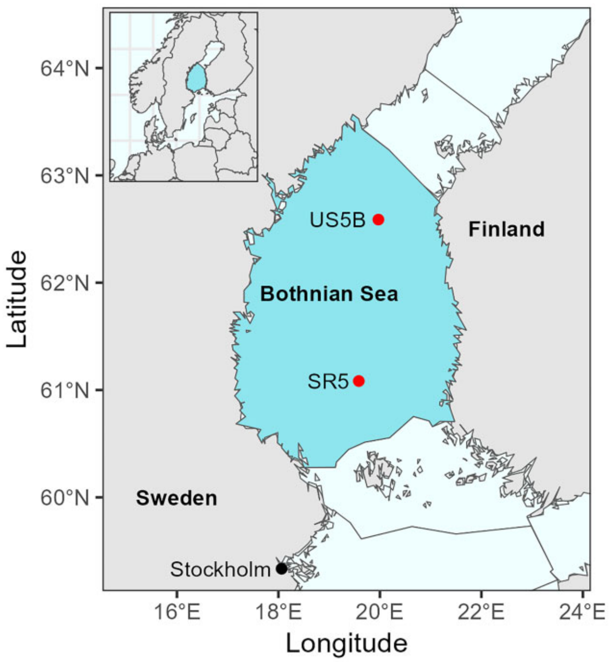

Figure 1. Location of the Bothnian Sea sub-basin in the Baltic Sea, and of the two monitoring stations from which data were used.

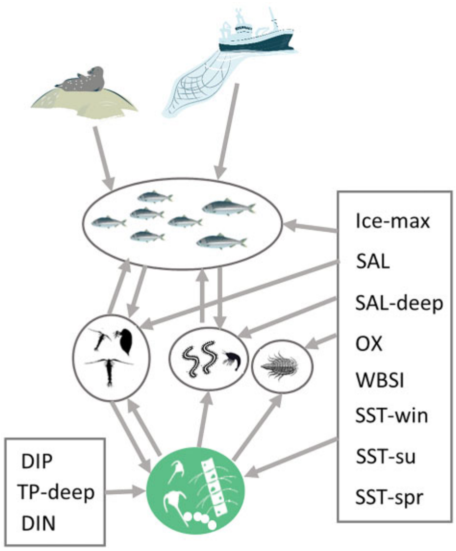

Figure 2. Simple food web diagram of the Bothnian Sea, showing the main trophic guilds included in the analyses; apex predators, planktivores, pelagic secondary producers, benthic deposit feeders, benthic predators, and pelagic primary producers. Arrows represent the known connections between trophic guilds and the relationships that were examined between trophic guilds (or key taxa) and the explanatory variables. Relationships with seals were not examined as their population dynamics suggests they are recovering to carry capacity from very low abundances (HELCOM 2023b).

on food web functioning (Blenckner et al. 2021, HELCOM 2023a).

However, environmental monitoring and data collection in the region provides the basis for assessing the status of species and populations individually and could also support evaluations of food web status provided adequate method development, potentially supplemented with complementary data collection. Several methods are available that could support this, including statistical and model-based approaches (HELCOM 2023a). One promising approach is integrated trend analysis, which has previously been used to elucidate regime shifts in the central Baltic Sea food web (Möllmann et al. 2009, Reckermann et al. 2012, Tomczak et al. 2022), and also provided the basis for food web studies of the Bothnian Bay (Pekcan-Hekim et al. 2016) and the Limfjord in Denmark (Tomczak et al. 2013). Such integrated analyses of trends in ecosystem components provide valuable insights on how the Baltic Sea ecosystem and its environmental status has developed in the recent past, although studies so far have not had the specific aim to align with formal assessment requirements of the MSFD.

This study focuses on the Bothnian Sea food web (Fig. 1), where herring (*Clupea harengus*) is a central component (Fig. 2) (Kiljunen et al. 2020). Being the most abundant planktivore in the sub-basin, herring can potentially drive top-down effects, regulating plankton abundances, while also being influenced by top-down predation and the bottom-up availability of zooplankton, and functioning as an important food source for birds, other fish and marine mammals (Cardinale et al. 2009, Östman et al. 2012, Karlson et al. 2020). External drivers such as changes in salinity, nutrients and temperature are potentially important for herring dynamics in the area, as for the pelagic community composition generally (Kuosa et al. 2017). As the Bothnian Sea has a low salinity of 4.8–6 at the surface and 6.4–7.2 in deeper waters (Lehmann et al. 2022), many species are living at the edge of their salinity tolerance. For example, in the Bothnian Bay food web, north of the Bothnian Sea, Pekcan-Hekim et al. (2016) found that salinity was the most important driver explaining changes in community composition. Over the last 40 years, environmental pressures on the Bothnian Sea have been gradually changing. Fishing pressure on herring populations in the Bothnian Sea has been increasing (ICES 2023a), deep-water temperatures and surface phosphorus have also increased, whereas deep water oxygen concentrations and surface salinity have decreased over time (Lehmann et al. 2022, Kankaanpää et al. 2023). Although previous studies have explored links between such changes and different taxonomic or trophic groups in the sub-basin or its vicinity (Suikkanen et al. 2007, Olsson et al. 2012, Olsson et al. 2015), the relative effects of such drivers on food web dynamics have so far not been thoroughly investigated.

The aim of the present study is to assess how key components of the food web of the Bothnian Sea have developed over the last 42 years (1979–2021) in relation to each other and to changes in ambient environmental drivers. Further, by structuring our analyses around trophic guilds, we evaluate our results against the criteria for ‘Good environmental status’ according to the EU MSFD food web descriptor (D4), focusing on the criteria for trophic guilds (MSFD D4C1 and D4C2; Decision 2017/848). Our first objective is to explore MSFD D4C2: ‘the balance of total abundance between the trophic guilds is not adversely affected due to anthropogenic pressures.’ Second, we focus on MSFD D4C1: ‘the diversity (species composition and their relative abundance) of the trophic guild is not adversely affected due to anthropogenic pressures.’ That is, we examine potential changes in the abundance between or within key trophic guilds of the Bothnian Sea food web over time, and to what extent climate change, i.e. changes in temperature, ice coverage and salinity, or other human pressures such as nutrient concentrations and fishing pressure, may be associated with any observed changes.

Methods

Study area

The Baltic Sea is one of the world's largest brackish-water seas and can be divided into six sub-basins separated by sills, each displaying unique salinity and ecological regimes (Kautsky and Kautsky 2000). The combination of inflow of marine water in the south with freshwater inflow from rivers creates a salinity gradient from around 20 in the Kattegat to two in the Bay of Bothnia (Lehmann et al. 2022). The Bothnian Sea (Fig. 1) has an average salinity of 4.8–7.2 and is located between maritime temperate and continental sub-Arctic climate zones (Meier et al. 2022). As it is on the boundary of many species' tolerances for salinity and climate, it is relatively species poor (Ojaveer et al. 2010, Koehler et al. 2022). The Bothnian Sea has a large catchment area (220 765 km^2) and high land runoff (Johansson 2017), which makes it highly susceptible also to anthropogenic pressures occurring on land (Korpinen et al. 2012). The current study focuses on the open sea part of the sub-basin, where characteristic species include e.g. grey seal (*Halichoerus grypus*), which is the dominant top predator, herring, and *Limnocalanus macrurus*, which is an omnivorous zooplankton species and a high quality prey for planktivores (Hiltunen et al. 2014). The Bothnian Sea is relatively shallow, with an average depth of 66 m and a maximum depth of 293 m, with benthic and pelagic coupling evident by vertical feeding migrations of both predators and prey (Kiljunen et al. 2020).

Analytical approach

We applied integrated trend analyses (ITA) using multivariate analyses coupled with generalized additive models (GAMs) to assess how relative abundances within and between trophic guilds in the open sea food web has changed over time in response to environmental and anthropogenic pressures. We used changes in relative abundances within and between trophic guilds, in alignment with MSFD criteria D4C1 and D4C2, respectively, to compare food web configuration over time. To divide species into trophic guilds we used the definitions provided by the European Commission (European Commission 2022), where at least three trophic guilds are to be included, which represent the top, middle and bottom of the food chain. Trophic guilds considered were pelagic primary producers, secondary producers, planktivores, demersal and pelagic sub-apex predators, and apex predators. However, not all of these guilds are monitored. Trophic guilds represented by long time series data in our studied system were pelagic primary producers (phytoplankton), pelagic secondary producers (zooplankton), benthic filter/deposit feeders, benthic predators, fish planktivores (dominated by herring), and apex predators (represented by grey seal) (Fig. 2). For details on data used see Table 1. We did not focus on evaluating the other two MSFD D4 criteria (C3, C4) due to data limitations. However, we included estimates for changes in size structure over time of a key representative of the planktivore guild (herring), which partly addresses D4C3 regarding size distribution within guilds in alignment with currently available guidance (European Commission 2022).

Data specifications

Data were collected from public databases and were quality controlled either by using time series verified for use in the Third holistic assessment of the ecosystem health of the Baltic Sea (HELCOM 2023a), or by consulting with experts on the concerned time series. The main databases used were hosted by the Finnish Environmental Institute (SYKE), the Swedish Meteorological and Hydrological Institute (SMHI), the International Council for Exploration of the Sea (ICES) and the Swedish University of Agricultural Sciences (SLU). To minimize potential error due to spatial variability between sampling points, we focused the data to as far as possible be representative of the situation around two open sea sampling stations, US5B (214 m deep) and SR5 (126 m deep) (Fig. 1), which have the longest consistent monitoring of pelagic and benthic fauna data in the Bothnian Sea. For phytoplankton, zooplankton and macrozoobenthos data, we used summer (May–July) means from these stations, which approximates the growing season and is when sampling took place. Phytoplankton were identified from integrated water samples collected between 0 and 10 m depth, zooplankton were collected with depth stratified vertical net tows from 5 m above the sea floor to the surface and macrozoobenthos were sampled from soft bottoms using a Van Veen grab (HELCOM 2014).

