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REPORT

Has eutrophication promoted forage fish production in the Baltic Sea?

Margit Eero, Helén C. Andersson, Elin Almroth-Rosell,
Brian R. MacKenzie

Abstract Reducing anthropogenic nutrient inputs is a major policy goal for restoring good environmental status of coastal marine ecosystems. However, it is unclear to what extent reducing nutrients would also lower fish production and fisheries yields. Empirical examples of changes in nutrient loads and concurrent fish production can provide useful insights to this question. In this paper, we investigate to what extent a multi-fold increase in nutrient loads from the 1950s to 1980s enhanced forage fish production in the Baltic Sea. We use monitoring data on fish stock dynamics covering the period of the nutrient increase, combined with nutrient concentrations from a 3-dimensional coupled physical-biogeochemical ocean model. The results suggest that nutrient enrichment enhanced the biomass level of forage fish by up to 50 % in some years and areas due to increased body weight of fish. However, the trends in fish biomasses were generally decoupled from changes in nutrient concentrations.

Keywords Nutrients · Fish production · Recruitment · Body weight

INTRODUCTION

Anthropogenic nutrient enrichment and resulting eutrophication is considered as one of the major human perturbations to marine ecosystems worldwide (e.g. Carpenter et al. 1998; Smith et al. 1999). Eutrophication is generally associated with negative impacts on the environment, such as toxic algal blooms, degradation of habitats, oxygen

deficiency and fish kills (e.g. Kemp et al. 2005; Anderson et al. 2008; Díaz and Rosenberg 2008). Consequently, minimizing human-induced eutrophication is necessary in order to achieve good environmental status of marine ecosystems. The historical, non-impacted status is often used as a basis for defining targets for nutrient reductions (e.g. HELCOM 2007). In this context, it is relevant to consider whether lowering nutrient concentrations to historical in some cases oligotrophic levels would involve tradeoffs in terms of potentially reduced fish production and subsequent fisheries yields.

The main undoubted effect of nutrient enrichment is elevated levels of primary production (e.g. Kerr and Ryder 1992). Regarding the effect of nutrients on secondary production, the views and evidences are diverse. Up to a certain level of nutrients, positive effects on fish production can be expected following the principles of an agricultural model, where the amount of production is determined by the food available (Nixon and Buckley 2002). However, the cascading effects of changes in nutrients and primary productivity on fish biomasses are often not apparent in empirical data or are difficult to demonstrate (Micheli 1999). However, several studies comparing nutrient levels or primary production with fish production or fisheries yields suggest that such relation may exist (e.g. Ware and Thomson 2005; Chassot et al. 2007, 2010).

The Baltic Sea offers a unique opportunity for such investigations due to long time series of observational data on fish production that span over a period of substantial increase in nutrient inputs. In the Baltic Sea, eutrophication first became an issue after World War II, when intensified agriculture with high fertilizer usage, lack of proper wastewater treatment and atmospheric deposition caused a dramatic nutrient-load increase over a few decades from the 1950s to 1980s (Jansson and Dahlberg 1999; Elmgren

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2001). Catches of forage fish, i.e. sprat (*Sprattus sprattus*) and herring (*Clupea harengus*), increased simultaneously from about 100 kt in the first half of the 1950s to above 500 kt in the mid-1980s, which could be considered as an effect of increased nutrient inputs (e.g. Österblom et al. 2007). However, fisheries landings can be influenced by various other mechanisms besides resource availability (Mcowen et al. 2015). A recent reconstruction of sprat dynamics, in fact, revealed a substantial decline in sprat biomass from the late 1960s to 1980s (Eero 2012), in contrast to increasing nutrient concentrations (Fig. 1). Dedicated analyses of individual components of fish production are therefore needed in order to elucidate the potential effects of increased nutrient availability.

In this paper, we assemble observational evidence for changes in recruitment (i.e. production of offspring) and individual growth of major forage fish species in the Baltic Sea, i.e. sprat and herring in the period from the 1950s to 1980s. We combine this information with nutrient concentrations from a 3-dimensional coupled physical-biogeochemical ocean model and investigate whether positive effects of nutrient enhancement on fish production potentially occurred. The present study provides useful insights to whether reduced fish production can be expected if historical trophic status of the sea is restored, and can contribute to defining good environmental status in a wider ecosystem context.

