



Original Article

The role of climate and fisheries on the temporal changes in the Bothnian Bay foodweb

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Climate change, eutrophication, and fishing are main pressures associated with changes in the abiotic and biotic environment in several sub-basins of the Baltic Sea. Identifying the nature of such changes is of relative importance for fisheries and environmental management. The Bothnian Bay is the northernmost sub-basin in the Baltic Sea and the responses of the foodweb to long-term changes in combined pressures have not been investigated. In this study, we explore long-term changes in the Bothnian Bay foodweb, represented by key species across all trophic levels over the past 34 years, and identify potential environmental and anthropogenic drivers. The results indicate that salinity is the most important driver to explain changes in the composition of the offshore biota in the Bothnian Bay. These changes are probably driven by indirect effects of salinity rather than bottom-up effects. A decline in the herring spawning-stock biomass was most plausibly attributed to an increased competition for food due to a parallel increase in vendace, which uses the same food resources (zooplankton and zoobenthos) and may benefit from declining salinity due to its limnic origin. A strong increase in the abundance of grey seal and ringed seal populations was seen in the late 2000s but was not related to any of the pressure variables analysed. Temperature and nutrients were not identified as important drivers of changes in the overall biota. Our study explores correlative relationships between variables and identifies potential interactions in the foodweb to generate hypotheses for further studies.

Keywords: climate, fisheries, grey seal, herring spawning-stock biomass, ringed seal, salinity.

Introduction

Anthropogenically induced climate change, eutrophication and fishing have played prominent roles as modifiers of the marine ecosystem structure and function over the last decades (Möllmann *et al.*, 2009; Hoegh-Guldberg and Bruno, 2010; Lotze *et al.*, 2011). These anthropogenic impacts have had consequences on ecosystem functioning with implications for the provision of ecosystem goods and services (Halpern *et al.*, 2009), on which human societies depend (Beaumont *et al.*, 2007). Understanding the role of these major pressures as drivers in changing the ecosystem and the components therein is basic for identifying relevant management actions.

Major changes in physical and biological conditions have been observed in recent decades in several marine ecosystems, such as the North Pacific and North Sea marine ecosystems (Weijerman *et al.*, 2005; Hare and Mantua, 2009) and coincide with major ecosystem changes in the Baltic Sea. Drivers of the ecosystem changes in the Baltic Sea ecosystem in the past decades have been identified as human-induced climate change and eutrophication together with direct effects of overfishing (Elmgren and Larsson, 2001; Casini *et al.*, 2009; Möllmann *et al.*, 2009). Climate change has been identified to affect fish species on a population level, as changes in abundance, size structure, and spatial distribution, and further to alter trophic interactions leading to changes in foodweb dynamics in the

Baltic Sea (Österblom *et al.*, 2007; Petitgas *et al.*, 2013; Bartolino *et al.*, 2014). Eutrophication entails increased primary productivity, which has altered species composition across trophic levels (phytoplankton, zooplankton, zoobenthos, and fish; Bonsdorff *et al.*, 1997; Micheli, 1999; Ådjers *et al.*, 2006) by shifting competitive advantages. Observed foodweb restructuring, including shifts in commercially important fish stocks, e.g. a decline in cod (*Gadus morhua*) and increase in sprat (*Sprattus sprattus*) in the central Baltic Sea (Alheit *et al.*, 2005), has been related to a combination of fishing and climate-dependent hydrological conditions (Casini *et al.*, 2008).

Although changes in foodweb composition in many sub-basins of the Baltic Sea have been studied extensively (Diekmann and Möllmann, 2010), equivalent investigations in the northernmost basin, the Bothnian Bay, are lacking and their potential causes have not been addressed. The Bothnian Bay is an important fishing ground for pelagic fish species and the major seal reproduction ground of the region (Meier *et al.*, 2004; ICES, 2014). The effects of eutrophication and other anthropogenic pressures are not as pronounced in the Bothnian Bay as in other basins due to low human population density, and low agricultural production surrounding the basin. In contrast, abiotic factors such as the extent of ice cover, temperature, and salinity may be more important variables in influencing the foodweb in the Bothnian Bay compared with other basins, as many of the species are at their physiological salinity and temperature limits. Thus, understanding the relative role of manageable human pressures, such as fisheries and nutrient loading, and climatic factors is important for identifying fisheries management and eutrophication abatement measures (Andersson *et al.*, 2015; Uotila *et al.*, 2015).

The aim of this paper is to identify and explain the changes that have occurred in the foodweb structure of the Bothnian Bay during the last three decades by analysing long-term environmental and biological data from several parts of the offshore ecosystem. The main questions that we address are: what are the changes that occurred in the abiotic and biotic environment of the Bothnian Bay in the recent three decades, and can changes in the biota be coupled to alterations in climatic factors, eutrophication, or fisheries?

Material and methods

Study site

The Bothnian Bay is the northernmost basin of the Baltic Sea with an area amounting to 36 260 km² (Figure 1). It is ice covered more than 120 d per year from November till April/May. The sub-basin is mainly shallow (mean depth 43 m), but the deepest basin extends to the depth of 147 m. Salinity is permanently low (2–3 psu) as a consequence of the combined effects of the large discharge of the northern rivers and the entering of well-oxygenized surface water masses above the halocline from the Baltic proper to the Gulf of Bothnia. The weak stratification and the seasonal turnover of the whole water body in spring and autumn extends down to the bottom promoting good oxygen conditions at the sediment–water interface.

