

Regime shifts, resilience and recovery of a cod stock

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ABSTRACT: In the North and Baltic seas Atlantic cod *Gadus morhua* stocks collapsed as part or one of the major factors inducing large-scale ecosystem regime shifts. Determining the relative contribution of overfishing and climate variability in causing these shifts has proven difficult. While facing similar climatic conditions, the Sound (i.e. a narrow strait located between the North and Baltic seas) differs from its neighbouring areas in the magnitude of fishing pressure as it is subjected to a local trawl fishing ban since 1932. By means of 3 independent multivariate analyses, we investigated the state and development of the Sound ecosystem, specifically testing for the occurrence of regime shifts and their potential drivers. By comparing the ecosystem development of the Sound with the neighbouring North and Baltic seas, we were able to demonstrate the positive effect of the trawl fishing ban on the resilience of the local cod stock to environmental change. The recovery and healthy condition of the Sound cod stock illustrate the need for adaptive marine management strategies that maximize ecosystem resilience.

KEY WORDS: Regime shift · Resilience · Ecosystem · Management · Atlantic cod · *Gadus morhua* · The Sound

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INTRODUCTION

Global fish production is under threat from overexploitation and climate change (Jackson et al. 2001, Hutchings & Reynolds 2004, Brander 2007). Besides causing an elevated risk of stock collapse (i.e. due to direct depletion by fishing), prolonged overfishing reduces the age, size and geographic diversity of fish populations, thereby increasing their vulnerability to climate driven recruitment stress (Brander 2005, Otersen et al. 2006, Anderson et al. 2008). To achieve sustainability, adaptive marine management strategies that maximize ecosystem resilience (i.e. the ability to withstand and buffer against change, Holling 1973) are needed (Folke et al. 2004, Steele 2004). The consequences of degrading resilience and increasing ecosystem vulnerability is clearly shown by the poor state of the Atlantic cod *Gadus morhua*, which was once among the commercially most important fish species in

the North Atlantic Ocean. Due to the joint effects of overfishing (Myers et al. 1997, Frank et al. 2005) and climate driven declines in productivity (Beaugrand et al. 2003) many of the stocks collapsed without showing signs of recovery (Hutchings & Reynolds 2004).

In several areas of the North Atlantic Ocean the collapse of cod stocks was part of or one of the major factors inducing large-scale reorganization of ecosystems (Frank et al. 2005, Kirby et al. 2009, Möllmann et al. 2009). These regime shifts are often driven by external forcing, including climate variability, overfishing and eutrophication (Collie et al. 2004). Determining the relative importance of these drivers in causing regime shifts is difficult due to co-occurring and often synergistic effects. The ability to separate these effects is of vital importance in developing ecosystem-based management strategies and achieving sustainable use of fisheries resources in the future (Pikitch et al. 2004, Marasco et al. 2007, Lindegren et al. 2009).

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In concert with large-scale patterns of ecosystem change across the North Atlantic Ocean (Bundy et al. 2009, Drinkwater et al. 2009, Link et al. 2009), simultaneous regime shifts (during the late 1980s) have been demonstrated for the North and Baltic seas (e.g. Beaugrand 2004, Alheit et al. 2005, Weijerman et al. 2005, Kenny et al. 2009, Möllmann et al. 2009). Both regime shifts were, to a large degree, triggered by climatic changes and overfishing with the collapse of the cod stocks being a major component of these ecosystem reorganizations. In the Baltic Sea the latter resulted in a pronounced trophic cascade leading to changes in the lower trophic levels (Österblom et al. 2007, Casini et al. 2008, Möllmann et al. 2008).

The narrow Sound is one of the straits linking the North and Baltic seas (Fig. 1). Though being hydrologically connected to the Baltic Sea by the northward flow of brackish surface water and to the North Sea by the southward flow of high-saline bottom water, the Sound shows marked differences in biotic conditions. These differences are manifested by locally spawning subpopulations of gadoids and flatfishes (Svedäng et al. 2004), similar to sedentary coastal populations found throughout the North Atlantic Ocean (e.g. Godø 1995, Robichaud & Rose 2004). Although a spill-over effect and an exchange with adjacent populations has not been quantified, the local cod population seems largely self-sustaining (Svedäng et al. 2004), as suggested by demographic differences (Svedäng et al. 2002), genetic studies (Nielsen et al. 2005) and tagging experiments (Pihl & Ulmestrand

1988, 1993), which points towards reproductive isolation through spawning site fidelity and/or juvenile retention (Robichaud & Rose 2004, Nielsen et al. 2005). In contrast to the depleted state of neighbouring cod stocks of the North and Baltic seas, the Sound fish stocks in general, and the cod stock in particular, are healthy not only in stock sizes but in the age-size structure of the populations (Svedäng et al. 2002). This difference is attributed to the absence of trawling activities (trawl fishing was banned in 1932 to facilitate shipping, Svedäng et al. 2004). Hence, while facing similar climatic conditions the Sound differs from its neighbouring areas in the magnitude of fishing pressure on the local fish stocks. An investigation of the ecosystem development in the Sound during the last decades and a comparison with the neighbouring North and Baltic seas may help determine the relative importance of the different drivers underlying regime shifts and fish stock collapses in marine ecosystems.

Based on a large multivariate data set we investigated the state and development of the Sound and specifically tested for the occurrence of regime shifts, trophic cascades and their potential drivers. By comparing the ecosystem development in the Sound with the neighbouring North and Baltic seas (i.e. through comparable methods across areas, Megrey et al. 2009) we demonstrated the positive effect of the trawl fishing ban on the resilience of the fish stocks and, in particular, the response of the local cod population to environmental change.

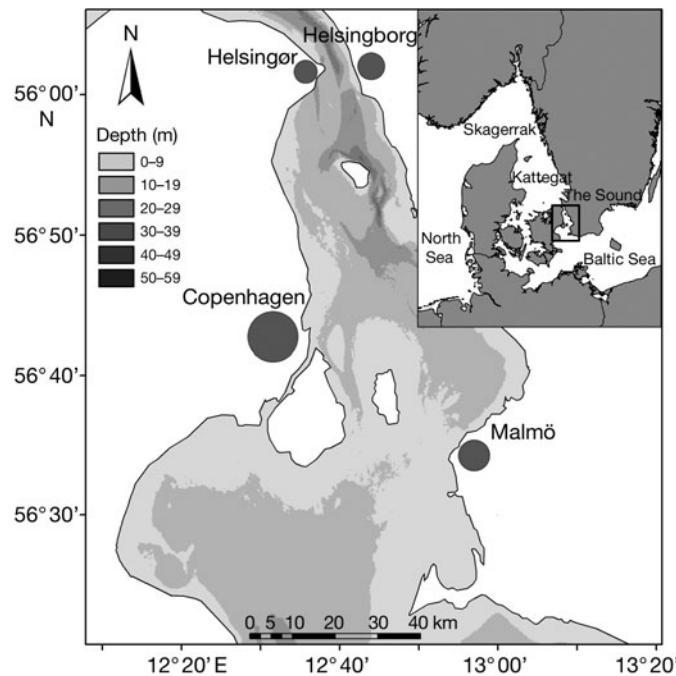


Fig. 1. The Sound (i.e. ICES Subdivision 23) and its position between the North and Baltic seas (inset)

