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Original Article

Temporal development of coastal ecosystems in the Baltic Sea over the past two decades

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Coastal areas are among the most biologically productive aquatic systems worldwide, but face strong and variable anthropogenic pressures. Few studies have, however, addressed the temporal development of coastal ecosystems in an integrated context. This study represents an assessment of the development over time in 13 coastal ecosystems in the Baltic Sea region during the past two decades. The study covers between two to six trophic levels per system and time-series dating back to the early 1990s. We applied multivariate analyses to assess the temporal development of biological ecosystem components and relate these to potential driving variables associated with changes in climate, hydrology, nutrient status, and fishing pressure. Our results show that structural change often occurred with similar timing in the assessed coastal systems. Moreover, in 10 of the 13 systems, a directional development of the ecosystem components was observed. The variables representing key ecosystem components generally differed across systems, due to natural differences and limitation to available data. As a result of this, the correlation between the temporal development of the biological components in each area and the driving variables assessed was to some extent area-specific. However, change in nutrient status was a common denominator of the variables most often associated with changes in the assessed systems. Our results, additionally, indicate existing strengths as well as future challenges in the capacity of currently available monitoring data to support integrated assessments and the implementation of an integrated ecosystem-based approach to the management of the Baltic Sea coastal ecosystems.

Keywords: eutrophication, fish, integrated assessment, management, multivariate analyses, phytoplankton, zoobenthos, zooplankton.

Introduction

Many marine ecosystems have gone through substantial structural changes during recent decades (Möllmann *et al.*, 2011). Despite their high ecological and socio-economic value, relatively little focus has been devoted to coastal ecosystems in this respect. Coastal areas are, however, often hot spots for multiple and conflicting human interests. Besides the effects of common pressures for coastal and open sea areas, such as the exploitation of living resources, large-scale climate forcing, eutrophication, pollution, and non-indigenous species, coastal areas are to a higher extent also influenced by human activities such as recreation, construction, boating, harbours, energy production, and aquaculture (Sandström *et al.*, 2005; Collie *et al.*, 2008; Sundblad and Bergström, 2014). An additional constraint to monitoring and assessment is that coastal biotic systems are to large extent locally structured, which may infer that their temporal development are expected to show divergent patterns. Recent studies have, however, challenged this view, showing that coastal fish and zoobenthos communities in different areas are influenced by changes in environmental variables acting at larger geographical scales (e.g. Olsson *et al.*, 2012, 2013).

Studies addressing the long-term development of ecosystems in an integrated context are crucial for the implementation of an ecosystem approach to management, the development of adaptive management strategies, and ensuring sustainable use of marine resources. Such studies are also pivotal for supporting integrated status assessments of ecosystems as required in international legislative acts and directives, such as the Baltic Sea Action Plan (HELCOM, 2007) and the EU Marine Strategy Framework Directive (European Commission, 2008). Integrated studies on the long-term development of marine ecosystems and their associated drivers have often focused on offshore ecosystems (Möllmann *et al.*, 2011). Due to the different environmental precondition, however, observations from offshore areas cannot be directly extrapolated to coastal systems. Little is also known about the generality of findings hitherto achieved in specific coastal areas (Tomczak *et al.*, 2012a).

There is evidence that variables related to eutrophication have had a significant impact on the structural development of marine ecosystems over the past decades (Daskalov *et al.*, 2007; Österblom *et al.*, 2007; Möllman *et al.*, 2009; Lindegren *et al.*, 2012; Tomczak *et al.*, 2012b), and other studies have also highlighted the impact of a changing climate and overfishing (Jackson *et al.*, 2001; Beugrand, 2004; Möllman *et al.*, 2009; Conversi *et al.*, 2010). Eutrophication, climate, and overfishing might all lead to a turnover in species composition (Beugrand, 2004; Möllman *et al.*, 2009; Conversi *et al.*, 2010), and in turn affect species interactions (Casini *et al.*, 2009). This might in turn ultimately influence ecosystem functioning and the provision of various ecosystem services, from fisheries yields to recreational values.

The Baltic Sea is the largest brackish water body in the world harbouring a unique mixture of organisms of both freshwater and marine origin (Voipio, 1981). The oceanographic properties of the area are characterized by strong environmental gradients in, for example, salinity, temperature, and nutrient levels, with almost marine conditions in the southwestern sub-basins to nearly freshwater conditions in the northernmost sub-basins (HELCOM, 2010). As a consequence, there are also strong differences in natural species composition and structure among ecosystems in the different parts of the Baltic Sea. The nutrient (trophic) status is typically high in the western, southern, and eastern Baltic Sea, due to elevated anthropogenic input, but significantly lower in the north (HELCOM, 2010). Exploitation from fisheries is recognized as another key issue for the region. In particular, overfishing on the key marine piscivorous fish species in the area, cod (*Gadus morhua*), in combination with unfavourable climatic conditions resulted in substantial change in ecosystem structure and function of the offshore Central Baltic Sea ecosystem in the late 1980s and early 1990s (Möllman *et al.*, 2009).

In this study, we apply a coherent approach to assess the temporal development of 13 coastal ecosystems in the Baltic Sea region, regarding key ecosystem components in the foodweb and potentially important pressure variables related to climate, hydrography, nutrient status, and fishing pressure. More specifically, we investigate: (i) the temporal development of biological ecosystem components across areas, (ii) the timing of any abrupt changes occurring in the structure of the biological ecosystem components in each system, and (iii) the relationships between biological ecosystem components and potential pressure variables.

