Reorganization of a large marine ecosystem due to atmospheric and anthropogenic pressure: a discontinuous regime shift in the Central Baltic Sea

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Abstract

Marine ecosystems such as the Baltic Sea are currently under strong atmospheric and anthropogenic pressure. Besides natural and human-induced changes in climate, major anthropogenic drivers such as overfishing and anthropogenic eutrophication are significantly affecting ecosystem structure and function. Recently, studies demonstrated the existence of alternative stable states in various terrestrial and aquatic ecosystems. These so-called ecosystem regime shifts have been explained mainly as a result of multiple causes, e.g. climatic regime shifts, overexploitation or a combination of both. The occurrence of ecosystem regime shifts has important management implications, as they can cause significant losses of ecological and economic resources. Because of hysteresis in ecosystem responses, restoring regimes considered as favourable may require drastic and expensive management actions. Also the Baltic Sea, the largest brackish water body in the world ocean, and its ecosystems are strongly affected by atmospheric and anthropogenic drivers. Here, we present results of an analysis of the state and development of the Central Baltic Sea ecosystem integrating hydroclimatic, nutrient, phyto- and zooplankton as well as fisheries data. Our analyses of 52 biotic and abiotic variables using multivariate statistics demonstrated a major reorganization of the ecosystem and identified two stable states between 1974 and 2005, separated by a transition period in 1988–1993. We show the change in Baltic ecosystem structure to have the characteristics of a discontinuous regime shift, initiated by climate-induced changes in the abiotic environment and stabilized by fisheries-induced feedback loops in the food web. Our results indicate the importance of maintaining the resilience of an ecosystem to atmospherically induced environmental change by reducing the anthropogenic impact.

Keywords: Baltic Sea, climate, eutrophication, fisheries, hysteresis, regime shift, resilience

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Introduction

Marine ecosystems are currently under strong atmospheric and anthropogenic pressure. Climate variability and change are known to affect the distribution and population dynamics of marine plant and animal populations (Beaugrand *et al.*, 2003; Richardson & Schoeman, 2004; Roessig *et al.*, 2004; Harley *et al.*, 2006; Pörtner & Knust, 2007), and overfishing of marine fish populations is a common phenomenon with effects not only on the exploited populations, but also on ecosystem structure and function (Myers & Worm, 2003; Frank *et al.*, 2005; Myers *et al.*, 2007). In addition, anthropogenic eutrophication is a major threat significantly affecting the health especially of coastal marine ecosystems (Cloern, 2001).

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Recently, studies demonstrated the existence of alternative stable states in various terrestrial and aquatic ecosystems (Scheffer *et al.*, 2001; Scheffer & Carpenter, 2003). The term regime shift, describing the transition between different states, was first used for marine ecosystems to describe dominance changes between fish populations, such as the fluctuations between anchovy and sardine in several regions of the world oceans (Lluch-Belda *et al.*, 1989). Nowadays, regime shifts are defined mainly on the basis of changes in the ecosystem as a whole (Collie *et al.*, 2004) and are typically characterized by infrequent and abrupt changes in ecosystem structure and function, occurring at multiple trophic levels and on large geographic scales (Collie *et al.*, 2004; Cury & Shannon, 2004; de Young *et al.*, 2004; Bakun, 2005; Lees *et al.*, 2006).

Marine ecosystem regime shifts have been explained mainly as a result of multiple causes, e.g. climatic regime shifts, overexploitation of resources or a combination of both (Scheffer & Carpenter, 2003; Lees *et al.*, 2006). They have been described for various marine ecosystems, with the most prominent examples relating to the North Pacific (Hare & Mantua, 2000), the Scotian Shelf off Canada (Choi *et al.*, 2005), the U.S. north-west continental shelf (Link *et al.*, 2002), the North Sea (Beaugrand, 2004; Weijerman *et al.*, 2005) and the Black Sea (Daskalov, 2002; Daskalov *et al.*, 2007).

The occurrence of ecosystem regime shifts has important management implications, especially within the evolving framework of the 'Ecosystem Approach to Management' (Browman & Stergiou, 2004; ICES, 2005; McLeod *et al.*, 2005). Regime shifts can cause losses of ecological and economic resources. Because of hysteresis in their response, restoring regimes considered as favourable may require drastic and expensive management actions (Scheffer *et al.*, 2001; Suding *et al.*, 2004).

The Baltic Sea is the largest brackish water body in the world, and its ecosystems are strongly affected by atmospheric and anthropogenic drivers. Model studies suggest two regime shifts to have occurred between 1900 and 1980 as a result of seal hunting and eutrophication (Österblom *et al.*, 2007). During the late 1980s, a regime shift was identified in the fish community which shifted from cod (*Gadus morhua*) to sprat (*Sprattus sprattus*) dominance. This change is considered to be mainly attributable to either hydrographic changes (Köster *et al.*, 2003, 2005) and/or cod overfishing (Harvey *et al.*, 2003; Österblom *et al.*, 2007). Based on a limited number of time series, but covering all trophic levels, the late 1980s event was shown to be mainly a climate-induced ecosystem regime shift (Alheit *et al.*, 2005). However, no statistical analysis covering time series from all components of the Baltic ecosystem including atmospheric and anthropogenic forcing was undertaken to support this assertion.

Here, we present results of an analysis of the state and development of the Central Baltic Sea ecosystem integrating hydroclimatic, nutrient, phyto- and zooplankton as well as fisheries data. Our study using multivariate statistics demonstrates a major reorganization of the ecosystem and identified two stable states between 1974 and 2005, separated by a transition period in 1988–1993. We show the change in Baltic ecosystem structure to have the characteristics of a discontinuous regime shift, initiated by climate-induced changes in the abiotic environment and stabilized by fisheries-induced feedback loops in the food web.

Material and methods

Data

We conducted an ecosystem assessment for the Central Baltic Sea, covering the areas of the Bornholm Basin, the Gdansk Deep and the Gotland Basin (Fig. 1). First, an inventory of available data characterizing the whole ecosystem and its abiotic environment was performed. Variables were selected based on the following criteria: (i) length of the covered period, (ii) number of missing data points, (iii) representativeness for a specific ecosystem component or a specific driver, (iv) low cross-correlation with other variables. Finally, we as far as possible avoided a potential overrepresentation of a single ecosystem component (e.g. a trophic group) by balancing the number of variables between components. This procedure was however constrained by ecosystem structure (e.g. number of important species within a trophic group) or the number of influential abiotic drivers. As a result, the selected set of variables represents a trade-off between all above-mentioned criteria. The finally selected data matrix contained 52 variables distributed over 12 fish, six zooplankton, 16 phytoplankton, eight nutrient and eight hydroclimatic time series and is given in Table A1. Information on cross- and autocorrelations of the selected time series can be found in Tables A2 and A3.

To represent the biotic part of the Central Baltic ecosystem, we used data of key components from fish, zoo- and phytoplankton communities. The three commercially and ecologically most important Central Baltic Sea fish stocks are cod (*G. morhua*), sprat (*S. sprattus*) and herring (*Clupea harengus*) (Köster *et al.*, 2003). To characterize their demography and stock development, spawner biomass, recruitment and individual weight were used, while fishing mortality was chosen to represent the pressure exerted by the fishery. Zooplankton is represented by the key species *Pseudocalanus acuspes*, *Acartia* spp. and *Temora longicornis* (Möllmann *et al.*, 2000). We used chlorophyll *a*
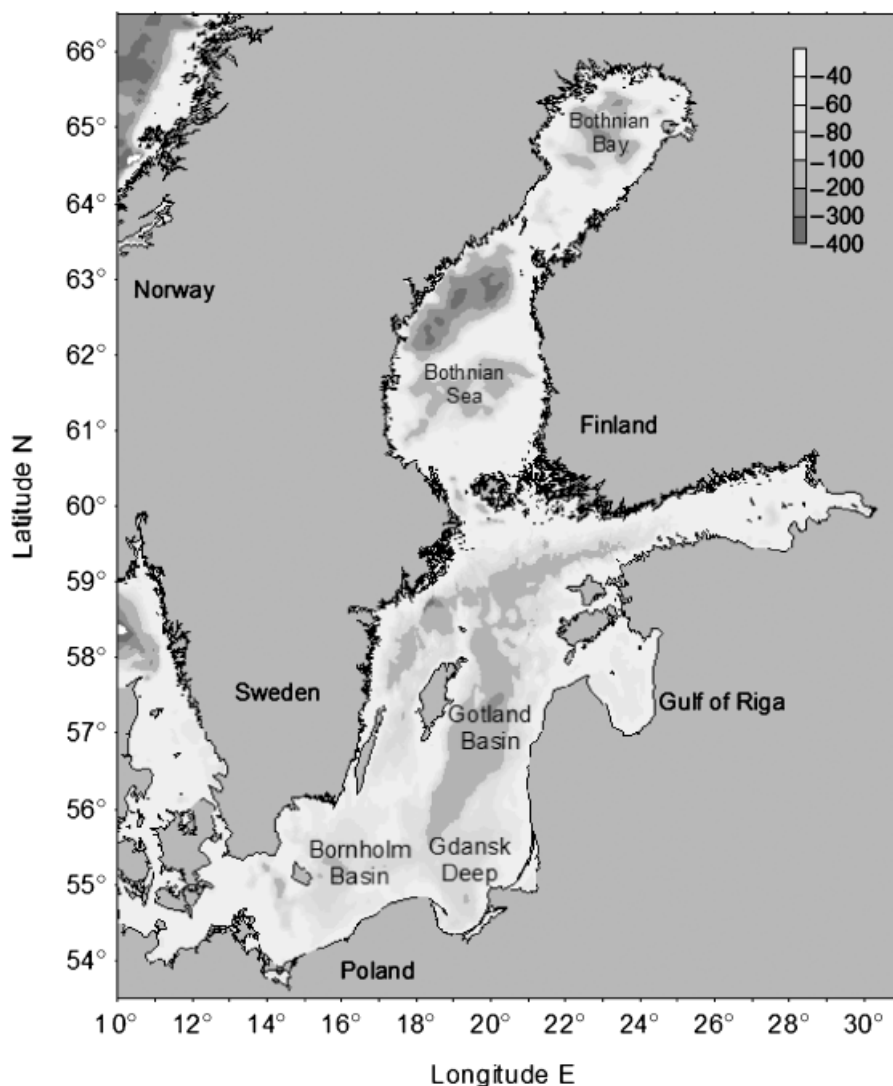
Fig. 1 Map of the Baltic Sea with the study area encompassing the deep basins, i.e. Bornholm Basin, Gdansk Deep and the Gotland Basin.

as a measure of total phytoplankton biomass, while biomass of diatoms, dinoflagellates and bluegreen algae was used to account for the changes in phytoplankton taxonomic composition (Wasmund et al., 1998).

