

Effects of climate and overfishing on zooplankton dynamics and ecosystem structure: regime shifts, trophic cascade, and feedback loops in a simple ecosystem

Christian Möllmann, Bärbel Müller-Karulis, Georgs Kornilovs, and Michael A. St John

Möllmann, C., Müller-Karulis, B., Kornilovs, G., and St John, M. A. 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.

The Central Baltic Sea is the largest brackish waterbody in the world ocean, containing a highly productive but low-diversity ecosystem. Climate-induced changes in hydrography recently caused an ecosystem regime shift with changes at all trophic levels. The most pronounced changes in the ecosystem occurred at the zooplankton and fish trophic levels. In the zooplankton, dominance changed between the copepods *Pseudocalanus acuspes* and *Acartia* spp., a result of reduced salinities and increased temperatures. The change in hydrography also affected the reproductive success of the major fish species, resulting in a change in dominance from the piscivorous cod (*Gadus morhua*) to the planktivorous sprat (*Sprattus sprattus*). First, we investigate statistically the occurrence of regime shifts in time-series of key hydrographic variables and the biomass time-series of key species. Second, we demonstrate a three-level trophic cascade involving zooplankton. Finally, we model the ecosystem effects of the abiotic and biotic changes on copepod biomass and recruitment of fish stocks. Our results demonstrate the linkage between climate-induced zooplankton and fish regime changes, and how overfishing amplified the climate-induced changes at both trophic levels. Hence, our study demonstrates (i) the multiple pathways along which climatic and anthropogenic pressures can propagate through the foodweb; (ii) how both effects act synergistically to cause and stabilize regime changes; and (iii) the crucial role of zooplankton in mediating these ecosystem changes.

Keywords: *Acartia* spp., Baltic Sea, climate, cod, overfishing, prey-to-predator loops, *Pseudocalanus acuspes*, regime shifts, sprat, trophic cascade.

Received 8 July 2007; accepted 10 November 2007; advance access publication 1 February 2008.

C. Möllmann and M. A. St John: Institute for Hydrobiology and Fisheries Science, University of Hamburg, Grosse Elbstr. 133, Hamburg D-22767, Germany. B. Müller-Karulis: Latvian Institute of Aquatic Ecology, Daugavgrivas Street 8, LV-1048 Riga, Latvia. G. Kornilovs: Latvian Fish Resources Agency, Daugavgrivas Street 8, LV-1007 Riga, Latvia. Correspondence to C. Möllmann: tel: +49 40 42838 6621; fax: +49 40 42838 6618; e-mail: christian.moellmann@uni-hamburg.de.

Introduction

Zooplankton plays a crucial role in the high impact that climate-induced changes in the physical environment have on pelagic ecosystems (e.g. Fromentin and Planque, 1996; Beaugrand *et al.*, 2002; Möllmann *et al.*, 2003; Chiba *et al.*, 2006) and in mediating these to upper trophic levels, i.e. commercially important fish populations (Beaugrand *et al.*, 2003; Möllmann *et al.*, 2005). These changes frequently co-occur with overall changes in the ecosystem, so-called regime shifts (e.g. Bakun, 2005; Lees *et al.*, 2006) that have been observed in various marine ecosystems of the world ocean, e.g. the North Pacific (Hare and Manuta, 2000) and the North Sea (Beaugrand, 2004). The term regime shift, describing the transition between different states, was first used for marine ecosystems to describe dominance changes between fish populations, e.g. the fluctuations between anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*) in several regions of the world ocean (Lluch-Belda *et al.*, 1989). Nowadays, regime shifts are defined mainly based on changes in the ecosystem as a whole (Collie *et al.*, 2004). They are usually low-frequency and abrupt changes in ecosystem structure and function, occurring at multiple trophic levels and on large geographic scales (Collie *et al.*, 2004;

Cury and Shannon, 2004; de Young *et al.*, 2004; Bakun, 2005; Lees *et al.*, 2006).

Recent investigations have demonstrated that ecosystem changes are also induced by human exploitation, both through direct effects on the target species and through indirect influences on ecosystem structure and function. Evidence is increasing for cascading trophic interactions in large marine ecosystems (Frank *et al.*, 2005, 2006; Myers *et al.*, 2007). These trophic cascades are mainly described as being caused by the depletion of top predators, leading to conspicuous reciprocal changes at trophic levels below, hence also involving zooplankton (Frank *et al.*, 2005).

Regime shifts and trophic cascades generally involve collapses of important exploited fish stocks. That it often takes longer for the resource population to recover than would be expected based on biological parameters (Hutchings, 2000; Steele and Schumacher, 2000) indicates the existence of important feedback processes operating in marine ecosystems (Bakun and Weeks, 2006). An example is the prey-to-predator (P2P) loop, which describes a stabilizing mechanism after the decline of a top-predator. The favoured prey increases as a result of decreased predation pressure and subsequently prevents the recovery of the

predator, e.g. by preying on the predator's eggs and larvae (Bakun and Weeks, 2006).

The brackish Central Baltic is a semi-enclosed sea containing a highly productive but low-diversity ecosystem, with only a few key species driving the system's dynamics. Recently, an ecosystem regime shift was described having pronounced changes at all trophic levels, mainly the result of climate-induced changes in salinity and temperature (Alheit *et al.*, 2005; Möllmann *et al.*, 2006). The clearest dominance changes in the ecosystem occurred at the zooplankton and fish trophic levels. In the zooplankton, dominance changed between the copepods *Pseudocalanus acuspes* and *Acartia* spp. (Möllmann *et al.*, 2003). Change in hydrography also affected the reproductive success of the major fish species, resulting in a change in dominance from the piscivorous cod (*Gadus morhua*) to the planktivorous sprat (*Sprattus sprattus*; Köster *et al.*, 2003).

First, we investigate the occurrence of regime shifts in time-series of key abiotic and biotic variables of the Central Baltic ecosystem. Second, we demonstrate a three-level trophic cascade involving zooplankton. Finally, we model the effects of the abiotic and biotic changes on copepod biomass and recruitment of fish stocks. Our results demonstrate the linkage between climate-induced zooplankton and fish regime changes, and how overfishing amplifies the climate-induced changes at both trophic levels. Further, our study demonstrates (i) the multiple pathways along which climatic and anthropogenic pressures can propagate through the foodweb; (ii) how both effects act synergistically to cause and stabilize regime changes; and (iii) the crucial role of zooplankton in mediating these ecosystem changes.