Material and methods

Data

The 13 coastal areas studied ranged across the Baltic Sea region from Denmark in the southwest to the northern parts of Sweden (Figure 1). The areas generally represented nearshore, shallow and sheltered coastal bays, archipelago areas, and lagoons. The total set comprised one area in Kattegat (Vendelsö), four areas in the central and southern Baltic Sea (Gulf of Gdańsk, Vistula lagoon, Curonian lagoon, Kvädöfjärden), two in the Gulf of Riga (Gulf of Riga SW, Gulf of Riga NE), two in the Gulf of Finland (Gulf of Finland E, Gulf of Finland W), two in the southern Bothnian Sea/Archipelago Sea (Forsmark, Archipelago Sea), and one in the southern Bothnian Bay (Holmön). In addition, one area in the Skagerrak (Limfjord) was included. For a more thorough description of the areas assessed, see ICES (2012). The biotic variables (biological ecosystem components) covered different trophic levels ranging from phytoplankton to seals (Table 1). Potential driving variables (environmental and fisheries-related variables) were categorized as related to climate, hydrology, nutrient status, or fishing pressure (Table 1; Supplementary material S1). The data for both types of variables

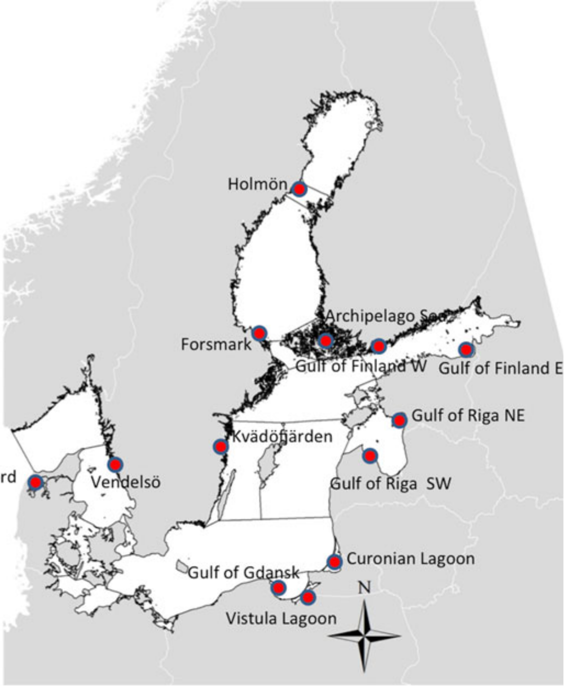

Figure 1. Map of the Baltic Sea and the areas included in this study.

Table 1. Data used in the study per coastal area, including basin, period considered, number of biotic, and environmental/fisheries variables.

Area	Basin	Period	# Biotic variables	# Env./Fish. variables	PP	ZP	ZB	P	F	S	N	H	C	FP
Limfjord (DK)	North Sea/Skagerrak	1992 – 2007	19	25	x		x		x		x	x	x	x
Vendelsö (SWE)	Kattegat	1992 – 2010	15	15			x		x		x	x	x	x
Gulf of Gdańsk (PL)	Southern Baltic	1994 – 2010	23	29	x	x			x		x	x	x	x
Vistula Lagoon (RUS)	Southern Baltic	1992 – 2011	23	15	x	x	x		x		x	x	x	x
Curonian Lagoon (RUS)	Southern Baltic	1992 – 2011	24	14	x	x	x		x		x	x	x	x
Kvädöfjärden (SWE)	W Baltic Proper	1992 – 2010	11	9			x		x	x	x	x	x	x
Gulf of Riga SW (LAT)	E Baltic Proper/Gulf of Riga	1992 – 2011	15	8	x	x			x		x	x	x	
Gulf of Riga NE (EST)	E Baltic Proper/Gulf of Riga	1993 – 2010	31	13	x	x	x	x	x		x	x	x	
Gulf of Finland E (EST)	Gulf of Finland	1993 – 2010	14	38	x	x	x				x	x	x	
Gulf of Finland W (FIN)	Gulf of Finland	1993 – 2010	23	12	x		x		x		x	x	x	
Archipelago Sea (FIN)	Archipelago Sea	1992 – 2009	19	7	x				x		x	x		
Forsmark (SWE)	Bothnian Sea	1992 – 2010	10	10			x		x	x	x	x	x	x
Holmön (SWE)	Bothnian Bay	1994 – 2010	16	14		x	x		x	x	x	x	x	x

Columns 6 – 15 indicate the type of variable included: PP, phytoplankton; ZP, zooplankton; ZB, zoobenthos; P, plants; F, fish; S, seal; N, nutrient loading and concentration; H, hydrology; C, climate; FP, fishing pressure.

were obtained from national and international monitoring programmes (Supplementary material S1). In each area, data to include were selected to as far as possible represent the biologically most relevant season and geographical scale. Hence, the data included were collected during different parts of the year (Supplementary material S1). As the focus of the study was to compare long-term temporal trends, differences in sampling season were not a factor that qualitatively affected the outcome of the analyses. The period assessed ranged from the early 1990s to 2010, to obtain a comparable period for all coastal areas included. However, for the most areas and variables, data are available also for later years (Table 1). In this paper, we restrict our analyses until 2010 due to limitations in data access and effort in data collation at the time of carrying out the analyses.

For the biological ecosystem components, between 11 and 31 variables were included in the analyses in each area (Table 1). The number of trophic levels covered differed to some extent across areas, depending on available data. The most commonly represented ecosystem component was fish, which was included in all areas but one. Data on phytoplankton were available for nine areas and were typically represented by chlorophyll *a* concentration, total phytoplankton biomass, or the biomass of key species groups (Supplementary material S1). Mesozooplankton data were included in seven areas and data on macrozoobenthos were available for ten of the areas. For both of these, data were represented by the biomasses of key species and species groups. For benthic vegetation, data were only available for one of the areas (Gulf of Riga, NE), and were represented by the biomass per square metre of higher plants and benthic macroalgae (*Charophyta*, *Rhodophyta*, *Phaeophyta*, and *Chlorophyta*). Fish were represented by several variables, including (in the different areas) larvae abundance and duration, fishery landings, abundance or catch per unit effort (cpue) from coastal fish monitoring programmes, estimates of spawning-stock biomass, fish recruitment, or mean weight of key species for the coastal fisheries. Data on seal abundance were only included for three of the areas, represented by local abundance estimates of seal populations.