For long term data on fish (1979–2021), we used the estimated herring spawning stock biomass (SSB) and recruitment of herring according to analytical stock assessments for the whole Gulf of Bothnia (ICES sub-divisions 30 and 31), in alignment with the current stock definitions (ICES 2023a). Herring SSB represents the total biomass of fish that are reproductively mature in the stock and herring recruitment represents the annual number of 1-year olds multiplied by their mean weight in the same year. While these two indicators had the advantage of covering a long time period, they derive from the same stock assessment model and could be expected to be interrelated and fisheries-dependent. Fisheries-independent data from surveys is available for the Bothnian Sea since 2007, based on the Baltic international acoustic survey (BIAS) performed yearly in Sept-Oct (ICES 2023b). This data was used in the analyses of the relationship among species within the planktivore guild, in a shorter time series (2007–2021). For this data, trends in fish biomasses are estimated from a combination of hydroacoustic data and trawl hauls to identify species and estimate size distributions, giving the estimated abundance and biomass of herring, stickleback (*Gasterosteus aculeatus*) and sprat (*Sprattus sprattus*) (ICES 2021; data available from the ICES database for acoustic and trawl surveys (ICES Acoustic Data Portal 2023). Additionally, to provide an estimate of long-term trends in herring size structure, approximating MSFD D4C3 ("The size distribution of individuals across the trophic guild is not adversely affected due to anthropogenic pressures") we used data on mean herring weights at age in catches (ICES 2023a). Based on the presented data per age group, we calculated the annual deviation in mean herring weight-at-age (g) from the average of the whole time series (1979–2012), using data for age classes 3–15 weighted by the biomass of each age class (ICES 2023a). Although this data series only represents one taxon rather than a whole trophic guild, it represents the most abundant species within the planktivore guild.

For marine mammals, grey seal monitoring was initiated in 1991 and population trends are reported at the level of the

Table 1. Trophic guilds and key focal taxa in the analysis of food webs for the open sea area of the Bothnian Sea, with specifications of the data used.

Trophic guild	Key taxa within guild	Season	Sampling station/ location	Unit	Source
Pelagic primary producers	Chlorophyta Chrysophyta Ciliophora Cryptophyta Cyanophyta Diatoms Dinophyta Euglenophyta Haptophyta	May–July	US5B, SR5	Biomass (ugl^{-1})	SYKE (2022)
Pelagic secondary producers	*Arcartia spp.* *Bosmina coregoni* *Eurytemora spp.* *L. macrurus* *Pleopis polyphemoides* *Podon spp.* *Pseudocalanus minutus*	May–July	US5B, SR5	Biomass (mg m^{-3})	SYKE (2022)
Benthic deposit feeders	*Marenzelleria* spp., *Macoma baltica*, *Monoporeia affinis*, *Pontoporeia* spp.	May–July	US5B, SR5	Wet Weight (g m^{-2})	SYKE (2022)
Benthic predators	*Saduria entomon*, *Bylgides sarsi*, *Halicryptus spinulosus*, *Harmothoe sarsi*	May–July	US5B, SR5	Wet Weight (g m^{-2})	SYKE (2022)
Herring	Herring spawning stock biomass (SSB) Herring recruit biomass Herring weight-at-age change	Yearly	ICES subdivisions 30, 31.	Biomass (tonnes) Biomass (tonnes) Average change in weight at age (g) age classes 3–15 + weighted by biomass.	ICES (2023a)
Planktivores	Herring Stickleback Sprat	Yearly (2007–2021)	ICES subdivision 30	Biomass (tonnes)	ICES (2023b)
Apex predators	Grey seal	May–June	Karlhällan, Klacken, Lövgrund, Norrkobbarn, Rödberget, Stenrevet, Sydvästbrotten, Sörbrotten	Total counted (on land, in water, pups). Modelled hindcasted from total Baltic counts between 1979–1990	SMHI (2023)

Unless otherwise is stated, the data covered years 1979–2021.

whole Baltic region (HELCOM 2023b). However, trends in seal abundance and condition between sub-basins can differ (HELCOM 2023b). To obtain a grey seal count specific to the Bothnian Sea, a relative index of grey seal abundance was calculated based on seal counts in haul-outs of the Northern Baltic proper, Åland Sea, Bothnian Sea and Bothnian Bay during May-June in alignment with HELCOM methods (2023b). For this, we summed the maximum count for each site during the survey period per year. Further specifications of all biotic data used is given in Table 1.

We assigned the key taxa to trophic guilds as shown in Table 1. Due to the naturally low species richness of the Bothnian Sea, only one or a few taxa were included in some of the guilds but still represent a significant part of the biomass. Among the biotic data, any phytoplankton, zooplankton and benthic taxa occurring in less than 10% of the studied years were excluded from the subsequent analyses of trends within that trophic guild. In all analyses, non-systematically missing data points (six incidences in phytoplankton and three in the zooplankton data) were replaced by mean values of the two years prior and two years after the missing data point. Seal data were missing prior to 1991, and were extrapolated backwards to 1979 using a logarithmic curve, which reflects the temporal pattern of the existing data and agrees with prior information that the grey seal population was at very low levels in the 1970s (HELCOM 2023b).

For environmental drivers, nutrient conditions were represented by winter means (November–March) of dissolved inorganic nitrogen (DIN) and phosphorus (DIP), total phosphorus (TP) bottom total phosphorus (TP-deep) and bottom water oxygen (OX). Climate and oceanographic conditions were represented by the winter Baltic Sea climate index (WBSI) (Hagen and Feistel 2005), spring, summer, and winter sea surface temperature (SST-spr, SST-su, SST-win, 0–10 m), winter surface salinity (SAL, 0–10 m), bottom salinity (SAL-deep, >100 m) and surface acidity (pH, sampled November–March), and the annual maximum extent of the ice sheet (ice-max; representing the wshole Baltic Sea (Table 2). The hydrochemical variables were monitored using a water sampler until 1991, and after 1991 a CTD was used. No systematic

Table 2. Environmental and anthropogenic drivers (explanatory variables) used in the analysis of food webs for the Bothnian Sea.

Abbreviation	Name used in text	Months	Depth (m)	Unit	Stations	Source
SST-win	Winter sea surface temperature	November–March	0–10	°C	US5B, SR5	SMHI (2023)
SST-spr	Spring sea surface temperature	March–May	0–10	°C	US5B, SR5, C3, C14 (years 2014–2021)	SMHI (2023)
SST-su	Summer sea surface temperatures	June–September	0–10	°C	US5B, SR5, C3, C14 (years 2014–2021)	SMHI (2023)
WBSI	Winter Baltic Climate Index	NA	NA		https://www.io-warnemuende.de/wibix.html	(Hagen and Feistel 2005)
Ice-max	Maximal ice extent	NA	NA	10^3 km^2	Whole Baltic Sea	SMHI (2023)
SAL-win	Winter surface salinity	November–March	0–10	[PSU]	US5B, SR5	SMHI (2023)
SAL-deep	Winter salinity of deep water	November–March	>100	[PSU]	US5B, SR5	SMHI (2023)
OX	Oxygen in the deep water, winter	November–March	>100	ml l^{-1}	US5B, SR5	SMHI (2023)
pH	pH	November–March	0–10	pH	US5B, SR5	SMHI (2023)
DIN	Dissolved inorganic nitrogen in the surface, winter	November–March	0–10	µmol l^{-1}	US5B, SR5	SMHI (2023)
DIP	Dissolved inorganic phosphorus in the surface, winter	November–March	0–10	µmol l^{-1}	US5B, SR5	SMHI (2023)
TP	Total phosphorus in the surface, winter	November–March	0–10	µmol l^{-1}	US5B, SR5	SMHI (2023)
TP-deep	Total phosphorus in the deep water, winter.	November–March	>100	µmol l^{-1}	US5B, SR5	SMHI (2023)
$F_{3\text{-}7}$	Fishing mortality of age 3–7 herring.	Yearly	NA		ICES subdivisions 30–31	ICES (2023a)

Unless otherwise is stated the data covered years 1979–2021.

differences were apparent between methods, however, as a precaution for years where both methods were used we used the method means, otherwise we used data from the method available. As an indicator of fishing pressure, we used the average fishing mortality of age 3–7 herring ($F_{3\text{-}7}$) modelled for subdivisions 30–31 to represent the mortality of the fully exploited age classes available from ICES (2023a). When explanatory variables were assessed in relation to the variables herring spawning stock biomass, recruitment, and weight-at-age, as well as the multivariate models, we used both the same-year data and 3-year moving average time lags (expressed as i.e. $F_{3\text{-}7}$ 3) to capture their potential immediate relationship as well as influence on cohorts. The time lag was identified after comparing with model fits using a 4-year lag, based on that for the last 13 years, 68%–92% of the herring stock have been between 1 and 5 years old (ICES 2023a). We did not test with a 5-year lag due to the loss of data in at the beginning of the time series.

Statistical methods

Figure 3 outlines the different steps applied in our analyses to explore the value of ITA in supporting the assessment of food web status in alignment with MSFD criteria D4C1 and D4C2, which are further detailed below. All analyses were carried out using data standardized to zero mean and unit variance to account for the comparison of data sets with different measurement units, and after transformation ($\ln(y + 1)$) the data met normal distribution of variances assumptions. We first explored how all variables changed over time, using GAMs with restricted maximum likelihood estimation, and checked the explanatory variables for co-variance and correlation. Some explanatory variables were predictably correlated, i.e. surface salinity, bottom salinity and pH, and the winter Baltic Sea index was correlated with the maximal ice extent. In addition, fishing mortality of herring was unexpectedly correlated with dissolved inorganic phosphorus and oxygen concentrations (Supplementary information, Anex 1). However, all variables where still interpreted as carrying unique information and were retained at the initial step. Possible interpretation biases due to covariation were considered by examination of variation inflation factors (VIF) in the multivariate analyses. Additionally, when examining relationships between explanatory and response variables using general additive models we only included data pairs where an ecologically relevant (first-order) causal relationship could be anticipated, which included top-down and bottom-up effects of key taxa, i.e. herring and phytoplankton taxa on zooplankton (Fig. 2).