Material and methods

Data

Because of limitations in the availability of the best data, we used time-series covering the period 1974–2005 in our analyses. Data for the copepods *P. acuspes* and *Acartia* spp. were collected in spring (mainly May) in the Gotland Basin (Figure 1), being largely representative for the entire Central Baltic (see Möllmann *et al.*, 2000; also for the sampling protocol), by the Latvian Fish Resources Agency (LatFRA) in Riga. Based on earlier knowledge, spring salinity in the halocline (80–100 m) was used as a predictor for *P. acuspes*, whereas spring temperature in the midwater (40–60 m) was used as a predictor for *Acartia* spp. biomass (Möllmann *et al.*, 2003). Depth ranges are used according to the vertical distribution of the copepods (Hansen *et al.*, 2006). In addition, we used dinoflagellates as a predictor for *Acartia* spp. biomass because it is an important food item (Peters, 2006) and promotes successful reproduction of the copepod (E. Gorokhova, pers. comm.).

Midwater temperature (40–60 m) was used to model sprat recruitment because it is known to influence egg and larval survival (Nissling, 2004). We also used the reproductive volume (RV) as a predictor for cod recruitment. RV is the water volume with a salinity >11 psu and an oxygen content >2 ml l⁻¹, representing the minimal conditions for successful cod egg development in the deep Baltic basins (MacKenzie *et al.*, 2000; Köster *et al.*, 2005). *Pseudocalanus acuspes* and *Acartia* spp. data were used in recruitment–environment models as variables influencing cod and sprat larval survival, respectively (Hinrichsen *et al.*, 2002; Voss *et al.*, 2003; Dickmann *et al.*, 2007).

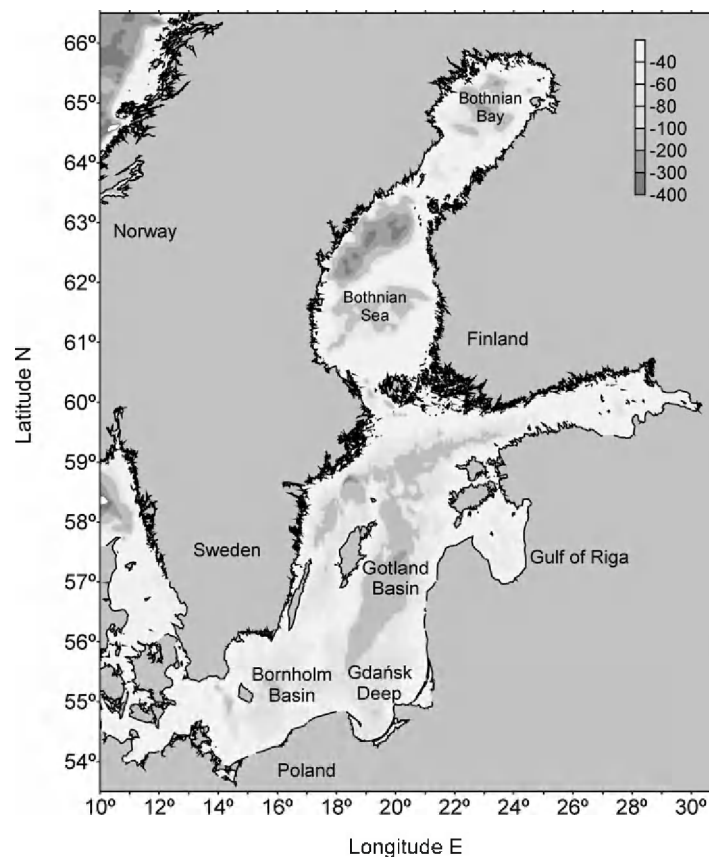


Figure 1. Map of the Baltic Sea with the study area encompassing the deep basins, i.e. Bornholm Basin, Gdańsk Deep, and the Gotland Basin.

All hydrographic as well as zoo- and phytoplankton biomass data are available from a database compiled and held by the ICES/HELCOM Working Group on Integrated Assessments of the Baltic Sea (ICES, 2007). We also accounted for climate effects other than temperature and salinity changes (e.g. drift) by using the winter NAO (North Atlantic Oscillation) index of Hurrell (1995; www.cgd.ucar.edu/cas/jhurrell/indices.data.html#naopcdjfm), the principal component time-series of the leading eigenvector of seasonal (December through March) sea-level pressure anomalies over the Atlantic Sector (20–80°N, 90°W–40°E).

Time-series of stock and spawning-stock biomass (SSB), recruitment at age 0 for cod (generally termed Eastern Baltic cod) and sprat, as well as fishing mortalities, were derived from multispecies virtual population analyses (MSVPA) for ICES Subdivisions 25–29 and 32 (ICES, 2006). MSVPA reconstructs the history of interacting fish stocks, based on landings (catch and individual weight) and survey data. Species interactions are estimated using information on diet, food selection, and consumption rates (Magnusson, 1995).

Numerical analyses

Regime Shifts: the sequential regime-shift detection method was used to identify shifts in the time-series of hydrographic variables, zooplankton and fish biomass, as well as fish recruitment (Rodionov, 2004; Rodionov and Overland, 2005). The method uses *t*-tests sequentially to determine whether 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 (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 targeted on decadal variability, we used *l* = 10. The significance level for the test was always set to *p* = 0.01.

The method used has a number of advantages over other methods for regime-shift detection: (i) it requires no *a priori* hypothesis on the timing of a regime shift; (ii) it can detect both abrupt and gradual regime changes; (iii) it is able to detect a regime shift relatively early (Rodionov and Overland, 2005). However, it has been demonstrated that stationary red noise processes may generate dynamics that can be misinterpreted as regime shifts (Rudnick and Davis, 2003; Rodionov, 2006). As a result, a “prewhitening” procedure has been implemented in the sequential regime-shift detection method that 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). The sequential regime-shift detection method is available as an MS EXCEL add-in and can be downloaded at www.beringclimate.noaa.gov.

Statistical modelling: we investigated the occurrence of a trophic cascade by using general linear models (GLM) of the relationships between cod, sprat, and *P. acuspes* biomass time-series. To account for autocorrelation in the data, the degrees of freedom in the statistical tests were adjusted using an equation by Chelton (1984), modified by Pyper and Peterman (1998).