The number of environmental and fisheries-related variables varied between 7 and 38 in the different areas (Supplementary material S1). In eight of the areas, variables from all four categories (climate, hydrology, nutrient status, and fishing pressure) were included (Table 1). Fisheries-related variables were not included in the remaining five areas, and in one area, climate-related variables were also missing. Variables related to climate were typically represented by water and air temperatures, water pH, windspeed, or ice retreat date. In addition, large-scale climatic indices (the Baltic Sea Index, BSI, Lehmann *et al.*, 2002; the North Atlantic Oscillation Index, NAO, Hurell, 1995; or the Arctic Oscillation Index, Kalnay *et al.*, 1996) were included. For variables related to hydrology, salinity levels, water column oxygen concentration, or bottom water oxygen concentration were included. Nutrient status was represented by concentrations of inorganic and organic nitrogen (N) and phosphorous (P) in the water column, concentrations of dissolved silica, loading of N and P from land and rivers, water colour, and water transparency (typically Secchi depth). For the fisheries-related variables, data on the landings of local coastal fisheries, fishing mortality, or fishing yield were included.

Analyses

Temporal development of ecosystem components in each area

The temporal development of the set of ecosystem components was initially assessed separately for each area. The analyses were performed using the multivariate analysis method of principal coordinate analysis (PCO; Zuur *et al.*, 2007) as implemented in the PERMANOVA + version of PRIMER (Anderson *et al.*, 2008). PCO is an analogue to a principal component analysis (PCA), but differs from this in that the ordination can be based on any index of similarity. Here, we used Chord distances (Orlóci, 1976), which is a metric index that does not treat double absence as an indication of resemblance, and give equal weights to rare and abundant observations (Legendre and Legendre, 1998). Further, since the Chord distance is a metric index, the axes of the ordination can be used directly in further analyses. Before analysis, all data were normalized (*z*-transformed) to remove the influence of differences in scaling of the different variables. The PCO identified the major changes over time in each area, and the projection of the sample scores on the first two PCO axes were used in subsequent analyses. The biotic components mainly associated with the changes along these two axes were identified by their factor loadings with the first PCO axis, separately for each area. Only those components with a multiple metric correlation >0.2 with any of the first two PCO axes were projected on the ordination plot (Supplementary material S2).

The incidence of abrupt changes in the structure of the biological ecosystem components over time was assessed using chronological clustering (Legendre and Legendre, 1998) as implemented in BRODGAR 2.5.7 (www.brodgar.com). For consistency with the PCO, we used Chord distance as the similarity index on normalized data in this analysis. A level of connectedness of 0.5 was used, and a temporal change was interpreted as statistically significant from 1 year to the next at $\alpha = 0.01$ and 0.05, to only include the strongest changes in each dataset (Zuur *et al.*, 2007).

Common development of biological ecosystem components across areas

Despite the differences in the data from different areas with respect to the coverage of different trophic levels and environmental variables, an attempt was also undertaken to address commonalities in the temporal development of biological ecosystem components across areas. This analysis was conducted by Min/max autocorrelation factor analysis (MAFA; Solow, 1994) as implemented in BRODGAR 2.5.7 (www.brodgar.com). Briefly, MAFA is a type of PCA which is based on autocorrelation factor analysis and which can be used to identify common patterns across datasets, for example, in time-series data (Zuur *et al.*, 2007). The autocorrelation factor analysis considers the trend of each individual time-series using an index function or smoothing curve, and for each identified common trend (MAFA-axis), a permutation test assesses whether or not the autocorrelation of the different datasets is significantly different from zero. The MAFA analysis was applied on data representing the first two axes of each area-specific PCO, and up to six potential common trends across areas were assessed. The cut-off level of significance between an individual time-series and an MAFA axis was set to the default value 0.45.

Association between biological ecosystem components and potential driving variables

The potential association between the biological components and driving variables (environmental and fisheries-related variables) was assessed at two different scales. First, potential driving variables were considered one at a time within each area, and second, a set of environmental variables was assessed across a subset of areas at regional scale. In the local scale analysis, the projected sample scores of the first two PCO axes were correlated with the potential driving variables, separately for each area using linear cross-correlation analyses as implemented in the PERMANOVA+ version of PRIMER (Anderson *et al.*, 2008). The variables exhibiting the highest correlation with PCO1 and PCO2 (based on the obtained *R*-values) were interpreted as the variables most strongly associated with the temporal development of biological components in that area.

Coastal ecosystems are thought to be rather isolated systems that respond mainly to local environmental perturbations (reviewed in Olsson *et al.*, 2012, 2013), but recent studies in the Baltic Sea have challenged this in showing impact of both large-scale climatic impact (Olsson *et al.*, 2012, 2013; Tomczak *et al.*, 2012a; Rousi *et al.*, 2013; Snickars *et al.*, 2015) and anthropogenic impact in nearby systems (Eriksson *et al.*, 2011; Casini *et al.*, 2012). A link to large-scale eutrophication is also perceivable as nutrient concentrations in coastal systems are strongly influenced by water exchange with adjacent offshore areas (Dimberg and Bryhn, 2014). Subsequently, we assessed the association between environmental variables reflecting changes on a regional scale and the temporal development of biological ecosystem components in the coastal areas. This analysis was performed on a subset of the coastal areas. Since the number of years considered in this study did not allow for a common comparison of the influence of a set of similar environmental variables across areas, we related the common MAFA axes of the first PCO axis across the seven systems being in direct contact to the Central Baltic Sea (Gulf of Gdańsk, Kvädöfjärden, Gulf of Riga SW, Gulf of Riga NE, Gulf of Finland W, Archipelago Sea, and Forsmark; Figure 1) to a set of regional environmental variables, assumed to potentially influence the environmental conditions in each of these areas. The dataset of regional variables included offshore sea surface (0–10 m) salinity, temperature, dissolved inorganic nitrogen (DIN) and phosphorous (DIP) from the Central Baltic Sea, the BSI index, and the NAO index (both December–March averages). No common variable representing fishing pressure or mortality was available for coastal systems. Data for environmental variables were extracted from the Swedish Hydrological and Meteorological Institute's SHARK database for stations BY4 and BY5 (Bornholm basin) and BY15 (Gotland basin), and aggregated into mean annual surface layer values for salinity, summer temperature (June–August), and winter (January–February) for DIN and DIP.