The data for the biotic components of the ecosystem differ in their spatial dimension. Fish stocks are generally assessed for areas encompassing their geographical distribution. Hence, cod and herring in our dataset are representative for the Central Baltic Sea, while population parameters for the Baltic sprat stock are available for the whole Baltic Sea only (ICES, 2007). Long-term zooplankton data were sampled in the Gotland Basin but temporal trends are largely representative for the entire Central Baltic Sea (Möllmann et al., 2000). Phytoplankton biomass and species composition were available for both the Bornholm and Gotland Basins and hence were used separately for both areas.

In our dataset, the abiotic environment of the Central Baltic Sea is represented by nutrient concentrations and hydroclimatic variables. We used winter concentrations of dissolved inorganic nitrogen (DIN) as well as phosphorus (DIP) in the mixed surface layer (represented by 0–10 m depth) to characterize the nutrient supply available to the developing phytoplankton community. Furthermore, deepwater nutrient concentrations (70–90 m and 200–220 m in the Bornholm and Gotland Basin, respectively) were used which indicate the nutrient reservoir that can potentially be transported into the euphotic zone over longer time scales. The Baltic Sea Index (BSI) is closely related to the index of the North Atlantic Oscillation (NAO) (Hurrell, 1995), but directly reflects the impact of climate variability on local oceanographic processes in the Central Baltic Sea (Lehmann et al., 2002). Atmospheric forcing is represented by the

BSI, which is defined as the difference of normalized sea-level pressure anomalies between the positions 53°30′N, 14°30′E (Szcecin, Poland) and 59°30′N, 10°30′E (Oslo, Norway). Positive values of the index correspond to approximately westerly winds over the Baltic, whereas a negative index corresponds more to easterly winds (Lehmann *et al.*, 2002). Here, we used the averages of the BSI for December, January and February. As hydrographic parameters, temperature, salinity and oxygen conditions were used from the Bornholm and Gotland Basins measured in spring and summer. Temperature data were used from the surface (0–10 m) and the intermediate (40–60 m) water, the layers mainly influenced by atmospheric forcing. Salinity data were used for the surface (0–10 m) influenced by runoff and precipitation, and the halocline, affected by the occurrence of major Baltic inflow events (Matthäus & Franck, 1992). Temperature in both layers and surface salinity was averaged over both basins because of the strong cross-correlation, while deepwater salinities were not because of their different trends. Further variables characterizing the deepwater conditions, important for a number of species such as cod and *P. acuspes* (Köster *et al.*, 2005; Schmidt, 2006), are oxygen conditions and the depth of the 11 psu isoline, the latter being only used for the Gotland Basin.

Numerical analyses

We performed principal component analysis (PCA) to analyse the finally selected multivariate data table. All time series had a frequency or were compiled to one value per year and covered in maximum the period 1974–2005. Missing values in the datasets were replaced by variable averages. To improve linearity between the variables and to reduce the relationship between the mean and the variance, biological as well as nutrient variables were $\ln(x + 1)$ transformed. PCAs were based on the correlation matrix. Initially, we performed a PCA using the whole dataset (PCA_all). Afterwards, additional PCAs were conducted using abiotic (PCA_abio) and biological variables (PCA_bio) separately. Abiotic variables included fishing mortalities, hydroclimatic as well as nutrient data.

To illustrate systematic patterns in the matrix of time series, and hence in the development of the ecosystem, the traffic light framework applied in fish stock assessments was used (Link *et al.*, 2002; Choi *et al.*, 2005). Raw values of each variable were categorized into quintiles, and each quintile was given a specific colour. Afterwards, the variables were sorted according to their loadings along the first PC axis (PC1).

We investigated the occurrence of regime shifts in the Central Baltic Sea by using the sequential regime shift detection method (STARS: Rodionov, 2004; Rodionov & Overland, 2005). STARS was applied to the first two PCs (PC1 and PC2) derived by the above-described PCAs. STARS uses *t*-tests sequentially to determine if the next value is significantly different from the previous regime. If so, the point is marked as a potential change point, and subsequent observations are used to confirm or reject the regime shift assumption (for details of the computation, see Rodionov, 2004). The determination of the regimes is strongly influenced by the choice of the cut-off length l, which determines the minimum length of a regime, and the significance level P of the *t*-test. For the analyses of our time series covering roughly three decades, we used $l = 5$ and $P = 0.05$. The applied method has a number of advantages compared with other methods for regime shift detection, e.g. (i) it requires no *a priori* hypothesis on the timing of regime shifts, (ii) it can detect both abrupt and gradual regime changes and (iii) it is able to detect a regime shift relatively early (Rodionov & Overland, 2005). However, it has been shown that stationary red noise processes may generate dynamics, which can be misinterpreted as regimes (Rudnick & Davis, 2003; Rodionov, 2006). Hence, a 'prewhitening' procedure has been implemented in STARS, which removes the red noise component from the time series. It involves subsampling and bias correction of the least-squares estimate for serial correlation (for details, see Rodionov, 2006).

We identified *key species and drivers* within regimes from the PCA_all output. For this, artificial vectors for each time period defined by STARS were calculated by averaging the PC1 and PC2 year scores and using the resulting coordinates as vectors' apices. Afterwards, the angles between variables and the new time vectors were determined. Variables showing an angle of less than 20° to one of the time vectors and being reasonably well represented on the first factorial plane (i.e. vector length > 0.2 of total length scaled to 1) were taken as characteristic of the respective regime.

Finally, to demonstrate that multiple drivers are responsible for regime changes in the Central Baltic ecosystem, we statistically modelled the different effects that the abiotic environment has on the development of the biotic part of the ecosystem. To this end, PC1 of PCA_bio was considered as an *ecosystem state index* and modelled as a function of *key abiotic drivers*. For this analysis, we selected the following abiotic variables based on the PCA analyses: the depth of 11 psu isoline as an index integrating deepwater salinity and oxygen conditions; Gotland Basin summer DIN, representing well the nutrient state of the system; surface salinity and temperature characterizing upper water layer hydrography; and cod fishing mortality, the most important exploitation effect on the system.

For the statistical analysis, generalized additive models (GAMs) implemented in the mgcv library of R

(Hastie & Tibshirani, 1990; Wood, 2007) were used. We estimated the optimal roughness of the smooth terms (i.e. thin plate smoothing splines) as well as the best combination of predictor variables by minimizing the generalized cross-validation criterion (GCV). GCV is a proxy for the model's out-of-sample predictive mean-squared error, and a model with the lowest GCV has the highest explanatory power (Wood, 2007). We tried all combinations of the selected predictor variables in GAMs, selecting the models with the best skills based on GCV. No significant autocorrelation of the residuals has been detected for all finally selected models.

PCAs were performed using the BRODGAR 2.5.6 program (www.brodgar.com). The STARS software is available as an MS EXCEL add-in and can be freely downloaded from www.BeringClimate.noaa.gov. GAMs were modelled using *R* (www.r-project.org).

Results

Time-series developments

The temporal change of all time series of the Central Baltic Sea was visualized by a 'traffic light plot' (Fig. 2). For each variable, values of the lowest quintile were drawn in green, of the highest quintile in red with a gradual colour changeover in-between. Variables were sorted according to their loadings along the first PC,

and by this, the plot shows a trend from variables placed at the bottom left with high values during the 1970s and early 1980s, to variables at the upper right with high values in the recent 15 years. The first group comprises biological variables related to cod, herring and *P. acuspes* whose time trajectories display a general negative trend (Fig. 3a and c). These are similar to the time series of surface salinity, while deepwater salinity increased again since the mid-1990s (Fig. 3e). The second group represents mainly sprat, *Acartia* spp. and *T. long-icornis*, whose biomass and abundances values showed a general increasing temporal trend (Fig. 3b and d). These biological variables have a similar time trend as the BSI and surface temperature, the latter being again on a lower level since the mid-1990s (Fig. 3f).

For variables with PC1 scores close to zero, relatively low values in the 1970s/1980s, high values between 1988 and 1993 and again low values afterwards were measured. This group included mainly time series of nutrients and phytoplankton. However, the phytoplankton dataset has gaps at the beginning of the investigation period, which might hide a clear temporal trend for this group.

Ecosystem changes

The first two principal components (PC1 and PC2) of PCA_all explained 24% and 13%, respectively, of the variability in the dataset, and the year scores of the first
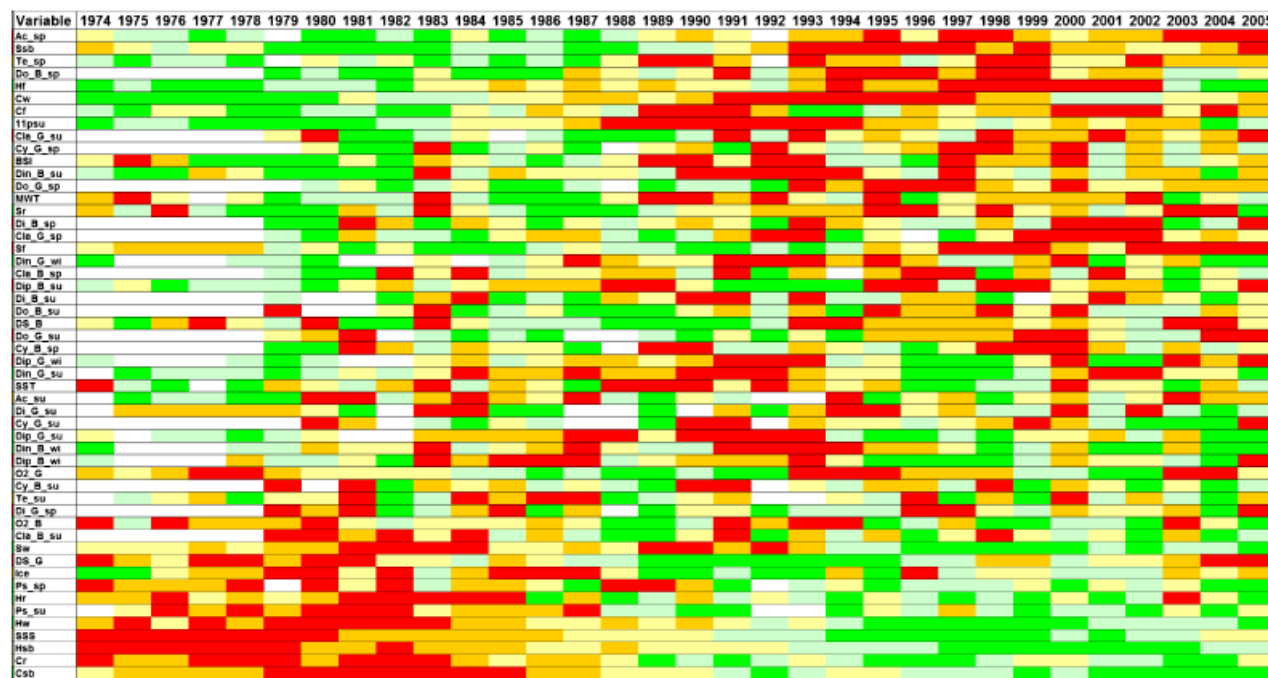