We found that environmental effects on *Acartia* spp. biomass are best described using linear models as well. First, we used temperature and the NAO to model *Acartia* spp. biomass for the whole period (1974–2005). We also modelled the effect of dinoflagellates

on *Acartia* spp. biomass. Data for the phytoplankton group are only available beginning in 1980, which limited the time horizon for the analyses. We constructed linear models by adding variables subsequently, checking thereafter for autocorrelation of the residuals. If autocorrelation was present, it was removed by first-order differencing, and models were refitted. If an intercept of a model was insignificant, additional models omitting the intercept were fitted. Models were compared using the explained variance (*r*²) and the Akaike information criterion (AIC; Akaike, 1974).

Pseudocalanus acuspes biomass, as well as cod and sprat recruitment, was best modelled using generalized additive models (GAMs; Hastie and Tibshirani, 1990; Wood, 2007). Using the mgcv library of R (Wood, 2001), we estimated the optimal roughness of the smooth terms as well as model structure (i.e. 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 (Wood, 2001, 2004). Hence, a model with the lowest GCV has the highest explanatory power, similar to the AIC (Wood, 2007). No significant autocorrelation has been detected for all fitted models.

We started the modelling of *P. acuspes* biomass with salinity and the NAO, adding sprat biomass thereafter as an indicator of top-down control. Cod and sprat recruitment modelling started using SSB, i.e. the effect of the size of the parent stock only. Thereafter, variables important for egg and larval survival were added, i.e. temperature and *Acartia* spp. for sprat, and the RV and *P. acuspes* for cod. Finally, a potential influence of the NAO was tested.

For copepod species, we used log-biomass as a response variable, whereas for fish species we modelled recruitment, the main process influencing stock biomass affected by bottom-up controls. We used a relative measure of recruitment, i.e. recruitment success, the logarithm of the ratio between the annual numbers of recruits and SSB as response (Stige *et al.*, 2006).

All statistical analyses were conducted using the R software (www.r-project.org).

Results

Trends, pathways, and regimes

Using the regime-shift detection method, we identified corresponding developments between the main hydrographic variables, temperature and salinity, and the key zooplankton and fish species. We detected regime shifts to higher temperatures in 1988 with the new regime lasting until 2003 (Figure 2a). *Acartia* spp. closely followed the shift to increased biomass at the end of the 1980s, but demonstrated an opposite shift at the beginning of this century (Figure 2c). The positive regime shift in sprat biomass occurred with a lag of 2 years in 1990 (Figure 2e). No regime shift was observed in the time-series of sprat recruitment success (Figure 2e).

We found a major regime shift in deep-water salinity to lower values in 1986 and reverse changes in 1996 and 2004 (Figure 2b). *Pseudocalanus acuspes* experienced only one regime change to lower biomass in 1991 (Figure 2d). Cod biomass experienced a regime shift already early in 1984 (Figure 2f). The decline in cod biomass was preceded by reduced recruitment success revealing a regime shift in 1983 (Figure 2f).

Time-series of fishing mortality coefficients demonstrate a variable pattern for sprat with a slight increase since the 1990s in parallel with the stock increase (Figure 2g). Cod fishing pressure was stable until the collapse of the stock in the late 1980s (Figure 2h). Fishing mortalities responded to the collapse of the stock with a lag

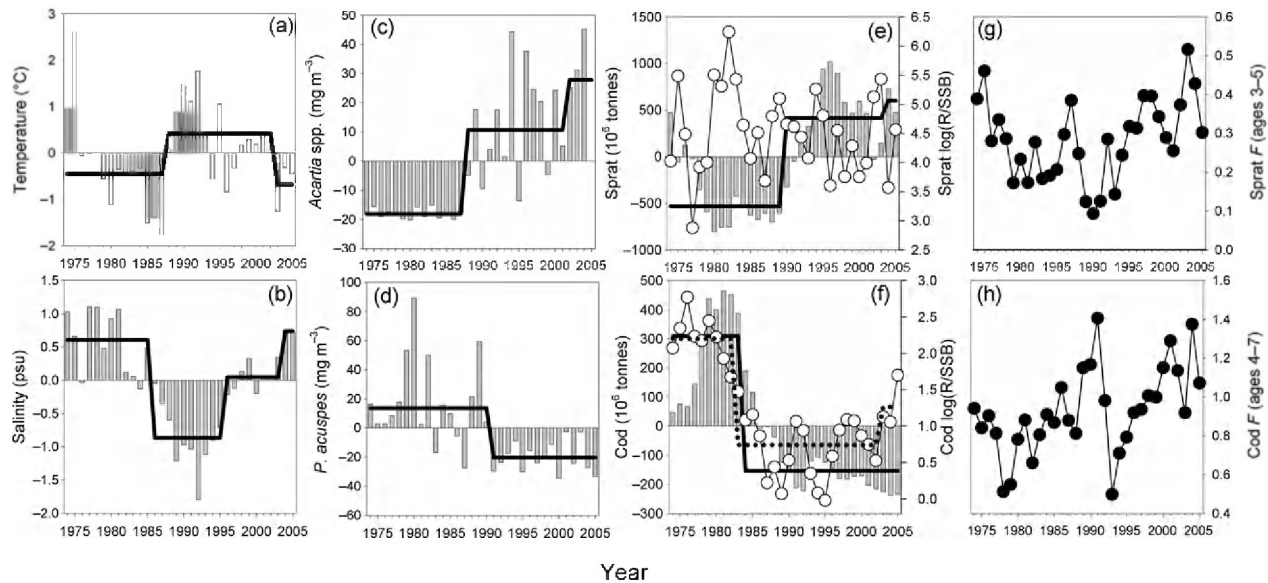


Figure 2. Dynamics of key ecosystem components in relation to hydrography: (a–d) anomaly time-series of salinity, temperature, and biomass of key copepod species (bold lines indicate regimes); (e and f) anomaly time-series of fish biomass (bars) and recruitment success (dots and lines); bold lines indicate biomass regimes; dotted line in (f) indicates regimes in cod recruitment success (no regimes detected for sprat); (g and h) time-series of fishing mortality coefficients (F).

of a few years and increased until the fishing ban in the early 1990s. Thereafter, fishing pressure increased, to the level of the late 1980s since the late 1990s.