Results

Temporal development of ecosystem components in each area

The first two axes of the PCO analysis on the biological ecosystem components (response variables) captured between 35 and 51% of the variation in the temporal development of the datasets from the different coastal areas (Table 2). The first axis explained between 19 and 33% of the variation, and the second axis between 15 and 22%.

In all 13 areas analysed, there had been a substantial change in the structure of the local ecosystem components assessed during the past 20 years (Figure 2a; Supplementary material S2 and S3). The temporal development in the different areas was, however, to a large extent unique and likely dependent on the identity of the ecosystem components and number of trophic levels included for each area (Table 2; Supplementary material S2). No overall and general patterns with respect to certain species groups could hence be deduced. The temporal development of the ecosystem components each coastal area is summarized briefly in the Supplementary material S2.

The timing of changes in the assessed biological ecosystem components was also to a large extent unique for each area, but some common patterns were apparent (Figure 2a; Supplementary material S3). In the majority of areas, significant structural changes were observed over time, mainly in the mid and late 1990s and early 2000s.

Common development of biological ecosystem components across areas

The MAFA analyses including the first PCO axes from all areas resulted in common development trajectories across the areas assessed. The first MAFA axis had a high autocorrelation coefficient ($r = 0.96$, $p = 0.024$) and described a directional development of the ecosystem components away from the state at the beginning of the period (Figure 2b). All areas except for Limfjord, Gulf of Gdańsk, and Gulf of Finland W exhibited a significant correlation with the first MAFA axis (Table 3a). The second MAFA axis ($r = 0.87$, $p = 0.098$) described a development where the system to some extent returned to its original state (Figure 2b). The temporal development of the Gulf of Gdańsk, Gulf of Finland W, Curonian Lagoon, and Kvädöfjärden was significantly correlated

Table 2. Summary of PCO analyses output for each area, with variation explained for each of the first two PCO axes (Expl var PCO1 and PCO2, respectively) and the summed variation for PCO1 and 2 (Σ PCO 1 and 2).

Area	Expl var PCO1 (%)	Expl var PCO2 (%)	Σ PCO 1 and 2	Variable 1		Variable 2	
Limfjord	20.4	17.6	38	Echinoderms	0.44 (+)	Chlorophyll *a*	0.40 (+)
Vendelsö	26.9	18.5	45.4	Shorthorn sculpin	0.37 (−)	Cumacea sp.	0.33 (−)
Gulf of Gdańsk	25	21.9	46.9	Aut. dinoflagellates	0.36 (+)	Het. dinoflagellates	0.35 (+)
Vistula Lagoon	23	15.9	38.9	Pikeperch weight	0.38 (−)	Polychaetes	0.32 (−)
Curonian Lagoon	19.2	14.7	33.9	Pikeperch recruitment	0.37 (+)	Pikeperch Weight	0.36
Kvädöfjärden	28.5	21.4	49.9	Cod	0.44 (+)	Grey seal	0.44 (+)
Gulf of Riga SW	21.3	15.8	37.1	Acartia	0.46 (−)	Chlorophyll *a*	0.45 (+)
Gulf of Riga NE	23.3	12.1	35.4	Smelt	0.35 (−)	Zoobenthos Community Index	0.32 (−)
Gulf of Finland E	30	20	50	Keratella sp. Spring	0.42 (+)	Nostocophyceae spring	0.37 (+)
Gulf of Finland W	23	18.1	41.1	Diatomophyceae sp.	0.39	Autotroph biomass	0.34
Archipelago Sea	29.5	15.8	45.3	Chrysophycae sp.	0.36	Ebriidae sp.	0.32
Forsmark	33.4	17.3	50.7	Marenzelleria spp.	0.57 (+)	Monoporeia affinis	0.38 (+)
Holmön	32.3	15	47.3	Grey seal	0.42 (+)	Ruffe	0.37 (+)

The variables exhibiting the highest (Variable 1) and second highest (Variable 2) correlation with the first PCO-axis are indicated together with their multiple metric correlation coefficient and the direction of development over time in parentheses; "+", linear increase; "−", linear decrease, and no sign no change at $\alpha = 0.05$.