We conducted distance-based redundancy analysis (dbRDA), which is a multivariate ordination method where response variables are constrained by explanatory variables in multiple dimensions, hence summarizing the variation in the biotic variables that can be explained by the environmental or anthropogenic drivers (Table 2). In contrast to RDA, which is based on Euclidean distances, dbRDA allows analyses based on more ecologically relevant measures of association. Here, we used chord distances, which are more suitable for abundance data and years are not sorted as similar based on common absences, which is otherwise problematic in data sets with many zeros (Legendre and Anderson 1999), such as our species abundance data within trophic guilds. We examined trends between and within trophic guilds separately for all biotic data sets using the *capscale* function (constrained

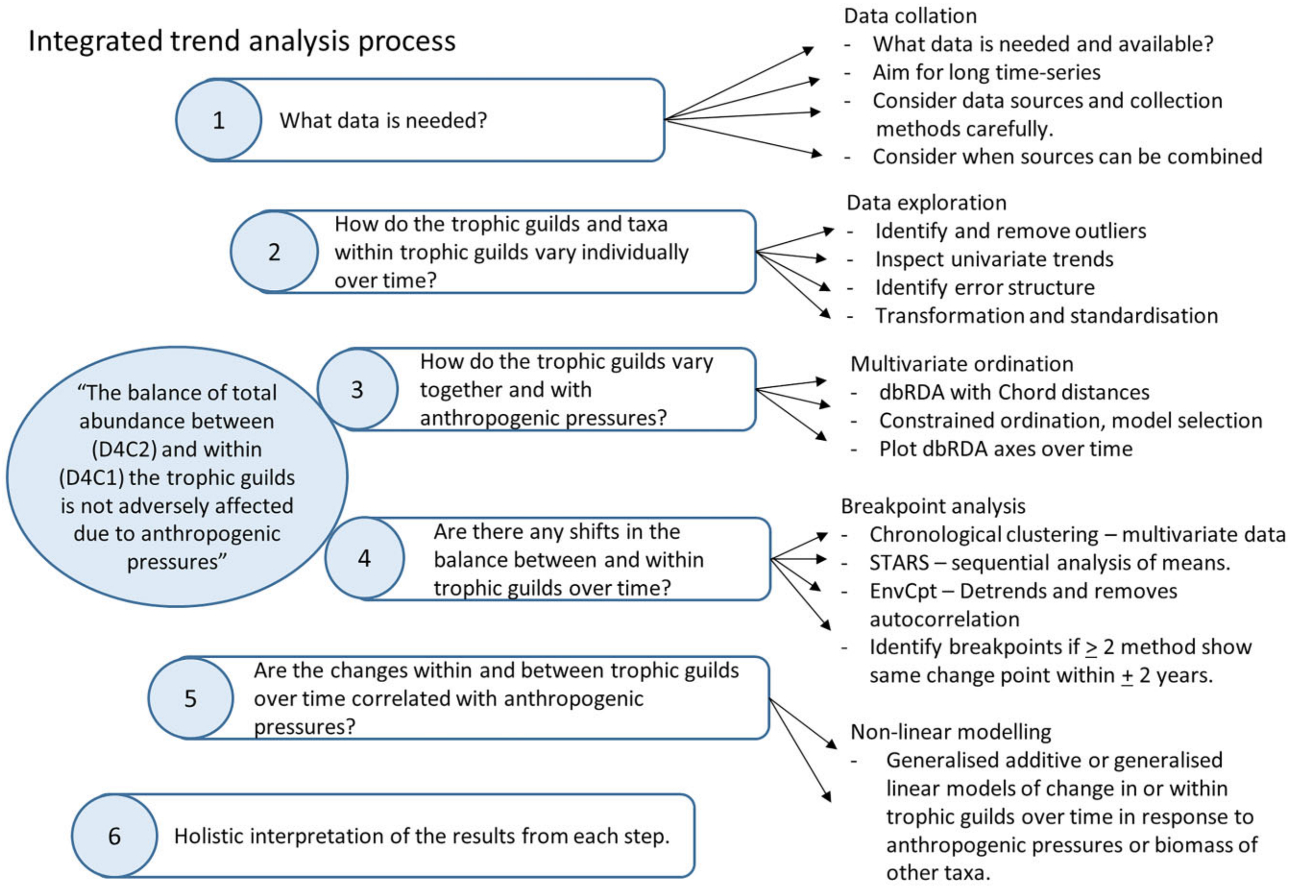

Figure 3. Process diagram of our methods for using integrated trend analysis to assess the status of food webs under the MSFD.

dbRDA) (see Table 1) in the *vegan* package (Oksanen et al. 2020) in the statistical freeware R (R Core Team 2021). To address multicollinearity, these models were checked to ensure that none of the included explanatory variables contributed to a VIF >5 (Zuur et al. 2010). When variables had VIFs >5 (indicating co-linearity) the one explaining the least amount of variation when tested with model selection was removed. We used the model selection tool *ordistep* and the lowest Akaike information criterion (AIC) to identify the most parsimonious models that explained the most variation and excluded non-significant explanatory variables. In the dbRDA analysis, the constrained variation (variation accounted for by the explanatory variables) and the fitted variation (variation explained by the explanatory variables and the relationships between the response variables) is presented for each axis.

We complemented the dbRDAs with breakpoint analyses to identify any distinct shifts in community composition over time. For this, we used a combination of three different methods as each have strengths and potential weaknesses. We used chronological clustering for analysing multiple time series simultaneously, using the Brodgar software (Highland statistics Ltd). Chronological clustering calculates a Euclidean distance matrix from which consecutive years are clustered if they meet a set proportion of common links of the maximum number of possible links (Legendre et al. 1985). We used a proportion of 50% common links and an alpha of 0.01, which is relatively conservative, as we aimed to only identify larger community shifts. To assess breakpoints based on the dbRDA axis scores, we used Sequential T-test Analysis of Regime Shifts (STARS v. 4.0), which detects shifts in the mean of the time series based on the students *t*-test using an Excel macro-enabled template file (Rodionov 2015). STARS has been previously used to estimate regime shifts in the Baltic Sea (i.e. Möllman et al. 2009, Tomczak et al. 2022), but may overestimate the number of breakpoints when autocorrelation or trends are present in the data (Beaulieu and Killick 2018), thus requiring de-trending or pre-whitening before analysis (Tomczak et al. 2022). Therefore, we compared the STARS results with changepoint analysis (Using the EnvCpt package in R; Killick et al. 2021), which fits up to 12 different models with variations in trends, means and autocorrelation, and identifies the most appropriate model according to the lowest AIC. Both STARS and EnvCpt analyses may overestimate the number of breakpoints especially in data with monotonous trends. We combined results for all the three methods by defining instances as a 'clear shift' where at least two methods identified the same breakpoint (±2 years) and breakpoints as a 'shift' where identified by only a single method (Beaulieu and Killick 2018).

As dbRDA is based on linear relationships we used GAMs to further investigate potential non-linear relationships between trophic guilds/key taxa and the explanatory variables, including top-down and bottom-up biotic drivers (Fig. 2). To focus the analyses on how the potential explanatory variables, and other taxa, may have influenced the focal biotic variable, we only included data where an ecologically relevant and first-order causal relationship could be anticipated (Fig. 2). For example, there is no biological basis for phosphorus to affect herring biomass directly, as effects of nutrient enrichment are mediated by intermediate trophic levels such as phytoplankton. Consequently, phosphorus was not used as an explanatory variable for herring. Further, factors affecting the abundance of apex predators were not examined in the GAMs as they show a growth trend over the studied period that most likely reflects a recovery from very low abundances, so that no ecologically relevant causal relationships to the examined factors could be anticipated over the studied time periods and variables (HELCOM 2023b). The GAMs were constructed using restricted maximum likelihood, and a maximum effective degrees of freedom (edf) of nine for the smooth terms, to balance the tradeoff between accurately representing the relationship between the model terms and ecological interpretation (Wood 2017). However the highest edf of 5.4 was well under the maximum of nine (Table 3). We used *k.check* to assess if the model accurately fitted the data using the available smoothing terms. Residuals were examined for autocorrelation and the model adjusted accordingly. Stepwise simplification and comparison of AIC values were used to determine the simplest model explaining the highest amount of variation (Wood 2017). When the best model did not contain nonlinear explanatory variables, general linear models (GLMs) were used in place of GAMs Results were retained in cases where the best model explained >30% of the variation in the time series. The GAM analyses were conducted using the *mgcv* package in the R freeware (Wood 2017).

Results

Changes over time between trophic guilds

The dbRDA analysis shows that the structure of the Bothnian Sea food web has changed between 1979 and 2021 in terms of the relative abundance between trophic guilds (Fig. 4). The first two axes of the constrained model explained 41% of the total constrained variation (Fig. 4a). The first axis (explaining 23% of the constrained variation) mainly reflected changes in apex predators (grey seal abundance), which was increasing over time (Figs 4–5). Pelagic primary and secondary producers (total phytoplankton and zooplankton biomass) were correlated with the first two dbRDA axes, also showing gradual increases over time (Fig. 4). The second axis was also correlated with changes in planktivores, represented by herring SSB (Fig. 4), which increased rapidly during the mid-1980s, followed by a steady decline for the remainder of the time series (Fig. 5d). Among the explanatory variables, fishing mortality ($F_{3–7}$ 3 year lag), DIP and surface salinity were the main factors correlated with changes along dbRDA axis 1, while deep salinity with a 3-year lag and surface salinity mainly correlated with dbRDA axis 2 (Fig. 4a).