The trophic cascade

Our time-series display a species-level trophic cascade involving three trophic levels (Figure 3). The decreasing cod biomass is significantly and negatively correlated with the sprat biomass, indicating top-down control (Figure 3a). Trophic cascading proceeded down to the copepod *P. acuspes*, whose biomass time-series is negatively related to the increased sprat stock (Figure 3b). The cascading effect over two trophic levels is further demonstrated by the significantly positive relationship between cod and *P. acuspes* (Figure 3c).

Bottom-up and top-down effects on *Acartia* spp. and *P. acuspes*

We conducted linear modelling to investigate the effect of environmental variables on *Acartia* spp. (Table 1). The linear models for the full period (1974–2005) explain only small proportions of the variance (maximum 25.5%). The most parsimonious model (lowest AIC) included temperature and the NAO, but excluded the intercept. Including dinoflagellates as an additional predictor, thereby reducing the period covered (1980–2005), resulted in significantly higher r^2 values. The best models included temperature, dinoflagellates, and the NAO; however, the last was not significant (explained variance >43%). Omitting the insignificant intercept resulted in a model that explained >90% of the variance and also displayed the best model quality in terms of the lowest AIC.

Significant predictors for *P. acuspes* biomass in GAMs were salinity and the biomass of the main predator sprat (Table 2). The best model, in terms of the lowest GCV and the largest proportion of the variance explained, also included the NAO.

Recruitment–environment relationships for sprat and cod

SSB was the most important predictor in all recruitment–environment GAMs for both sprat and cod (Table 3). For sprat, we found all other variables, for example, the variables important for egg and larval survival, i.e. temperature and *Acartia* spp. biomass, to be significant predictors of recruitment. Adding the NAO to the model significantly improved model fit. The final model, having the lowest GCV, explained >90% of the variance (Figure 4).

In contrast to sprat, the NAO was not a significant predictor for recruitment–environment models for cod (Table 3). The best model explained >80% of the variance and included, in addition to the SSB, variables influencing egg and larval survival, respectively, i.e. RV and *P. acuspes* biomass (Figure 4).

Discussion

A climate-induced regime shift amplified by a fishing-induced trophic cascade

Our analyses confirmed regime shifts in the biomass of Central Baltic key zooplankton and fish species (Alheit *et al.*, 2005). Two pathways of change could be identified: a decrease in *P. acuspes* and cod, related to decreasing salinity (path 1), and an increase in *Acartia* spp. and sprat (path 2), related to increased temperatures. These regime shifts in the two pathways together caused an ecosystem regime shift, i.e. a major restructuring of the upper trophic levels.

The changes were initiated by the decreased salinity in path 1. As a result, cod recruitment success decreased, followed by a decrease in biomass (Köster *et al.*, 2005). Cod recruitment failure was clearly related to decreased salinities, although the regime-shift detection method indicated a later salinity decrease than observed in recruitment success and biomass. This apparent disagreement was caused by anomalously high salinity in 1985,

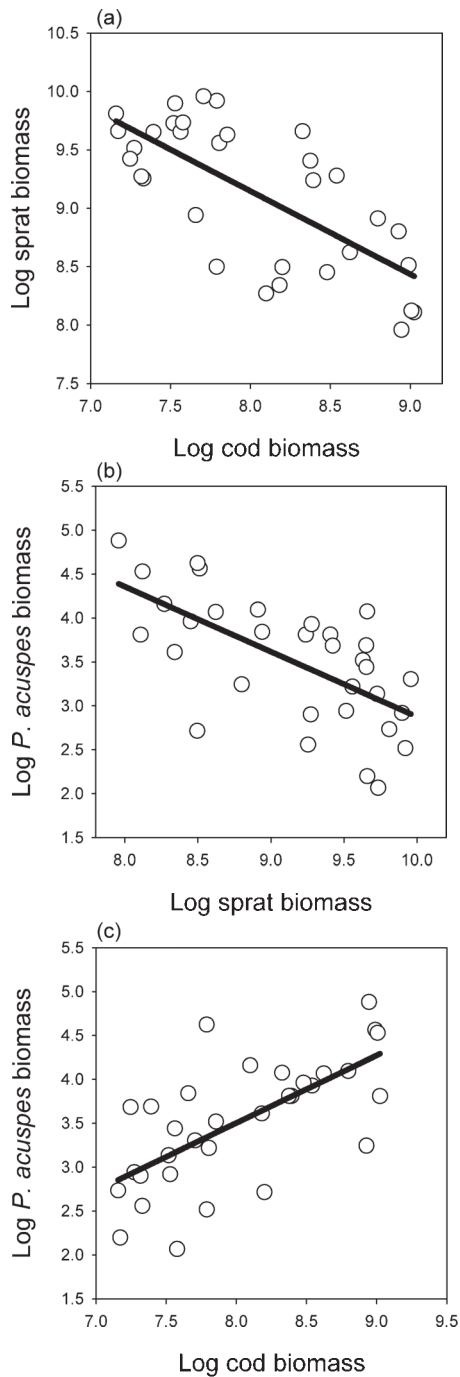


Figure 3. Trophic cascading in the Central Baltic: relationships between (a) sprat and cod biomass ($r^2 = 0.50$, $p < 0.05$); (b) *P. acuspes* and sprat ($r^2 = 0.41$, $p < 0.05$), and (c) *P. acuspes* and cod biomass ($r^2 = 0.46$, $p < 0.05$).

forcing the method to detect the regime shift later, in 1986, although salinity clearly had already decreased before then.

In addition to the changes in path 1, temperature increased at the end of the 1980s, causing changes in path 2. *Acartia* spp. responded immediately to the hydrographic change, whereas the sprat stock reacted with a lag of a few years. No increase in sprat recruitment success was observed, indicating that low predation pressure by the collapsed cod stock leading to a larger SBB was

the main driver for large sprat year classes during the 1990s (Köster *et al.*, 2003).

Clearly, cod fishing amplified, but did not initiate, the collapse of the stock, because fishing mortalities increased only after the decline in biomass had already occurred. Currently, fishing pressure on cod is still high, preventing recovery of the stock and allowing the sprat stock to control the copepod *P. acuspes*, so exerting cascading trophic interactions. Hence, a sequence of events has caused the observed ecosystem regime shift in the Central Baltic Sea, starting with a climate-induced salinity and temperature change and amplified by cod overfishing, cascading down to the zooplankton trophic level.