MATERIALS AND METHODS

Data collection. A data inventory was performed on available time series characterising the Sound ecosystem and its abiotic environment. Selection of variables was based on their ecological importance, the length of the time series and the completeness of the dataset. Furthermore, data collection was restricted to the Sound, excluding the larger western Baltic/Kattegat area, due to (1) data availability, (2) lack of comparable integrated ecosystem analysis in these areas, (3) a primary interest in studying an area that has experienced limited effects from a fishery. In total, 74 biotic and abiotic time series from 1970 to 2006 were compiled. Due to cross-correlations between variables and missing values at the beginning of the investigated period 48 datasets were used for subsequent analyses (Table 1), which covered a period from 1979 to 2005.

To reflect the abiotic environment variables representing both physical oceanographic and nutrient conditions were assembled. Spring and summer values of temperature and salinity were included, which covered the main seasons for primary and secondary

Table 1. Description of time series used in multivariate analysis. For a more detailed description and data requests, please contact the ICES/HELCOM Working Group on Integrated Assessments of the Baltic Sea (WGIAB) or the corresponding author. For abbreviations see 'Materials and methods: Data collection'

Variable	Abbreviation	Season	Unit	Source
Surface salinity	H1	Spring	psu	DMU/SMHI
Surface salinity	H2	Summer	psu	DMU/SMHI
Bottom salinity	H3	Spring	psu	DMU/SMHI
Bottom salinity	H4	Summer	psu	DMU/SMHI
Surface temperature	H5	Spring	°C	DMU/SMHI
Surface temperature	H6	Summer	°C	DMU/SMHI
Bottom temperature	H7	Spring	°C	DMU/SMHI
Bottom temperature	H8	Summer	°C	DMU/SMHI
Baltic Sea Index	H9	Winter	IFM	
Volume outflow	H10	Annual	km ³	SMHI
Volume inflow	H11	Annual	km ³	SMHI
Bottom oxygen	N1	Spring	ml l ⁻¹	DMU/SMHI
Nitrate	N2	Winter	µmol l ⁻¹	DMU/SMHI
Ammonium	N3	Winter	µmol l ⁻¹	DMU/SMHI
Silica	N4	Winter	µmol l ⁻¹	DMU/SMHI
Total phosphorus	N5	Winter	µmol l ⁻¹	DMU/SMHI
Chl a	P1	Summer	µg l ⁻¹	DMU
Diatoms	P2	Spring	µg C l ⁻¹	DMU
Dinoflagellates	P3	Spring	µg C l ⁻¹	DMU
Cryptophyceans	P4	Spring	µg C l ⁻¹	DMU
Nanoplankton	P5	Spring	µg C l ⁻¹	DMU
Dinoflagellates	P7	Summer	µg C l ⁻¹	DMU
Cryptophyceans	P8	Summer	µg C l ⁻¹	DMU
Nanoplankton	P9	Summer	µg C l ⁻¹	DMU
Cyanobacteria	P10	Summer	µg C l ⁻¹	DMU
Flagellates (microzooplankton)	M1	Spring	µg C l ⁻¹	DMU
Other microzooplankton	M2	Spring	µg C l ⁻¹	DMU
Flagellates (microzooplankton)	M3	Summer	µg C l ⁻¹	DMU
Other microzooplankton	M4	Summer	µg C l ⁻¹	DMU
<i>Acartia</i> spp.	Z1	Summer	µg C l ⁻¹	DMU
<i>Centropages</i> spp.	Z2	Summer	µg C l ⁻¹	DMU
<i>Pseudocalanus</i> spp.	Z3	Summer	µg C l ⁻¹	DMU
<i>Temora longicornis</i>	Z4	Summer	µg C l ⁻¹	DMU
<i>Evdadne</i> spp.	Z5	Summer	µg C l ⁻¹	DMU
<i>Oithona similis</i>	Z6	Summer	µg C l ⁻¹	DMU
<i>Podon</i> spp.	Z7	Summer	µg C l ⁻¹	DMU
<i>Bosmina</i> spp.	Z8	Summer	µg C l ⁻¹	DMU
Crustaceans	B1	Annual	g m ⁻²	DMU
Echinoderms	B2	Annual	g m ⁻²	DMU
Molluscs	B3	Annual	g m ⁻²	DMU
Polychaetes	B4	Annual	g m ⁻²	DMU
Whiting landings	F1	Annual	t yr ⁻¹	FD
Dab landings	F2	Annual	t yr ⁻¹	FD
Plaice landings	F3	Annual	t yr ⁻¹	FD
Flounder landings	F4	Annual	t yr ⁻¹	FD
Cod landings	F5	Annual	t yr ⁻¹	FD
Herring landings	F6	Annual	t yr ⁻¹	FD

production as well as the relevant periods for fish reproduction. Due to a strong and permanent stratification, both surface and bottom values were used. Total annual inflow (southward) and outflow (northward) of water through the Sound, which accounts for only a fraction of the total water flux between the North and Baltic seas (Fischer & Matthäus 1996), were

included to represent the hydrodynamics of the area. Furthermore, the Baltic Sea Index (BSI), which reflects the effect of climate variability on oceanographic processes in the area (Lehmann et al. 2002), was included. Oxygen conditions were represented by bottom concentrations during spring and nutrient conditions by winter concentrations of nitrate, ammonium, silica and total phosphorus.

The selected biotic variables cover all trophic levels from primary producers to top-predatory fish. Summer chlorophyll a (chl a) was used as a proxy for total phytoplankton biomass. To account for changes in the relative taxonomic composition of the phytoplankton groups during spring and summer the biomass of diatoms, dinoflagellates, cryptophyceans, nanoplankton and cyanobacteria (summer) were used in the analysis. The zooplankton community is represented by summer biomass values of copepods (*Acartia* spp., *Centropages* spp., *Pseudocalanus* spp. and *Temora longicornis*) and cladocerans (*Evdadne* spp., *Oithona similis*, *Podon* spp. and *Bosmina* spp.). Benthos is characterised by annual biomass averages of molluscs, polychaetes, echinoderms and crustaceans. Annual landings from the local gill net fishery of the commercially most important fish species Atlantic cod, whiting *Merlangius merlangus*, Atlantic herring *Clupea harengus*, plaice *Pleuronectes platessa*, flounder *Platichthys flesus* and dab *Limanda limanda* were chosen to characterise the fish community. Landings of seasonally occurring species such as garfish *Belone belone*, Atlantic mackerel *Scomber scombrus* and European eel *Anguilla anguilla* were excluded. However, herring landings consisting of both a local population and the Rügen spring-spawning herring were included since it resides in the Sound during a major part of the year from August to March (Nielsen et al. 2001).