Fig. 2 Traffic-light plot representing the development of the Central Baltic Sea ecosystem; time-series transformed into quintiles and sorted according to PC1 of PCA_all; red represents high values while green represents low values of the respective variable; factor loadings for PC1 and PC2 next to the variable abbreviation; abbreviations see Table A1.
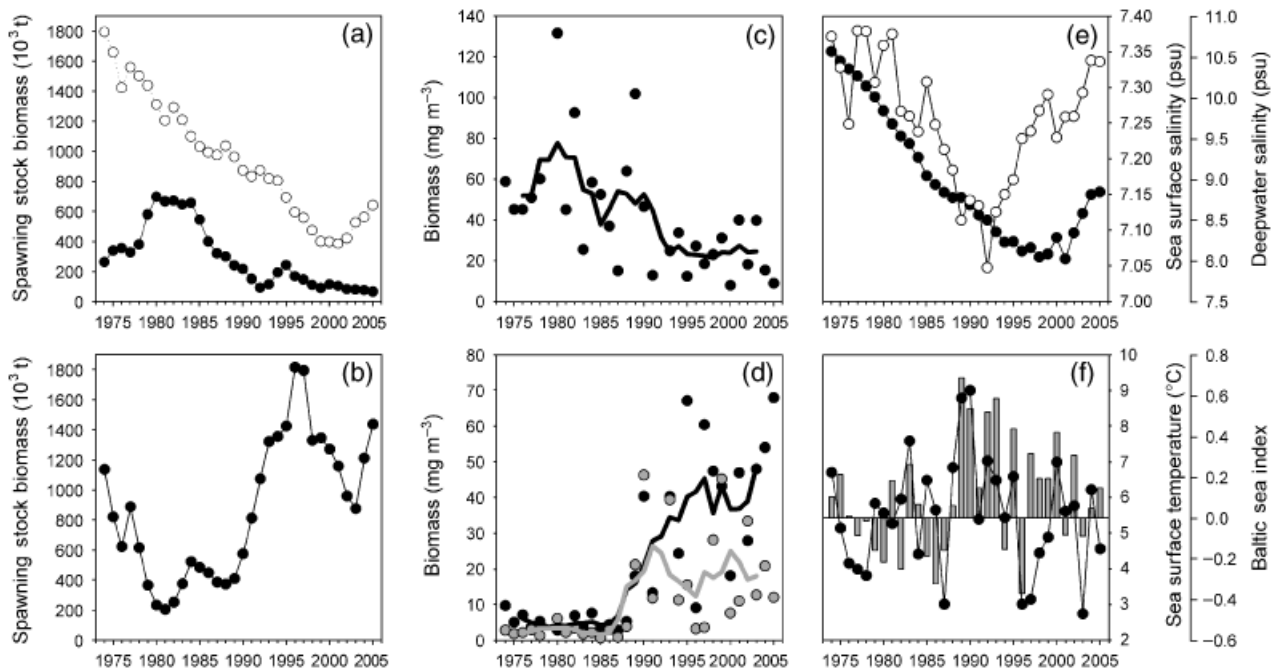
Fig. 3 Time-series on main ecosystem trends; (a) spawner biomass of cod (black dots) and herring (white dots); (b) spawer biomass of sprat; (c) biomass of *Pseudocalanus acuspes*, line represents 3-point moving averages; (d) biomass of *Acartia* spp. (black dots) and *Temora longicornis* (grey dots), lines represent 3-point moving averages; (e) sea surface (black dots) and Gotland Basin deepwater salinity (white dots); (f) Baltic Sea Index (bars) and sea surface temperature (black dots).

factorial plane can be interpreted as indicators displaying the main trends in the ecosystem and its abiotic environment. The trajectory of PC1 scores is characterized by a rapid shift from positive to negative values at the end of the 1980s, and remaining negative until the end of the period (Fig. 4a). PC2 displayed a steady increase until 1988 and a sharp decrease to negative values from 1993 onwards.

To disentangle the temporal trends of biotic variables and the environmental and anthropogenic drivers, we performed two additional PCAs (PCA_bio, PCA_abio). The trajectories of the first two biotic PCs (explaining 30% and 12% of the variability; Fig. 4b) revealed similar patterns compared with those derived by PCA_all. However, the change to negative PC1 scores at the end of the 1980s is less abrupt. The first two abiotic PCs explained 28% and 17% of the variance in the data subset and showed different trends compared with those of PCA_all and PCA_bio. In accordance with the biological variables, the late 1980s shift in PC1 can be observed (Fig. 4c); however, PC1 scores turn back to the same level as extracted before the shift, with the exception of a few years at the beginning of the 21st century. Accordingly, PC2 scores were similar at the beginning and the end of the investigation period although experiencing a rapid increase in the early 1990s. This indicates that the present abiotic conditions

in the Baltic Sea are similar to those that predominated in the 1970s, which is in contrast to the biotic conditions.

Plotting time scores of PC1 vs. PC2 visualizes the overall changes in the ecosystem of the Central Baltic Sea as well as in its biotic and abiotic components. Using the output of PCA_all, we found the years 1974–1987 being concentrated on the right-hand side of the plot (Fig. 4d). Over time, the scores moved to the left part of the plot, first between 1988 and 1993 to the upper quadrant, then to the lower quadrant where they concentrate for the remaining period. A similar pattern with two separate regimes but a shorter transition period was detected when using the PCA_bio output (Fig. 4e). In contrast, the pattern of scores resulting from the PCA_abio analysis was different (Fig. 4f). The transition period in the late 1980s and early 1990s is clearly visible, but abiotic conditions have returned to a similar state by the end of the period.

Regime shifts

We applied the sequential regime shift analysis on the time series of PC1 and PC2 scores to verify the observations in the dataset and to detect the timing of potential regime shifts. We found 1988 to be a strong regime shift year (displayed by the Regime Shift Index) on PC1 data independent of which PCA results were used (Table 1),
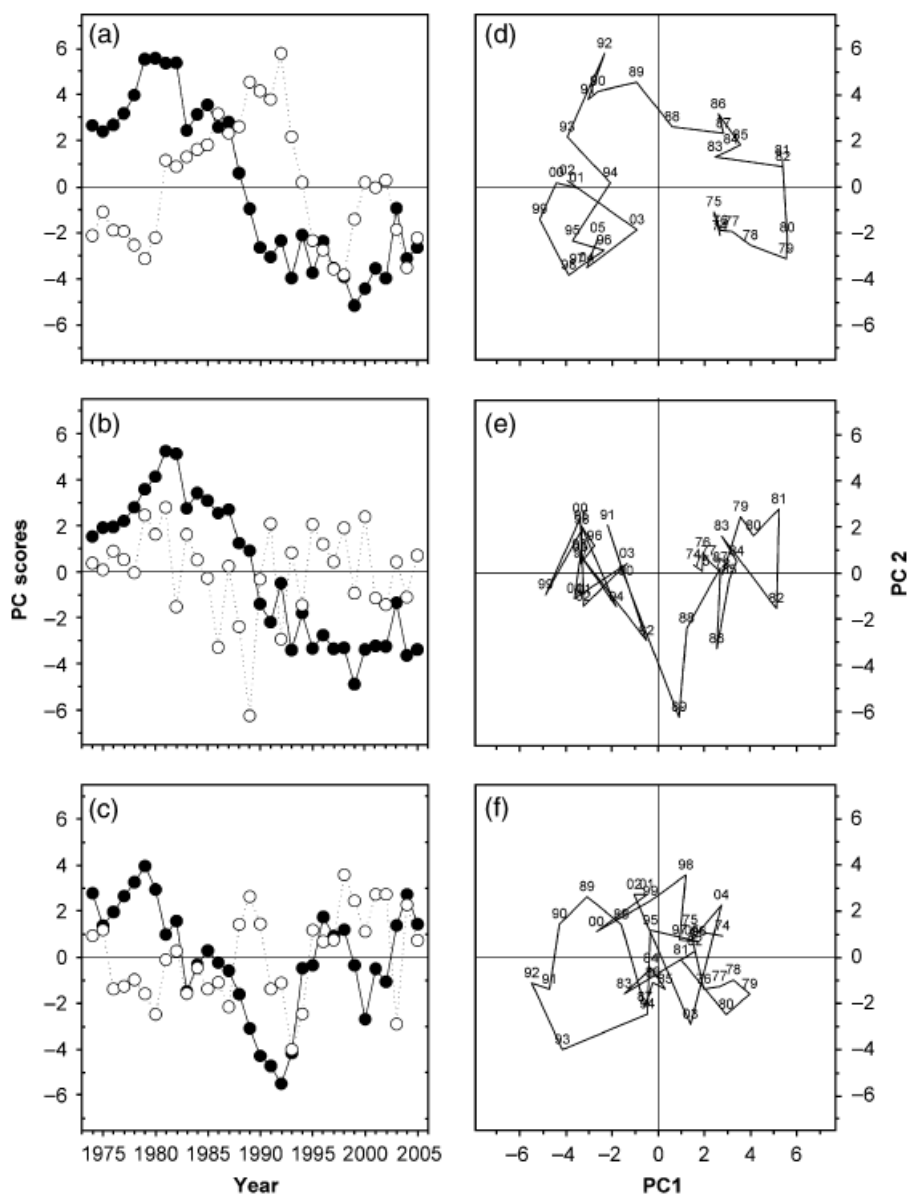
Fig. 4 Results of Principal Component Analyses; (a) time-scores of PCA-all, (b) PCA_bio and (c) PCA_abio, (black dots PC1, white dots PC2); (d) time-trajectory of PC1 vs. PC2 of PCA-all, (e) PCA_bio and (f) PCA_abio.

indicating the beginning of a transition period between two regimes. We further detected strong regime shifts of PC1 from the biological data in 1993, indicating the beginning of a new regime. In the temporal development of PC1 scores extracted from abiotic variables only, this pronounced shift occurred in 1994, defining the end of the transition period and the return of the abiotic variables to their previous state. Regime shifts were further observed on PC2 of the full PCA in 1994, again characterizing the transition period. Further but comparatively weak shifts on PC2 were also detected for PCA_abio in 1998 and the full PCA in 1981.