Considering the biota, salinity is one of the determining factors in the Bothnian Bay: it gives rise to a strong dominance of freshwater species, but marine species are represented due to the open connection to the rest of the Baltic Sea (Elmgren and Larsson, 2001). Grey seals (*Halichoerus grypus*) and ringed seal (*Phoca hispida botnica*) represent the top mammal predators and have increased in abundance during the last decades (Härkönen *et al.*, 2013). Eutrophication has not been viewed as a serious environmental problem in the Bothnian Bay, mainly due to smaller external nutrient loading compared with the other Baltic Sea basins and the lack of areas receiving substantial

internal loading (Andersen *et al.*, 2015). Primary productivity is limited by phosphorus in contrast to other basins in the Baltic Sea where nitrate is the limiting nutrient (Andersson *et al.*, 1996; Tamminen and Andersen, 2007), which is due to the presence of high amount of iron in the sediments that remove phosphorus from the water and the sediment surface (Lehtoranta *et al.*, 2008). The main exploited fish species in the Bothnian Bay include herring (*Clupea harengus*), vendace (*Coregonus albula*; Rudstam *et al.*, 1994; Bergenius *et al.*, 2013), and salmon (*Salmo salar*; ICES, 2014).

Data

We assembled a dataset including time-series over more than three decades (1980–2013; 34 years) from the monitoring of the abiotic and biotic environment of the Bothnian Bay ecosystem. The variables included were selected to achieve a balanced representation of the main trophic levels and potential pressures, to represent relevant sampling seasons for analysing long-term trends, and to provide consistent time-series based on available data.

Potential pressure variables were selected to represent changes in climate, nutrient conditions, and fishing. In total, ten pressure variables were included in the analyses (Table 1). The data were mainly obtained from offshore areas. Average spring values of sea surface temperature (TEMP) were calculated based on monthly means. Average winter values of near-bottom water salinity (SAL) and oxygen (OX), and surface water pH calculated based on monthly means along with number of annual ice cover days (ICE) were used as climate-related variables (Table 1). These variables are expected to influence the biota directly by effecting recruitment and survival or species physiology and metabolism (Rijnsdorp *et al.*, 2009). To represent the atmospheric forcing, December–February averages of the Baltic Sea Index (BSI) were included in the analyses. BSI is closely related to the North Atlantic Oscillation (NAO) but is considered a better estimate of climate-related variability to describe local oceanographic processes of the Baltic Sea region (Lehmann *et al.*, 2002; Table 1). BSI represents the difference of normalized sea level pressure anomalies between Oslo (Norway) and Szczecin (Poland; Lehmann *et al.*, 2002). We used average winter values of dissolved inorganic phosphorus (DIP) and nitrogen (DIN) in productive surface layer to represent the general nutrient status (HELCOM, 2009; Table 1). Winter values of nutrients were used in this study to represent the overall nutrient situation, as the winter values give a more stable measure of the total pool of inorganic nitrogen and phosphate compared with values during the growth season which are more variable (HELCOM, 2009). To represent fishing, we included data on herring trawl fishing effort (TRWL) and trapnet effort (TRPN; Table 1). We used effort instead of catch data or modelled fishing mortality because it is a direct measure of the fishing intensity and does not stem from the same estimation model as is used for estimating herring spawning-stock biomass (SSB; as fishing mortality does). Trawling effort was calculated as the total annual trawling hours times the estimated trawl size coefficient, and trapnet effort as the number of trapnets per year (ICES, 2014; Table 1).

The biotic data were represented by 15 variables that covered trophic levels from primary producers to marine mammal top predators in the offshore Bothnian Bay area (Table 1). Spring and summertime values of chlorophyll *a* (Chl*a*) in productive surface layer were used to represent primary production. Direct data on phytoplankton abundance were not available in a consistent way over the whole assessed period, and were therefore not included. However, chlorophyll *a* correlated with phytoplankton biomass



Figure 1. Map of the Baltic Sea and its sub-basins including the study area the Bothnian Bay (ICES Subdivision 31) with the location of sampling stations F2, F9, B03, Välimatala, and Sydvästbrotten (see Table 1 for further details).

for the years when both types of data were available (Pearson's correlation, $n = 23$, $r^2 = 0.53$, $p = 0.009$). Zooplankton data were available for the summer season only and represented by the biomass ($\mu\text{g m}^{-3}$) of the cladoceran species *Bosmina* sp., *Daphnia*

sp., *Evadne* sp., and the copepod species *Cyclops* sp., *Limnocalanus* sp., and *Eurytemora* sp. (Table 1). These were the zooplankton taxa occurring with a frequency of at least 30% in the overall time-series. To represent the benthic fauna, we included biomass (wet weight,

Table 1. Variables used in the analyses.