Environmental and biological data were extracted from published reports and the databases hosted by The Danish National Environmental Research Institute (DMU) (www.dmu.dk) and the Swedish Meteorological and Hydrological Institute (SMHI) (www.smhi.se). Fish

survey data were extracted from International Council for the Exploration of the Sea (ICES) database (www.ices.dk) and commercial landings from The Danish Directorate of Fisheries (FD) (www.fd.dk) and the Swedish Board of Fisheries (www.fiskeriverket.se).

Regime shift analysis. Principal component analysis (PCA) was used to extract the most important modes of variability in the time series. Beforehand, we replaced missing values in the dataset by variable averages. To improve linearity between variables and to reduce the relationship between the mean and the variance, all biological variables were $\ln(x + 1)$ transformed. Our analyses included a PCA using all 48 time series, followed by 2 separate PCAs for either abiotic (16 series) or biotic variables (32 series). All 3 PCAs were conducted based on the correlation matrix and the first factorial plane was visualised as a correlation biplot.

To identify potential regimes in the data sets chronological clustering was performed to objectively identify the years where the largest shifts occurred. This method describes discontinuities in a multivariate series of samples and takes into account the sequence of sampling, which makes it possible to eliminate singletons (Legendre et al. 1985, Legendre & Legendre 1998). To show the most important breakpoints in the dataset, the significance level alpha, which can be considered as clustering intensity parameter, was set to 0.01 and the connectedness level to 50 %. Corresponding to the methodological approach used in the PCA data were first standardised and then the Euclidean distance function was calculated to determine the similarity between years.

In a further analysis we applied the sequential *t*-test analysis of regime shifts (STARS) method (Rodionov 2004) to normalized averages (e.g. Hare & Mantua 2000) of hydrographic and nutrient time series as well as for each functional group, i.e. phytoplankton, zooplankton, benthos and fish separately. The STARS algorithm is designed to detect statistically significant shifts in the mean level and the magnitude of fluctuations in time series by using modified 2-sided Student's *t*-tests. STARS can detect shifts at different time scales and magnitudes by varying the probability level of the tests and the cut-off length that controls the duration of regimes (Rodionov & Overland 2005). In the present study we applied a significance level of $p = 0.05$ and a cut-off length of 10 yr. More information on the STARS method and Excel add-in software is available online at www.beringclimate.noaa.gov.

Trophic cascade analysis. Trophic cascades are defined by alternating top-down and bottom-up regulation and the propagation of indirect positive feedbacks between nonadjacent trophic levels (Pace et al. 1999, Casini et al. 2008). To first provide an understanding of the underlying processes of ecosystem regulation in the

Sound we investigated the potential occurrence of trophic cascades by applying a simple linear regression analysis on selected time series representing key components of the different trophic levels of the ecosystem. In addition, a regression analysis on aggregated biomasses for each trophic level was performed. All time series were log transformed to stabilise the variance. Model diagnostics were applied to test for the assumption of normality and independence of residuals.

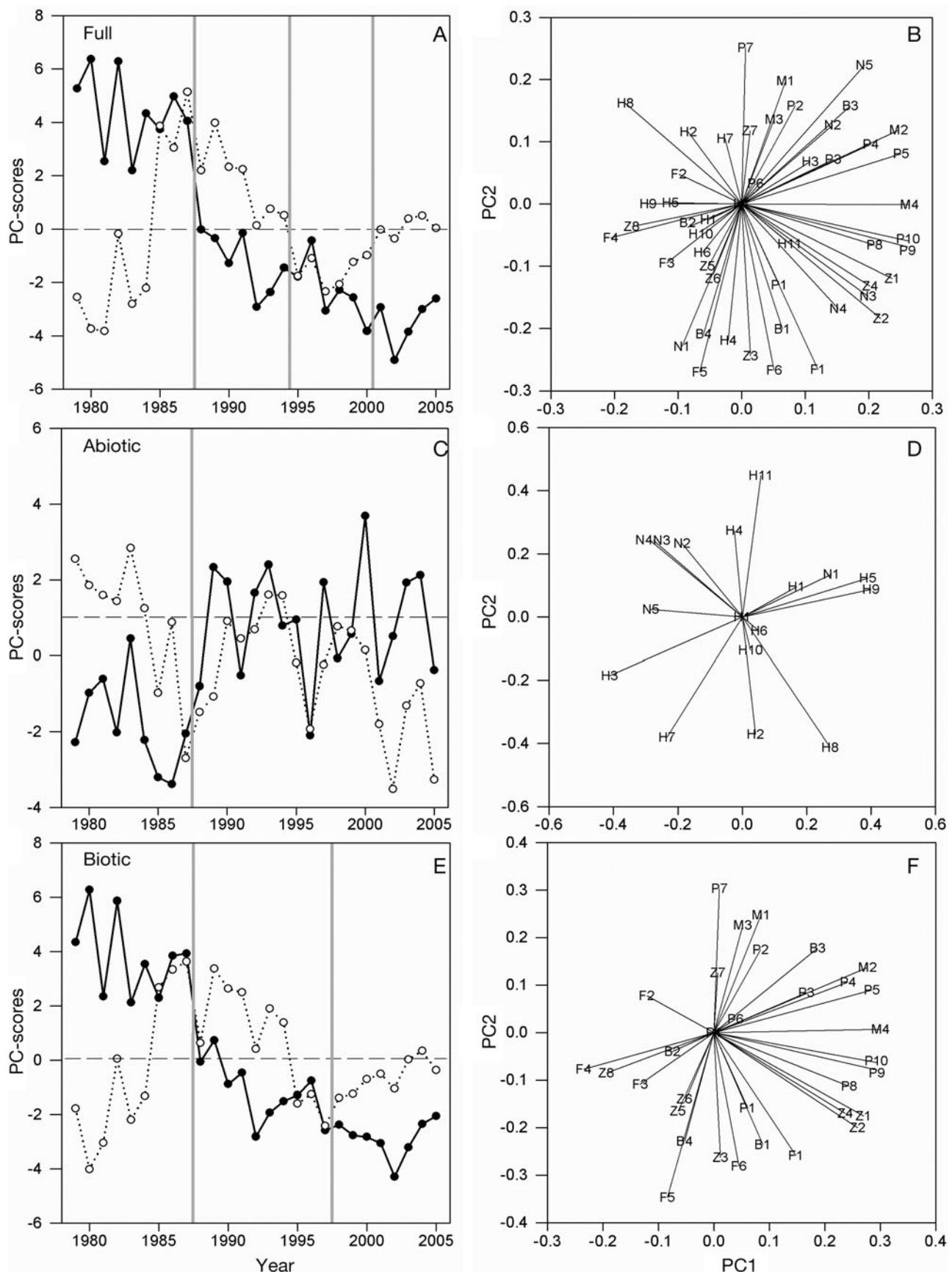
Cross-ecosystem comparisons. For the cross-ecosystem comparison, principle component 1 (PC1) scores from regime shift studies in the North Sea (Weijerman et al. 2005) and the central Baltic Sea (Möllmann et al. 2009) were collected (i.e. chosen to cover the whole period from 1979 to 2005). PC1 can be considered as an integrated indicator of ecosystem state and development (Möllmann et al. 2009). The STARS method was then applied to the PC1 scores, including the Sound, to compare the timing and magnitude of the regime shifts. We also compared the spawning stock biomass (SSB), i.e. derived from standard stock assessments in the North and Baltic seas, and landings of the cod and the dominant pelagic fish stock between areas. Since landings may not accurately reflect the true stock dynamics in the Sound, we additionally collected independent survey data and catch per unit effort (CPUE) estimates (landings per trawling hour) available for cod from 1991 to 2006 and 1996 to 2006, respectively. All statistical analyses were conducted with the Brodgar (www.brodgar.com) and R software (www.r-project.org).