Key species and key drivers

To allow a better visualization of the results extracted by PCA_all from the whole set of the 52 variables, we performed an analysis to identify species and drivers that are characteristic of the regimes and the transition period observed by PCA_all (Fig. 5a). Variables highly positively correlated to the first period (1974–1987) were cod and herring spawner biomass, cod recruitment as well as *P. acuspes* summer biomass and surface salinity. In more recent years (1994–2005), the dominating signals in the time series were the large sprat spawning

stock biomass, high *Acartia* spp. as well as dinoflagellate spring biomasses in the Bornholm Basin and summer chlorophyll *a* in the Gotland Basin. In the transition period (1988–1993), no key species could be identified, and these years were exclusively characterized by abiotic variables, i.e. the depth of the 11 psu isoline and the BSI.

The relation of the various biological variables to the observed regimes is shown by the factor loadings of PC1 and PC2 from PCA_bio (Fig. 5b). The two regimes are mainly visible by comparison of the variables on PC1. The early regime (1974–1987) is characterized by positive loadings and hence high values of cod and herring recruitment and spawner biomass. Further variables positively related to this regime are *P. acuspes* biomass as well as herring and sprat individual weight. Negatively correlated to these variables, that is showing

Table 1 Results of the regime shift analysis (STARS) on principal component analysis (PCA) output: regime shift years identified in time series of PC1 and PC2 scores and Regime Shift Index (RSI) (Rodionov, 2004)

Analysis	PC1	PC2	RSI
PCA_all	1988		−2.06
		1981	0.60
		1994	−1.28
PCA_bio	1980		−0.08
	1988		−1.46
	1993		−0.80
PCA_abio	1983		−0.12
	1988		−0.56
	1994		1.38
		1998	−0.41

opposite temporal trends and thus negative loadings on PC1, are sprat spawner biomass, spring *Acartia* spp. and *T. longicornis* biomass as well as spring dinoflagellate biomass in the Bornholm Basin. All these groups can be seen as key representatives of the late regime (1994–2005). However, for both phyto- and zooplankton, the clear affiliation to the second regime is only true for spring time series. Most of the phytoplankton variables, e.g. diatoms, dinoflagellates, cyanobacteria and total chlorophyll *a* concentration, but as well zooplankton summer time series are positively related to PC2. The time trajectory of these groups is characterized by an increase during the transition period, but in contrast to key groups from the recent regime, declined again later.

Vector loadings of the abiotic PCA (Fig. 5c) display high salinity and oxygen values in parallel to low temperatures characteristic for the early regime. At the beginning of the transition period, high temperatures were observed in parallel to high BSI values which also coincided with high fishing pressure on cod and herring. The end of the transition period is characterized by high winter surface DIN and DIP concentrations in the Central Baltic, as well as the respective deep water concentrations in the Gotland Basin. At the same time, deepwater salinity in the Eastern Gotland Basin was low, leading to a deep 11 psu isoline. At the end of the study period, abiotic conditions returned to higher salinity as well as lower temperatures and nutrient concentrations.

Ecosystem state index and abiotic drivers

To investigate the relationship between the biotic ecosystem and the abiotic drivers, we considered PC1 of
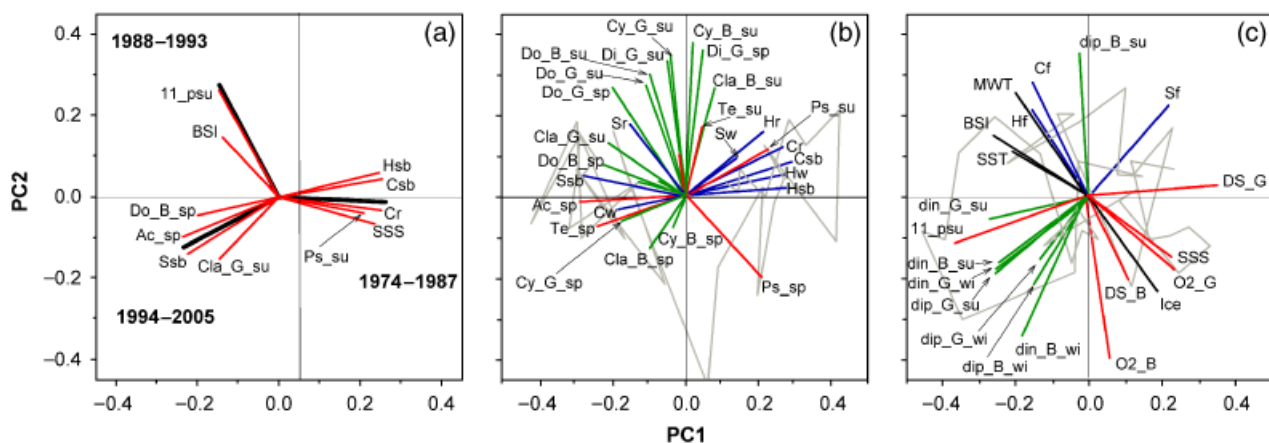
Fig. 5 Factor loadings of (a) key species and driver analysis using PCA_all (bold black vectors represent mean vectors for identified regimes [1974–1987 vs. 1994–2005] and the transition period [1988–1993]), (b) PCA_bio (green vectors represent phytoplankton, red vectors zooplankton and blue vectors fish-related variables), and (c) of PCA_abio (green vectors represent nutrient, red vectors salinity/oxygen, black vectors temperature-related and blue vectors fisheries-related variables; grey background lines in (b) and (c) are time-trajectories of PC1 vs PC2 of PCA_bio (from Fig. 3e) and PCA_abio (from Fig. 3f), respectively; abbreviations see Table 1.

Table 2 Finally selected generalized additive models relating the ecosystem state index (PC1 of PCA_bio) to environmental variables

Predictors	r^2	GCV
SSS**, 11psu***, SST**†, Din_G_su**	84.8	1.53
SSS***, 11psu***, SST†, Cf*	87.6	1.63
SSS***, 11psu***, Cf**	87.5	1.50

*$P < 0.01$. **$P < 0.001$. ***$P < 0.0001$.
†Parametric term in the model.
For abbreviations, see Table A1.
r^2, explained variance; GCV, general cross-validation criterion.

PCA_bio as an *ecosystem state index* and modelled it statistically as a function of abiotic drivers. The finally selected models based on r^2 and GCV always included the effect of salinity, both in the surface as well as in the deepwater, the latter represented by the depth of the 11 psu isoline (Table 2). Including different combinations of sea surface temperature, DIN and cod fishing mortality in the analysis resulted in only slightly different model skills. All abiotic drivers, however, represented highly significant predictors in the finally selected models.

Discussion

Regime shift characteristics

Our study identifies and describes a regime shift in the pelagic ecosystem of the Central Baltic Sea during the late 1980s and early 1990s. The timing of the Baltic regime shift is in accordance with similar events detected especially in many North Pacific and North Atlantic marine ecosystems (e.g. Hare & Mantua, 2000; Link *et al.*, 2002; Beaugrand, 2004; Choi *et al.*, 2005; Weijerman *et al.*, 2005). The event can be further described as abrupt and one which has affected multiple trophic levels and occurred on a wide geographic scale such as that of a large marine ecosystem, all characteristics of a real ecosystem regime shift (Collie *et al.*, 2004; Cury & Shannon, 2004; de Young *et al.*, 2004; Bakun, 2005; Lees *et al.*, 2006).

Using the sequential regime shift analysis on PCA results, we identified two regimes (1974–1987 and 1994–2005). The 'key species and driver analysis' using the output of PCA_all showed the two regimes to be best characterized by the opposite dominance of key fish and zooplankton species, i.e. cod and *P. acuspes* as well as sprat and *Acartia* spp. (MacKenzie *et al.*, 2007; Möllmann *et al.*, 2008). As shown by PCA_bio, herring is another important component of the first regime, similar as *T. longicornis* for the recent regime. Our analyses did not fully confirm the dominance change in the phytoplankton from diatoms to dinoflagellates (Wasmund *et al.*, 1998; Alheit *et al.*, 2005). While dinoflagellates seem to be generally abundant in the second regime especially in the Bornholm Basin, no consistent trend has been observed for diatoms and cyanobacteria.

Characteristic for the shift between the two regimes is that it occurred in a transition period during 1988–1993. As shown by our multivariate analysis, this period is characterized by low salinity and oxygen conditions, high temperatures and nutrient levels as well as high cod fishing pressure, which probably all contributed to forcing the biotic part of the ecosystem into a new state.

Multiple drivers of the regime changes

Our analyses support the notion that ecosystem regime shifts are most likely caused by a number of confounding factors (Scheffer & Carpenter, 2003; Lees *et al.*, 2006). However, the results of our 'key species and driver analysis' displayed the primary importance of changes in the abiotic environment for triggering the Baltic regime shift. We showed deepwater salinity and oxygen conditions (indicated by the depth of the 11 psu isoline) and the BSI (indicating thermal conditions) to be the primary agents of the change. These trends in abiotic conditions, especially at the end of the 1980s and early 1990s, were a result of the changes in atmospheric forcing. During the identified transition period between 1988 and 1993, the BSI, which is similar to the NAO (Lehmann *et al.*, 2002), increased stepwise to positive values. High values of the BSI result in a transport of warm and humid air to the area increasing sea surface temperatures and lowering surface salinity (Lehmann *et al.*, 2002). Hence, the vector loadings of PCA_abio indicate parallel trends of the BSI and midwater temperatures, but opposite trends with surface salinity. In addition, Central Baltic deepwater hydrographic conditions are strongly dependent on the intrusion of highly saline and oxygenated water masses from the North Sea (Fonselius & Valderrama, 2003). Increased rainfall and runoff as a result of the changed atmospheric forcing caused sea-level variations which may explain the low frequency of these major Baltic inflows since the 1980s and hence lowered salinity and oxygen levels (Matthäus & Franck, 1992; Matthäus & Schinke, 1999).