Variable	Unit	Abbreviation	Sampling time	Sampling depth	Station/sampling area	Source
Climate variables						
P Water temperature	°C	TEMP	April–June	1–10 m	F9	SMHI ^a
P Salinity	psu	SAL	November–December	≥30 m	F9	SMHI
P Ice cover days	Number of days	ICE			Vällimatala	FMI ^b
P Oxygen	mg l ⁻¹	OX	November–December	≥30 m	F9	SMHI
P pH	–	pH	November–December	0–10 m	F9	SMHI
P Baltic Sea index	–	BSI	December–February	–	–	–
Nutrient variables						
P Dissolved inorganic phosphorus	µM	DIP	November–December	0–10 m	F9	SMHI
P Dissolved inorganic nitrogen	µM	DIN	November–December	0–10 m	F9	SMHI
Fishing variables						
P Herring trawl effort	Trawling hours/estimated trawl size	TRWL	April–November	–	ICES SD31	ICES ^c
P Herring trapnet effort	Number of trapnets	TRPN	April–November	–	ICES SD31	ICES
Biotic variables						
R Chlorophyll <i>a</i>	mg m ⁻³	Chla	May–September	0–10 m	BO3	NAOO ^d /FEI ^e
R <i>Monoporeia affinis</i> , wet weight	g m ⁻²	Monoporeia	May–June	100–115 m	BO3	NAOO/FEI
R <i>Saduria entomon</i> , wet weight	g m ⁻²	Saduria	May–June	100–115 m	BO3	NOOA/FEI
R <i>Cyclops</i> sp., biomass	µg m ⁻³	Cyclops	August	0–100 m	F2	NOAA/FEI
R <i>Limnocalanus macrurus</i> , biomass	µg m ⁻³	Limnocalanus	August	0–100 m	F2	NOAA/FEI
R <i>Eurytemora</i> sp., biomass	µg m ⁻³	Eurytemora	August	0–100 m	F2	NOAA/FEI
R <i>Bosmina</i> sp., biomass	µg m ⁻³	Bosmina	August	0–100 m	F2	NOAA/FEI
R <i>Daphnia</i> sp., biomass	µg m ⁻³	Daphnia	August	0–100 m	F2	NOAA/FEI
R <i>Evadne</i> sp., biomass	µg m ⁻³	Evadne	August	0–100 m	F2	NOAA/FEI
R Herring (<i>Clupea harengus</i>), recruit biomass	t	HerrRecBiom	April–November	–	ICES SD31	ICES
R Herring (<i>Clupea harengus</i>), spawning-stock biomass	t	HerrSSB	April–November	–	ICES SD31	ICES
R Grey seal (<i>Halichoerus grypus</i>)	Numbers	Grey seal	May–June	–	Sydvästbrödden	–
R Ringed seal (<i>Phoca hispida botnica</i>)	Numbers	Ringed seal	May–June	–	Sydvästbrödden	–
R Vendace (<i>Coregonus albula</i>), recruit biomass	t	VendRecBiom	September–October	0–50 m	ICES SD31	ICES
R Vendace (<i>Coregonus albula</i>), spawning-stock biomass	t	VendSSB	September–October	0–50 m	ICES SD31	ICES

Most data series covered years 1980–2013 except for vendace recruit and SSB, which was from years 1991 till 2013. The first column indicates whether the variable was used as a pressure (P) or response (R) variables in the analyses. For the position of sampling stations BO3, F2, and F9, ICES Subdivision 31 (SD31), and sampling areas Vällimatala, and Sydvästbrödden, see Figure 1.

^aSwedish Meteorological Institute (SMHI), <http://www.smhi.se/en>.

^bFinnish Meteorological Institute (FMI), <http://en.ilmatieteentaitos.fi/>.

^cInternational Council for the Exploration of the Sea (ICES), <http://www.ices.dk/Pages/default.aspx>.

^dNational Oceanic and Atmospheric Administration (NOAA), <http://www.noaa.gov/>.

^eFinnish Environment Institute (SYKE), <http://www.syke.fi/en-US>.

g m⁻²) of the two dominating species in the area, the amphipod *Monoporeia affinis* and its predator, the isopod *Saduria entomon* (Table 1).

Fish was represented by herring and vendace, which are the main zooplanktivores in the system, although they also feed on zoobenthos (Valtonen, 1983; Casini *et al.*, 2004). The only offshore piscivorous fish species in this system is salmon. We chose, however, to not include salmon in these analyses, as the populations of salmon in the Bothnian Bay are migrating and consist of both stocked reared salmon and wild salmon (ICES, 2014), and hence are affected by conditions in their spawning rivers as well as in their main feeding grounds in southern Baltic Sea (Suuronen and Jounela, 2010). We included data on the two main life stages of herring, biomass of recruits (HerrRecBiom), and of the spawning stock (HerrSSB; Table 1). Data were obtained from the annual stock assessment (ICES, 2014), as produced by a state-space assessment model (Extended survival analysis, XSA). Herring recruit biomass is the annual number of 1-year olds times their mean weight in the same year, and herring SSB is the total biomass of fish that are reproductively mature in the stock. Whereas the recruit biomass is primarily affected by environmental factors, such as temperature and salinity (Cardinale *et al.*, 2009), the SSB is the part of the stock that is directly influenced by fishing (Houde, 2009). Vendace recruit and SSB were included in a separate set of analyses, due to the shorter available time-series. By using biomass data, we account for the changes in abundance, individual growth, as well as size composition of the two fish stocks.

For vendace, a Pope cohort stock assessment model was used to estimate recruit and SSB (Pope, 1972). The model input data were catch-at-age from the fishery for the years 1991–2013, including age groups 0–5. Natural mortality was set at 0.2 for all ages. Fishing mortality in the final year was set to 0.13, 0.39, 0.70, 0.71, and 0.97 for age groups 0–4, respectively, which are the averages across years 2005–2013. During this period, most of the fishers used trawls equipped with selectivity grids. Fishing mortality for the oldest age group (5 year) was set to 0.70, estimated from the average fishing mortality across the entire time-series for age group 4. The estimated number of 5-year olds in the population was low in all years (~2%), so the fishing mortality in this older age group has an insignificant impact on the assessment. Data from both commercial samples (2002–2013) and fisheries-independent hydroacoustic survey (Kaljuste and Heimbrandt, 2010) were used to estimate the proportion of mature individuals. Taken as the median estimate of these data, maturity-at-age was set to 0.02, 0.87, and 0.97 for ages 0, 1, and 2, respectively. All 3- to 5-year olds were considered mature. The estimated biomass of 1-year olds was used as recruitment, as the introduction of a sorting grid to the trawling gear in 2004 changed the selection of 0-year olds preventing a comparison of 0-year olds before and after this introduction was unreliable.

For seals, data on the abundance of the two seal species (grey and ringed seals) occurring in the Bothnian Bay were included (Table 1). Both species are known to be predators on herring, vendace, and salmon (Lundström *et al.*, 2010; Suuronen and Lehtonen, 2012). Grey seal data were obtained from yearly counts during May–June at Sydvästbrotten, which is the largest grey seal haul out in the Bothnian Bay (Harding *et al.*, 2007). Ringed seal abundances were estimated based on the counts on the sea ice in spring (Härkönen *et al.*, 2013).