Although the ecosystem changes in the Baltic fulfil the general definition of a regime shift by occurring on a large geographic scale and over several trophic levels (Collie *et al.*, 2004), the more gradual change in salinity and cod biomass in path 1 does not correspond to the characteristic of an abrupt change. The change in path 1 might, therefore, better be termed a phase transition, where the system flips to another state when passing a threshold (Scheffer and Carpenter, 2003). We found the applied regime-shift detection method especially useful because it was also able to resolve these changes (Rodionov and Overland, 2005). In general, however, we believe that the changes in the Baltic ecosystem can be considered an ecosystem regime shift.

Bottom-up effects of hydrographic change

Our analyses provide evidence that climate-induced salinity and temperature changes initiated the ecosystem regime shift. In this context, path 1 was initiated by the decreasing frequency of major Baltic inflow (MBI) events, starting in the early 1980s (Matthäus and Franck, 1992; Fonselius and Valderrama, 2003). Because of the strong stratification in the deep Baltic basins, saline waters and oxygen can only be introduced by lateral advection from the North Sea. The absence of these events results in low salinities and oxygen deficiency in the deep water. The low salinity has caused the decrease in *P. acuspes*, as demonstrated by our GAMs. The females of this copepod reproduce in spring in the halocline of the deep Central Baltic basins (Hansen *et al.*, 2006). In stagnant conditions, i.e. longer periods without MBIs, reproductive success suffers from the adverse hydrographic conditions (Renz and Hirche, 2006).

The decrease in salinity and oxygen also caused the collapse of the cod stock as a result of low recruitment (Köster *et al.*, 2005). Our GAMs demonstrate that, in addition to the importance of the SSB, the direct effect of hydrography on the eggs, as indexed by the RV (MacKenzie *et al.*, 2000), is also significant. Furthermore, the indirect effect of hydrography through the biomass of *P. acuspes* was confirmed (Hinrichsen *et al.*, 2002), resulting in a model that explained a large proportion of the variance in cod recruitment.

Using a similar GAM approach, an earlier study investigated the effects of SSB and climate on a number of North Atlantic cod stocks (Stige *et al.*, 2006). In contrast to our study, this analysis demonstrated no relationship between recruitment and SSB for Central Baltic cod, called Eastern Baltic cod in their study (see Supplementary Material in Stige *et al.*, 2006). The reason for this difference is most likely the use of different time-series on recruitment and SSB, because our study used output of recruitment at age 0 from a MSVPA, whereas Stige *et al.* (2006) used estimates of recruitment at age 2 from the single-species VPA. Age 0 depends much more on the SSB because a number of factors can

Table 1. Results of linear models relating *Acartia* spp. biomass to environmental variables. If autocorrelation in the residuals was detected, time-series were first-order differenced (DIF) and models refitted. If intercepts (IC) of the models were not significant, models were additionally fitted omitting the IC. AIC, Akaike information criterion, r^2 , explained variance; and p , probability.

Predictors	Period	DIF	IC	AIC	r^2 (%)	p
Temperature*	1974–2005	+	+	74.85	15.1	0.0205
Temperature*+NAO**	1974–2005	+	+	72.80	25.5	0.0161
Temperature*	1974–2005	+	–	73.13	14.9	0.0292
Temperature**+NAO**	1974–2005	+	–	71.07	25.3	0.0145
Temperature*+Dinoflagellates*	1980–2005	–	+	73.12	43.2	0.0015
Temperature*+Dinoflagellates*+NAO	1980–2005	–	+	75.11	43.2	0.0053
Temperature***+Dinoflagellates*	1980–2005	–	–	71.17	92.0	<0.0001
Temperature***+Dinoflagellates*+NAO	1980–2005	–	–	73.17	92.0	<0.0001

* $p < 0.01$; ** $p < 0.05$; *** $p < 0.0001$.

Table 2. GAMs relating *P. acuspes* biomass to environmental variables; GCV, general cross validation criterion; r^2 , explained variance.

Predictors	GCV	r^2 (%)
Salinity*	0.028	63.5
Salinity*, NAO	0.026	75.4
Salinity**, Sprat biomass**	0.022	71.3
Salinity**, Sprat biomass**, NAO	0.020	81.6

* $p < 0.0001$; ** $p < 0.001$.

obscure the relationship during the subsequent 2 years of juvenile Baltic cod (Köster *et al.*, 2005). Furthermore, differences between the studies may have been induced by the different periods covered by the respective datasets (1974–2005 for this study and 1966–2001 for Stige *et al.*, 2006).

Our results further demonstrate that neither *P. acuspes* nor cod biomass increased with the rise in salinity after the inflows in 1993 and 2003. This indicates a change to other processes than pure bottom–up control, i.e. overfishing and top–down control (see below).

The current dominance of path 2 was initiated by the sudden increase in temperature at the end of the 1980s (Alheit *et al.*, 2005). This increase was caused by the change in atmospheric

Table 3. GAMs for recruitment–environment relationships for sprat and cod; GCV, general cross validation criterion; r^2 , explained variance.

Predictors	GCV	r^2 (%)
Sprat		
SSB*	0.448	31.4
SSB*, Temperature*	0.381	55.6
SSB**, Temperature**, NAO**	0.292	87.7
SSB*, Temperature*, <i>Acartia</i> spp.*	0.373	57.5
SSB**, Temperature**, <i>Acartia</i> spp.***, NAO**	0.214	96.6
Cod		
SSB***	0.255	76.2
SSB***, RV	0.242	79.7
SSB***, RV, NAO	0.264	79.7
SSB***, RV*, <i>P. acuspes</i> **	0.187	85.8
SSB**, RV*, <i>P. acuspes</i> ***, NAO	0.205	85.8

* $p < 0.01$; ** $p < 0.001$; *** $p < 0.0001$.

forcing, associated with the sudden increase in the NAO (Hurrell, 1995), and has also caused regime shifts in other areas, such as the North Pacific and the North Sea (Hare and Mantua, 2000; Beaugrand, 2004; Weijerman *et al.*, 2005). In the Baltic, higher temperatures have favoured the development of *Acartia* spp. (Möllmann *et al.*, 2003), as indicated by our linear modelling efforts. Temperature has a direct positive effect on the magnitude of resting egg hatching in Baltic *Acartia* spp. (Alheit *et al.*, 2005). An indirect effect is apparent through the significant effect of dinoflagellates in our models. This phytoplankton group flourished during the 1990s, potentially as a result of reduced winter mixing in this period (Wasmund *et al.*, 1998; Wasmund and Uhlig, 2003). The increased food supply together with accelerated growth in warmer temperatures may thus have caused the increase in *Acartia* spp.