The results from the breakpoint analyses (chronological clustering, change point analysis, and STARS) gave somewhat different results as to which years changes in the food web occurred (Table S1). However, all three methods identified two clear shifts, around 1984–1988 and 2013–2014, indicating three main phases of food web configuration over time (Fig. 4b). The period from 1979 to 1984 can be characterized as a relatively low productivity phase, with low biomasses of all trophic guilds, low nutrient concentrations, high winter ice coverage, and high salinity (Figs 5 and 6a,b,g,h,k). The following period from 1988 to 2013 was characterized by rapid change across several trophic guilds, including benthic deposit feeders, herring SSB, and apex predators. Further inspection of the underlying data mainly associated this period of change with the introduction and establishment of the non-indigenous species *Marenzelleria* spp. causing a spike in benthic deposit feeder abundance (Fig. 5c,e), and with grey seal increasing steadily (Fig. 5f). Herring SSB increased at first and subsequently declined (Fig. 5e). Over the same period, salinity and ice coverage declined, while phosphorus concentrations increased slowly (Fig. 6a,b,g,k). The most recent period, 2014–2021, was characterized by further declines in herring spawning stock biomass, as well as declines in benthic filterer and seal abundance (Fig. 5). The drivers of the food web in this period appear to be a combination of top-down and bottom-up factors such as increasing nutrient concentrations (mainly phosphorus) and a time-lagged effect of increasing fishing mortality (Figs 4a–c and 6g, l). The abundance of higher trophic levels, i.e. apex predators (grey seal) and planktivores (herring) decreased rapidly, while the abundance of lower trophic levels, i.e. zooplankton, and phytoplankton increased gradually (Fig. 5).

Changes within trophic guilds

For the planktivore guild, which was assessed based on the shorter survey-based data (2007–2021), sticklebacks increased over time, while sprat and herring decreased (Fig. 7a–c). This was reflected in the correlations of these taxa with the first two dbRDA axes (Fig. 8a,c) and the changes in species scores over time (Fig. 8b). The only significant explanatory variable was fishing mortality (applying a 3-year lag), which was positively correlated with dbRDA axis 1 (Fig. 8a). All breakpoint analyses found a shift in 2012–2013 associated with increased sticklebacks and decreases in herring and sprat (Fig. 8b).

Among benthic species, taxa within both the assessed guilds showed highly variable abundances over time (1979–2021; Fig. 7d–f). The most prominent pattern was among the benthic deposit feeders, where the polychaete *Marenzelleria* spp. and the amphipod *Pontoporeia femorata* abundance increased and were positively correlated with dbRDA axis 1, while *Mo. affinis* was negatively correlated, reflecting a decrease over time (Fig. 8d–f). The predatory polychaete *Har. sarsi* was correlated with dbRDA axis 2 and positively associated with winter surface salinity, which decreased over time. The isopod predator and scavenger *S. entomon* was not correlated with any of the explored explanatory variables and did not show any clear trends over time (Figs 7d and 8d). Both chronological clustering and STARS found a clear shift in community composition linked to the appearance of *Marenzelleria* spp. (Fig. 8e), which first appeared in the data set in 2003 and increased to a peak in 2005 after which it declined (Fig. 7e). Change point analysis identified several shifts, at 1989, 1995, and 2001, which could be associated with variability in *M. affinis* and *S. entomon* over time. Oxygen (OX) concentrations, which decreased around the same time in the Bothnian Sea, were negatively correlated with dbRDA axis 1 (Fig. 8d).

For pelagic secondary producers (zooplankton), the first two dbRDA axes only explained 27% of the constrained variation. Changes along the first axis reflected a decline of marine taxa that require sufficient salinities such as *Arcartia spp.* and *Pseudocalanus minutus*, and an increase of freshwater taxa *B. coregoni* and *L. macrurus*, in parallel with a decline in

Table 3. Output of GAMs on factors potentially explaining changes in trophic guilds and key taxa within guilds.

Trophic guild/Key taxa	**Model variables**	**Edf**	**Shape /Slope**	**P-values**	**DevEx (%)**
Planktivores*	$F_{3\text{-}7}$, 3 year lag	1.8	⤴	0.063	**39.2**
Stickleback *	$F_{3\text{-}7}$, 3 year lag	0.9	↗	<0.001	**71.6**
Sprat*	$F_{3\text{-}7}$, 3 year lag	2.4	↪	<0.001	**73.7**
Herring SSB	$F_{3\text{-}7}$, 3 + SAL-deep 3				**95.2**
	$F_{3\text{-}7}$, 3 year lag	5.4	↪	<0.001	
	SAL-deep 3 year lag	2.6	↷	<0.001	
Herring recruitment	*B. coregoni* + Ice-max + Weight-at-age change				**41.7**
	B. coregoni	0.9	↗	<0.001	
	Ice-max	0.8	↘	0.021	
	Weight-at-age change	0.9	↗	0.002	
Herring weight-at-age change	$F_{3\text{-}7}$ 3 + SST-spr 3				**89.4**
	$F_{3\text{-}7}$ 3 year lag	2.9	⤴	<0.001	
	SST-spr 3 year lag	2.7	↪	<0.001	
Pelagic secondary producers (Zooplankton)	SAL + WBSI + Cyanophyta				**39.5**
	SAL	1	-190	<0.001	
	WBSI	1	19.2	0.06	
	Cyanophyta	1	-0.262	0.06	
L. macrurus	SAL-deep + Herring + Ice-max				**68.7**
	SAL-deep	3.4	↪	<0.001	
	Herring SSB	2.8	↷	0.01	
	Ice-max	2.3	↷	0.03	
M. affinis	TP + SST-su				**63.1**
	TP	2.1	⤵	<0.001	
	SST-su	2.2	↷	<0.001	

Table 3. Continued

Pelagic primary producers **(Phytoplankton)**	SAL-deep + SST-su				**40.1**
	SAL-deep	1.9	↷	0.004	
	SST-su	1.5	↪	0.005	
Cyanophyta	DIP	1.9	↗	<0.001	**37.6**

Results are only shown for models that explained >30% of the variation in the guilds and taxa time series, hence results for benthic deposit feeders and benthic predators and some key taxa within the other trophic guilds are not shown (compared with Table 1). Edf (estimated degrees of freedom) = 1 indicates that the relationship is linear. Shape/slope shows the shape of the relationship if the model is non-linear (GAM) and the slope of the linear (GLM) models. The actual model relationships are visualized in Figs S6–S8. DevEx is the percent variance explained by the full model. All models are based on time series from 1979 to 2021 ($N = 43$), except those marked $*$, which are from 2007 to 2021 ($N = 15$).

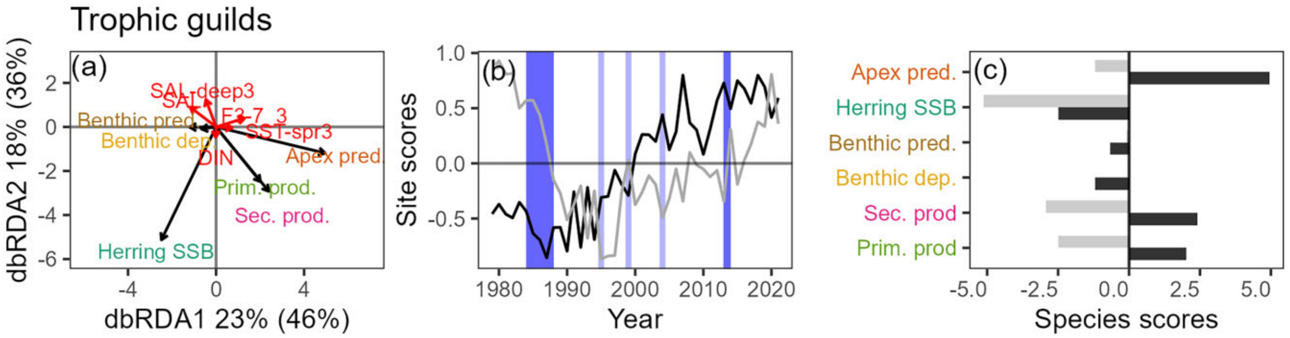

Figure 4. Results of dbRDA on the relative abundance between all included trophic guilds (a–c) 1979–2021. The biplot (a) shows the linear relationships between the response variables and the significant explanatory variables for the first and second dbRDA axes. dbRDA 1 accounts for 46% of the fitted variation (shown in brackets) and 23% of the total constrained variation and dbRDA 2 accounts for 36% of the fitted variation and 18% of the total constrained variation. The change in site scores (b) for dbRDA axes 1 (black) and 2 (grey) over time delineates three main periods. White areas represent relatively stable periods with no breakpoints identified by chronological clustering, change point analysis and STARS, the dark shaded areas represent where two methods show similar breakpoints and the shaded area represents a less stable period where multiple breakpoints were found (shown as lines). The species scores for each taxa and their correlation with the first two dbRDA axes and are shown in figure c. Planktivorous fish are only represented by herring in the analyses of longer-time series, as this is spawning stock biomass based on fisheries dependent data. For explanations of abbreviations, see Tables 1–2.

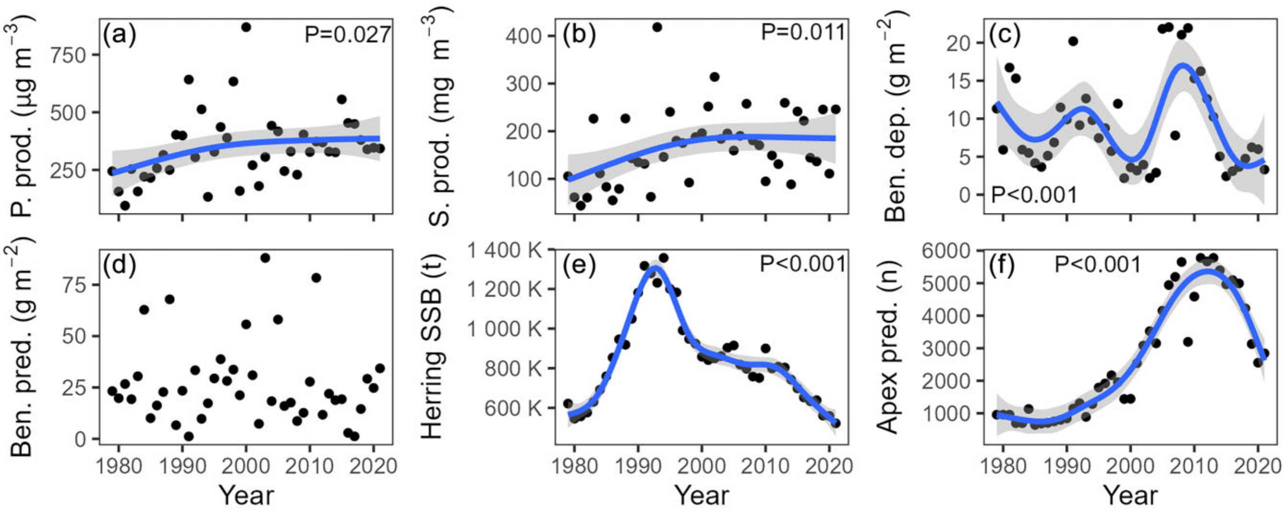

Figure 5. Temporal development of trophic guilds included in the study, P. prod, Pelagic primary producers; S. prod, Pelagic secondary producers; Ben. dep, Benthic deposit feeders; and Ben. pred, Benthic predators. Significant general additive model trends over time ($P < 0.05$) with 95% confidence intervals and P-values are shown. Note that apex predator data (grey seal) before 1991 is extrapolated.