The lack of inflows between the early 1980s and the early 1990s also had a pronounced impact on the nutrient state of the Central Baltic Sea. In the deepwater of the Gotland Basin, NH_4 and PO_4 generated by the mineralization of organic substances in the sediment accumulated. Nutrient accumulation in the deepwater is a combined effect of physical stagnation in the absence

of inflows, and of biogeochemical processes under anaerobic conditions. Under anaerobic conditions during the stagnation period, NH_4 cannot be oxidized to NO_3 and further denitrified. Consequently, DIN accumulates in the bottom water (Nausch et al., 2003). Biogeochemical processes contributing to the increase in deepwater DIP are the release of previously accumulated, most likely iron oxide-bound PO_4 (Conley et al., 2002; Nausch et al., 2003) from anoxic bottom sediments and the low efficiency of sediments in adsorbing newly mineralized PO_4 under anaerobic conditions (Hille et al., 2005).

The described changes in the abiotic environment occurred in a sequence of events, accumulating during the transition period. First, the salinity and oxygen levels in the deepwater of the Central Baltic Sea decreased as a result of a lack of inflows of North Sea water (Fonselius & Valderrama, 2003). In parallel, nutrient levels increased as a result of organic matter degradation in the bottom sediments (Nausch et al., 2003). The second development contributing to the regime shift was the sudden shift in the atmospheric forcing in 1988, displayed by the change in the BSI to positive values, therefore causing an abrupt increase in temperatures (Alheit et al., 2005).

The changes in the food web of the Central Baltic ecosystem can be partly explained by the above-described changes in the abiotic environment. Species such as cod and P. acuspes, which dominated the first regime, suffered from low salinity and oxygen conditions that negatively affected the survival of their offspring (Köster et al., 2005; Renz & Hirche, 2006;

Schmidt, 2006). In contrast, species such as sprat and the copepods Acartia spp. and T. longicornis benefited from the sudden warming in the early 1990s (Köster et al., 2003; Möllmann et al., 2003), as did dinoflagellates (Wasmund et al., 1998).

The PCA on abiotic data further demonstrated that in addition to the physical and chemical conditions, unsustainable fishing pressure might have contributed to the ecosystem changes. During the 1980s, the cod fishery boomed due to the extraordinary high stock sizes. However, when reproductive success declined and the stock size decreased, fishing effort has not been reduced. Hence, fishing mortality on cod was especially in the transition period too high for the level of reproductive success, which is still true today (Köster et al., 2005; Möllmann et al., 2008). The present results also suggest high fishing mortality on herring to have contributed to the decline of the stock biomass, while the sprat stock seemed to be resilient to the present level of fishing due to its high reproductive potential (Möllmann et al., 2008).

The transition period between the two regimes ended in 1993, when a strong inflow of North Sea water improved the deepwater conditions (Fonselius & Valderrama, 2003). In addition, temperature decreased due to changed atmospheric forcing. Cod fishing pressure decreased as well due to management regulations, however only for a short period of time, being on a high level until present (Köster et al., 2005). The results of the separate PCAs for biotic and abiotic variables indicate the return of the abiotic state to similar conditions as
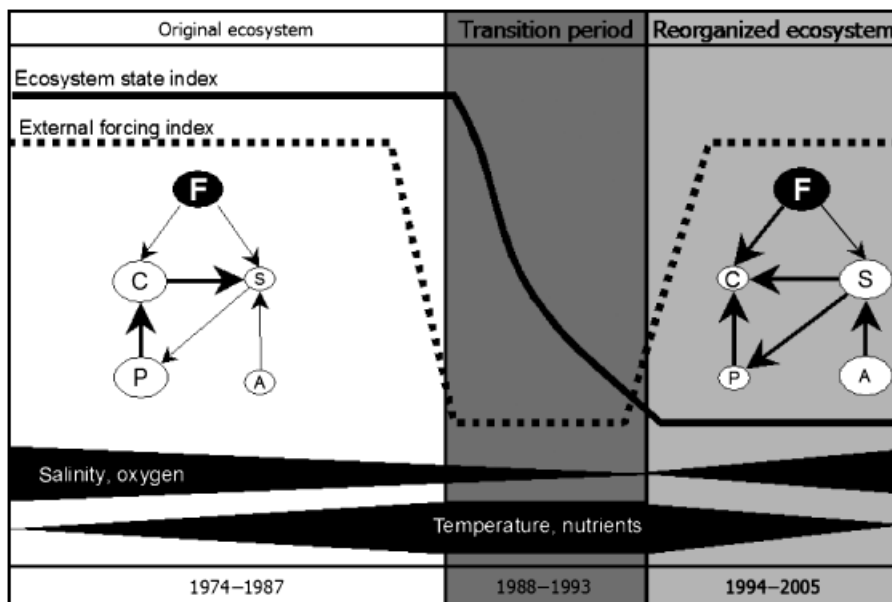

Fig. 6 Conceptual diagram displaying the changes in the Baltic Sea ecosystem; F, fishing pressure; C, cod; S, sprat; P, Pseudocalanus acuspes and A, Acartia spp.; arrows represent direction and strength of a control.

observed at the start of the time series, while the biotic state has shifted to a new regime.

Our statistical models relating different key abiotic variables to the *ecosystem state index* support the hypothesis that multiple drivers are responsible for the regime changes. The finally selected models explaining a large proportion of the variance in the *ecosystem state index* included salinity, temperature, nutrient conditions and cod fishing mortality, all being significant predictors.

A discontinuous regime shift

Figure 6 summarizes the changes in the Central Baltic ecosystem in a conceptual diagram. The *ecosystem state index* (an idealization of the PC1 of PC_bio) decreased as a response of the *external forcing index* (an idealization of the PC1 of PC_abio). The change occurred during the transition period when the most extreme abiotic conditions prevailed, i.e. lowest salinity and oxygen, but highest temperature and nutrient levels. After the transition period, the external forcing index returned to its original state, while the ecosystem state index did not.

The observation that most of the biotic variables did not return to their initial state in contrast to the observed trends in the abiotic variables (shown by the separate biotic and abiotic PCAs) indicates the existence of hysteresis in the Central Baltic Sea ecosystem and characterizes the observed changes as a discontinuous regime shift (Scheffer & Carpenter, 2003; Collie *et al.*, 2004).

Theory explains discontinuous regime shifts by the occurrence of feedback loops stabilizing the new regime (Scheffer *et al.*, 2001; Bakun, 2006). For the Central Baltic Sea, we explain this by changes in the control pattern between major food web components (Fig. 6). In the 'original ecosystem', high salinity and oxygen levels promote large *P. acuspes* and cod populations, the latter controlling the sprat population. These formerly abundant populations are now dominated by sprat and *Acartia* spp. which profited from the changed abiotic conditions. Additionally, cod fishing pressure is still unsustainable at present and the effect of the resulting low cod biomass cascaded down to the copepod *P. acuspes* via low predation rates on sprat (Möllmann *et al.*, 2008). This trophic cascade has established a stabilizing prey-to-predator (P2P) loop (Bakun, 2006), because *P. acuspes* which is controlled by the now large sprat stock (Möllmann & Köster, 2002) is important for cod larval survival and hence recruitment (Hinrichsen *et al.*, 2002; Köster *et al.*, 2005; Möllmann *et al.*, 2008). A second P2P loop has been described by Bakun & Weeks (2006), because sprat not only control *P. acuspes* but also prey on cod eggs diminishing recruitment success as well (Köster & Möllmann, 2000). These feedback loops indeed seem to stabilize the present regime,

for which an indication is that the *ecosystem state index* remains in the new regime. Typical examples are the failure of recovery of *P. acuspes* and cod after the inflow in 1993, but also in 2003 (Möllmann *et al.*, 2008).

In addition to these feedback loops, climate-induced bottom-up processes potentially stabilize the new regime. The increased dinoflagellate stock due to the recent warming (Wasmund *et al.*, 1998) has a positive effect on the population of *Acartia* spp., being important for the recently high level of sprat recruitment (Dickmann *et al.*, 2007; Möllmann *et al.*, 2008).

Management implications – maintaining ecosystem resilience

The present study provides evidence in support of the assertion that combined climatic and anthropogenic disturbances can trigger regime shifts in ecosystems (Scheffer *et al.*, 2001; Scheffer & Carpenter, 2003). In the case of the Baltic Sea, this trigger was the sudden increase in temperature due to changed atmospheric forcing in the late 1980s and unsustainable cod fishing pressure, both favouring the dominance of sprat and *Acartia* spp. However, a prerequisite for this to happen was a loss of resilience, which made the system more fragile to perturbations (Folke *et al.*, 2002; Folke, 2006). In the Baltic Sea ecosystem, reduced resilience was due to unfavourable reproductive conditions (i.e. low salinity and oxygen conditions) for cod and too high fishing pressure. The resulting decrease in the cod stock has caused a reduced control of the sprat stock, which was then able to increase due to the changed hydrographic conditions (Möllmann *et al.*, 2008).

Discontinuous regime shifts as described in the present study may result in significant costs for society (Scheffer *et al.*, 2001), such as the low cod stock. Restoring the ecosystem to a more desired and often earlier state following a regime shift usually involves drastic and expensive interventions (Scheffer & Carpenter, 2003; Suding *et al.*, 2004). Furthermore, the goal of management must be to sustain the stability of regimes, rather then trying to control fluctuations (Scheffer *et al.*, 2001; Folke, 2006). For the Baltic Sea, this means maintaining the resilience of the ecosystem, which is determined by deepwater conditions and cod fishing pressure. The former can only be influenced by reduction in anthropogenic nutrient input accelerating the oxygen consumption in the deepwater, while the frequency of inflows is certainly not manageable. Therefore, closing the fishery for Eastern Baltic cod would help the recovery of the stock by developing a more healthy age structure in the population (Berkeley *et al.*, 2004). This would make the stock more able to profit from potentially improving environmental conditions,

and hence lead to a more balanced ecosystem. In parallel, early warning systems for changes in the hydrographic environment, but also in the structure of the food web need to be established for a future sound ecosystem-based management.