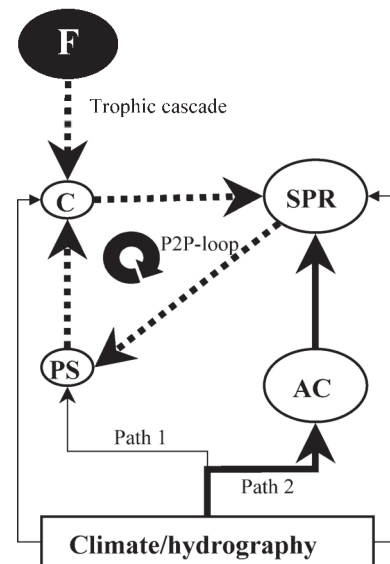


Figure 4. Conceptual model of the changes in the Central Baltic ecosystem: F, fishing pressure; C, cod; SPR, sprat; PS, *P. acuspes*; AC, *Acartia* spp. Thin arrows at the edges symbolize the direct effect of hydrography on cod and sprat recruitment (e.g. on egg and larval survival); path 1 indicates salinity-related trends, whereas path 2 temperature-related ones (bold arrows indicate the current dominance of this path); dotted arrows indicate the trophic cascade and the establishment of the P2P loop.

Warmer ambient conditions further helped the sprat stock to increase to record stock sizes during the 1990s, mainly through high reproductive success (Köster *et al.*, 2003). Temperature directly influences egg and larval survival (Nissling, 2004). Our results further reveal that the increase in *Acartia* spp., which increased larval survival (Voss *et al.*, 2006; Dickmann *et al.*, 2007), contributed to the increase in sprat recruitment. Therefore, on both the salinity and temperature paths, direct and indirect effects of hydrographic change caused the observed restructuring of the ecosystem, with zooplankton species having central importance.

Interestingly, including the NAO in our statistical analyses has only increased the performance of the models for *Acartia* spp. and sprat, but not for *P. acuspes* and cod. This can be explained by the strong vertical habitat segregation in the Central Baltic. Key processes for *Acartia* spp. and sprat occur at intermediate depth, which is strongly affected by NAO-related effects, like warming and changes in circulation. These results are in accordance with a study demonstrating the importance of temperature and transport patterns for the survival of Baltic sprat larvae (Baumann *et al.*, 2006). In contrast, *P. acuspes* and cod depend heavily on the hydrographic conditions in the deep water. Although the absence of MBIs might also be related to the NAO (Hänninen *et al.*, 2000), deep-water conditions are less influenced by the NAO, explaining the marginal importance in our models. Relating the NAO as a proxy for temperature changes (Stige *et al.*, 2006) to cod recruitment therefore seems to be inappropriate for the special case of Eastern Baltic cod.

Top-down effects of cod overfishing

Recently, evidence for indirect effects of overfishing has been reported for large marine ecosystems such as the Eastern Scotian Shelf off Canada (Frank *et al.*, 2005). We could demonstrate a similar trophic cascade, although only for three trophic levels. Overfishing has significantly contributed to the decrease of the Central Baltic cod stock, which cascaded via the sprat stock down to the copepod *P. acuspes* (Möllmann and Köster, 2002; Köster *et al.*, 2005). The trophic cascade has occurred only at the species level, because herring (*Clupea harengus*), the other main food item of cod, has not increased in abundance (Köster *et al.*, 2003). Similarly, other important copepods, such as *Acartia* spp. and *Temora longicornis*, have not suffered from the increase in sprat abundance (Möllmann *et al.*, 2003). This points to the importance of hydrography for Baltic zooplankton and fish populations, as described above. However, our results reveal that top-down effects, potentially caused by an unsustainable fishing pressure on cod, add to the effect of the hydrographic change. Incorporating the biomass of the predator sprat into the GAMs for *P. acuspes* significantly improved the model, demonstrating that both controls acted synergistically in determining the development of the copepod. The importance of top-down control seems to have increased when the new regime was established. We could find no increase in biomass of *P. acuspes* and cod after the MBIs in 1993 and 2003, indicating that fishing and predation effects are now limiting the dynamics of these populations.

Conceptual model of the changes in the Central Baltic ecosystem

We summarized in a conceptual model the different processes that led to the restructuring in the Central Baltic ecosystem (Figure 4). The changes were initiated by the decreasing salinity (path 1),

causing the decline of *P. acuspes* and cod. Increased temperature (path 2) resulted in the increase in *Acartia* spp. and sprat. In addition, high fishing pressure on cod contributed to its decline and cascaded down to *P. acuspes*. Both pathways have established the current regime of *Acartia* spp. and sprat dominance.

Interestingly, these developments established a stabilizing P2P loop. Bakun and Weeks (2006) discuss a similar feedback loop occurring in the Central Baltic via cod egg predation by sprat (Köster and Möllmann, 2000). We demonstrate another P2P loop in the ecosystem: the low cod stock caused the sprat stock to increase, now limiting the main food for cod larvae, i.e. *P. acuspes* (Voss *et al.*, 2003). These feedback loops, together with fishing pressure that is too high, now seem to have stabilized the current regime, an indication of which is the failure of recovery of *P. acuspes* and cod after the MBIs in 1993 and 2003.

Our study reveals that a holistic understanding of both the influence of climate and fishing on ecosystem structure and function is crucial to sound, ecosystem-based fishery management approaches (Bakun, 2006). Therefore, future studies on ecosystem function should consider both drivers, and models for ecosystem-based fishery management should reflect their relative importance and interactions.

In conclusion, our results demonstrate the linkage between climate-induced zooplankton and fish-regime changes, and how overfishing amplified and stabilized the climate-induced changes. Our study demonstrates (i) the multiple pathways along which climatic and anthropogenic pressures can propagate through the foodweb; (ii) how both effects acted synergistically to cause and stabilize regime changes; and (iii) the crucial role of zooplankton in mediating these ecosystem changes.