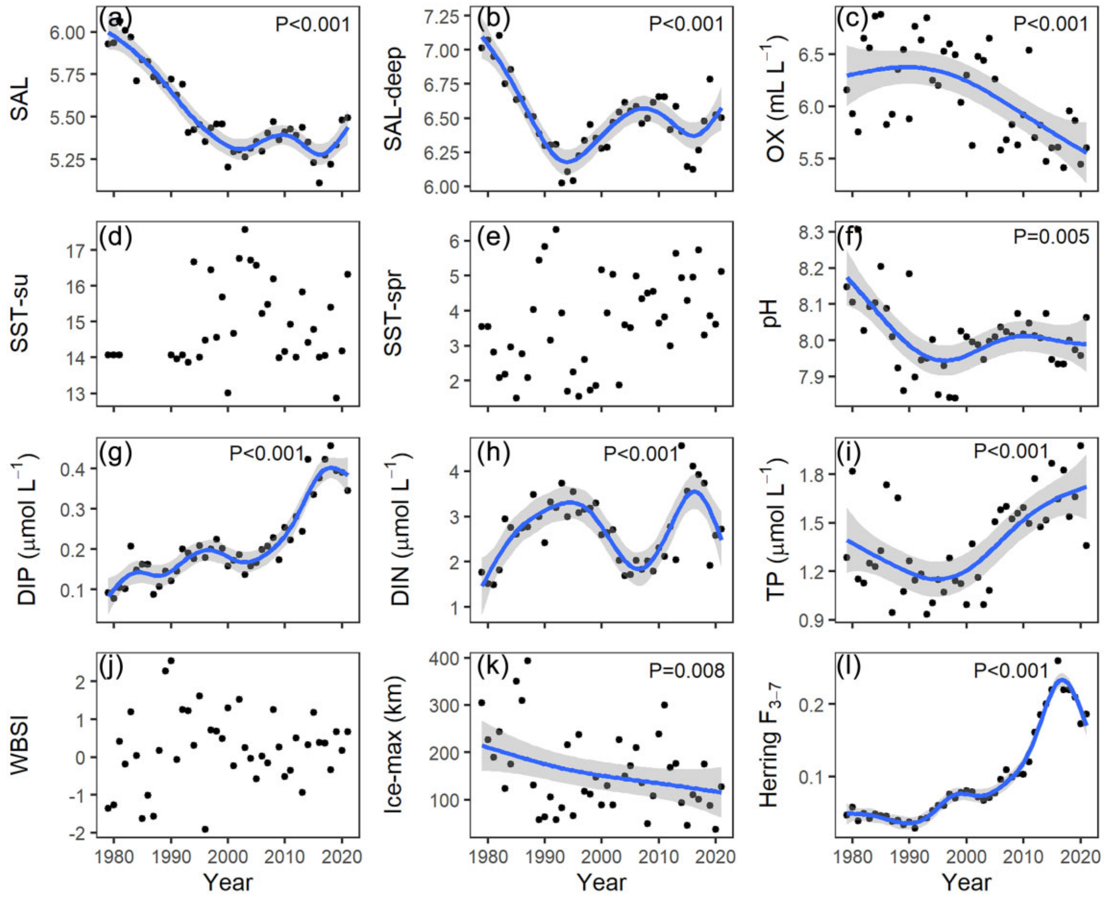

Figure 6. Temporal development in environmental and anthropogenic drivers over time in the Bothnian Sea. Significant general additive model trends over time ($P < 0.05$) with 95% confidence intervals and P-values are shown. For explanation of abbreviations, see Table 2.

surface salinity over time (Figs 7g–i and 8g). The three breakpoint analyses detected many shifts between 1984 and 2011 (Table S1), suggesting that there have been no distinct changes in community composition during this time but a gradual transition (Fig. 8h).

Representing pelagic primary producers, total phytoplankton biomass increased until 1999 and was thereafter relatively constant over the studied years (Fig. 5a). However, major changes in the relative abundance of different phytoplankton taxa occurred (Figs 7j–l and 8j–l). Key changes along dbRDA axis 1 reflected increased abundance of cyanobacteria, diatoms, and ciliophora (mostly *Listomatea*) and a decrease in dinophsytes and euglenoids, coinciding with a clear shift in species composition around 1999 (Fig. 8k–l). The changes were associated with decreasing salinity and increasing DIP concentrations (Fig. 8j). Three periods were recognized by the chronological clustering, change point analyses, and STARS, where all methods identified clear shifts between 1996–2002 and 2008–2011 (Fig 8j); before 1996, haptophytes, chlorophytes, and dinophytes were abundant or increasing, and after 2010, ciliates, cyanobacteria, and diatoms dominated the total phytoplankton biomass.

Changes in explanatory variables over time

Most environmental variables showed some kind of directional trend over the studied time period, with the exceptions of the Baltic Sea winter index (WBSI) and spring and summer sea surface temperatures (SST-spr, SST-su) (Fig. 6). Hence, maximal ice cover (ice-max) was the only climate-related variable that reflected increasingly warmer conditions. Salinity was slightly higher in deep water than at the surface, showing a declining trend in both layers from 1979 to 1995. After this, surface salinity was relatively stable over time and deeper water salinity slightly increased again. Oxygen in deep waters declined over time but did not reach levels corresponding to hypoxia or causing release of phosphorus bound in sediments. Although DIP increased over time, DIN showed no clear direction of change but cycled through increasing and decreasing concentrations. Fishing mortality of herring increased over time, with a peak in 2015 (Fig. 6l).

Changes in trophic guilds in response to explanatory variables

The GAMs showed that for most trophic guilds (planktivores, benthic predators, benthic deposit feeders, and pelagic secondary producers), the deviance explained by the explanatory variables was less for the whole trophic guild than when the dominant taxa were modelled separately (Table 3). As illustrated in the dbRDA results, this reflects cases when taxa within each guild show opposite patterns in relation to some pressures. For example, among the planktivores, sprat decreased and stickleback increased with increased fishing pressure (Table 3).

For the longer time series (1979–2021) 95% of the variation in herring SSB was explained by salinity and fishing pressure (Table 1). Herring SSB was negatively associated

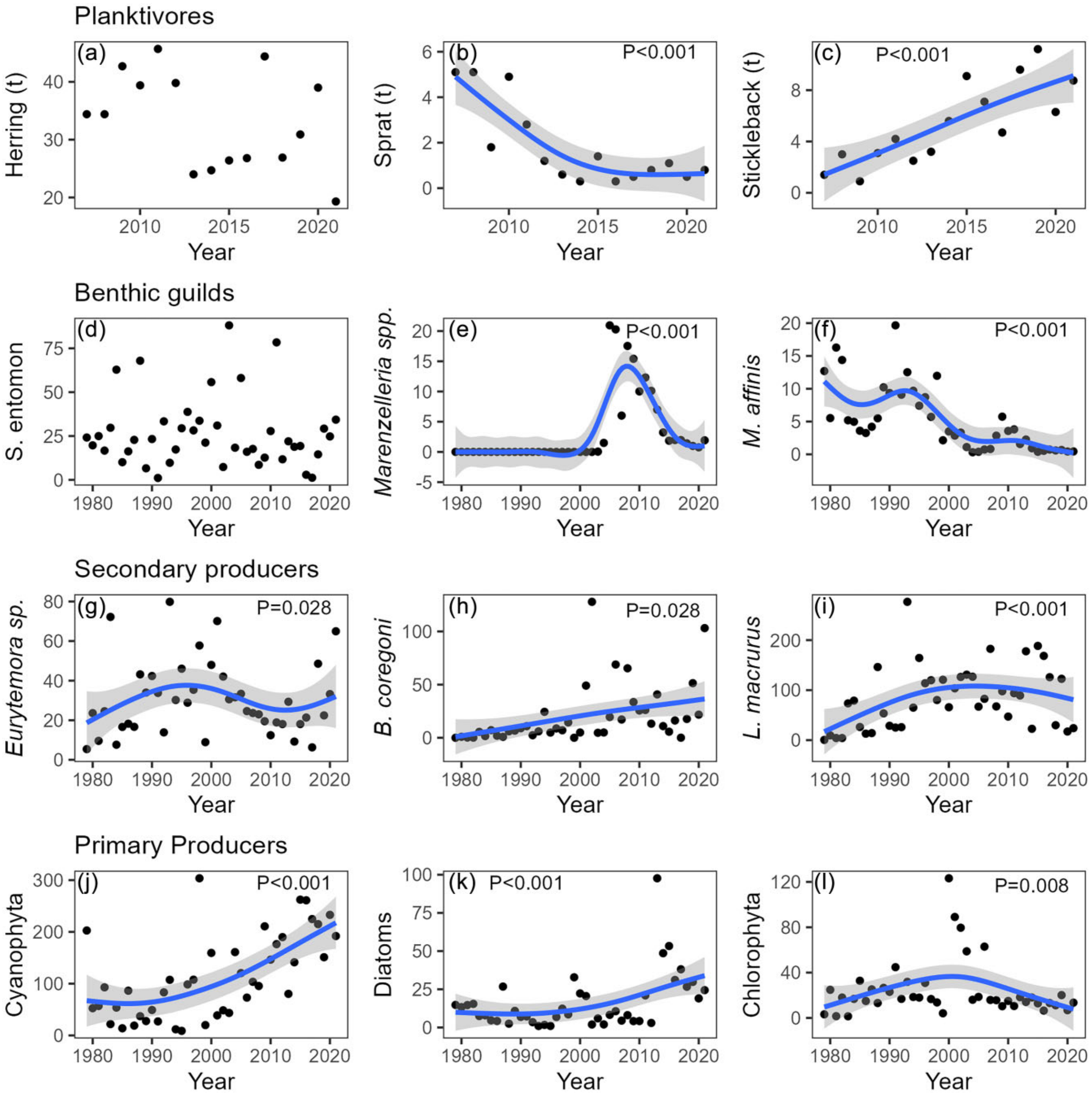

Figure 7. Temporal development in selected key species from the trophic guilds planktivores, benthic predators and benthic deposit feeders, pelagic secondary producers, and pelagic primary producers, in the Bothnian Sea. Significant general additive model trends over time ($P < 0.05$) with 95% confidence intervals and P-values are shown.