RESULTS

Ecosystem analysis

The PCA of the full data set, which takes into account both abiotic and biotic variables, resulted in 35.6 % explained variance on the first 2 PCs (a plot of eigenvalues for each principle component of the 3 PCAs is shown in Fig. S1 in the supplement available at www.int-res.com/articles/suppl/m402p239_app.pdf). Scores along the first PC (24.2 %) showed a clear temporal trend from positive values in the early years and negative values from the 1990s onwards separated by a sharp decrease in scores between 1987 and 1988

Fig. 2. Year scores at the first 2 axes (PC1 [solid] and PC2 [dotted]) resulting from the principle component analysis (PCA) of (A) full, (C) abiotic and (E) biotic dataset. Vertical lines indicate the time of the most important breakpoints obtained from chronological clustering using an alpha value of 0.01. (B,D,F) Correlation biplots from each normalised PCA. The angles between eigenvectors represent the degree of correlation between variables (see Table 1) and PC axes



(Fig. 2A). The variable loadings, i.e. the length and orientation of vectors on the correlation biplot, visualise the degree of correlation with the respective PC (Fig. 2B). Thus, nutrients (N2, N5), small-sized phytoplankton (P4, P5, P8, P9), cyanobacteria (P10), copepods (Z1, Z2, Z4), microzooplankton (M4) and molluscs (B3) were mainly positively correlated to PC1, while flatfish (F2 to F4), *Bosmina* spp. (Z8) and summer bottom temperatures (H8) showed negative correlations. The negative correlation thus indicates an increasing trend in each of these variables within the last 15 yr, e.g. higher flatfish landings. The second PC (11.4 %) showed an initial sharp increase in scores followed by a gradual decrease and a rather stable period in the last 10 yr. Large-sized phytoplankton (P2, P7) and microzooplankton (M1, M3) showed positive correlations to this axis, while landings of herring (F6), cod (F5) and whiting (F1) and biomass of *Pseudocalanus* spp. (Z3) were negatively correlated with PC2. This means that these variables generally increased since the mid-1990s. Finally, the outflow (H10) and inflow (H11) did not explain much of the variation on the first 2 PCs (Fig. 2B), indicating that transport and advection, no matter how important for the physical environment (Fig. 2C), seem to be uncorrelated to the temporal dynamics of most ecosystem components.

The second PCA, using only abiotic time series, explained 39.2 % of the variance on the first factorial plane. PC1 scores (21.5 %) showed strong fluctuations with an overall increasing trend since the late 1980s (Fig. 2C). In the correlation biplot (Fig. 2D), BSI (H9) and spring surface temperature (H5) were positively correlated to PC1, indicating their overall increase during the last decades. In contrast, spring bottom salinity (H3) and nutrient conditions (N2 to N5) decreased and showed negative correlations to the first axis. PC2 scores (17.7 %) oscillated with high values at the beginning and low values at the end of the investigated period. Volume inflow (H11) and summer bottom salinity (H4) showed positive correlations, while bottom temperatures (H7, H8) and surface salinity (H2) showed negative correlations to PC2.

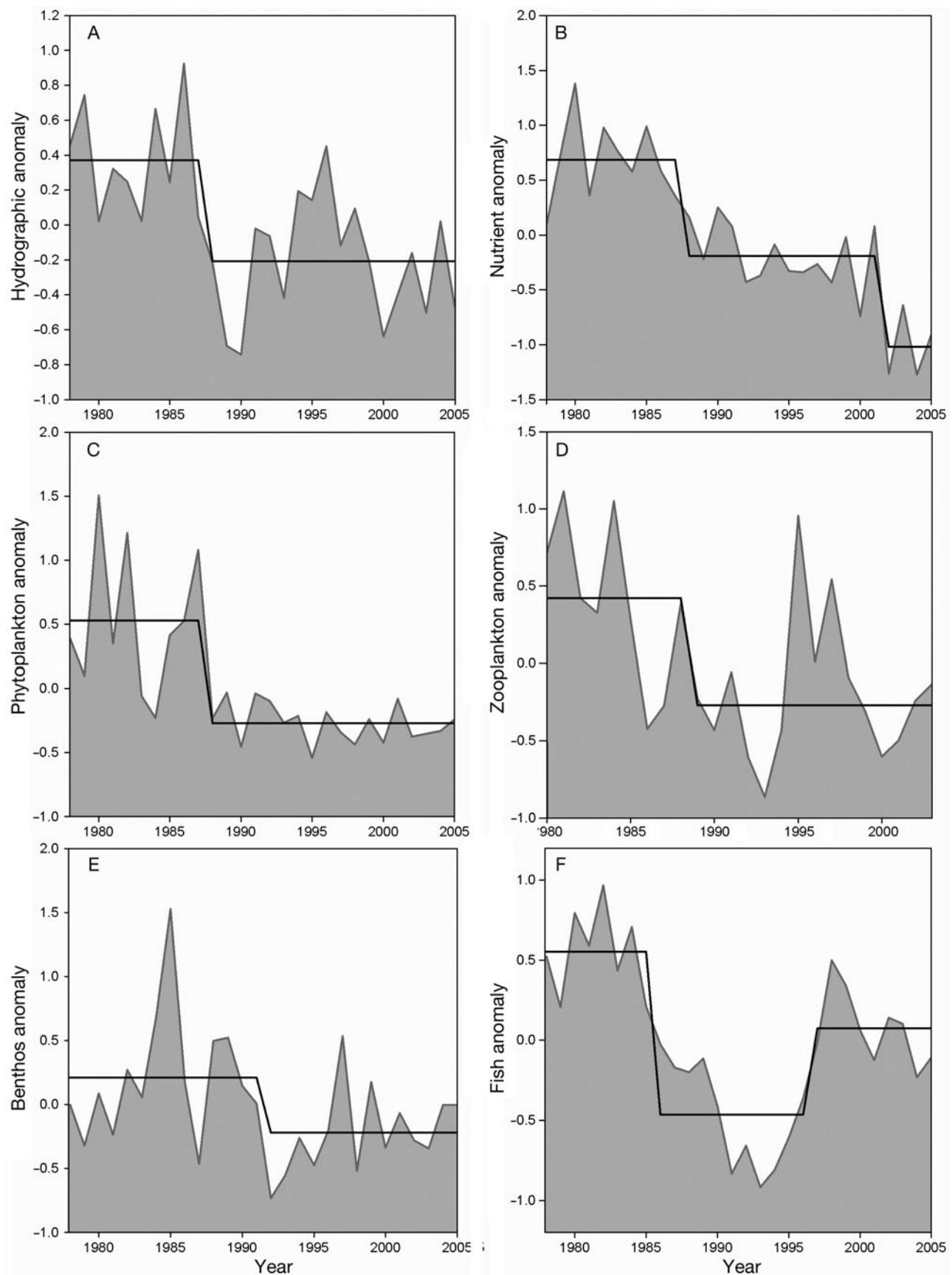
The third PCA, which used only biological time series, explained 41.3 % of the variance on the first factorial plane. The temporal development of PC1 and PC2 scores (Fig. 2E) were relatively similar to the results of the first PCA that used the full data set (Fig. 2A). During the first years PC1 scores (28.3 %) showed positive values, but shifted to negative values following a sharp decrease from 1987 to 1988 (Fig. 2E). The eigenvectors (Fig. 2F) of small-sized phytoplankton (P4, P5, P9), cyanobacteria (P10), microzooplankton (M2, M4), copepods (Z1, Z2, Z4) and molluscs (B3) were positively correlated to PC1, while landings of flatfish (F3, F4) and biomass of *Bosmina* spp. (Z8) showed negative