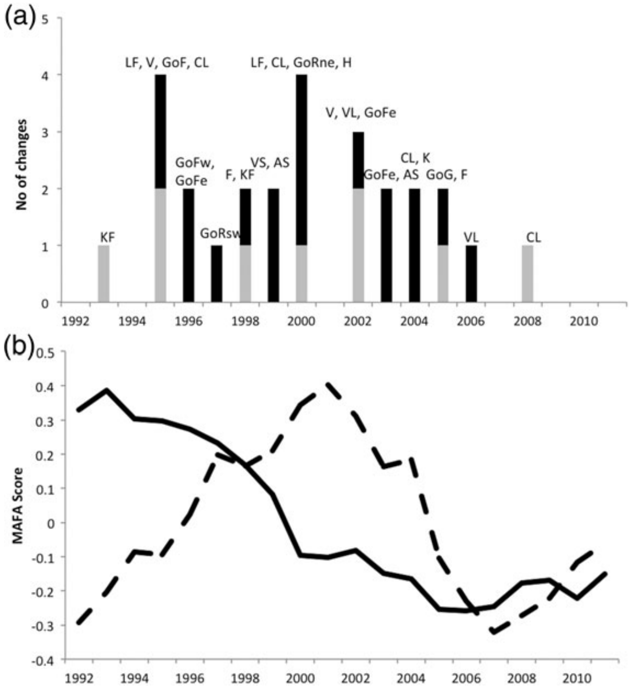

Figure 2. (a) Number of changes per year in the structure of biological ecosystem components in the different areas as derived from the chronological clustering analyses. Grey bars denote changes at $\alpha = 0.05$ and black bars changes at $\alpha = 0.01$. For more detailed information, see Supplementary material S3. LF, Limfjord; V, Vendelsö; GoG, Gulf of Gdańsk; VL, Vistula Lagoon; CL, Curonian Lagoon; KF, Kvädöfjärden; GoRsw, Gulf of Riga SW; GoRne, Gulf of Riga NE; GoFe, Gulf of Finland E; GoFw, Gulf of Finland W; AS, Archipelago Sea; F, Forsmark; H, Holmön. (b) The temporal development of the first two MAFA axes from the analysis on the first PCO-axis from all 13 areas. Solid line represents MAFA 1, and broken line MAFA 2. The MAFA axes combine the temporal development of the first PCO-axis across areas. Only MAFA 1 was significant.

with the shape of the second MAFA axis (Table 3a). The Limfjord area was the only area significantly related to the third MAFA axis ($r = 0.79$, $p = 0.093$: Table 3a). Neither of the axes in the MAFA analysis for the second PCO axis had a significant autocorrelation. The diversity of data used in the analysis across areas is likely to limit the potential for extracting common patterns, but the systems that exhibited a directional temporal development all included data on seals (two areas) and often zoobenthos and zooplankton (nearly all areas with data on these ecosystem components were included). It might hence be that a common and directional development of these ecosystem components across areas influences the outcome of the analysis.

Association between biological ecosystem components and driving variables

The cross-correlation analysis between data representing first two PCO axes from each area and the set of driving variables identified the highest level of correlation for variables related to nutrient status in 13 out of 26 possible comparisons (with the first PCO axis in eight areas, and the second axis in five areas) when considering the effects of each variable alone (Table 4). Fisheries-related variables were correlated with any of the first two PCO axes in six of the areas, variables related to hydrology in five, and climate-related variables in two area-level comparisons. Nutrient status variables and phytoplankton were correlated in six out of the nine areas where both these types of variables were available, and in five out of ten areas that included both nutrient status variables and data on zoobenthos. A correlation was seen in three out of eight of the areas where both fish and fisheries-related variables were included. The variables relating to hydrology showed no clear correlations with the PCO axes for any area. The climate-related variables mainly showed correlations in areas where data on fish and seal were included. Hence, despite the difference in the types of data included for different areas, some common patterns were seen, particularly with respect to the correlations between nutrient status and the phytoplankton and zoobenthos variables, and between the fisheries-related variables and fish.

The MAFA analysis at larger geographical scale, assessing data for seven areas in direct connection to the Central Baltic Sea, yielded a very similar outcome as the common analysis including all 13 areas. The first MAFA axis ($r = 0.94$, $p < 0.001$) described a directional development away from the state at the beginning of the period assessed (Figure 3). All areas except for Gulf of Gdańsk and Gulf of Finland W were significantly related to this developmental trajectory (Table 3b). The second MAFA axis was also significant ($r = 0.79$, $p = 0.007$), and described a development where the system to some extent returned to the state at the beginning of the period (Figure 3). The Gulf of Gdańsk, Gulf of Finland W, and Kvädöfjärden areas exhibited a significant correlation to this axis. The third MAFA axis was not significant ($r = 0.55$, $p = 0.058$). The overall development of the biological datasets as captured on the first MAFA axis was significantly related to the development of DIN and DIP in the offshore Central Baltic Sea (Table 5; Figure 4). In addition, water temperature, BSI, and NAO were also associated with the first MAFA axis, but the relationship was not significant. The correlation between the driving variables in this analysis was typically low (not exceeding 0.25 in any comparison expect for that between BSI and NAO, results not shown), suggesting that they are not redundant and alone describe a unique environmental pressure. The results further suggest that changes in surface nutrient concentrations in the Central Baltic Sea, either increasing or decreasing, have had an impact on the temporal development of the biota in the majority of seven coastal areas included in the analysis, during the past 20 years. The second MAFA axis was significantly related only to DIP, and an almost significant correlation also to salinity (Table 5; Figure 4). Over the period assessed, there was an increase in DIP (linear regression, $r^2 = 0.34$, $p = 0.007$), and a decrease in DIN ($r^2 = 0.38$, $p = 0.004$; Figure 5) in the offshore Baltic Sea.

Table 3. Summary of the MAFA analysis for the first PCO axis from (a) the analyses of all areas and (b) joint analyses of the seven areas connected to the central Baltic Sea.