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References

Alheit J, Möllmann C, Dutz J, Kornilovs G, Löwe P, Mohrholz V, Wasmund N (2005) Synchronous ecological regime shifts in the North and Central Baltic Sea in 1987–88. *ICES Journal of Marine Science*, **62**, 1205–1215.

Bakun A (2005) Regime shifts. In: *The Sea, Vol. 13, The Global Coastal Ocean, Multiscale Interdisciplinary Processes* (eds Robinson AR, Brink K), pp. 971–1026. Harvard University Press, Cambridge, MA, USA.

Bakun A (2006) Wasp-waist populations and marine ecosystem dynamics: navigating the ''predator pit'' topographies. *Progress in Oceanography*, **68**, 271–288.

Bakun A, Weeks SJ (2006) Adverse feedback sequences in exploited marine systems: are deliberate interruptive actions warranted? *Fish and Fisheries*, **7**, 316–333.

Beaugrand G (2004) The North Sea regime shift: evidence, causes, mechanisms and consequences. *Progress in Oceanography*, **60**, 245–262.

Beaugrand G, Brander KM, Lindley J, Souissi S, Reid PC (2003) Plankton effect on cod recruitment in the North Sea. *Nature*, **426**, 661–664.

Berkeley SA, Chapma C, Sogard SM (2004) Maternal age as a determinant of larval growth and survival in a marine fish, *Sebastes melanopses*. *Ecology*, **85**, 1258–1264.

Browman HI, Stergiou KI (2004) Perspectives on ecosystem-based approaches to the management of marine resources. *Marine Ecology Progress Series*, **274**, 269–303.

Choi JS, Frank KT, Petrie BD, Leggett BD (2005) Integrated ecosystem assessment of a large marine ecosystem: a case study of the devolution of the Eastern Scotian Shelf, Canada. *Oceanography and Marine Biology: An Annual Review*, **43**, 47–67.

Cloern JE (2001) Our evolving conceptual model of the coastal eutrophication problem. *Marine Ecology Progress Series*, **210**, 223–253.

Collie JS, Richardson K, Steele JH (2004) Regime shifts: can theory illuminate the mechanisms? *Progress in Oceanography*, **60**, 281–302.

Conley DJ, Humborg C, Rahm L, Savchuk OP, Wulff F (2002) Hypoxia in the Baltic Sea and basin-scale changes in phosphorus biogeochemistry. *Environmental Science and Technology*, **36**, 5315–5320.

Cury P, Shannon LJ (2004) Regime shifts in the Benguela ecosystem: facts, theories, and hypothesis. *Progress in Oceanography*, **60**, 223–243.

Daskalov G (2002) Overfishing drives a trophic cascade in the Black Sea. *Marine Ecology Progress Series*, **225**, 53–63.

Daskalov GM, Grishin AN, Rodionov S, Mihneva V (2007) Trophic cascades triggered by overfishing reveal possible mechanisms of ecosystem regime shifts. *Proceeding of the National Academy of Sciences of the United States of America*, **104**, 10518–10523.

de Young B, Harris R, Alheit J, Beaugrand G, Mantua N, Shannon L (2004) Detecting regime shifts in the ocean: data considerations. *Progress in Oceanography*, **60**, 143–164.

Dickmann M, Möllmann C, Voss R (2007) Feeding ecology of Central Baltic sprat (*Sprattus sprattus* L.) larvae in relation to zooplankton dynamics – implications for survival. *Marine Ecology Progress Series*, **342**, 277–289.

Folke C (2006) Resilience: the emergence of a perspective for social-ecological systems analyses. *Global Environmental Change*, **16**, 253–267.

Folke C, Carpenter S, Elmqvist T, Gunderson L, Holling CS, Walker B (2002) Resilience and sustainable development: building adaptive capacity in a world of transformations. *Ambio*, **31**, 437–440.

Fonselius S, Valderrama J (2003) One hundred years of hydrographic measurements in the Baltic Sea. *Journal of Sea Research*, **49**, 229–241.

Frank KT, Petrie BD, Choi J, Leggett BD (2005) Trophic cascades in a formerly cod-dominated ecosystem. *Science*, **308**, 1621–1623.

Hare SR, Mantua NJ (2000) Empirical evidence for North Pacific regime shifts in 1977 and 1989. *Progress in Oceanography*, **47**, 103–145.

Harley CDG, Hughes AR, Hultgren KM *et al.* (2006) The impacts of climate change in coastal marine systems. *Ecology Letters*, **9**, 228–241.

Harvey CJ, Cox SP, Essington TE, Hansson S, Kitchell JF (2003) An ecosystem model of food web and fisheries interactions in the Baltic Sea. *ICES Journal of Marine Science*, **60**, 939–950.

Hastie T, Tibshirani R (1990) *Generalized Additive Models*. Chapman & Hall, London.

Hille S, Nausch G, Leipe T (2005) Sedimentary deposition and reflux of phosphorus (P) in the Eastern Gotland Basin and their coupling with P concentrations in the water column. *Oceanologia*, **47**, 663–679.

Hinrichsen HH, Möllmann C, Voss R, Köster FW, Kornilovs G (2002) Bio-physical modelling of larval Baltic cod (*Gadus morhua*) survival and growth. *Canadian Journal of Fisheries and Aquatic Sciences*, **59**, 1958–1873.

Hurrell JW (1995) Decadal trends in the North Atlantic Oscillation: regional temperatures and precipitation. *Science*, **269**, 676–679.

ICES (2005) *Guidance on the application of the ecosystem approach to management of human activities in the European marine environment.* ICES Cooperative Research Report, no. 273, 22 pp.

ICES (2007) *Report of the Baltic Fisheries Assessment Working Group (WGBFAS).* International Council for the Exploration of Sea, C.M. 2007/ACFM:15.

Köster FW, Möllmann C (2000) Trophodynamic control by clupeid predators on recruitment success in Baltic cod? *ICES Journal of Marine Sciences*, **57**, 310–323.

Köster FW, Möllmann C, Hinrichsen HH *et al.* (2005) Baltic cod recruitment – the impact of climate and species interaction. *ICES Journal of Marine Science*, **62**, 1408–1425.

Köster FW, Möllmann C, Neuenfeldt S *et al.* (2003) Fish stock development in the Central Baltic Sea (1976–2000) in relation to variability in the physical environment. *ICES Marine Science Symposia*, **219**, 294–306.

Lees K, Pitois S, Scott C, Frid C, Mackinson S (2006) Characterizing regime shifts in the marine environment. *Fish and Fisheries*, **7**, 104–127.

Lehmann A, Krauss W, Hinrichsen HH (2002) Effects of remote and local atmospheric forcing on circulation and upwelling in the Baltic Sea. *Tellus*, **54**, 299–316.

Link JS, Brodziak JKT, Edwards SF *et al.* (2002) Marine ecosystem assessment in a fisheries management context. *Canadian Journal of Fisheries and Aquatic Science*, **59**, 1429–1440.

Lluch-Belda D, Crawford RJ, Kawasaki T, McCall AD, Parrish RH, Schwartzlose RA, Smith PE (1989) Worldwide fluctuations in sardine and anchovy stocks: the regime problem. *South African Journal of Marine Science*, **8**, 195–205.

MacKenzie BR, Gislason H, Möllmann C, Köster FW (2007) Impact of 21st century climate change on the Baltic Sea fish community and fisheries. *Global Change Biology*, **13**, 1–20.

Matthäus W, Franck H (1992) Characteristics of major Baltic inflows – a statistical analysis. *Continental Shelf Research*, **12**, 1375–1400.

Matthäus W, Schinke H (1999) The influence of river runoff on deep water conditions of the Baltic Sea. *Hydrobiologia*, **393**, 1–10.

McLeod KL, Lubchenco J, Palumbi SR, Rosenberg AA (2005) *Scientific consensus statement on marine ecosystem-based management.* Communication Partnership for Science and the Sea, available online at: www.compassonline.org/pdf_files/EBM_Consensus_Statement_v12.pdf.

Möllmann C, Kornilovs G, Sidrevics L (2000) Long-term dynamics of main mesozooplankton species in the Central Baltic Sea. *Journal of Plankton Research*, **22**, 2015–2038.

Möllmann C, Köster FW (2002) Population dynamics of calanoid copepods and the implications of their predation by clupeid fish in the Central Baltic Sea. *Journal of Plankton Research*, **24**, 959–977.

Möllmann C, Köster FW, Kornilovs G, Sidrevics L (2003) Interannual variability in population dynamics of calanoid copepods in the Central Baltic Sea. *ICES Marine Science Symposia*, **219**, 294–306.

Möllmann C, Müller-Karulis B, Kornilovs G, St John MA (2008) Effects of climate and overfishing on zooplankton dynamics and ecosystem structure – regime shifts, trophic cascade and feedback loops in a simple ecosystem. *ICES Journal of Marine Science*, **65**, 302–310.

Myers RA, Baum JK, Shepherd TD *et al.* (2007) Cascading effects of the loss of apex predatory sharks from a coastal ocean. *Science*, **315**, 1846–1850.

Myers RA, Worm B (2003) Rapid worldwide depletion of predatory fish communities. *Nature*, **423**, 280–283.

Nausch G, Matthäus W, Feistel R (2003) Hydrographic and hydrochemical conditions in the Gotland Deep area between 1992 and 2003. *Oceanologia*, **45**, 557–569.

Österblom H, Hansson S, Larsson U, Hjerne O, Wusff F, Elmgren R, Folke C (2007) Human-induced trophic cascades and ecological regime shifts in the Baltic Sea. *Ecosystems*, doi: 10.1007/s10021-007-9069-0.

Pörtner HO, Knust R (2007) Climate change affects marine fishes through the oxygen limitation of thermal tolerance. *Science*, **315**, 95–97.

Renz J, Hirche HJ (2006) Life-cycle of *Pseudocalanus acuspes* Giesbrecht (Copepoda, Calanoida) in the Central Baltic Sea: I. Seasonal and spatial distribution. *Marine Biology*, **148**, 567–580.