All data were $\ln(x + 1)$ transformed to improve linearity and normalized due to differences in measurement units of the variables used in the analyses (Clarke and Warwick, 2001). Missing values were replaced with 4 year (2 years before and 2 years after) moving averages.

In total, there were three missing data points from the abiotic dataset. For the biotic dataset, zooplankton was not sampled for 7 of the years (1983, 1989, 1990, 1997, 1998, 2000, and 2009 were missing).

Statistical methods

To assess the temporal development of the potential pressure variables and the biota during the studied period, we conducted principal coordinate analysis (PCO, Zuur *et al.*, 2007), separately for each dataset. The analyses were done as implemented in PERMANOVA+ of PRIMER v6 (Anderson *et al.*, 2008). For the pressure and biotic variables, similarities were assessed based on chord distances, which is a metric index that does not treat double absences as an indication of resemblance and gives equal weights to rare and abundant observations (Legendre and Legendre, 1998). The data were visualized in an ordination biplot with species vectors and with a temporal trajectory to highlight the relative position of adjacent years. The presence of discontinuities over time in the biotic dataset was assessed by chronological clustering, with similarities among years assessed by chord distances (Legendre and Legendre, 1998) using Brodgar 2.7.4 (www.brodgar.com). Significant shifts were identified at $\alpha = 0.01$ to include only the most marked changes (Zuur *et al.*, 2007).

The relationship between the potential pressure variables and biotic variables was assessed with distance-based linear models (DistLM). DistLM is a multivariate regression method where a resemblance matrix of the response dataset is regressed against a set of explanatory variables. The resemblance matrix of the response dataset was based on chord distances (Anderson *et al.*, 2008). As the variables salinity (SAL) and herring trawl effort (TRWL) were highly correlated (Spearman correlation, $n = 34$, $r = 0.87$, $p \leq 0.001$), the analyses were run in two sets including only one of these at a time. Each run only included variables with Variance Inflation Factors (VIF) < 3 (Zuur *et al.*, 2010). Also, the abundance of grey seal and ringed seal showed a steep increase during the last decade, and according to preliminary runs, these variables had a great influence on the obtained pattern. To assess the overall influence of the seal variables, the DistLM analyses were run twice, both including and excluding data on seal abundance. The variables included in the final DistLM-models were selected using the BEST selection procedure in PRIMER v6 (Anderson *et al.*, 2008) based on the corrected Akaike information criterion (AICc; Burnham and Anderson, 2002) and Bayes information criterion (BIC; Schwarz, 1978). We selected the best models which fell within the two units of the AICc as well as the BIC.

Further, the relationship between all potential pressure variables and the biotic dataset was visualized by distance-based redundancy analyses (db-RDA) using Brodgar 2.7.4. This is an extension of a PCA (principal component analysis) that explicitly models response variables as a function of explanatory variables (Zuur *et al.*, 2007).

Results

In the PCO on the biotic variables, the first two axes of the PCO explained 26.6 and 22.7%, of the variation in the dataset (Figure 2). The variables that mainly contributed to the pattern along the first axis (PCO1) were grey seal, ringed seal, the copepods *Cyclops*, and *Limnocalanus* and on the second axis (PCO2), the cladoceran species *Daphnia*, *Bosmina*, and *Evdadne* (Figure 2). According to the chronological clustering, the main changes over time occurred in 1995 and 2000 (Figure 2). The first period was associated with relatively high herring SSB and by low abundances of both grey and ringed seals (Figure 3). In addition, the biomass of the copepod *Cyclops* sp. was very low till year 1995 and increased thereafter,

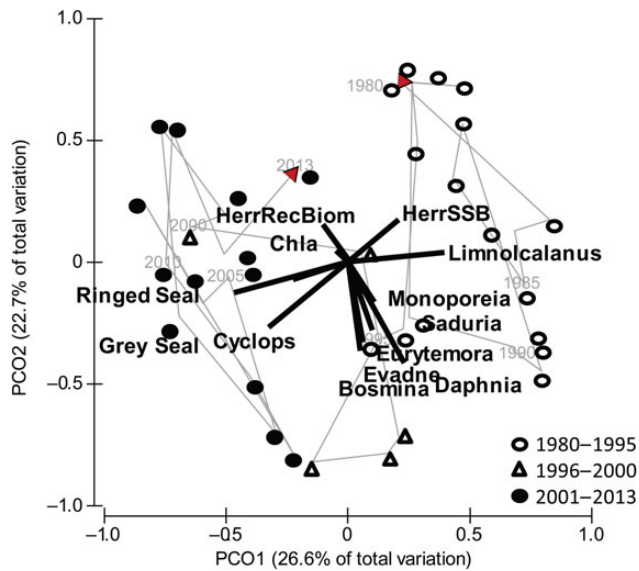


Figure 2. PCO biplot on the biotic dataset. Projected vectors show the correlation of variables with the two first ordination axes, as identified by a multiple metric correlation. The grey line indicates the temporal trajectory and the arrows mark the beginning and ending of the time-series. Consecutive years with similar biotic composition according to chronological clustering are identified by the same symbols. Chla, Chlorophyll a ; Limnocalanus, *Limnocalanus macrurus*; Cyclops, *Cyclops* sp.; Eurytemora, *Eurytemora* sp.; Daphnia, *Daphnia* sp.; Bosmina, *Bosmina* sp.; Evadne, *Evadne* sp.; Monoporeia, *Monoporeia affinis*; Saduria, *Saduria entomon*; HerrSSB, herring spawning-stock biomass; HerrRecBiom, herring recruit biomass; ringed seal; grey seal. This figure is available in black and white in print and in colour at ICES Journal of Marine Science online.

showing higher values during the last two decades. The data on several other zooplankton species (*Bosmina* sp., *Evadne* sp., *Daphnia* sp., and *Eurytemora* sp.) also showed peaks in 1995; however, there was no consistent increase following that year (Figure 3). In addition, the biomass of the benthic fauna (*M. affinis* and *S. entomon*) both showed low levels after the mid-1990s. The biomass of *Limnocalanus* sp. was relatively high in the 1980s but remained low since after the early 1990s. The period after 2000 was characterized by low herring SSB and a clear increase in the abundance of both grey seal and ringed seal, and a further increase in *Cyclops* sp.