MATERIALS AND METHODS

Data sources

Fish biomasses are determined by a combination of recruitment, individual growth and mortality. Nutrients are expected to impact on adult fish biomass mainly via recruitment and growth, while biomasses of forage fish in the Baltic Sea are additionally heavily influenced by mortality due to fishing and predation by cod (Köster et al. 2003). In order to minimize the effect of mortality interfering with biomass dynamics, we investigated the potential effect of nutrient increase separately on recruitment and growth. The analyses used biomass and recruitment estimates of sprat that were available back to the 1950s (Eero 2012), separately for three sub-regions, i.e. (i) Western Baltic and Bornholm Basin, (ii) Gdansk and Gotland Basins and (iii) northern (N) Baltic Proper (Fig. 2). The borders for the sub-regions were defined based on the Subdivisions used in ICES, and are further referred to as southwest (SW), southeast (SE) and northern (N) Baltic Proper, respectively. For herring, estimates of population dynamics covering the period of nutrient increase from the 1950s to 1980s were available only for the northern Baltic Proper (Ojaveer 2003). Growth was represented by mean body weight of fish with observations originating roughly from the same sub-regions as the biomass and recruitment

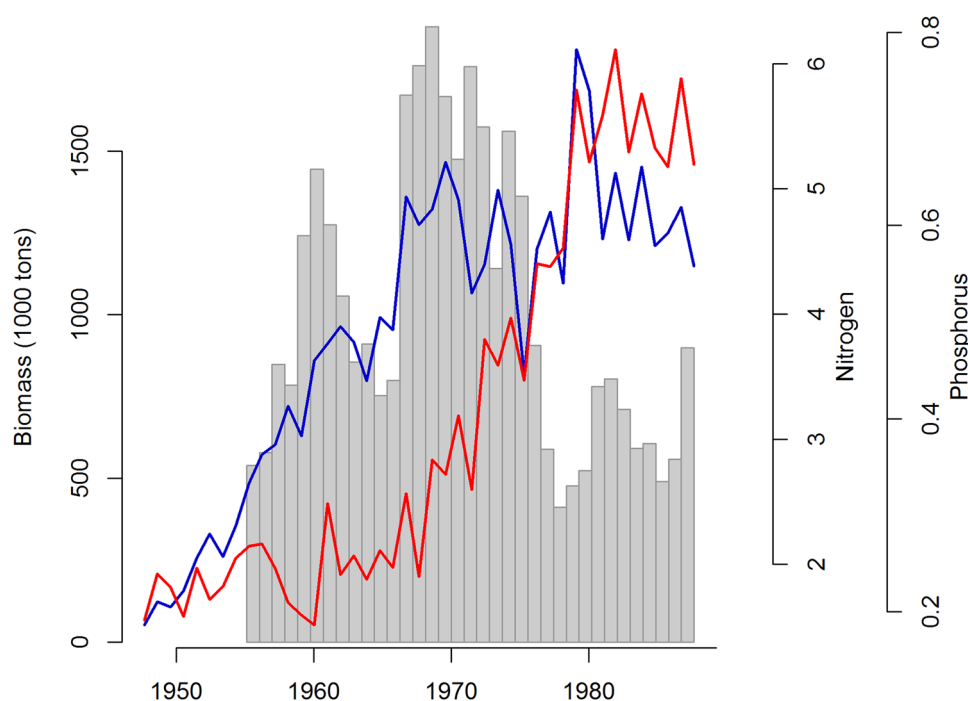**Fig. 1** Development of winter nitrogen (*blue line*) and phosphorus (*red line*) concentrations (mmol m3^{-1}) in the Baltic Sea (average of sub-areas, based on results from this study) in comparison with trends in sprat biomass (*bars*) (Eero 2012)
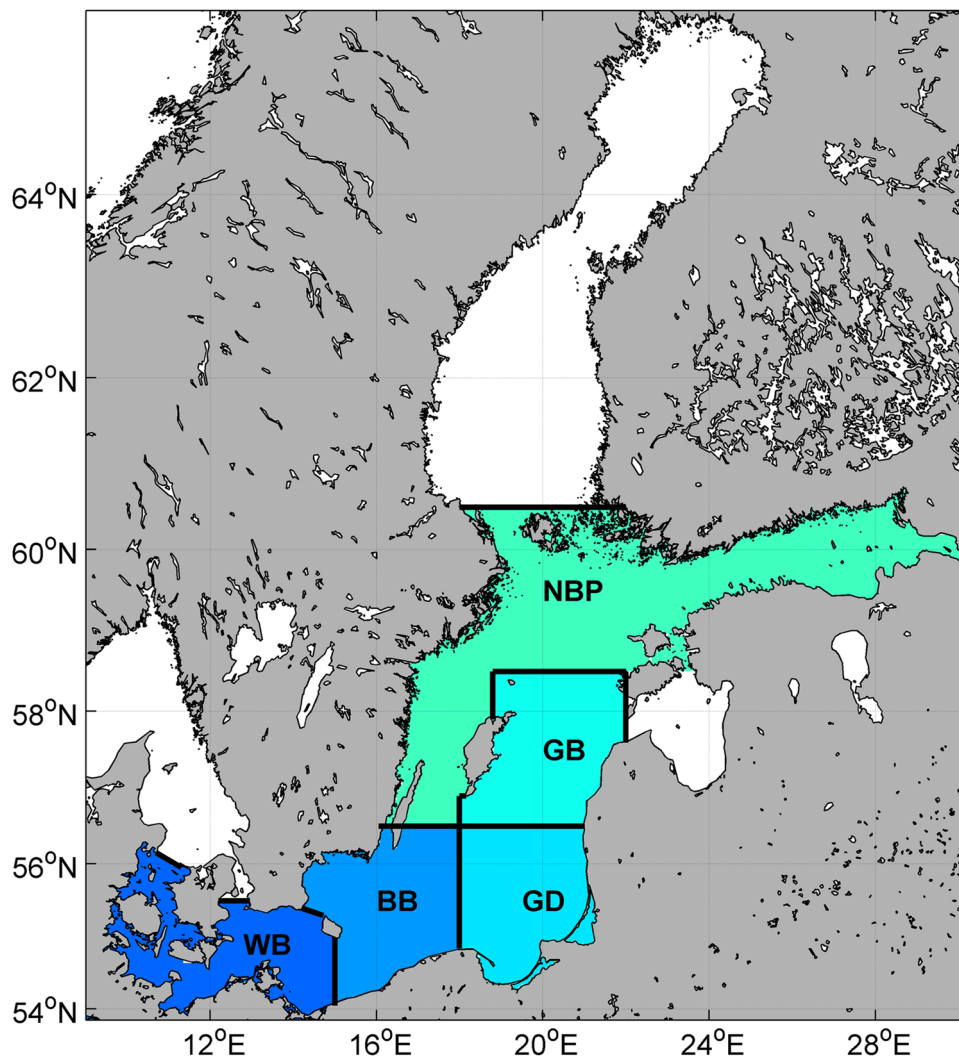
Fig. 2 Map of the Baltic Sea showing the sub-regions referred to in the paper: *WB* Western Baltic; *BB* Bornholm Basin; *GD* Gdansk Deep; *GB* Gotland Basin; and *NBP* Northern Baltic Proper