Richardson AJ, Schoeman DS (2004) Climate impact on plankton ecosystems in the Northeast Atlantic. *Science*, **305**, 1609–1612.

Rodionov SN (2004) A sequential algorithm for testing climate regime shifts. *Geophysical Research Letters*, **31**, L09204, doi: 10.1029/2004GL019448.

Rodionov SN (2006) The use of prewhitening in climate regime shift detection. *Geophysical Research Letters*, **31**, L12707, doi: 101029/2006GL025904.

Rodionov SN, Overland JE (2005) Application of a sequential regime shift detection method to the Bering Sea ecosystem. *ICES Journal of Marine Science*, **62**, 328–332.

Roessig JM, Woodley CM, Cech JJ, Hansen LJ (2004) Effects of global climate change on marine and estuarine fishes and fisheries. *Reviews in Fish Biology and Fisheries*, **14**, 251–275.

Rudnick DL, Davis RE (2003) Red noise and regime shifts. *Deep-Sea Research*, **50**, 691–699.

Scheffer M, Carpenter S, Foley JA, Folke C, Walker B (2001) Catastrophic shifts in ecosystems. *Nature*, **413**, 591–596.

Scheffer M, Carpenter SR (2003) Catastrophic regime shifts in ecosystems: linking theory to observation. *Trends in Ecology and Evolution*, **18**, 648–656.

Schmidt JO (2006) *Small and meso-scale distribution patterns of key copepod species in the Central Baltic Sea and their relevance for larval fish survival.* PhD Thesis, University of Kiel, Germany, 89 pp.

Suding KN, Gross KL, Houseman GR (2004) Alternative states and positive feedbacks in restoration ecology. *Trends in Ecology and Evolution*, **19**, 46–53.

Wasmund N, Nausch G, Matthäus W (1998) Phytoplankton spring blooms in the southern Baltic Sea – spatio-temporal development and long-term trends. *Journal of Plankton Research*, **20**, 1099–1117.

Wasmund N, Uhlig S (2003) Phytoplankton trends in the Baltic Sea. *ICES Journal of Marine Science*, **60**, 177–186.

Weijerman M, Lindeboom H, Zuur AF (2005) Regime shifts in marine ecosystems of the North and Wadden Sea. *Marine Ecology Progress Series*, **298**, 21–39.

Wood SN (2007) *Generalized Additive Models. An Introduction with R.* Chapman & Hall, Boca Raton, FL, USA.

Appendix A

Tables A1–A3

Table A1 Description of time series used in the meta-analysis of the Central Baltic Sea

Variable	Abbreviation	Unit	Area	Season	Source
Cod Spawner biomass	Csb	Tonnes	SD 25-32	Annual	ICES
Cod recruitment	Cr	No age 2 (10^3)	SD 25-32	Annual	ICES
Cod weight	Cw	kg (age 3)	SD 25-32	Annual	ICES
Cod fishing mortality	Cf	Age 4–7	SD 25-32	Annual	ICES
Sprat Spawner biomass	Ssb	Tonnes	SD 22-32	Annual	ICES
Sprat recruitment	Sr	No age 1 (10^3)	SD 22-32	Annual	ICES
Sprat weight	Sw	kg (age 3)	SD 22-32	Annual	ICES
Sprat fishing mortality	Sf	Age 3–5	SD 22-32	Annual	ICES
Herring Spawner biomass	Hsb	Tonnes	SD 25-29 + 32excl. GOR	Annual	ICES
Herring recruitment	Hr	No age 1 (10^3)	SD 25-29 + 32excl. GOR	Annual	ICES
Herring weight	Hw	kg (age 3)	SD 25-29 + 32excl. GOR	Annual	ICES
Herring fishing mortality	Hf	Age 2–6	SD 25-29 + 32excl. GOR	Annual	ICES
Acartia spp.	Ac_sp	mg m^{-3}	Gotland Basin	Spring	LATFRA
Acartia spp.	Ac_su	mg m^{-3}	Gotland Basin	Summer	LATFRA
Temora longicornis	Te_sp	mg m^{-3}	Gotland Basin	Spring	LATFRA
Temora longicornis	Te_su	mg m^{-3}	Gotland Basin	Summer	LATFRA
Pseudocalanus acuspes	Ps_sp	mg m^{-3}	Gotland Basin	Spring	LATFRA
Pseudocalanus acuspes	Ps_su	mg m^{-3}	Gotland Basin	Summer	LATFRA
Chlorophyll *a*	Cla_B_sp	mg m^{-3}	Bornholm Basin	Spring	ICES
Chlorophyll *a*	Cla_B_su	mg m^{-3}	Bornholm Basin	Summer	ICES
Chlorophyll *a*	Cla_G_sp	mg m^{-3}	Gotland Basin	Spring	ICES
Chlorophyll *a*	Cla_G_su	mg m^{-3}	Gotland Basin	Summer	ICES
Diatoms	Di_B_sp	mg m^{-3}	Bornholm Basin	Spring	Wasmund & Uhlig (2003)
Dinoflagellates	Do_B_sp	mg m^{-3}	Bornholm Basin	Spring	Wasmund & Uhlig (2003)
Cyanobacteria	Cy_B_sp	mg m^{-3}	Bornholm Basin	Spring	Wasmund & Uhlig (2003)
Diatoms	Di_B_su	mg m^{-3}	Bornholm Basin	Summer	Wasmund & Uhlig (2003)
Dinoflagellates	Do_B_su	mg m^{-3}	Bornholm Basin	Summer	Wasmund & Uhlig (2003)
Cyanobacteria	Cy_B_su	mg m^{-3}	Bornholm Basin	Summer	Wasmund & Uhlig (2003)
Diatoms	Di_G_sp	mg m^{-3}	Gotland Basin	Spring	Wasmund & Uhlig (2003)
Dinoflagellates	Do_G_sp	mg m^{-3}	Gotland Basin	Spring	Wasmund & Uhlig (2003)
Cyanobacteria	Cy_G_sp	mg m^{-3}	Gotland Basin	Spring	Wasmund & Uhlig (2003)
Diatoms	Di_G_su	mg m^{-3}	Gotland Basin	Summer	Wasmund & Uhlig (2003)
Dinoflagellates	Do_G_su	mg m^{-3}	Gotland Basin	Summer	Wasmund & Uhlig (2003)
Cyanobacteria e	Cy_G_su	mg m^{-3}	Gotland Basin	Summer	Wasmund & Uhlig (2003)
Dissolved inorganic nitrogen (surface)	Din_B_wi	mmol m^{-3}	Bornholm Basin	Winter	BED/SMHI/ICES
Dissolved inorganic phosphorus (surface)	Dip_B_wi	mmol m^{-3}	Bornholm Basin	Winter	BED/SMHI/ICES
Dissolved inorganic nitrogen (surface)	Din_G_wi	mmol m^{-3}	Gotland Basin	Winter	BED/SMHI/ICES
Dissolved inorganic phosphorus (surface)	Dip_G_wi	mmol m^{-3}	Gotland Basin	Winter	BED/SMHI/ICES
Dissolved inorganic nitrogen (deepwater)	Din_B_su	mmol m^{-3}	Bornholm Basin	Summer	BED/SMHI/ICES
Dissolved inorganic phosphorus (deepwater)	Dip_B_su	mmol m^{-3}	Bornholm Basin	Summer	BED/SMHI/ICES
Dissolved inorganic nitrogen (deepwater)	Din_G_su	mmol m^{-3}	Gotland Basin n	Summer	BED/SMHI/ICES

(Contd.)

Table A1 (*Contd.*)

Variable	Abbreviation	Unit	Area	Season	Source
Dissolved inorganic phosphorus (deepwater)	Dip_G_su	$mmol\,m^{-3}$	Gotland Basin	Summer	BED/SMHI/ICES
Maximum ice cover	Ice	km^2	Baltic	Annual	FIMR
Baltic Sea Index	BSI		Central Baltic	Winter	IFM
Depth of 11 psu isoline	11psu	m	Gotland Basin	Annual	LATFRA
Sea surface temperature	SST	°C	Central Baltic	Spring	BED/SMHI/ICES
Midwater temperature (40–60 m)	MWT	°C	Central Baltic	Spring	BED/SMHI/ICES
Sea surface salinity	SSS	psu	Central Baltic	Spring	BED/SMHI/ICES
Deepwater salinity (70–90 m)	DS_B	psu	Bornholm Basin	Spring	BED/SMHI/ICES
Deepwater salinity (80–100 m)	DS_G	psu	Gotland Basin	Spring	BED/SMHI/ICES
Deepwater oxygen	O2_B	$mL\,L^{-1}$	Bornholm Basin	Spring	BED/SMHI/ICES
Deepwater oxygen	O2_G	$mL\,L^{-1}$	Gotland Basin	Spring	BED/SMHI/ICES

SD, ICES Sub-Division; ICES, International Council for the Exploration of the Sea, Copenhagen, Denmark; LATFRA, Latvian Fish Resources Agency, Riga, Latvia; BED, Baltic Environment Database, Stockholm University, Stockholm, Sweden; SMHI, Swedish Meterological and Hydrological Institute, Norrköping, Sweden; FIMR, Finnish Institute of Marine Research, Helsinki, Finland; IFM, Leibniz Institute for Marine Science Kiel, Germany.