To separate the potentially strong influence of seal abundance on the results, we also conducted the PCO and chronological clustering excluding the data on grey seal and ringed seal. The variation explained by the first two axes of the PCO was similar as with seals included (27.5 and 20.7% on PCO1 and PCO2, respectively), and the overall pattern of the PCO biplot remained the same (Supplementary Figure S1). When data on seals were excluded, a change was only detected in year 1995 according to the chronological clustering analyses (Supplementary Figure S1).

For the pressure dataset, the first two axes of the PCO explained 29.6 and 19.6% of the variation and significant changes in the pressure variables were detected by chronological clustering in years 1989 and 2004 (Figure 4). The variables that mainly contributed to the overall pattern in the PCO were herring trawling and trapnet effort (TRP and TRWL), salinity (SAL), and ice cover days (ICE) on the first axis. Salinity, ice cover days, and effort were all lower towards the end of the time-series (Figure 5). Temperature

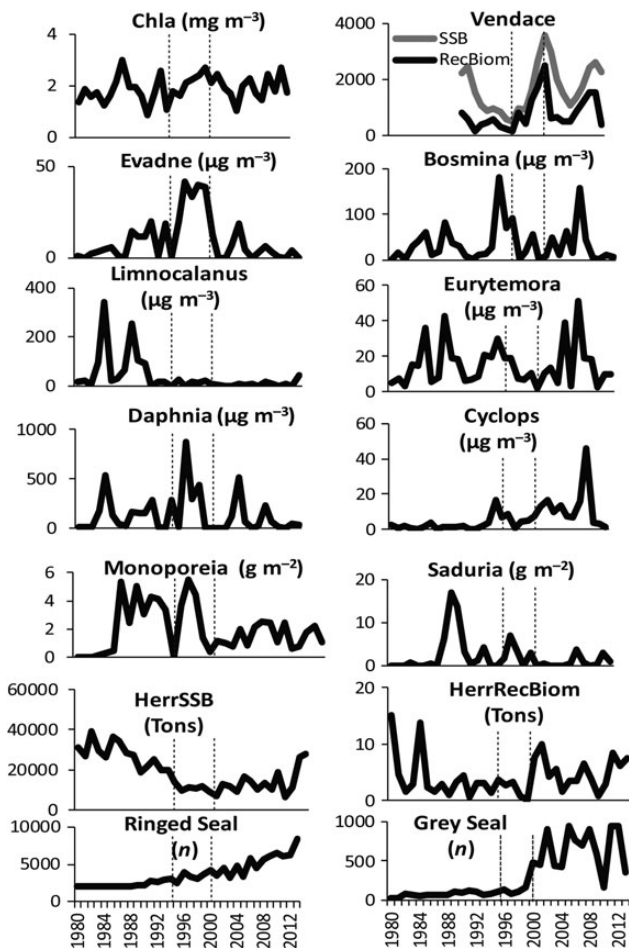


Figure 3. Temporal development of the biotic variables from 1980 till 2013 in the Bothnian Bay. Dashed lines indicate the main changes that occurred over time in 1995 and 2000 according to the chronological clustering. Chla, Chlorophyll a ; VendSSB, vendace spawning-stock biomass; VendRecBiom, vendace recruit biomass; Limnocalanus, *Limnocalanus macrurus*; Cyclops, *Cyclops* sp.; Eurytemora, *Eurytemora* sp.; Daphnia, *Daphnia* sp.; Bosmina, *Bosmina* sp.; Evadne, *Evadne* sp.; Monoporeia, *Monoporeia affinis*; Saduria, *Saduria entomon*; HerrSSB, herring spawning-stock biomass; HerrRecBiom, herring recruit biomass; ringed seal; grey seal.

(TEMP), pH, dissolved inorganic nitrogen (DIN), and oxygen (OX) contributed most to the pattern on the second axis (Figure 4).

The DistLM identified two alternative best models, explaining the variation in the biota of the Bothnian Bay, one for each set of analyses. In the analyses without herring trawl effort, a model with only salinity or one with salinity and BSI together were selected (Table 2), whereas when excluding the salinity data, the best models included herring trawl effort, or trawl effort together with BSI. The selected models remained the same in the case where data on grey seal and ringed seal were not included in the response dataset, but the level of explanation of the models decreased (Table 2).

According to the db-RDA analysis, all pressure variables together explained 42% of the variation in the biotic data and 70% of the variation was captured by the first two axes (Figure 6). Herring SSB and *Limnocalanus* biomass were positively related to salinity as well as to herring trapnet and trawl effort, whereas the biomass of *Cyclops* and the abundance of grey seal and ringed seal were negatively related