estimates. The temporal and spatial coverage of the data used and data sources are provided in Table S1.

Recruitment and mean weight of sprat and herring in the Baltic Sea are influenced by a number of environmental and ecological factors, in addition to the potential effect of nutrients. Environmental variables used in the analyses (Table S1) included sea surface temperature (SST) and average temperature and salinity in the 0–50 m water layer. Additionally, the Baltic Sea environmental index (BSE) was used, which consists of the Arctic oscillation index, the salinity between 120 and 200 m in the Gotland Sea, the integrated river runoff into the Baltic Sea and the relative vorticity of geostrophic wind over the Baltic Sea area (Dippner et al. 2012). Average winter values (December–February) of nitrogen (Nc) and phosphorus (Pc) concentrations in the surface layers (0–9 m) at different sub-areas (Fig. S1) were extracted from the Swedish Coastal and

Ocean Biogeochemical model coupled to the Rossby Centre Ocean circulation model (RCO-SCOBI). The model system is described in Eilola et al. (2009) and Meier et al. (2003) and has been used in various ocean-climate and process studies. A brief description of the model is provided in the electronic supplementary material.

Analyses of changes in mean body weight of fish

Annual mean weight (W) of fish, averaged over specific age classes (Table S1), was used to represent inter-annual changes in body weight. This is following similar approach as used by Casini et al. (2010), as the trends in mean weights of different age-groups of a species were similar. Previous studies focusing on recent decades have related the weight of sprat and herring in the Baltic Sea to temperature, salinity and sprat abundance via intra-specific

competition (Cardinale et al. 2002; Möllmann et al. 2005; Casini et al. 2010). Based on this knowledge, at first step, region-specific temperature and salinity at 0–50 m depth in spring–summer and sprat abundance were included as explanatory variables for mean weight of both sprat and herring in all sub-areas, in addition to Nc and Pc. Analyses of temporal changes in mean weight were conducted using multiple linear regressions that have a generic form:

$$W = a_0 + a_1 * \text{Var1} + a_2 * \text{Var2} + \varepsilon, \qquad (1)$$

where a_0, a_1 and a_2 are model parameters and Var1 and Var2 are explanatory variables. The number of elements in specific models depends on the number of explanatory variables (*Var*) included. Non-significant variables were removed from final models, except for Nc and Pc that were kept in order to demonstrate their level of significance.