Acknowledgements

We thank all colleagues involved in the data collection, especially Ludvigs Sirevics (Riga, Latvia), Norbert Wasmund (Warnemünde, Germany), and Eske Teschner (Kiel, Germany). The present study was partly supported by the EU-funded projects UNCOVER and PROTECT, as well as the GLOBEC-GERMANY project, funded by the German Ministry for Education and Research (www.globec-germany.de). Three anonymous referees significantly improved the manuscript.

References

- Akaike, H. 1974. A new look at statistical model identification. *IEEE Transactions on Automatic Control*, AU-19: 716–722.
- Alheit, J., Möllmann, C., Dutz, J., Kornilovs, G., Löwe, P., Mohrholz, V., and Wasmund, N. 2005. Synchronous ecological regime shifts in the Central Baltic and the North Sea in the late 1980s. *ICES Journal of Marine Science*, 62: 1205–1215.
- Bakun, A. 2005. *Regime Shifts*. Ed. by A. R. Robinson, and K. Brink. Harvard University Press, Cambridge, MA.
- Bakun, A. 2006. Wasp-waist populations and marine ecosystem dynamics: navigating the “predator pit” topographies. *Progress in Oceanography*, 68: 271–288.
- Bakun, A., and Weeks, S. J. 2006. Adverse feedback sequences in exploited marine systems: are deliberate interruptive actions warranted? *Fish and Fisheries*, 7: 316–333.
- Baumann, H., Hinrichsen, H.-H., Malzahn, A., Möllmann, C., Köster, F. W., and Temming, A. 2006. Recruitment variability in Baltic sprat, *Sprattus sprattus*, is tightly coupled to temperature and transport patterns affecting the larval and early juvenile stages. *Canadian Journal of Fisheries and Aquatic Sciences*, 63: 2191–2201.

- Beaugrand, G. 2004. The North Sea regime shift: evidence, causes, mechanisms and consequences. *Progress in Oceanography*, 60: 245–262.
- Beaugrand, G., Brander, K. M., Lindley, J. A., Souissi, S., and Reid, P. C. 2003. Plankton effect on cod recruitment in the North Sea. *Nature*, 426: 661–664.
- Beaugrand, G., Reid, P. C., Ibañez, F., Lindley, J. A., and Edwards, M. 2002. Reorganization of North Atlantic marine copepod biodiversity and climate. *Science*, 296: 1692–1694.
- Chelton, D. B. 1984. Commentary: short-term climate variability in the Northeast Pacific Ocean. *In* *The Influence of Ocean Conditions on the Production of Salmonids in the North Pacific*, pp. 87–99. Ed. by W. Pearcy. Oregon State University Press, Corvallis, OR.
- Chiba, S., Tadokoro, K., Sugisaki, H., and Saino, T. 2006. Effects of decadal climate change on zooplankton over the last 50 years in the western Subarctic North Pacific. *Global Change Biology*, 12: 907–920.
- Collie, J. S., Richardson, K., and Steele, J. H. 2004. Regime shifts: can theory illuminate the mechanisms? *Progress in Oceanography*, 60: 281–302.
- Cury, P., and Shannon, L. J. 2004. Regime shifts in the Benguela ecosystem: facts, theories, and hypothesis. *Progress in Oceanography*, 60: 223–243.
- de Young, B., Harris, R., Alheit, J., Beaugrand, G., Mantua, N., and Shannon, L. 2004. Detecting regime shifts in the ocean: data considerations. *Progress in Oceanography*, 60: 143–164.
- Dickmann, M., Möllmann, C., and Voss, R. 2007. Feeding ecology of Central Baltic sprat *Sprattus sprattus* larvae in relation to zooplankton dynamics: implications for survival. *Marine Ecology Progress Series*, 342: 277–289.
- Fonselius, S., and Valderrama, J. 2003. One hundred years of hydrographic measurements in the Baltic Sea. *Journal of Sea Research*, 49: 229–241.
- Frank, K. T., Petrie, B., Choi, J. S., and Leggett, W. C. 2005. Trophic cascades in a formerly cod-dominated ecosystem. *Science*, 308: 1621–1623.
- Frank, K. T., Shackell, N. L., Petrie, B., and Choi, J. S. 2006. Reconciling differences in trophic control in mid-latitude marine ecosystems. *Ecology Letters*, 9: 1–10.
- Fromentin, J.-M., and Planque, B. 1996. *Calanus* and environment in the eastern North Atlantic. 2. Influence of the North Atlantic Oscillation on *C. finmarchicus* and *C. helgolandicus*. *Marine Ecology Progress Series*, 134: 111–118.
- Hänninen, J., Vuorinen, I., and Hjelt, P. 2000. Climatic factors in the Atlantic control the oceanographic and ecological changes in the Baltic Sea. *Limnology and Oceanography*, 45: 703–710.
- Hansen, F. C., Möllmann, C., Schütz, U., and Neumann, T. 2006. Spatio-temporal distribution and production of calanoid copepods in the Central Baltic Sea. *Journal of Plankton Research*, 28: 39–54.
- Hare, S. R., and Mantua, N. J. 2000. Empirical evidence for North Pacific regime shifts in 1977 and 1989. *Progress in Oceanography*, 47: 103–145.
- Hastie, T. J., and Tibshirani, R. J. 1990. *Generalized Additive Models*. Chapman and Hall, London.
- Hinrichsen, H. H., Möllmann, C., Voss, R., Köster, F. W., and Kornilovs, G. 2002. Bio-physical modelling of larval Baltic cod (*Gadus morhua*) survival and growth. *Canadian Journal of Fisheries and Aquatic Sciences*, 59: 1858–1873.
- Hurrell, J. W. 1995. Decadal trends in the North Atlantic Oscillation: regional temperatures and precipitation. *Science*, 269: 676–679.
- Hutchings, J. A. 2000. Collapse and recovery of marine fishes. *Nature*, 406: 882–885.
- ICES. 2006. Report of the Study Group on Multispecies Assessment in the Baltic. ICES Document CM 2006/BCC: 07.
- ICES. 2007. Report of the ICES/HELCOM Working Group on Integrated Assessments of the Baltic Sea. ICES Document CM 2007/BCC: 01.
- Köster, F. W., and Möllmann, C. 2000. Trophodynamic control by clupeid predators on recruitment success in Baltic cod? *ICES Journal of Marine Science*, 57: 310–323.
- Köster, F. W., Möllmann, C., Neuenfeldt, S., Vinther, M., St. John, M. A., Tomkiewicz, J., Voss, R., *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.
- Köster, F. W., Möllmann, C., Hinrichsen, H.-H., Tomkiewicz, J., Wieland, K., Kraus, G., Voss, R., *et al.* 2005. Baltic cod recruitment—the impact of climate and species interaction. *ICES Journal of Marine Science*, 62: 1408–1425.
- Lees, K., Pitois, S., Scott, C., Frid, C., and Mackinson, S. 2006. Characterizing regime shifts in the marine environment. *Fish and Fisheries*, 7: 104–127.
- Lluch-Belda, D., Crawford, R. J., Kawasaki, T., MacCall, A. D., Parrish, R. H., Schwartzlose, R. A., and Smith, P. E. 1989. Worldwide fluctuations in sardine and anchovy stocks: the regime problem. *South African Journal of Marine Science*, 8: 195–205.
- MacKenzie, B. R., Hinrichsen, H.-H., Plikshs, M., Wieland, K., and Zezera, A. S. 2000. Quantifying environmental heterogeneity: habitat size necessary for successful development of cod *Gadus morhua* eggs in the Baltic Sea. *Marine Ecology Progress Series*, 193: 143–156.
- Magnusson, K. G. 1995. An overview of the multispecies VPA—theory and applications. *Reviews in Fish Biology and Fisheries*, 5: 195–212.
- Matthäus, W., and Franck, H. 1992. Characteristics of major Baltic inflows—a statistical analysis. *Continental Shelf Research*, 12: 1375–1400.
- Möllmann, C., Kornilovs, G., and Sidrevics, L. 2000. Long-term dynamics of main mesozooplankton species in the Central Baltic Sea. *Journal of Plankton Research*, 22: 2015–2038.
- Möllmann, C., and Köster, F. W. 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, F. W., Kornilovs, G., and Sidrevics, L. 2003. Interannual variability in population dynamics of calanoid copepods in the Central Baltic Sea. *ICES Marine Science Symposia*, 219: 220–230.
- Möllmann, C., Kornilovs, G., Fetter, M., and Köster, F. W. 2005. Climate, zooplankton, and pelagic fish growth in the Central Baltic Sea. *ICES Journal of Marine Science*, 62: 1270–1280.
- Möllmann, C., Müller-Karulis, B., Diekmann, R., Flinkman, J., Kornilovs, G., Lysiak-Pastuszak, E., Modin, J., *et al.* 2006. An integrated ecosystem assessment of the Central Baltic Sea and the Gulf of Riga. ICES Document CM 2006/P: 03.
- Myers, R. A., Baum, J. K., Shepherd, T. D., Powers, S. P., and Peterson, C. H. 2007. Cascading effects of the loss of apex predatory sharks from a coastal ocean. *Science*, 315: 1846–1850.
- Nissling, A. 2004. Effects of temperature on egg and larval survival of cod (*Gadus morhua*) and sprat (*Sprattus sprattus*) in the Baltic Sea—implications for stock development. *Hydrobiologia*, 514: 115–123.
- Peters, J. 2006. Lipids in key copepod species of the Baltic Sea and North Sea—implications for life cycles, trophodynamics and food quality. PhD thesis, University of Bremen. 177 pp.
- Pyper, B. J., and Peterman, R. M. 1998. Comparison of methods to account for autocorrelation in correlation analyses of fish data. *Canadian Journal of Fisheries and Aquatic Sciences*, 55: 2127–2210.
- Renz, J., and Hirche, J. 2006. Life-cycle of *Pseudocalanus acuspes* Giesbrecht (Copepoda, Calanoida) in the Central Baltic Sea: I. Seasonal and spatial distribution. *Marine Biology*, 148: 567–580.