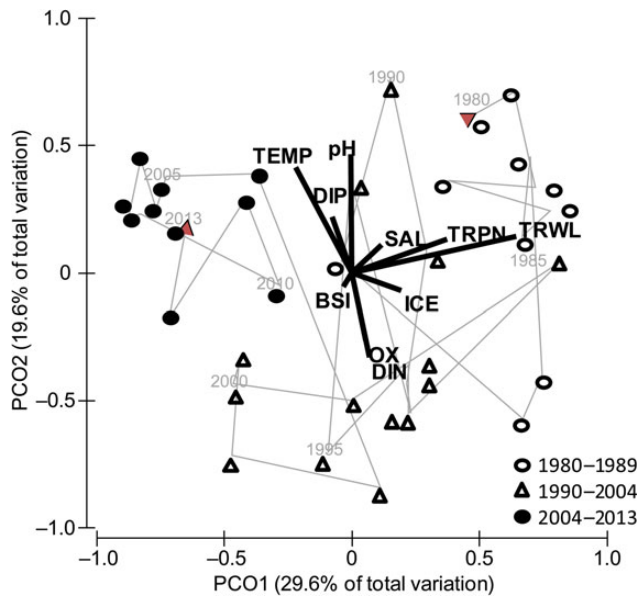


Figure 4. PCO biplot on the pressure dataset. Projected vectors show the correlation of the main contributing variables with the two first ordination axes, as identified by a multiple metric correlation. The grey line indicates the temporal trajectory and the arrows mark the beginning and ending of the time-series. Consecutive years with similar abiotic composition according to chronological clustering are identified by the same symbols. TEMP, temperature; SAL, salinity; ICE, number of ice cover days; TRPN, herring trapnet effort; TRWL, herring trawl effort; OX, oxygen; pH; DIN, dissolved inorganic nitrogen; DIP, dissolved inorganic phosphorus; BSI, Baltic Sea index. This figure is available in black and white in print and in colour at *ICES Journal of Marine Science* online.

to these. Along the second axis, the biomass of the benthic fauna (*M. affinis* and *S. entomon*) and of the zooplankton taxa *Bosmina*, *Evadne*, *Daphnia*, and *Eurytemora* were positively related to the BSI and to DIN (Figure 6). Herring recruit biomass showed a positive relationship with temperature but had a minor contribution to the overall variation explained. In the analyses without seals, the main pattern of the db-RDA remained the same and less of the variation in the biotic data (34%) was explained by the pressure variables (Supplementary material S2).

The analyses including vendace were performed on the shorter time-series (1991–2013), comparing biotic datasets with and without vendace (Supplementary Figure S3). Compared with the long-term analyses 1980–2013 (Figure 2), herring SSB had a lower contribution to the overall variation in the biota (Supplementary Figure S3). Herring SSB correlated with *Limnocalanus* in the shorter time-series as well and additionally with their zoobenthic prey *M. affinis* and *S. entomon* (Supplementary Figure S3). Vendace contributed greatly to the overall variation in the biota during 1991–2013 (Supplementary Figure S3), although the overall variation explained by the first two PCO axes did not increase [25.5% (PCO1) and 16.4% (PCO2), compared with 25.3 and 16.4% without vendace]. Vendace biomasses, grey seals, and the zooplankton *Evadne*, *Daphnia*, and *Bosmina* were the variables that correlate most with PCO1. The DistLM identified a large number (12) of redundant models for the dataset including vendace, but in accordance with the longer time-series [without vendace (1980–2013)], salinity was the variable that was selected in most models (in 8 out of 14 models, Supplementary Table S1).

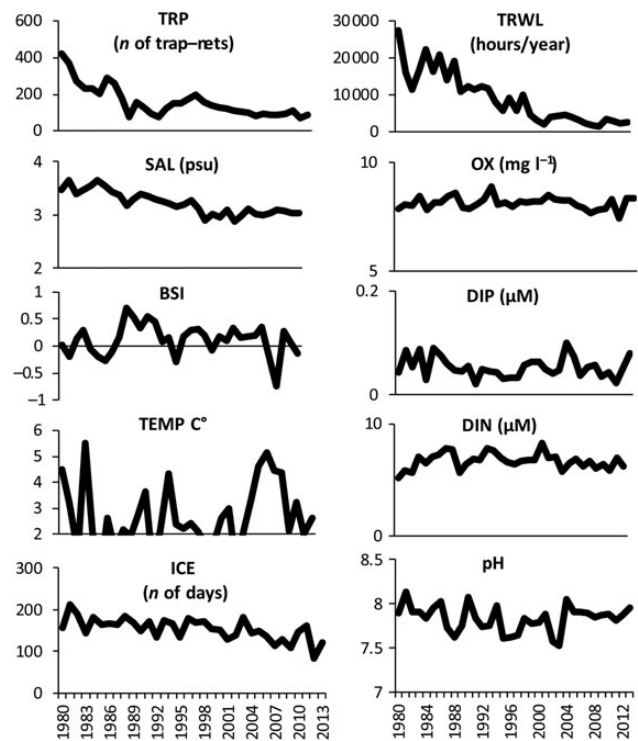


Figure 5. Temporal development in the pressure variables during 1980 till 2013 in the Bothnian Bay. TEMP, temperature; SAL, salinity; ICE, number of ice cover days; TRPN, herring trapnet effort; TRWL, herring trawl effort; OX, oxygen; pH; DIN, dissolved inorganic nitrogen; DIP, dissolved inorganic phosphorus; BSI, Baltic Sea index.

Table 2. Alternative models selected by the DistLM including or excluding seals for the time-series from 1980 until 2013.

Model	AICc	BIC	R ²
With seals			
Salinity	−3.489	−0.823	0.206
Salinity + BSI	−3.558	0.220	0.262
Trawl effort	−3.696	−1.031	0.211
Trawl effort + BSI	−3.109	0.669	0.252
Without seals			
Salinity	0.2758	2.941	0.113
Salinity + BSI	0.4818	4.261	0.169
Trawl effort	0.5769	3.242	0.105
Trawl effort + BSI	1.2396	5.018	0.150

All models were within 2 units of the minimum AICc and the BIC.