correlations. PC2 scores (13.1 %) showed an increasing trend until 1991, followed by a gradual decrease and a more stable period with negative values occurring in recent years. Dinoflagellates (P7), diatoms (P2) and microzooplankton (M1, M3) showed positive correlations to this axis, while landings of herring (F6), cod (F5) and whiting (F1) and biomass of *Pseudocalanus* spp. (Z3) were negatively correlated, thus indicating comparatively high values during the last 10 yr.

The vertical lines superimposed on the PCA plots (Fig. 2) show the most important breakpoints identified by chronological clustering using an alpha value of 0.01. In all 3 data sets, i.e. the full (Fig. 2A), abiotic (Fig. 2C) and biotic data set (Fig. 2E), respectively, significant breakpoints were detected from 1987 to 1988. Furthermore, 2 breakpoints were identified in the full data set from 1994 to 1995 and 2000 to 2001 (Fig. 2A) and in the biotic data set from 1997 to 1998.

The STARS method identified significant regime shifts that largely coincided with the breakpoints detected by chronological clustering. The hydrographic data (Fig. 3A) showed a clear regime shift from 1987 to 1988, corresponding to a dramatic shift mainly in bottom salinity, SST and BSI. The increase and decrease in the mid-1990s were not identified as separate states. Due to a sharp decrease in nitrogen and phosphorus, the nutrient data (Fig. 3B) showed 2 regime shifts from 1987 to 1988 and 2001 to 2002, respectively. Coinciding with the decrease in nutrients, primary producers (Fig. 3C) also demonstrated a shift from 1987 to 1988. Zooplankton showed a regime shift from 1988 to 1989, which thus lagged by 1 yr compared with the 1987 to 1988 regime shifts. The sharp increase from 1994 to 1995 and the consecutive period of high values were due to its short duration, and was not identified as a separate regime (Fig. 3D). Benthos data (Fig. 3E) showed one significant shift from 1991 to 1992, which was delayed in comparison with the previously mentioned groups. As in all other groups, the fish data showed a sharp decrease since the mid-1980s (Fig. 3F). Though showing 2 consecutive declines from 1985 to 1987 and 1989 to 1991, respectively, only the first shift was found to be significant. Additionally, an opposite shift was observed from 1996 to 1997, possibly following the sharp decrease in the hydrography and increase in zooplankton variables from 1994 to 1995.

Fig. 3. Regime shifts in climate, nutrient and biological time series: (A) climate, (B) nutrient, (C) primary producers, (D) zooplankton, (E) benthos, (F) fish. Variables of each group are standardised to zero mean and unit variance and reverted such that the steps show the same sign in all time series. Significant stepwise shifts in means (black line) were detected using significance level $p = 0.05$ and a cut-off length of 10 yr



Trophic cascade analysis

To visualise top-down and bottom-up regulation in the Sound, selected time series from each functional group were graphically displayed as standardised anomalies (Fig. 4). Based on the similarities in temporal dynamics of the selected variables, the analysis suggests 2 parallel pathways of bottom-up regulation in the Sound, the first linking hydrographic-climatic processes to zooplankton and fish and the second linking nutrient dynamics to primary producers and benthos. The first pathway is clearly visible in the relationships between bottom salinity, *Pseudocalanus* spp., herring and cod (Fig. 4A,C,E). The variables were chosen as they represent key hydrographic variables and the dominant zooplankton and fish species in the area. The second pathway is visualised by the similar temporal dynamics of winter concentration of phosphorus (considered to be the limiting nutrient in the area, Wasmund & Uhlig 2003), total photosynthetic biomass and mollusc biomass, the latter representing the most abundant benthic group in the Sound. A regression analysis on the selected time series showed a highly significant and positive relationship between each trophic level (Table 2), i.e. between zooplankton (*Pseudocalanus* spp.), planktivorous fish (herring) and piscivorous fish (cod) as well as between primary producers and benthos (molluscs). Furthermore, these patterns are consistent when also considering aggregated biomasses for each trophic level (Table 3). This indicates strong bottom-up regulation in all parts of the ecosystem and rules out the possibility of trophic cascades, since trophic cascades are generally identified by inverse (negative) relationships between adjacent trophic levels (Pauly et al. 1998, Worm & Myers 2003, Casini et al. 2008).