Area	MAFA 1	MAFA 2	MAFA 3
(a)			
Limfjorden	0.44	0.13	**0.48**
Vendelsö	**−0.89**	−0.16	−0.23
Gulf of Gdańsk	0.09	**−0.70**	0.17
Vistula Lagoon	**0.95**	−0.01	−0.08
Curonian Lagoon	**0.80**	**0.52**	−0.03
Kvädöfjärden	**0.78**	**0.48**	0.06
Gulf of Riga SW	**0.80**	−0.05	−0.13
Gulf of Riga NE	**0.88**	0.05	0.40
Gulf of Finland E	**0.72**	−0.32	0.19
Gulf of Finland W	−0.31	**0.79**	−0.01
Archipelago Sea	**0.76**	0.17	−0.08
Forsmark	**0.94**	0.02	0.19
Holmön	**0.70**	0.41	0.39
(b)			
Gulf of Gdańsk	0.22	**−0.75**	**−0.51**
Kvädöfjärden	**0.72**	**0.62**	0.09
Gulf of Riga SW	**0.79**	0.05	0.18
Gulf of Riga NE	**0.91**	0.22	−0.30
Gulf of Finland W	−0.44	**0.76**	−0.02
Archipelago Sea	**0.69**	0.31	0.29
Forsmark	**0.94**	0.18	−0.06

Numbers give the correlation coefficient between each area and the first three MAFA axes. The level of significance was set to 0.45 and significant correlations are highlighted.

Discussion

In this study, we assess the temporal development of biological ecosystem components in 13 coastal areas in the Baltic Sea over the past two decades. The analyses were to some extent restricted by data availability, as it was not possible to obtain identical variables across areas, and in several cases, data on certain ecosystem components and potential driving variables were not available. Despite the

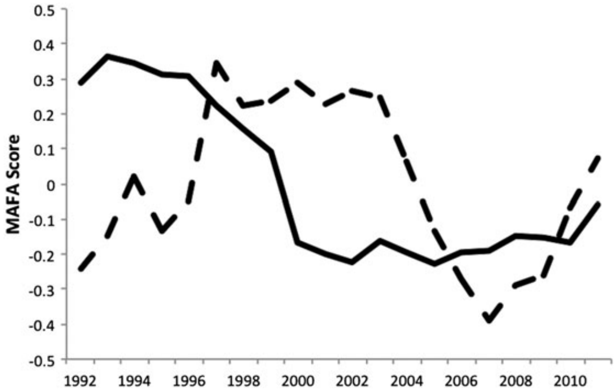

Figure 3. Temporal development of the first two MAFA axes from the analysis on the first PCO-axis from the seven areas connected to the Central Baltic Sea. Solid line represents MAFA 1, and broken line MAFA 2.

Table 4. Summary of the linear cross-correlation analyses between the first two axes of the PCO (PCO1 and PCO2) and the set of potential driving variables in each area.

Area	PCO1	R	Category	PCO2	R	Category
Limfjord	DIP winter	0.69	N	Yield crusteaceans	0.61 (+)	FP
Vendelsö	DIP	0.69	N	F-cod	0.19	FP
Gulf of Gdańsk	Flatfish landings	0.49 (−)	FP	NH4 winter	0.60 (−)	N
Vistula Lagoon	N summer	0.67 (+)	N	F pikeperch	0.55	FP
Curonian Lagoon	F pikeperch	0.76 (+)	FP	Oxygen summer	0.52	H
Kvädöfjärden	DIN	0.65 (+)	N	AO	0.42 (−)	C
Gulf of Riga SW	Tot N	0.54 (−)	N	Tot P	0.44 (−)	N
Gulf of Riga NE	SiO_4	0.79 (+)	N	Oxygen	0.54	H
Gulf of Finland E	Oxygen	0.86 (−)	H	Tot P	0.66 (+)	N
Gulf of Finland W	Oxygen	0.34 (−)	H	NH4 summer	0.46	N
Archipelago Sea	PO4-P	0.57 (+)	N	PO4-P	0.42 (+)	N
Forsmark	P runoff	0.49 (−)	N	F herring	0.66	FP
Holmön	Salinity	0.73 (−)	H	BSI	0.44	C

The variables exhibiting the highest correlation with the first two PCO-axes are shown, together with the correlation coefficient of the variables and the direction of their development over time in parentheses; "+", linear increase; "−", linear decrease, and no sign no change at $\alpha = 0.05$. The category of each variables is given as: N, nutrient loading and concentration; H, hydrology; C, climate; FP, fishing pressure.

data shortcomings, however, 10 of the 13 areas assessed exhibited a common and unidirectional development away from the initial ecosystem state at the beginning of the assessment period. This pattern was most strongly associated with a directional development of zooplankton, zoobenthos, and seals. In half of studied areas, the temporal development was associated with a concurrent change in nutrient variables. A common analysis of the coastal areas connected to the Central Baltic Sea indicated that common directional developments in these ecosystems were mainly associated with changes in off shore DIP (increasing) and DIN (decreasing) during the assessment period. Associations between the development of biological ecosystem components and climate-related variables (i.e. temperature and pH), hydrography (i.e. salinity), and fishing pressure were also found, although our findings suggest that variables related to nutrient status are of relatively higher importance for the temporal development of coastal ecosystems in the Baltic Sea during the past two decades.

Table 5. Summary of the MAFA analysis on the first PCO-axis from each of the seven areas connected to the central Baltic Sea and the set of common environmental/fisheries-related variables.

Variable	MAFA 1	MAFA 2	MAFA 3
BSI	0.27	−0.05	0.19
NAO	0.32	−0.08	0.21
Temperature	−0.12	−0.13	0.19
Salinity	0.35	0.40	−0.07
DIN	**0.62**	0.18	0.21
DIP	**−0.54**	**−0.46**	0.09

Given is the correlation coefficient (*r*) between the first three MAFA axes and each of the environmental/fisheries-related variables. The level of significance was set to 0.45 and bold figures represent significant correlations. BSI, Baltic Sea Index; NAO, North Atlantic Oscillation; DIN, dissolved inorganic nitrogen; DIP, dissolved inorganic phosphorous.