Recruitment analyses

Recruitment of forage fish in the Baltic Sea, especially sprat, shows high inter-annual variability. Earlier studies covering the period from the 1970s onwards have identified a number of processes and variables influencing sprat recruitment, such as climate variability, transport of larvae, food availability and predation on early life stages (Voss et al. 2012 and references therein). Also, the size of the parent stock is traditionally considered to affect the amount of offspring. Among the variables investigated, sprat recruitment in a Baltic wide scale has been found to be most correlated with SST in summer that affects the recruitment possibly via impacting on feeding and growth of early life stages (e.g. Margonski et al. 2010). SST has also been found to influence herring recruitment in the central Baltic Sea (Margonski et al. 2010). In a more coastal environment, such as the Gulf of Riga, herring recruitment has been related to the Baltic Sea index (BSI), which is the difference of normalized sea level pressures between Oslo, Norway and Szczecin, Poland (Lehmann et al. 2002). Based on this knowledge, region-specific SST in summer (August), Baltic Sea environmental index (BSE) and spawning stock biomass (SSB) were included as explanatory variables in recruitment (*R*) models, both for sprat and herring. We used the more recently developed climate index BSE that shows a better performance than other climate indices such as BSI (Dippner et al. 2012). Additionally, Nc and Pc were included in recruitment models to explore their significance in explaining recruitment fluctuations. A standard stock-recruitment model (Ricker 1954) was applied, incorporating environmental variables. The model has a generic form:

$$R = a * \text{SSB} * \exp(b * \text{SSB} + c * \text{env}), \qquad (2)$$

where *a*, *b* and *c* are model parameters, and *env* represents an environmental variable. The number of elements in specific models depends on the number of environmental variables (*env*) included. Similarly to the analyses of mean weight, non-significant variables were removed from final models, except for Nc and Pc that were kept in order to demonstrate their significance levels.

Quantifying the contribution of nutrient increase in the 1950s–1980s to sprat biomass

In a next step, we calculated what the biomass of sprat in the Baltic Sea in the period from the 1950s to 1990s would have been if the observed nutrient increase would not have taken place, using the results from the mean weight and recruitment analyses described above. To eliminate the effect of nutrient increase in the 1950s–1980s, the nutrient concentrations in this period were kept constant at the level estimated for the beginning of the analysed time series. These adjusted nutrient concentrations were then entered in the regression models for mean weight (described above) to derive the adjusted fitted values for mean weight ($W_{\text{fitted\_adj}}$). The ratio between $W_{\text{fitted\_adj}}$ and the fitted weights from the original model using the realized nutrient levels (W_{fitted}) was used as a factor to adjust the observed mean weights (W_{obs}):

$$W_{\text{adj}} = W_{\text{obs}} * \frac{W_{\text{fitted\_adj}}}{W_{\text{fitted}}}. \qquad (3)$$

Changes in mean weight impact on biomass in two ways, i.e. (i) directly, as a larger body weight of individual fish results in a higher biomass, and (ii) indirectly through recruitment, given that a larger spawner biomass produces a higher recruitment. To account for the indirect effects of changes in mean weight on recruitment, the stock-recruitment models (described above) were fitted again using the spawner biomass values adjusted for W_{adj} (SSB_{adj}). The ratio between the fitted recruitment ($R_{\text{fitted\_adj}}$) from the model using SSB_{adj} and the recruitment from the model with observed SSB (R_{fitted}) was used as a factor to adjust the observed recruitment values (R_{obs}):

$$R_{\text{adj}} = R_{\text{obs}} * \frac{R_{\text{fitted\_adj}}}{R_{\text{fitted}}}. \qquad (4)$$

These analyses did not account for direct impacts of nutrient increase on recruitment as nutrients were not found to explain significant amounts of variability in recruitment dynamics in the recruitment analyses described above (see "Results" section).