Discussion

The results from our study indicate that there have been substantial changes in the biota of the Bothnian Bay during the period from 1980 to 2013, and that these may be linked to changes in climate variables. Three periods with significantly different species composition were distinguished; the period till the mid-1990s was characterized by high herring SSB, which declined from the mid-1980s till the beginning of 1990s, and has remained low till the most recent 2 years studied. In the second period from 1995 to 2000, herring biomass was low, whereas all cladoceran species studied peaked and the benthic amphipod *M. affinis* increased in biomass. During the 2000s, the biomasses of herring, amphipod, and cladocerans have all been low, while seal abundance has increased.

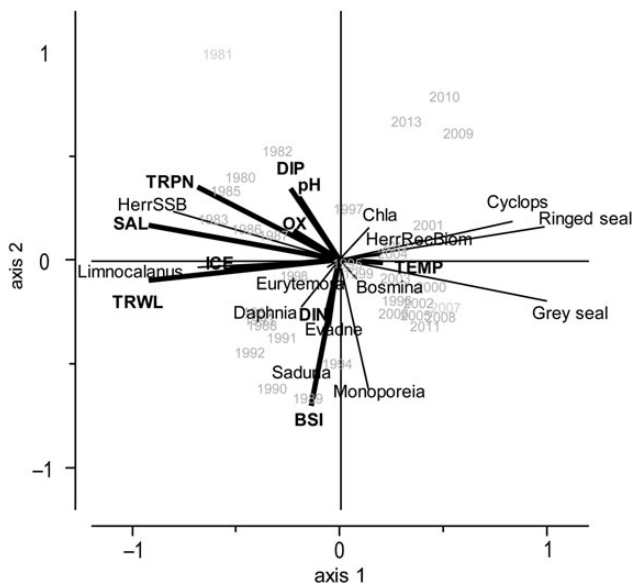


Figure 6. Output from db-RDA explaining the variation in the biotic dataset using the pressure variables. Projected vectors show the correlation of the main contributing variables with the two first ordination axes. Bold vectors illustrate the explanatory variables and non-bold vectors the response variables. Pressure variables explained 42% of the variation in the biotic data and 70% of the variation was captured by the first two axes. Chla, Chlorophyll *a*; Limnocalanus, *Limnocalanus macrurus*; Cyclops, *Cyclops* sp.; Eurytemora, *Eurytemora* sp.; Daphnia, *Daphnia* sp.; Bosmina, *Bosmina* sp.; Evadne, *Evadne* sp.; Monoporeia, *Monoporeia affinis*; Saduria, *Saduria entomon*; HerrSSB, herring spawning-stock biomass; HerrRecBiom, herring recruit biomass; ringed seal; grey seal; TEMP, temperature; SAL, salinity; ICE, number of ice cover days; TRPN, herring trapnet effort; TRWL, herring trawl effort; OX, oxygen; pH; DIN, dissolved inorganic nitrogen; DIP, dissolved inorganic phosphorus; BSI, Baltic Sea index.

The main pressure variables associated with overall changes in the Bothnian Bay biota were two of the climatic variables (salinity and BSI for the long time-series, and a dominance of salinity as an explanatory variable in the selected models for the short time-series). An alternative best model was considered, where fishing effort was included instead of salinity. However, fishing effort showed a positive relationship with herring SSB and did not reflect a pressure driving changes in the biota, but instead higher fishing effort was seen during times when the herring stock has been large. In contrast, the correlation between decreasing salinity and the biotic changes observed may indicate some relevant causal relationships. Decreasing salinity is likely to have a direct impact on the zooplankton species composition that will consequently also lead to changes at the upper trophic levels, such as herring weight-at-age and biomass (Flinkman *et al.*, 1998; Rönkkönen *et al.*, 2004). Declining salinity has been associated with a decrease in large marine zooplankton species in other basins of the Baltic Sea, such as *Pseudocalanus elongatus* and other large copepods in the Gulf of Finland (Flinkman *et al.*, 1998), the Baltic Proper, and the Archipelago Sea (Vuorinen *et al.*, 1998). However, in the Bothnian Bay, most copepod and cladoceran plankton, which also are important prey for herring, are of limnic origin (e.g. *Limnocalanus* sp. and *Daphnia* sp., respectively), and have not increased following the decrease in salinity. The observed changes in species composition across trophic levels in the Bothnian Bay are

therefore likely to be more indirectly coupled to salinity, than directly affecting the productivity base.

The BSI was the second most important variable explaining overall long-term (1980–2013) changes in the biota, in combination with either salinity or trawl fishing effort. According to the db-RDA, the BSI correlated mainly with the biomass of the zoobenthic species *M. affinis* and *S. entomon*, and to some extent also with the cladoceran species *Daphnia* sp., *Bosmina* sp., and *Evadne* sp. The BSI is an index of climate variability and reflects general changes in climatic conditions (Lehmann *et al.*, 2002). Positive and negative values of BSI indicate lower and higher summer surface temperatures, respectively, and changes in the prevailing wind direction from easterly to westerly wind, which could affect the transport of plankton in the water column (Baumann *et al.*, 2006). The high amphipod and cladoceran biomasses during the late 1990s, paralleled by positive BSI-values, may therefore have been coupled to altered plankton transport in the Bothnian Bay. However, BSI did not contribute strongly to explaining the biotic changes observed in the shorter time-series (1991–2013) when salinity was found to be the clearly dominating variable in the set of best models. This suggests that, overall, salinity is the more important driver of observed changes in the composition of offshore biota in the Bothnian Bay.