with increasing fishing mortality, which could be expected based on that the two variables derive from the same source (as described in the methods section). Herring SSB was also positively correlated with decreasing salinity, which may appear counterintuitive, as herring is a marine species. However, changes in salinity were also associated with changes in important prey for herring, for example the freshwater zooplankton species *L. macrurus* declined with increasing salinity (Table 3). The most important variable associated with herring recruitment was the abundance of the cladoceran *B. coregoni,* a documented prey species (Table 3). For the shorter, survey-based time series, total planktivore biomass (including herring, sprat, and stickleback), showed a concave relationship with herring fishing mortality. This shape was explained by sprat and stickleback biomass showing opposite relationships with herring fishing mortality, sprat decreasing, and sticklebacks increasing with increased herring fishing mortality. Herring biomass, however, was not associated with any explanatory variables in this time series (Table 3). Herring weight-at-age was negatively associated with fishing mortality, showing a sharp decrease already as mortality increased to 0.1, thereafter it increased slightly and flattened out (Supplementary information, Fig. S7d). Herring weight-at-age was also negatively correlated with spring sea surface temperature (Table 3) and showed a positive relationship to recruitment.

GAMs for the benthic trophic guilds (benthic predators and deposit feeders, respectively) did not explain >30% of the deviance of the guilds and hence changes in abundance were not

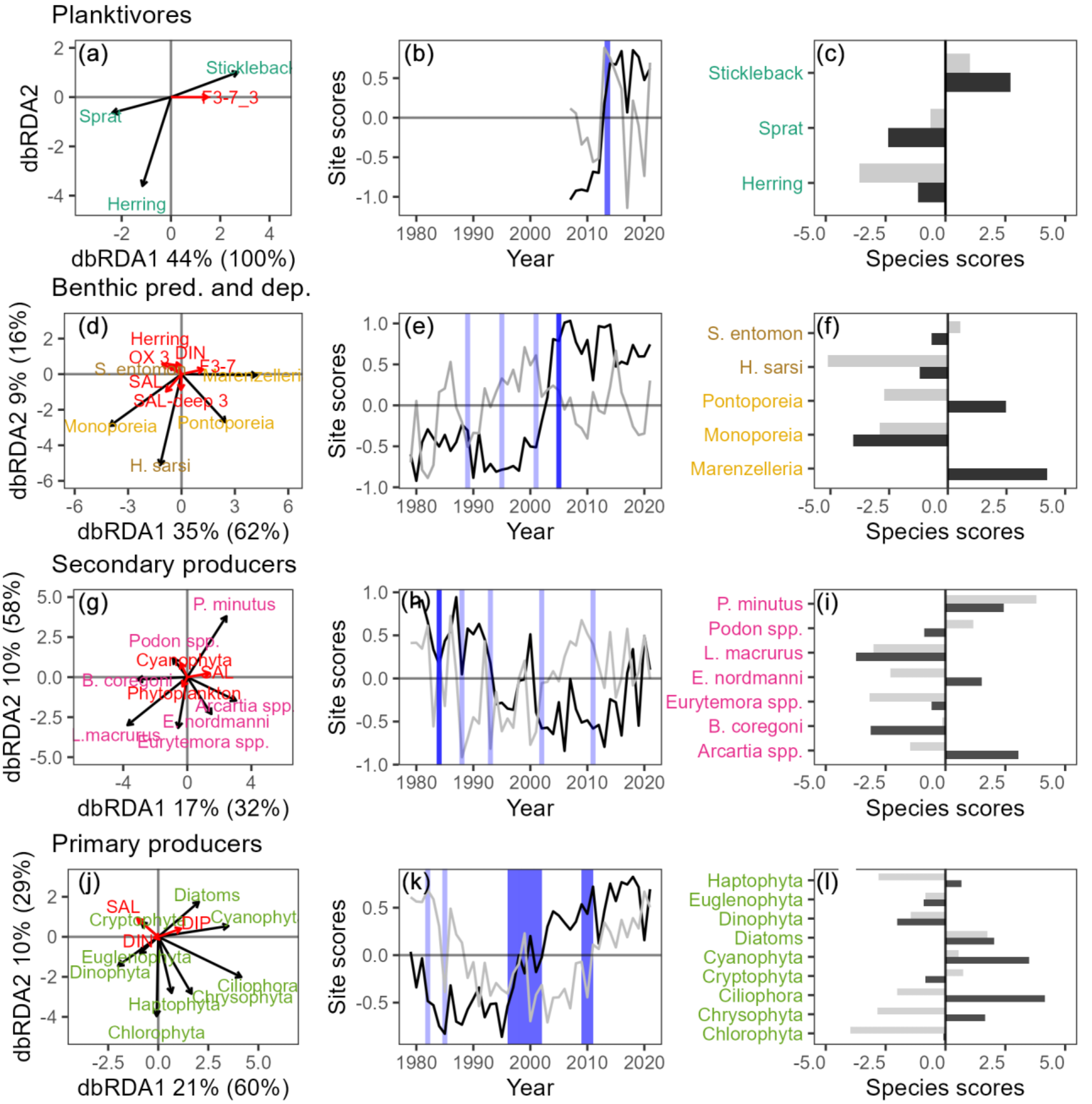

Figure 8. Results of constrained dbRDA on compositional changes within the trophic guilds of planktivores (a–c) (based on fisheries independent surveys 2007–2021), benthic producers and deposit feeders (d–f), pelagic secondary producers (g–i), and pelagic primary producers (k–l). Biplots for each guild are in the first column (a, g, and j) and show the linear relationships between the response variables and the significant explanatory variables for the first and second dbRDA axes. The dbRDA axes show the percentage of total constrained variation (variation accounted for by the explanatory variables) and the percentage of total fitted variation for each dbRDA axis in brackets. The change in site scores for dbRDA axes 1 (black) and 2 (grey) over time are shown in the middle column (b, e, h, and k), and the shaded areas represent shifts in guild composition identified by chronological clustering, change point analysis, and STARS. The species scores for each included taxon, which represent the correlation between the taxa and the RDA axes are shown in the third column (c, f, i, and l). Explanations of abbreviations can be found in Tables 1 and 2.

attributed to any combination of the explanatory variables. For the GAMs on key taxa, 63% of the variation in *M. affinis* biomass was explained by total phosphorus in deep waters, and summer sea surface temperature (Table 3). For the other benthic taxa, the best models did not explain >30% of the variation.

Changes in the pelagic secondary producers were attributed to a negative correlation with salinity and a positive correlation with maximum ice extent (iice-max), indicating that the guild is favored by cold winters. The results primarily reflected the similar relationships between these environmental factors and *L. macrurus*, a cold stenothermic brackish water copepod. In addition, *L. macrurus* was potentially top-down controlled by herring predation, being positively correlated with increasing herring SSB to about 800 kt but decreasing at higher herring SSB (Table 3, Supplementary information Fig. S8c).

Total pelagic primary producer (phytoplankton) biomass was mainly negatively correlated with salinity and summer sea surface temperature, with the model including these two factors explaining 43% of the deviance. Winter dissolved

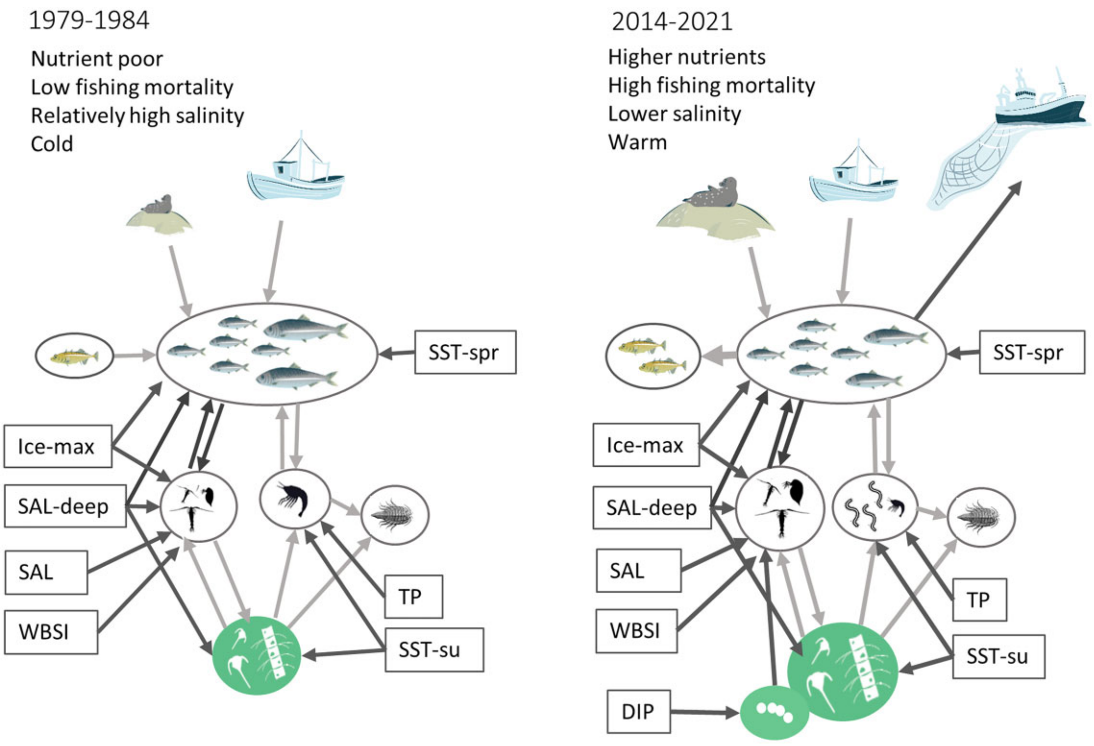

Figure 9. Conceptual diagram of the Bothnian Sea food web and the two stable food web configurations found for the periods 1979–1984 and 2014–2021. The arrows represent the direction of energy transfer (or effect), with the light grey arrows representing documented relationships between trophic guilds and pressures and the dark grey arrows representing the relationships found in this study. Abbreviations can be found in the text.

inorganic nitrogen and phosphorus did not contribute to explaining the variation in total phytoplankton biomass. However, in the GAMs on key taxa, dissolved inorganic phosphorus had a positive relationship with cyanobacterial biomass, which has been increasing over time (Table 3).