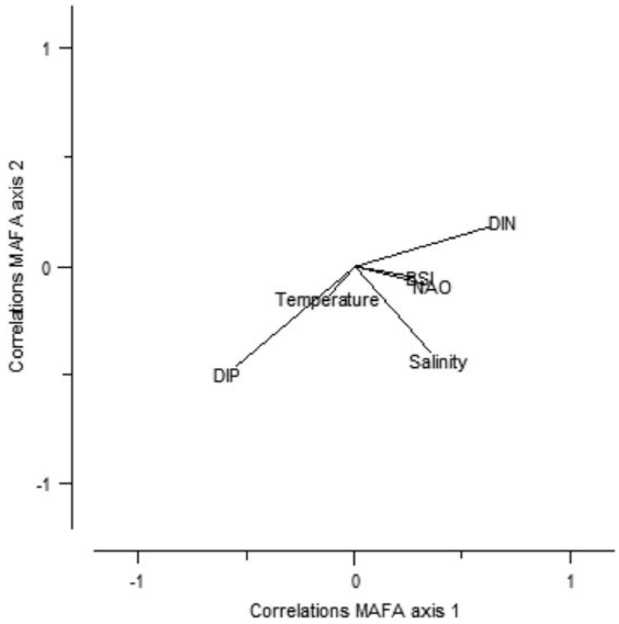

Figure 4. Ordination of the correlation between the set of common environmental/fisheries-related variables and the first two MAFA axes as derived from the first PCO-axis from each of the seven areas connected to the Central Baltic Sea. BSI, Baltic Sea Index; NAO, North Atlantic Oscillation; DIN, dissolved inorganic nitrogen; DIP, dissolved inorganic phosphorous.

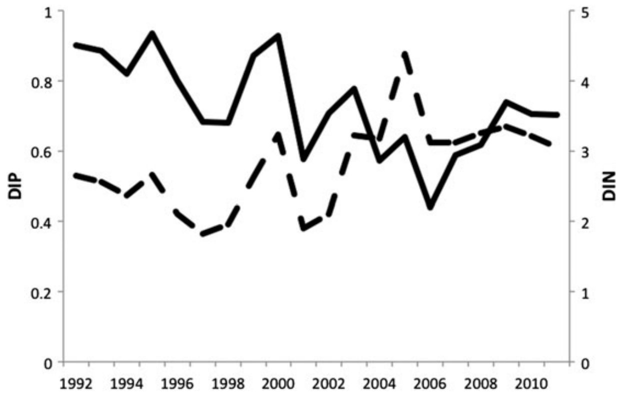

Figure 5. Temporal development between 1992 and 2011 for surface values (0–10 m) of DIN (μmol l^{-1}, solid line) and DIP (μmol l^{-1}, broken line) for the Central Baltic Sea.

Development of ecosystem components

Generally, only few studies have previously assessed the temporal development of coastal ecosystems over time in an integrated manner. Collie *et al.* (2008) suggested that the temporal development of the coastal fish community in Narragansett Bay (Rhode Island, USA) was associated with changes in climate and eutrophication status. In the Baltic Sea, the long-term temporal development of coastal fish- and zoobenthos communities has been linked to the impact of climate, nutrients, and top-down control on species composition (Olsson *et al.*, 2012, 2013; Tomczak *et al.*, 2012a). Neither of these studies did, however, address the long-term development of several trophic levels in concert as has been previously done for offshore systems (Casini *et al.*, 2009; Möllman *et al.*, 2009; Conversi *et al.*, 2010; Lindegren *et al.*, 2012).

In our study, we assess the temporal development of several parts of the ecosystem in each area in an integrated manner. As expected, a rather complex picture with unique developmental trajectories in different coastal areas was seen. There were both increases and decreases in the abundance of species favoured by a warmer and less saline Baltic Sea in the different areas, and the same pattern was seen for species sensitive to changes in nutrient concentrations and load, and fishing pressure. Species expected to be favoured by increasing water temperatures and decreased salinities were, for example, the fish species perch (*Perca fluviatilis*) and roach (*Rutilus rutilus*, Olsson *et al.*, 2012), which increased in the Archipelago Sea, Holmön, and Gulf of Riga SW. However, they decreased in Kvädöfjärden and Forsmark. The amphipod *Monoporeia affinis* that is expected to be sensitive to increased water temperatures (Olsson *et al.*, 2013) also increased in some areas (Forsmark and Kvädöfjärden) and decreased in others (Gulf of Finland W and Holmön). Pikeperch (*Sander lucioperca*) is a fish species that generally benefits from more eutrophic conditions (Bergström *et al.*, 2013), but is also to a substantial degree exploited by coastal fisheries (Mustamäki *et al.*, 2013; Heikinheimo *et al.*, 2014). Pikeperch increased in both the Vistula and Curonian Lagoons, despite stable fishing pressure in the former and increased fishing pressure in the latter. As pikeperch is a species with a very local population structure (Björklund *et al.*, 2007), the common response across systems is not likely to result from direct links between the populations, but rather reflect a joint response to a common pressure other than fishing pressure across systems. Overall, not many general patterns for the development of the different ecosystem components across areas were hence identified, indicating that coastal systems generally are rather local in their appearance and their response to changes in environmental conditions (Wootton, 1998). The results also reflect that the data assessed cover substantial natural environmental gradients in important physical and hydrographical variables (Voipio, 1981) and species diversity (Ojaveer *et al.*, 2010).

Despite the observed differences, some common developmental trajectories across areas were observed. There were similar patterns in the timing of significant changes in the structure of ecosystem components across areas, and a similar and directional development of the systems in the majority of areas. The results suggest that the state characterizing the most recent years has departed from that in the early/mid-1990s. Earlier studies have demonstrated that the ecosystem in the offshore central Baltic Sea has changed towards a deteriorated environmental state during recent decades (Casini *et al.*, 2008; Möllman *et al.*, 2009). Whether or not the common and directional development as observed in our study represents a development away from a desirable state in coastal areas is outside the scope of this paper, but to the best of our knowledge, our study is the first to highlight that coastal ecosystems in the Baltic Sea have undergone a common directional development over the past decades.