The analyses of changes in the biota during 1991–2013 suggest potential mechanisms for how salinity may have contributed to the observed changes in species composition. Vendace, which is a freshwater zooplanktivore, contributed highly to the observed biotic variation in the dataset. Our results show that salinity was the variable best explaining the biotic variation in this dataset (irrespective of whether vendace was included or not in the biotic response data), and that vendace recruitment increased while salinity decreased over time. For freshwater species living on the margin of its physiological tolerance in the Bothnian Bay, even small fluctuations in salinity may potentially have large influences on the population dynamics. Bergenius *et al.* (2013) found that salinity and winter temperature explained much of the variation in vendace recruitment in the Bothnian Bay. As vendace and herring both are pelagic zooplanktivores and also both feed on zoobenthos (Valtonen, 1983), competition for food resources combined with different physiological tolerances may be mechanisms by which changes in salinity impact also on herring; decreasing salinity favours recruitment of the freshwater species vendace but not marine species herring. Due to the explorative nature of the analyses conducted here, building on correlative analyses, it is not possible to discriminate causal relationships. However, the results suggest a potential mechanism of salinity-induced changes in competitive balances that warrants further study.

The other environmental variables studied were little or not at all represented in the set of best models for all studied time-series (1980–2013, 1991–2013 with and without vendace). While nutrient concentrations may drive changes in zooplankton and benthos productivity via effects on phytoplankton growth, DIN and DIP changes were not associated with the overall changes in the biota. Eutrophication has not been considered a major environmental issue in the Bothnian Bay, in the same way as for other areas of the Baltic Sea (Andersen *et al.*, 2015), although more recent studies suggest that there is still a considerable anthropogenic component (Fleming-Lehtinen *et al.*, 2015). However, our results suggest that changes in nutrient concentrations during the last three decades have not led to large-scale changes in species composition across trophic levels in the Bothnian Bay.

Spring temperature did not explain the overall changes in biota according to the DISTLM, and correspondingly, the overall observed relationship between temperature and biota was small. Some relationship between temperature and herring recruit biomass was indicated (based on observations of vector loadings, Figure 6), but this was minor relative to the observed correspondence between changes in salinity and adult herring biomass. Along the same axis, a relationship between declining herring SSB and the freshwater copepod *Limnocalanus* was also implied. *Limnocalanus* was at low levels in the Bothnian Bay since the early 1990s. In the Bothnian Sea, which is the most adjacent sub-basin to the Bothnian Bay, high biomass of the freshwater copepod *Limnocalanus* sp. along with declining salinity have been connected to the improvement in the condition of adult herring (Rajasilta *et al.*, 2014). The zooplankton data used here were based on sampling in August, as spring data were not available. However, if the trend that was observed for zooplankton in August in our dataset holds true also for the full growing season of herring (June–August), the results suggest that the low herring SSB observed in the Bothnian Bay in later years may be due to limited food resources. However, the low biomass of *Limnocalanus* sp. was probably not directly attributed to changes in salinity, since it is a limnic species and a positive effect of decreasing salinity would have been expected (Rajasilta *et al.*, 2014). This indicates that there is some other additionally limiting factor for *Limnocalanus* sp. in this sub-region. In addition, the mismatch in the timing of these key abiotic and biotic variables, due to limitations in available data, could result in missing out on some relationships between variables.

Although herring is mainly a zooplanktivore, it also feeds on amphipods during its adult life stages (Casini *et al.*, 2004). The biomass of the amphipod *M. affinis* dropped after 1995 in the Bothnian Bay and remained low thereafter. The observed pattern is in correspondence to results from the adjacent Bothnian Sea (Olsson *et al.*, 2013; Wiklund and Andersson, 2014) and north Bothnian proper (Rousi *et al.*, 2013). In the Bothnian Sea, the decrease in *M. affinis* has been attributed mainly to food limitation due to decline in primary productivity (Eriksson *et al.*, 2009; Wiklund and Andersson, 2014). The decline in herring SSB in the Bothnian Bay may therefore additionally be linked to decreased availability of benthic prey, via a decline in herring weight-at-age. In addition, selective predation by seals on larger herring (Gårdmark *et al.*, 2012) may leave populations dominated by small sizes (as shown for Bothnian Sea herring, Östman *et al.*, 2014), particularly in the last decade of the time-series in the Bothnian Bay.

The increase in seals in the Bothnian Bay had a strong contribution to the overall pattern but is not likely to be explained by the studied abiotic variables. It is rather explained by recovery from extremely low population sizes, in early and mid-1900s, when populations were decimated by contaminants and hunting (Harding *et al.*, 2007; Härkönen *et al.*, 2013). Seals may, however, affect other parts of the foodweb due to their high consumption rate of fish (Lundström *et al.*, 2010). Changes in seal abundance do not give a full explanation to the observed decrease in herring SSB in this study, as the decrease in herring biomass was initiated earlier in time than the increase in seals. However, seal predation could be one reason for the continued low herring SSB biomasses in the recent decade (Gårdmark *et al.*, 2012; Lundström *et al.*, 2014) and has been attributed to lower population mean weight-at-age in herring in the adjacent Bothnian Sea (Östman *et al.*, 2014).

A crucial part of successful management of marine environments and resources is to have an understanding of the current state of the ecosystem and ongoing processes affecting it (Levin *et al.*, 2009;

Österblom *et al.*, 2010; Möllmann *et al.*, 2014). This study provides an understanding of the changes that have taken place in species composition across five trophic levels in the Bothnian Bay, and explores the predominating set of underlying abiotic drivers. The multivariate analyses that we have used in this study explore only correlative relationships between variables. However, in the near to absence of costly controlled experiments to established causative relationships, the results of our study generate hypotheses for further focused experiments and monitoring. Our results indicate that the Bothnian Bay foodweb is strongly influenced by ongoing decrease in salinity, which may be expected to decrease further due to climate change (Meier *et al.*, 2012). A further increased understanding of foodweb dynamics and potential causes in the area is therefore highly motivated. Our results indicating salinity-driven shifts in competitive balance in the fish community call for further studies on environment-dependent species interactions. In particular, studies focusing on changes in zooplankton community structure and potential links to the growth rate of pelagic fish species, as well as the implications for changes in these variables for the productivity of the system and potential resource use.

Supplementary data

Supplementary material is available at the ICESJMS online version of the manuscript.

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