Discussion

The ITA applied to food web data for the Bothnian Sea revealed several relationships between variables representing key ecosystem components and their potential relationships to environmental drivers applicable for addressing food web status (MSFD D4 criteria). Overall, the long-term ITA (1979–2021) demonstrated how the relative abundance between trophic guilds (MSFD C4C2) has changed over 42 years. During this time, three main phases were identified, including a relatively low biomass phase (1979–1983), followed by a period with changes in many trophic guilds (1984–2013) to the most recent prevailing state (2014–2021), which was characterized by relatively low biomass of herring and increasingly nutrient rich conditions (Fig. 9). These changes over time between trophic guilds (MSFD C4C2) were associated with increased anthropogenic pressures such as fishing mortality and dissolved inorganic phosphorus concentrations. Climate-related factors, such as salinity and temperature, also contributed to the rise and decline of herring SSB and a slight increase in pelagic primary and pelagic secondary producers (phytoplankton and zooplankton biomass) over time. The combination of environmental factors associated with the changes in food web structure aligns with previous results for the Central Baltic and the Bothnian Bay. Previous analyses for the Central Baltic Sea have attributed increasing nutrient levels to a shift from a low to high productivity food web regime in 1972–1973, which was followed by a shift from a cod to a planktivore dominated fish community in 1989–1990, driven by high fishing mortality and changes in climate (Alheit et al. 2005, Möllman et al. 2009, Tomczak et al. 2022). North of our study area, changes in salinity, and temperature were found to be the main drivers of food web dynamics in the Bothnian Bay (Pekcan-Hekim et al. 2016); however, nutrient dynamics and fishing were not identified as key drivers at that time. Hence, the trajectory of the Bothnian Sea food web appears to be similar to what has been previously observed for the Central Baltic, but the changes have occurred over a longer time period and with an apparent delay of about 20 years, concurring with a later increase in nutrients and introduction of increased fishing pressure.

Changes within trophic guilds (MSFD D4C1) were observed for all examined guilds (planktivores, benthic deposit feeders, and pelagic primary producers), although their relationships to anthropogenic drivers varied. The plankivore guild (addressed by the shorter time series, 2007–2021) was represented by small pelagic fish species that are central in the food web of the Bothnian Sea, both as a prey for apex predators and regulator of secondary producers via predation pressure (Kiljunen et al. 2020). Of these, herring and sprat biomass generally decreased over time and stickleback increased, with a clear change observed within this trophic guilds in 2013, concurrent with the last observed clear shift in abundance between trophic guilds. In relation to drivers, the temporal dynamics within the group of planktivores were most clearly associated with changes in fishing mortality (Table 3). The changes could additionally reflect that the three taxa compete for food, or synergistic effects. As large herring can control stickleback abundance through predation, reductions in the herring population could release sticklebacks from both competition and predation pressure (Parmanne et al. 2004, Peltonen et al. 2004, Olin et al. 2022). Although herring is the key target species for fisheries in the Baltic Sea, one explanation for the association of sprat with herring fishing mortality could be effects of mixed catches in the pelagic fisheries. However, estimating the proportion of herring and sprat in the catches is difficult due to the large volumes and associated uncertainties in reporting (Section 7 in ICES 2023a).

Interestingly, for herring, the association with explanatory variables differed for the different time series and response variables used. In the longest time series (1979–2021), the GAMs identified a strong relationship between the 3-year time lagged fishing mortality and herring SSB, which is not unexpected as the two indicators ($F_{3–7}$ and SSB) derive from the same model and are not independent. In addition, salinity was identified as an explanatory variable, with herring SSB decreasing at higher salinities. Such a relationship could be linked to salinity-related changes in food availability, as both *B. coregoni* and *L. macrurus*, which are freshwater species, are important food for herring in the Bothnian Sea (Cardinale et al. 2009, Rajasilta et al. 2014, Von Weissenberg et al. 2024). Our analysis extends that by Cardinale et al. (2009) for herring recruitment, adding 15 years to the time series. In both studies, herring recruitment was strongly related to the biomass of *Bosmina coregoni*, which is an important food source for newly hatched herring. Both studies also noted a positive effect of a warmer climate on recruitment, although in our analysis, this was seen as a (negative) correlation with ice extent rather than a positive correlation with summer sea surface temperature. A positive association was seen between herring weight-at-age and herring recruitment, which is line with previous work showing that larger and better-condition fish are more fecund (Óskarsson et al. 2002), and that the abundance of larger fish correlates with recruitment (Van Deurs et al. 2023). Overall, herring weight-at-age, which we included to represent changes in size structure (MSFD D4C3), decreased strongly over time and showed a negative relationship to fishing already at relatively low fishing pressure compared to the highest values in the time series. Although our study is based on correlative analyses, these observations are in line with published model predictions and observed smaller body sizes in response to fishing pressure (de Roos et al. 2006, Barnett et al. 2017). Declines in body size can decrease overall biomass and catches (Audzijonyte et al. 2013), increase density dependent competition (Östman et al. 2014, Van Deurs et al. 2023), or competition with smaller species such as sprat, as observed in the Central Baltic (Cardinale and Arrhenius 2000, Rönkkönen et al. 2004, Casini et al. 2010). In addition, increasing temperature may contribute to a decrease in body size (Audzijonyte et al. 2020). A relationship between these factors was noted in our results and previously in the Central Baltic (Möllmann et al. 2003, Dippner et al. 2019). Declines in herring weight-at-age in Baltic Sea basins have previously been observed in the Central Baltic (Cardinale and Arrhenius 2000), Gulf of Riga (Raid et al. 2010), and Gulf of Finland (Rönkkönen et al. 2004).

Clear changes over time were also observed within the benthic deposit feeder guild as indicated by the break point analysis. These mainly reflected a decline in *M. affinis* associated with steady declines in salinity, and the previously documented invasion of the *Marenzelleria* species complex (Wiklund and Andersson 2014, Kauppi et al. 2015). The decline in *M. affinis* began before *Marenzelleria* spp. densities reached high levels and has been related to a drop in diatom biomass and quality of phytoplankton as food in the early 2000s (Wiklund and Andersson 2014, Kauppi et al. 2015). However, *Marenzelleria* spp. may also have contributed to maintaining *M. affinis* biomass at low levels as they compete for both food and space (Kotta and Ólafsson 2003, Neideman et al. 2003). The observation that *M. affinis*, which is a glacial relict in the Baltic Sea, was negatively correlated with increasing temperature is in accordance with previous studies (Rousi et al. 2013) and could be due to higher egg mortality (Wiklund and Sundelin 2001), or increased sensitivity to contaminants (Jacobson et al. 2008), which are a widespread problem in the Baltic Sea (HELCOM 2023a). For the benthic predators, no clear relationships to the explored explanatory variables or other taxa were found, neither at the guild level nor for key taxa. This may be explained by that key taxa within the group, *S. entomon* and *Har. sarsi* have a generalist diet, enabling them to survive on many types of detritus and prey under variable conditions (Sarvala 1971, Sandberg and Bonsdorff 1990).

For pelagic secondary producers, (zooplankton), total biomass within the guild was positively correlated with the winter Baltic Sea index, being higher during North Atlantic oscillations of warm humid westerly winds across Europe resulting in warmer winters with lower ice cover, higher rainfall, and increased freshwater discharge into the Baltic (Hagen and Feistel 2005). The compositional change that was observed within this guild over time, away from taxa with higher salinity requirements towards freshwater taxa that cope with lower salinities, such as *L. macrurus* and *B. coregoni,* does hence not necessarily represent changes attributed to anthropogenic pressures. The changes in secondary producers also do not represent worsened conditions in terms of environmental status or the function of the guild as food for higher trophic levels. Both the mean size and biomass of zooplankton have increased in the Bothnian Sea over time, which represents improving environmental status (HELCOM 2023a), and the large-bodied copepod *L. macrurus* is an important lipid rich spring food for herring (Rajasilta et al. 2014, Von Weissenberg et al. 2024). *Limnocalanus macrurus* biomass may also be influenced by top-down predation, as it varied with herring SSB. Although *L. macrurus* is a generalist feeder (Von Weissenberg et al. 2024), it may additionally be affected by bottom-up factors such as phytoplankton food quality (Ruokolainen et al. 2006), as shown by the negative correlation with cyanobacterial biomass.

Within the pelagic primary producer guild, compositional changes identified by the break point analysis were attributed to an increase in cyanobacteria since 2000 and increases in diatoms and ciliates since 2010. The increase in cyanobacteria was linked to increasing concentrations of dissolved inorganic phosphorus, an anthropogenic pressure influenced by nutrient inputs from land and the inflow of phosphorus-rich water from the Central Baltic (Gustafsson et al. 2012, Räike et al. 2020).