Cross-ecosystem comparisons

As illustrated by the generally declining PC1 scores from the North Sea (Fig. 5A), the Sound (Fig. 5C) and the central Baltic Sea (Fig. 5E), the areas show similar ecosystem dynamics during the observed period. Likewise, the timing and magnitude of regime shifts detected by STARS all coincide during the period from 1987

Fig. 4. Selected time series from each trophic level (i.e. standardised to zero mean and unit variance) visualising the 2 pathways of ecosystem regulation in the Sound. (A) Summer bottom salinity (dotted) and summer biomass of *Pseudocalanus* spp. (solid). (B) Winter total phosphorus concentrations (dotted) and total phytoplankton biomass (solid). (C) Summer biomass of *Pseudocalanus* spp. (dotted) and landings of herring (solid). (D) Winter total phosphorus concentrations (dotted) and biomass of molluscs (solid). (E) Landings of herring *Clupea harengus* (dotted) and cod *Gadus morhua* (solid). (F) Summer total phytoplankton biomass (dotted) and biomass of molluscs (solid). (A regression analysis of the presented time series is presented in Table 2)

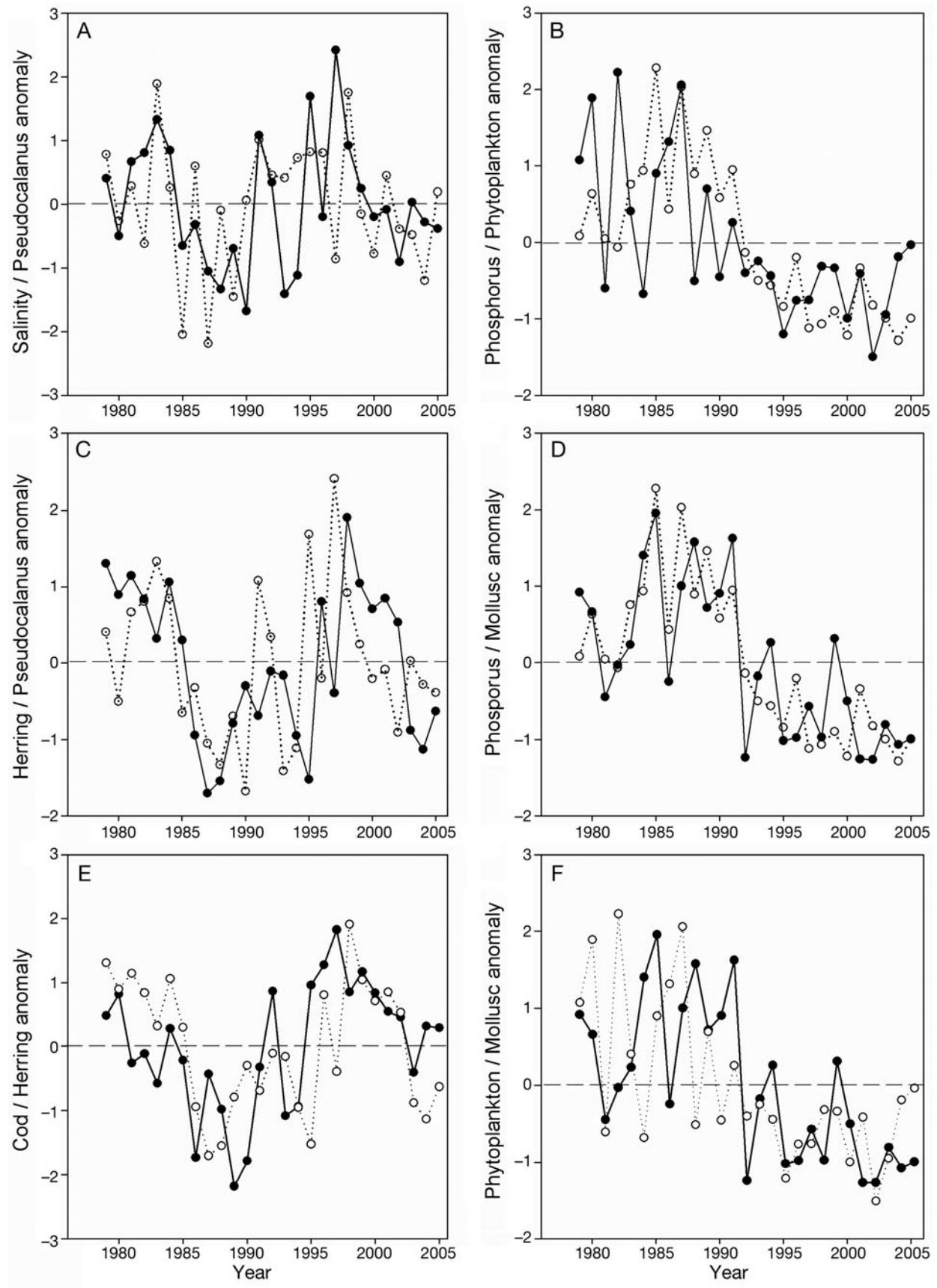
to 1988. The dynamics of cod stocks from the North Sea (Fig. 5B) and central Baltic Sea (Fig. 5F) largely follow the ecosystem developments, while for cod stock in the Sound the initial decrease is followed by an increase since the mid-1990s (Fig. 5C). Since landings data may not adequately describe the cod stock dynamics, we additionally plotted landings data with independent survey data available from 1991 to 2006. The strong correlation with survey data ($r = 0.79$, $p <$

Table 2. Linear regression analysis on selected time series. Following the 2 suggested pathways of regulation, the analysis is divided into (A) a hydrographic-climatic section and (B) a nutrient section. TP: winter total phosphorus. Model significance via p-values (p), degrees of freedom (df) and regression coefficients, the intercept a and the slope b with associated significance levels (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$) are indicated. To emphasize the type of linear relationship, a positive (+) and negative (-) sign is indicated. The coefficient of determination (R^2) is shown in percent

Response	Predictor	df	p	a	b	Sign	R^2
(A) Hydrographic-climatic pathway							
<i>Pseudocalanus</i> spp.	Herring	24	<0.001	-6.3***	0.50***	+	52
<i>Pseudocalanus</i> spp.	Cod	24	0.007	-7.1*	0.58**	+	23
Herring	Cod	24	<0.001	0.03	1.04***	+	37
(B) Nutrient pathway							
Total phytoplankton	TP	24	<0.001	7.1*	9.3***	+	40
Molluscs	TP	25	<0.001	-3.2***	4.0**	+	62
Total phytoplankton	Molluscs	24	0.008	16.3***	1.4**	+	22

Table 3. Linear regression analysis on aggregated biomasses for each trophic level or functional group. Model significance via p-values (p), degrees of freedom (df) and regression coefficients, the intercept a and the slope b with associated significance levels (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$) are indicated. To emphasize the type of linear relationship, a positive (+) and negative (-) sign is indicated. The coefficient of determination (R^2) is shown in percent

Response	Predictor	df	p	a	b	Sign	R^2
Zooplankton	Climate	25	0.03	2.3***	0.34*	+	14
Pelagic fish	Zooplankton	24	<0.001	11.3***	1.5***	+	46
Demersal fish	Pelagic fish	25	0.04	11.6***	0.2*	+	13
Phytoplankton	Nutrients	25	<0.001	19.8**	5.2***	+	46
Benthos	Phytoplankton	23	0.02	3.3***	0.05*	+	17