Seals and some of the fish species (i.e. cod) included in the analyses are highly mobile with panmictic populations in the Baltic Sea. The trends in these ecosystem components might hence not be independent across systems, and could to some extent drive the observed common development across areas. However, this is likely not the main explanation behind our findings, since seals and cod were only included in three of the systems each (for cod only two systems in the Central Baltic Sea; Supplementary material S1), and contributed significantly to ecosystem development in only two areas (Holmön and Kvädöfjärden, see Table 2).

Association with environmental and fisheries-related variables

Unique associations between the development of each system and the environmental and fisheries-related variables were observed in each area when considering the local variables one at a time. Moreover, in the majority of areas, variables reflecting more than one category of drivers (hydrography, climate, fishing pressure, and nutrients) were associated with the first two PCO axes. Although we did not test for the combined and/or interactive effects of these variables, these results indicate that more than one type of environmental or anthropogenic pressure, potentially acting in concert or additively, could be influential for the temporal development of coastal ecosystems in the Baltic Sea region (Kotta *et al.*, 2009). However, variables related to nutrient status were overrepresented in the analyses at local scale, and also in the regional scale analyses, when the developments of seven coastal areas in direct connection to the Central Baltic Sea. At the regional scale, the strongest correlation was seen for DIN and DIP, where DIN has decreased and DIP increased in the Central Baltic Sea during the studied period. Despite these differences in direction, the results corroborate earlier findings that eutrophication is the most important pressure impacting the ecosystem in the Baltic Sea, and that changes in nutrient status have substantial impacts on the biodiversity, with effects, for example, on the environmental targets within the HELCOM Baltic Sea Action Plan (HELCOM, 2007). Interestingly, earlier studies assessing the temporal development (>30 years) of Baltic coastal fish- and zoobenthos communities have not found any links to nutrient concentrations (Olsson *et al.*, 2012, 2013; Rousi *et al.*, 2013). This might either be a result of differences in studied time range, so that the effects of a gradually changing climate might mainly be observed over a longer time-perspective (>20 years), whereas changes in nutrient status are more evident at shorter time-scales. Or that the effects of eutrophication only play a role if other factors, as, for example, fishing pressure, are accounted for. Neither of these potential explanations is mutually exclusive, but our findings highlight the need for considering shifting baselines and also potential additive and combined effects of pressures when assessing the current state of marine ecosystems.

We also found some relationship with changes in climate, hydrology, and fishing pressure for the development of the systems in the different coastal areas, but to a much lesser extent. Such responses have been demonstrated in earlier studies of Baltic ecosystems (Österblom *et al.*, 2007; Möllman *et al.*, 2009; Lindegren *et al.*, 2012; Olsson *et al.*, 2012, 2013), and also highlight the sensitivity of coastal systems in the Baltic to climate change and overexploitation of key species.

Management perspectives

The results presented in this study could be biased towards the availability of data being sensitive to changes in nutrient state, differences in the coverage of the number and type of data considered across areas, and by the analytical methods used. We have furthermore not considered foodweb interactions in the assessment of coastal ecosystem development in this study, something that might influence the outcome of the analyses. Moreover, earlier studies have demonstrated major changes in the structure and function of Baltic Sea ecosystems in the late 1980s (Möllman *et al.*, 2009; Lindegren *et al.*, 2012; Olsson *et al.*, 2012, 2013), a period not covered by the data used in this study. This might to some extent limit our analyses, but our results nevertheless suggest several significant structural changes (likely of a comparably smaller magnitude) in the systems assessed during the mid and late 1990s and early 2000s. To that end, we also find a directional development away from the state characterizing the structure of the systems in the early 1990s in the majority of areas assessed, suggesting that coastal ecosystems in the Baltic Sea are still affected by environmental perturbations and are hence under continuous change.

One of the key messages of this study is besides describing a strong directional development and significant changes in the structure of coastal ecosystem components in the Baltic Sea over the past two decades, the collation of data currently available to support integrated ecosystem assessments of coastal systems in the Baltic Sea from many countries and sources. The studied coastal systems are typically very local in their structure and dynamics, and under increasing anthropogenic impact, but current monitoring of several key ecosystem components is missing or monitored with poor temporal and spatial coverage in many areas. For example, four or more trophic levels were only covered by monitoring in 4 of the 13 systems assessed. The geographical coverage was best represented for fish and fisheries data and macro-zoobenthos, whereas data on phytoplankton, zooplankton, and top-predators were poorer both regarding the temporal and spatial perspective. A future sampling strategy to facilitate integrated ecosystem assessments should obviously include monitoring also of the ecosystem components for which data are currently lacking, and the temporal and spatial resolution should be representative for the system assessed. Our study hence highlight current data gaps to support an integrated status assessment of Baltic Sea coastal ecosystems as required in Baltic Sea

Action Plan and Marine Strategy Framework Directive. With the current amount of data available, the prospects for integrated monitoring and assessment in coastal ecosystems in the Baltic Sea seem to be limited to a few areas only.

To that end, we also suggest that future studies should address further the importance of shifting baselines and effects of differences in the temporal coverage for status assessments and management advice. Extending the analyses beyond the period currently assessed would highlight more recent changes in ecosystem structure and cast light on the past status of coastal ecosystems in the Baltic Sea. Including also additional sectors as tourism, recreation, and industry as well as valuation of ecosystem services in a more multi-sectorial framework approach would also provide additional input on the status and use of heavily impacted coastal ecosystems, as well the cultural and social services that they provide.

Supplementary data

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

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