Potential connection to food web status

Currently, there are no established methods to evaluate the status of food webs in the Baltic Sea region, or generally under the EU MSFD (Boschetti et al. 2021). The present analyses were carried out to support the further development of such assessments. Identifying quantitative threshold values or formally assessing the environmental status of food webs was outside of the scope of our study, but the results clarify trends in the structure of the food web and address potential relationships between these and anthropogenic pressures. Consequently, by exploring a wide range of variables in a coherent way under a structured framework, the integrated trend analyses can contribute to identifying priorities in the development of ecosystem-based management. They can also support a discussion about desired directional developments for different food web components, which can inform societal decisions about management objectives for food webs as a next step.

With regard to diversity within trophic guilds (MSFD D4C1), the species composition and relative abundance of taxa within key trophic guilds clearly changed in several cases in the Bothnian Sea over the studied years, even when the total biomass within a guild was relatively unchanged, i.e. pelagic primary and secondary producers. For the primary producer guild, the increase of cyanobacteria observed in parallel with increases in phosphorus indicates an increased risk for harmful algal blooms and decline in food web status according to MSFD D4C1, which states that the composition within the guild should not be adversely affected due to anthropogenic pressures (Commission Decision). In the Baltic Sea, cyanobacterial blooms are assessed under D5C3 (eutrophication status) using a pre-core indicator (HELCOM 2023a), with levels in the Bothnian Sea being indicative of poor environmental status at the end of our time series (HELCOM 2023c). Changes in the secondary producers over time were also linked to increases in cyanobacterial biomass and hence to phosphorus, but additionally to climate-related factors such as the winter Baltic Sea index. However, as also discussed in the section above, changes in composition within the guild of secondary producers primarily reflected increases in zooplankton species which are important prey for herring (*L. macrurus* and *B. coregoni*) (Cardinale et al. 2008, Rajasilta et al. 2014). The observed change represents an improved environmental status according to the regionally agreed HELCOM indicator on food webs under descriptor 1 (Biodiversity; HELCOM 2023a), illustrating the complexity of the task to develop status assessment approaches for food webs, even for a relatively simple system such as the Bothnian Sea. Within the benthic deposit-feeding guild, the compositional changes mainly reflected a decrease of *M. affinis*, which is a high quality prey for herring (Ejdung and Elmgren 2001, Casini et al. 2004, Kiljunen et al. 2020), and a shift towards higher biomasses of the *Marenzelleria* species complex, which is potentially less utilized by higher trophic levels (Golubkov et al. 2021). Although there is currently no threshold value for these benthic taxa in the region, the results suggest that their role as prey for higher trophic levels is decreasing (Karlson et al. 2020). As the changes within benthic deposit-feeders were associated with anthropogenic pressures, i.e. increasing phosphorus and the introduction of a non-indigenous species, the results in all would suggest a decline in food web status according to the D4 criteria for this guild. For the planktivore guild, increasing stickleback abundance along with decreases in herring and sprat (Fig. S5), are also indicative of adverse effects on other parts of the food web (Olsson et al. 2019, Olin et al. 2022, also discussed under D4C2 below). With the changes occuring in parallel with increased fishing pressure, this also indicates a decline in D4 food web status. Further, whereas this study represents the open sea system, effects may also extend to coastal food webs due to species' migrations, where increases in sticklebacks may interfere with coastal fish recruitment and have been linked to decreases in coastal predatory fish populations (Bergström et al. 2015, Olin et al. 2022).

MSFD D4C2 states that the balance of total abundance between the trophic guilds should not be adversely affected due to anthropogenic pressures (Commission Decision). Overall, our results show that the main compositional shifts observed between guilds in the Bothnian Sea food web were associated with changes in anthropogenic drivers, mainly represented by fishing pressure and increased phosphorus concentrations (Fig. 9). Here, the declines in herring SSB linked to fishing pressure must be interpreted carefully as the metrics are not independent. However, fishing pressure was also associated with reduced herring weight-at-age, which can be linked to adverse effects on other parts of the food web (Casini et al. 2010, Van Deurs et al. 2023), including humans in terms of loss of cultural values and local income through decreased fishing opportunities (Ignatius et al. 2019). In fact, declining catches of large herring along the Bothnian Sea coast have already led to conflicts between small-scale fishers and large industrial trawlers and a strong societal debate where different stakeholders have pointed to either eutrophication, rising temperatures, or high fishing pressure as explanations for altered food web dynamics and changes in the herring stocks (Hedberg et al. 2023). Effects on other parts of the food web could also be considered in the light of a recent deterioration of grey seal health, which may be due to reduced food availability (HELCOM 2023a). Thus, the decline in herring SSB and herring weight-at-age, independent of their cause, can be considered as undesirable both from a human and biodiversity perspective. The overall situation, including data gaps and remaining issues, illustrates the importance of securing and analyzing ecosystem-based monitoring data and implementing ecosystem-based management of marine food webs to avoid unsustainable ecosystem effects (Eero et al. 2021).

Evaluation of the method

Integrated trend analyses support the ecosystem-based assessment of food webs as they enable several ecosystem components to be addressed simultaneously and relate observed trends to multiple potential drivers. The multivariate analyses (dbRDA) provided a comprehensive overview of how the food web developed over time, where identified key aspects can be further interpreted by more detailed analyses and in relation to ecological understanding of the system. However, an uncertainty of the analyses lies in that observed correlations do not necessarily imply causation and that only linear relationships are investigated. The GAMs examined only one taxon at a time but complement the multivariate analyses by addressing non-linear trends and by isolating plausible causal relationships for the focal response variable. The breakpoint analyses enabled defining stable periods and key periods of change in the multivariate and univariate data. This can be particularly helpful for identifying threshold values and management reference points, although it remains difficult to determine the exact timing of a certain change in complex systems where key components interact with each other. Additionally, it can be challenging to decide how large compositional changes need to be in order to be identified as a regime shift, or as a consistent shift over time (Möllmann et al. 2009, Yletyinen et al. 2016). The combination of these analyses gives a view of the main temporal patterns in the Bothnian Sea food web, including issues to highlight in the further prioritization of assessments and management strategies.

Addressing food webs at the level of biomass within trophic guilds has been suggested as a suitable approach for a food web indicator due to being generally supported by adequate availability and quality of data, association with key processes, as well as being easily interpretable, relevant to management and with estimable management targets (Tam et al. 2017). Although all of these aspects were not in focus here, these conclusions were generally not contradicted in our study. However, our studied system represents a very simple food web in terms of taxonomic structure, compared to most marine systems, but the analyses still revealed complexities that may complicate the interpretation of the results. Further, the trophic guild concept only identifies a selection of aspects of relevance for food web function, while other functional groupings may be more relevant in some cases, depending on management priorities (Blondel 2003). For example, several benthic taxa contribute to food web productivity as prey but also for example to nutrient and carbon sequestration through their behaviour, and the latter aspects are not specifically captured in the currently applied definitions. Adjusting the guild concept to focus on feeding rather than trophic guilds is a potential method refinement (Thompson et al. 2020), although in the Bothnian Sea it is not likely that using feeding guilds would alter the results significantly as the food web is relatively simple.

In our study, the analyses of relationships to drivers were restricted by available data on potential explanatory variables. One example is the problems with obtaining independent estimates of trends in fish biomass and fishing mortality, as discussed above, which should be improved in coming research. It would also be valuable to supplement the analyses with data on the natural mortality for species within different guilds over time, given the structural changes observed. For example, levels of seal predation are likely increasing from very low levels in the beginning of the studied time period (Fig. 5f), while predation on herring and other planktivores from piscivorous fish is likely to have been higher in the past. Cod was present in the Bothnian Sea in the 1980s (Kuosa et al. 2017), but the decline of the Baltic cod stock has constrained its northern distributional range (Tomczak et al. 2022). Including various aspects of food web dynamics (i.e. productivity, size, edibility, and trophic linkages) could also be expected to further enhance the results, help identify suitable threshold values for good status and support management decisions (Tam et al. 2017, Eero et al. 2021). Lastly, although our studied system is relatively data-rich compared to many other systems, we did still not assess MSFD D4C3 in detail or D4C4 at all (i.e. size distribution of individuals across the trophic guild and productivity of the trophic guild, respectively; Commission Decision), due to a lack of adequate data across trophic levels. In future work, metrics on these aspects, such as individual size structure, population resilience, or the productivity of the system, would be important additional components for assessing how changes in structure affect food web function. For example, information about how efficiently energy and nutrients are transferred to higher trophic levels is highly relevant, e.g. for making adequate decisions about the potential for harvesting (Modica et al. 2014, Stäbler et al. 2019, Griffiths et al. 2024).

Conclusions

The integrated trend analyses, using multivariate analyses and GAMs, show how the relative abundance within and between trophic guilds has changed in the Bothnian Sea food web over the past four decades. The changes in food web structure occurred in parallel with changes in anthropogenic (fishing mortality and increasing phosphorus) and climate related (salinity and temperature) factors. Although determining the status of the food web, or deciding on threshold values for good status was beyond the scope of this study, the results provide information to support the further development of such assessments. The direction of trends in the studied guilds and taxa, when evaluated against the EU MSFD criteria for good environmental status for food webs and supported by observed trends and levels for existing operational HELCOM status indicators where appropriate, indicate a deteriorating status of the Bothian Sea food web status over time. Structural changes within the trophic guilds were mainly identified for planktivores, benthic deposit feeders and pelagic primary producers (referring to MSFD D4C1). For the entire food web, changes in the balance of total abundance between the trophic guilds (D4C2) were identified as becoming more adverse in connection to increasing phosphorus concentrations and increased fishing mortality. While final management objectives for food webs remain to be defined, the results imply that measures to reduce phosphorus loads and leave more herring in the ecosystem are likely to remediate the currently observed deprecation in the system.

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Author contributions

Both CLF and LB contributed to the conceptualization, methodology and writing and editing of the manuscript. CLF curated, analysed and visualized the data.

Supplementary data

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

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Data availability

All data used here are available in the public domain and included in the reference list.

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