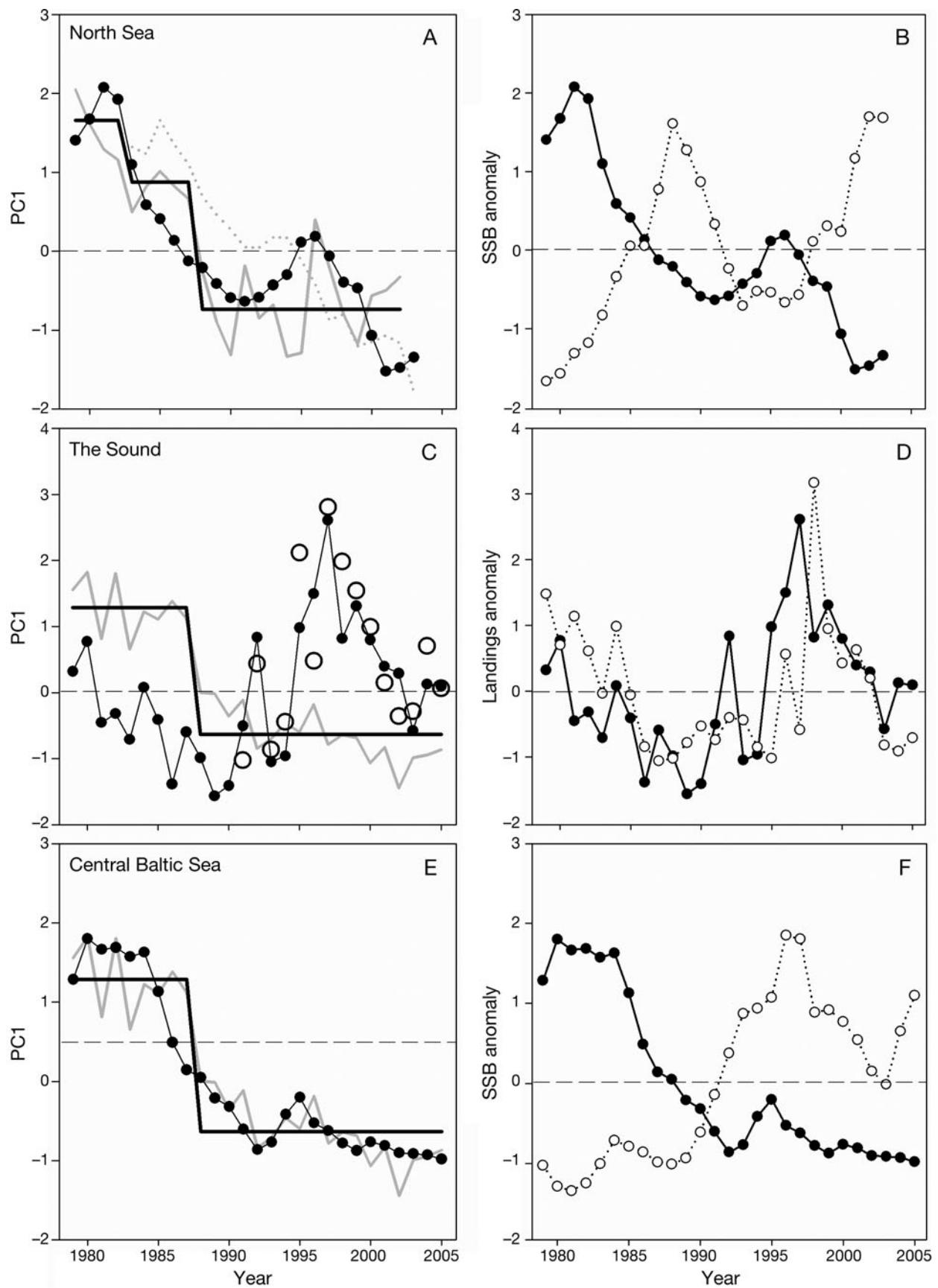


Fig. 5. Comparison of normalised PC1 scores (grey line), spawning stock biomass (SSB) values of cod *Gadus morhua* (black line) and pelagic fish species (dotted lines) from (A,B) the North Sea, (C,D) the Sound and (E,F) the central Baltic Sea. Herring *Clupea harengus* is shown for the North Sea and the Sound, while sprat *Sprattus sprattus* is shown for the central Baltic Sea. As a complement, PC1 scores from Kenny et al. (2009), which covered a shorter time period between 1983 and 2003, are shown for (A) the North Sea as a dotted grey line. Bold black lines represent the regime shifts as detected by the sequential *t*-test analysis of regime shifts (STARS) method. Cod landings from the Sound are compared with normalised (i.e. to zero mean and unit variance) survey data available from 1991 to 2006 (large circles)

0.001) as well as with CPUE estimates (i.e. landings per trawling hour, $r = 0.82$, $p < 0.001$) indicated that landings may reflect the true stock dynamics, at least from the early 1990s onwards.

In the North and Baltic seas, the regime shift and collapse of the cod stocks triggered a trophic cascade causing changes in the lower trophic levels (Österblom et al. 2007, Casini et al. 2008, Möllmann et al. 2008, Kirby et al. 2009). The trophic cascade is illustrated by the strong negative correlation between cod and sprat *Sprattus sprattus* ($r = -0.72$, $p < 0.001$), the dominating planktivorous species in the Baltic Sea (Fig. 5F), and between cod and herring ($r = -0.81$, $p < 0.001$), one of the main planktivorous fish species in the North Sea (Fig. 5B). As opposed to the neighbouring areas, the positive relationship between the Sound cod and herring (Table 2) suggests no trophic cascade, but instead a strong bottom-up regulation in the area.

DISCUSSION

In the North Sea and central Baltic Sea the cod stocks collapsed simultaneously with large-scale ecosystem reorganisations (Reid et al. 2003, Beaugrand 2004, Weijerman et al. 2005, Casini et al. 2008, Möllmann et al. 2008). These regime shifts are considered driven by the combined and synergistic effects of both overfishing and climate variability (Weijerman et al. 2005, Möllmann et al. 2009). Despite the absence of commercial trawl fishing, we also demonstrated a clear shift in the Sound ecosystem. Given the coherent patterns and synchronous timing of regime shifts across the entire North Atlantic Ocean (Bundy et al. 2009, Drinkwater et al. 2009, Link et al. 2009), atmospheric-oceanographic changes are the most likely driver. In the North and Baltic seas, regional climate and hydrographic conditions are mainly influenced by large-scale circulation patterns causing periodic inflow events from the North Atlantic Ocean (Hänninen et al. 2000, Reid et al. 2003). These events affect all parts of

the ecosystem from lower trophic levels (Reid et al. 1998, Möllmann et al. 2000, Beaugrand et al. 2003, Wasmund & Uhlig 2003) to higher trophic levels (Kröncke et al. 1998, Möllmann et al. 2003, Durant et al. 2004) and involve a suite of different physical and biological processes, mainly related to effects of temperature, salinity, oxygen, turbulence and advection (Ottersen et al. 2001). In the mid-1980s, the North Atlantic Oscillation (NAO) and BSI shifted sharply from a negative to a positive phase, giving rise to anomalous temperatures, salinities and oxygen conditions throughout the whole area. These climate anomalies, by means of direct and indirect biological feedbacks, most probably induced the simultaneous regime shift observed in the North Sea, central Baltic Sea and the Sound from 1987 to 1988.