- Rodionov, S. N. 2004. A sequential algorithm for testing climate regime shifts. *Geophysical Research Letters*, 31: L09204; doi: 10.1029/2004GL019448.
- Rodionov, S. N. 2006. The use of prewhitening in climate regime shift detection. *Geophysical Research Letters*, 31: L12707; doi: 10.1029/2006GL025904.
- Rodionov, S. N., and Overland, J. E. 2005. Application of a sequential regime shift detection method to the Bering Sea ecosystem. *ICES Journal of Marine Science*, 62: 328–332.
- Rudnick, D. L., and Davis, R. E. 2003. Red noise and regime shifts. *Deep Sea Research I*, 50: 691–699.
- Scheffer, M., and Carpenter, S. R. 2003. Catastrophic regime shifts in ecosystems: linking theory to observation. *Trends in Ecology and Evolution*, 18: 648–656.
- Steele, J. H., and Schumacher, M. 2000. Ecosystem structure before fishing. *Fisheries Research*, 44: 201–205.
- Stige, L. C., Ottersen, G., Brander, K., Chan, K-S., and Stenseth, N. C. 2006. Cod and climate: effect of the North Atlantic Oscillation on recruitment in the North Atlantic. *Marine Ecology Progress Series*, 325: 227–241.
- Voss, R., Clemmesen, C., Baumann, H., and Hinrichsen, H. 2006. Baltic sprat larvae: coupling food availability, larval condition and survival. *Marine Ecology Progress Series*, 308: 243–254.
- Voss, R., Köster, F. W., and Dickmann, M. 2003. Comparing the feeding habits of co-occurring sprat (*Sprattus sprattus*) and cod (*Gadus morhua*) larvae in the Bornholm Basin, Baltic Sea. *Fisheries Research*, 63: 97–111.
- Wasmund, N., Nausch, G., and 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., and Uhlig, S. 2003. Phytoplankton trends in the Baltic Sea. *ICES Journal of Marine Science*, 60: 177–186.
- Weijerman, M., Lindeboom, H., and Zuur, A. F. 2005. Regime shifts in marine ecosystems of the North and Wadden Sea. *Marine Ecology Progress Series*, 298: 21–39.
- Wood, S. N. 2001. mgcv: GAMs and generalized ridge regression for R. *R News*, 1–2: 20–25.
- Wood, S. N. 2004. Stable and efficient multiple smoothing parameter estimation for generalized additive models. *Journal of the American Statistical Association*, 99: 673–686.
- Wood, S. N. 2007. *Generalized Additive Models—An Introduction with R*. Chapman and Hall, London.

doi:10.1093/icesjms/fsm197