Table A2 Autocorrelation coefficients of the used time series for three lags (for abbreviations, see Table A1)

Variable	Lag 1	Lag 2	Lag 3
Temora_Sum	−0.254	−0.035	0.023
dino_BB_sum	−0.068	0.353	0.065
cyano_GB_spr	0.009	0.223	0.028
dia_GB_sum	0.038	−0.322	−0.032
Chla_BBSum	0.042	0.191	0.021
Chla_BBSpr	0.048	0.034	−0.328
SPRR1	0.056	0.099	0.125
dia_GB_spr	0.059	−0.049	−0.029
cyano_BB_sum	0.097	0.077	−0.192
dia_BB_sum	0.102	−0.052	−0.038
dino_BB_spr	0.113	0.034	0.292
Acartia_Sum	0.135	−0.184	0.42
cyano_BB_spr	0.147	−0.351	−0.158
O2_BB	0.156	−0.067	0.1
DIP_BB_10_win	0.165	0.245	−0.043
SST_Spr	0.173	0.062	−0.042
Pseudo_Spr	0.193	0.371	0.11
cyano_GB_sum	0.25	−0.247	−0.354
DIN_BB_90_sum	0.293	0.223	0.217
DIP_BB_90_sum	0.325	0.079	0.293
DIN_BB_10_win	0.329	0.053	0.306
Temora_Spr	0.33	0.059	0.343
BSI	0.333	0.101	−0.062
dia_BB_spr	0.361	−0.098	−0.063
T_60_spr	0.373	0.196	−0.08
Chla_GBSpr	0.38	−0.043	−0.143
DIN_GB_10_win	0.395	0.144	0.161
S90_BB	0.4	0.052	0.124
MaxIce	0.413	0.235	−0.02
HERR1	0.427	0.377	0.345
dino_GB_sum	0.428	0.048	−0.117
DIP_GB_10_win	0.441	0.057	−0.142
Chla_GBSum	0.451	0.245	0.158
dino_GB_spr	0.473	0.417	0.357
Pseudo_Sum	0.51	0.556	0.495
O2_GB	0.514	0.113	−0.042
Cod_F47	0.516	0.234	0.154
Acartia_Spr	0.526	0.747	0.523
DIN_GB_220	0.537	0.315	0.319
DIP_GB_220	0.548	0.466	0.217
Spr_F35	0.771	0.66	0.415
S100_GB	0.798	0.662	0.648
CODR2	0.807	0.612	0.632
var11psu_GBAnn	0.825	0.616	0.487
Her_F26	0.845	0.683	0.431
HERWC3	0.846	0.84	0.742
CODWC3	0.853	0.785	0.671
SPRWC3	0.87	0.706	0.543
SPRSSB	0.895	0.744	0.652
CODSSB	0.95	0.849	0.741
HERSSB	0.979	0.953	0.935
SSS	0.987	0.966	0.937

Table A3 Cross-correlation coefficients between the used time series (for abbreviations, see Table A1)

	Cod_F47	CODR2	CODSSB	CODWC3	Her_F26	HERR1	HERSSB	HERWC3	Spr_F35	SPRR1	SPRSSB	SPRWC3	Acartia_Spr	Acartia_Sum	Temora_Spr	Temora_Sum	Pseudo_Spr	Pseudo_Sum	Chla_BBSpr	Chla_BBSum	Chla_GBSpr	Chla_GBSum	dia_BB_spr	dia_GB_spr	dia_BB_sum	dia_GB_sum
dino_GB_spr	0.09	−0.61	−0.52	0.32	0.32	−0.27	−0.55	−0.49	0.20	0.19	0.18	−0.22	0.28	0.09	0.27	0.12	−0.26	−0.55	0.17	−0.23	0.24	0.12	0.12	−0.27	0.26	−0.31
dino_BB_sum	0.02	0.53	0.73	−0.62	−0.54	0.54	0.77	0.75	−0.24	−0.31	−0.57	0.50	−0.57	−0.08	−0.46	0.07	0.43	0.71	−0.27	0.30	−0.19	−0.43	−0.13	0.33	−0.17	−0.17
dino_GB_sum	0.16	0.22	0.73	−0.46	−0.43	0.65	0.70	0.84	−0.51	−0.26	−0.65	0.67	−0.65	0.08	−0.51	0.15	0.57	0.68	−0.18	0.42	−0.48	−0.47	−0.33	0.36	−0.12	−0.12
cyano_BB_spr	−0.04	−0.05	0.25	0.46	0.46	−0.35	−0.71	−0.64	−0.09	0.25	0.48	−0.22	0.45	0.24	0.31	0.15	−0.50	−0.46	0.24	−0.19	0.16	0.02	−0.04	−0.04	0.03	0.03
cyano_GB_spr	−0.02	0.30	0.29	0.08		0.00	−0.73	−0.57	0.16	0.14	−0.55	−0.44	0.32	−0.02	−0.40	0.25	0.34	−0.39	−0.05	0.31	0.21	−0.42	0.29	−0.14	0.04	−0.07
cyano_BB_sum	0.07	−0.10	0.25	0.20	0.20		0.52	0.56	−0.27	0.15	−0.59	0.57	−0.44	0.36	−0.40	−0.01	0.53	0.61	−0.17	0.23	−0.21	−0.40	−0.32	0.20	−0.08	−0.08
cyano_GB_sum	0.55	−0.11	0.06	−0.14	−0.08	−0.12		0.84	−0.34	−0.29	−0.81	0.60	−0.68	−0.22	−0.53	0.02	0.59	0.53	−0.25	0.25	−0.35	−0.49	−0.26	0.21	−0.08	0.08
DIN_BB_10_win	0.17	0.04	0.18	0.37	0.24	0.11	0.06		−0.54	−0.36	0.51	0.77	−0.71	−0.09	−0.41	−0.26	−0.28	−0.14	0.08	−0.08	−0.35	0.38	0.08	−0.26	0.08	−0.01
DIP_BB_10_win	−0.12	−0.36	−0.26	−0.41	−0.16	−0.07	0.06	0.08		0.34	0.37	−0.83	0.48	−0.04	0.06	−0.09	−0.40	−0.19	0.00	0.06	0.07	0.24	−0.09	−0.21	−0.20	−0.42
DIN_GB_10_win	0.41	0.07	0.19	−0.22	−0.07	−0.21	−0.05	0.11	0.27			−0.25	0.38	0.01	0.13	−0.12	−0.59	−0.45	0.40	−0.17	0.29	0.60	0.26	−0.07	−0.02	−0.20
DIP_GB_10_win	−0.04	−0.23	−0.09	−0.19	−0.01	−0.07	0.15	0.27	0.73	0.24		−0.75	0.64	−0.01	0.26	0.17	0.51	0.38	−0.17	0.16	−0.17	−0.59	−0.20	−0.03	0.24	−0.02
DIN_BB_90_sum	0.26	0.17			0.21	−0.17	−0.01	0.26	0.11	0.61	0.38		−0.64	0.05	−0.22	−0.33	−0.47	−0.47	0.13	−0.01	0.17	−0.59	0.24	−0.20	0.07	−0.01
DIP_BB_90_sum	0.13	0.02	−0.01	−0.35	−0.13	0.28	−0.29	0.06	0.44	0.36	0.42	0.22		0.04	−0.11	0.46	−0.09	0.07	−0.21	−0.04	−0.05	−0.14	−0.06	0.25	0.39	−0.09
DIN_GB_220	0.03	−0.41	−0.29	0.25	0.25	0.05	0.18	0.07	−0.26	−0.03	0.01	−0.08	−0.31			−0.20	−0.25	−0.13	−0.21	0.06	0.32	0.31	0.25	0.14	−0.04	0.02
DIP_GB_220	−0.03	−0.39	−0.40	−0.36	−0.12	−0.20	0.14	0.23	0.23	0.35	0.39	0.26	0.31	−0.07	0.63			0.24	−0.21	0.23	0.22	−0.23	0.14	−0.23	−0.04	−0.24
MaxIce	−0.12	−0.22	−0.27	−0.04	−0.04	−0.20	0.09	−0.06	0.48	0.37	0.34	0.27	0.34	−0.14	−0.02	0.03	0.36	0.36		0.33	−0.45	−0.37	−0.15	0.00	−0.04	0.07
X11psu_GBAnn	−0.01	0.06	0.00	−0.03	0.39	0.46	0.08	0.11	0.12	0.15	0.20	−0.10	−0.27	0.07	−0.02	0.26	−0.78			−0.24	−0.21	−0.39	0.12	0.43	−0.31	0.07
SST_Spr	0.19	−0.03	−0.09	−0.42	−0.06	0.13	0.07	0.09	0.02	0.20	0.19	0.29	0.34	0.01	0.20	0.60	−0.33	0.07		0.33	−0.10	0.09	0.12	−0.11	0.00	0.27
T_60_spr	−0.15	−0.33	0.10	−0.17	0.15	0.25	0.08	0.00	0.53	0.24	0.71	0.30	0.63	−0.07	0.55	0.28	−0.47	0.47		−0.27			−0.21	0.01	0.18	0.06
SSS	0.13	0.07	0.19	0.02	−0.06	0.15	0.08	0.00	0.00	0.06	0.04	0.04	0.20	−0.05	0.27	0.28	−0.94	0.40	0.54				0.62	0.29	0.16	−0.20
S90_BB	−0.32	−0.31	−0.07	−0.05	0.01	0.01	−0.07	0.16	−0.09	−0.15	0.05	−0.02	0.20	−0.02	0.11	0.08	0.74	0.74	0.01	0.54		0.38	0.38	−0.30	0.20	0.21
S100_GB	0.16	0.36	0.32	0.22	−0.21	0.10	0.22	−0.03	0.15	−0.11	0.02	0.07	0.32	−0.43	−0.36	−0.31	−0.22	−0.13	−0.31	0.01	−0.13		−0.07		0.33	0.13
O2_BB	−0.20	−0.03	0.02	0.45	0.10	−0.15	−0.01	0.04	−0.48	−0.10	−0.16	−0.53	−0.03	−0.35	−0.52	−0.46	−0.13	−0.45	−0.35	−0.32	−0.14	0.58	0.16	0.16	−0.15	0.19
O2_GB	−0.04	0.02	−0.03	−0.24	−0.23	−0.19	0.20	−0.08	0.36	−0.04	0.05	0.01	0.17	−0.82	−0.03	0.15	−0.13	−0.13	−0.19	−0.19	−0.25	0.33	0.45	0.45	0.33	−0.19
	0.14	0.39	0.26	0.24	−0.01	−0.16	−0.11	−0.14	−0.03	−0.27	−0.12	0.02	0.00	−0.27	−0.54	−0.46	−0.30	−0.30		−0.38	−0.22	0.19	0.73	0.73	0.19	−0.20

Column abbreviation key (bottom of table): dino_BB_spr, dino_GB_spr, dino_BB_sum, dino_GB_sum, cyano_BB_spr, cyano_GB_spr, cyano_BB_sum, cyano_GB_sum, DIN_BB_10_win, DIP_BB_10_win, DIN_GB_10_win, DIP_GB_10_win, DIN_BB_90_sum, DIP_BB_90_sum, DIN_GB_220, DIP_GB_220, MaxIce, BSI, X11psu_GBAnn, SST_Spr, T_60_spr, SSS, S90_BB, S100_GB, O2_BB, O2_GB