Depending on the internal structure and the type of external forcing, ecosystem regime shifts may be classified into 3 qualitatively different types: smooth, abrupt and discontinuous (Collie et al. 2004). While the first two represent generally reversible transitions between alternative ecosystem states, a discontinuous shift involves hysteresis, a process preventing the system from switching back to the previous state even if external conditions are restored (Scheffer et al. 2001). In the North and Baltic seas, the regime shift and collapse of the cod stock resulted in a pronounced trophic cascade leading to changes in the lower trophic levels (Österblom et al. 2007, Casini et al. 2008, Möllmann et al. 2008, Kirby et al. 2009). This internal restructuring of the food web may presently maintain the ecosystem in its currently less desirable ecosystem state by means of negative feedbacks (Bakun 2006, Casini et al. 2009, Möllmann et al. 2009). While the regime shifts of the North and Baltic seas may be described as discontinuous, the Sound regime shift shows no signs of trophic cascade or shift in trophic control (i.e. between top-down and bottom-up regulation) and is, therefore, probably of the abrupt, but still reversible, kind. Given similar external physical forcing, the observed difference between regime shifts in the North Sea, Baltic Sea and the Sound are probably due to a different magnitude of anthropogenic influences, e.g. with respect to eutrophication and fishing pressure, which both affect the internal structure and resilience of the ecosystem.

Eutrophication has caused regime shifts in lakes (Carpenter et al. 1987, Scheffer & van Nes 2007) and estuarine ecosystems (Daskalov et al. 2007, Hansson et al. 2007, Oguz & Gilbert 2007, Österblom et al. 2007). The Sound faced severe eutrophication in the early 1980s; however, due to the implementation of efficient waste water treatment, river run-off (mainly of phosphate) was markedly reduced (The Sound Water Cooperation 2004). In combination with limited inflow

of nutrient-rich bottom water from the North Sea, the nutrient reductions probably caused the strong decline in nutrient conditions during this period. Furthermore, Wasmund & Uhlig (2003) related decreasing trends in cyanobacteria and chl *a* to increasing temperatures and a decrease in nutrient loadings, in particular of phosphorus, which is considered a co-limiting nutrient in this area (HELCOM 2002). The shift from small-sized phytoplankton species and N-fixing cyanobacteria to larger-sized diatoms and dinoflagellates in the early 1990s may be explained by a combination of climate changes and nutrient forcing (Wasmund & Uhlig 2003, Henriksen 2009).

Henriksen et al. (2001) showed significant positive response of macrobenthos abundances to winter nutrient input and spring primary production in Danish waters. Likewise, Kröncke et al. (1998) showed a similar effect on macrozoobenthos in the North Sea. Decreasing nutrient loadings and primary production in combination with a milder climate probably induced the observed changes in the benthic community in the Sound, especially the drastic decrease of filter-feeding molluscs (bivalves). The changes may not be attributed to fishing activities because towed bottom-fishing gear, i.e. trawls, has been banned since 1932. The invasion of the alien polychaete species, *Marenzelleria viridis*, may further explain the shift in dominance to polychaetes in the early 1990s (Strömberg & Persson 2005).

Overfishing results in a reduction of the mean age, mean size and geographic diversity of populations and has been shown to increase the sensitivity of fish stocks to climate-driven recruitment stress (Brander 2005, Ottersen et al. 2006, Anderson et al. 2008), thereby impairing their resilience to withstand and buffer against environmental change (Folke et al. 2004). For the North Sea cod, recruitment stress is primarily caused by a temperature driven mismatch in prey availability, which reduces the survival of young cod (Beaugrand et al. 2003); For eastern Baltic cod, low salinities and low oxygen concentrations directly impair recruitment through increased egg and larvae mortalities (Köster et al. 2005). Furthermore, the large sprat stock may impose negative key feedbacks by preying on cod eggs (Köster & Möllmann 2000) and reducing the main food source of cod larvae, the copepod *Pseudocalanus acuspes* (Möllmann & Köster 2002). Though mechanisms are not investigated in detail, our study suggests a positive effect of both bottom salinity and zooplankton availability (i.e. *Pseudocalanus* spp.) on cod recruitment in the Sound.

Following the regime shift and collapse of the cod stocks in the North and Baltic seas, the populations remained at historically low levels with no or only weak signs of recovery (A slight increase in eastern

Baltic cod has been observed during the recent year). In contrast, the Sound fish stocks in general and the local cod population in particular show a clear recovery in the mid-1990s after the regime shift. The resilience and recovery potential of the cod stock in the Sound is probably due to the absence of commercial trawl fishing, as only local gill net fisheries are allowed in the area (Svedäng et al. 2004). As a consequence, the cod stock shows demographic conditions (age and size distribution) to be far better than the overexploited neighbouring stocks (Svedäng et al. 2002, this paper Fig. S2). With many large, old and experienced individuals and several generations contributing to spawning (Ottersen et al. 2006, Anderson et al. 2008), the cod stock in the Sound seems more resilient to recruitment stress and could therefore recover after experiencing years of potentially unfavourable climate conditions for spawning. Whether the trawling ban increases resilience of the ecosystem by protecting important benthic habitats and organisms, which are vital for growth and recruitment of demersal fish species such as cod (Collie et al. 2000), is presently unclear. To that end, we stress the need for further investigations on the local fish stocks in general, and the cod population in particular, to provide detailed understanding of the mechanisms underlying fish stock resilience in the Sound.

CONCLUSIONS

Ecosystems worldwide have already shown clear evidence of change in response to changing climate (Walther et al. 2002, Rosenzweig et al. 2008) and even more pronounced alterations might be encountered in the future, especially as climate scenarios predict drastic changes in atmospheric–oceanographic forcing (IPCC 2007). Resilient ecosystems are able to absorb extreme events without changing fundamentally, but if the resilience once is weakened it can be restored only slowly (Folke et al. 2004). Furthermore, hysteresis may even prevent the ecosystem from switching back to the previous state as it is not sufficient to restore external conditions (Scheffer et al. 2001). External conditions can be only partly influenced (e.g. by reducing nutrient loads), but we are able to control fisheries through appropriate and ecologically sound management actions. While the regime shifts in the North and Baltic seas may involve hysteresis, and as such be described as discontinuous, the Sound regime shift shows no signs of trophic cascade or hysteresis and may therefore be of the abrupt but still reversible kind. The present study indicates that low fishing pressure and, hence, healthy fish population sizes and structures can obviously change

the response of an ecosystem to external forcing. The cod stock in the Sound recovered to preshift conditions whereas those in neighbouring areas remained in a depleted state. The socioeconomic costs of an ecosystem switch with a decline of commercially valuable fish species can be enormous and, therefore, the maintenance and restoration of ecosystem resilience is an important part of a successful ecosystem-based fisheries management strategy (Folke et al. 2004, Marasco et al. 2007).

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