Finally, simulations of sprat stock development from the 1950s to 1990s were performed using the adjusted mean

weight (W_{adj}) and recruitment values (R_{adj}) corresponding to constant nutrient concentrations at the level of the 1950s. The simulations used observed stock numbers in 1956 as a starting point and applied fishing and natural mortalities from the original stock assessments for the three sub-regions, i.e. SW, SE and N Baltic Proper (Eero 2012). The stock numbers were projected forward in time using the standard stock numbers at age equation (e.g. Haddon 2001).

RESULTS

Nutrient concentrations and mean body weight of sprat and herring

The nutrient levels estimated from the RCO-SCOBI model show a fivefold increase in nitrogen concentration (Nc) from the 1950 to early 1970s, after which concentrations fluctuated without a trend. The concentration of phosphorus (Pc) was relatively stable from the 1950s to 1970s, but increased three to four times from the beginning of the 1970s to the first half of the 1980s when it levelled off (Fig. 1). The increase is visible in all areas of the Baltic Sea, although the absolute levels vary by sub-regions (Figs. S1, S2).

The mean body weight of sprat (average of ages 3–6) in SW and SE Baltic Sea was approximately 10–15 % higher in the 1970s–1980s compared to the early 1950s (Fig. 3a, b). A more pronounced increase in mean weight was recorded in the northern Baltic Proper, where an average sprat was up to 1.7 times heavier in the mid-1980s compared to the early 1960s (Fig. 3c). A similar increase in mean weight (average of ages 2 and 4) was recorded for herring in the northern Baltic, where the data extending back to 1948 show stable mean weights until the mid-1960s and an increase to approximately 1.5 times higher weights in the 1970s (Fig. 3d). The positive trends in both sprat and herring body weight in the 1970s–1980s coincided with the pronounced increase in Pc. Accordingly, Pc was found to explain significant amount of variability in mean weight of both sprat and herring in all sub-areas (Table 1). Nc was significant only for herring in the northern Baltic Sea. Changes in sprat weight in SE and N Baltic were additionally found to be correlated with temperature and sprat abundance, respectively (Table 1).

Nutrient concentrations and recruitment of sprat and herring

Sprat recruitment models including SSB and SST as explanatory variables explained significant amounts of recruitment variability in all three sub-regions in the Baltic Proper. In the northernmost area, including additionally BSE as an explanatory variable significantly improved the explained variability in recruitment (Table 2). For herring in the northern Baltic, SST was not found to be significant and the final model therefore only included SSB and BSE as explanatory variables. Nc and Pc did not appear significant in any of the recruitment models. The effect of nutrients on recruitment was tested both on longer (1957–2010) and shorter time series until 1987 (results not shown), with similar results. Indirectly, the nutrient increase was found to have affected recruitment via mean weight of individual fish (see above) that enhanced the biomass, which in turn influenced recruitment.

The fitted recruitment models were able to describe sprat recruitment dynamics relatively well in SW and SE Baltic Proper (Fig. 4a, b). In the north, the magnitude of variation between year-classes and single events of outstanding year-classes were often not well captured by the recruitment model that generally underestimated recruitment in these years (Fig. 4c). These strong year-classes occurred mainly in the beginning of the time series and are therefore unlikely resulting from increased nutrients but probably are related to some other unaccounted processes. For herring, major long-term variations in recruitment were captured by SSB and BSE (Fig. 4d). The residuals of the recruitment models did not reveal significant trends ($p < 0.1$) for any of the areas or species, besides sprat in the northern Baltic, where recruitment was underestimated in the beginning of the time series in the 1960s, resulting in a significant trend from positive to negative residuals (Fig. S3).

Impact of nutrient increase on sprat biomass

The increase in nutrients from the 1950s to 1980s coincided with increased body weight of both sprat and herring. Changes in body weight of individual fish modify the biomass directly. Additionally, given that a larger SSB produces a higher recruitment, the increase in mean body weight promotes the stock further via enhanced recruitment. Both of these processes were taken into account when simulating sprat biomass dynamics under stable nutrient concentrations from the 1950s. The simulated biomass dynamics in terms of major fluctuations in stock size were similar to the estimates from original stock assessment (Fig. 5a–c). However, the proportional difference between the two time series increased from the 1950s to 1980s and reached up to 50 % (in the 1980s) higher observed sprat biomass in northern Baltic Sea compared to the simulated scenario with no increase in nutrients (Fig. 5f). The relative effect of nutrient increase on biomass was lower in SW and SE, up to 30 and 40 %, respectively
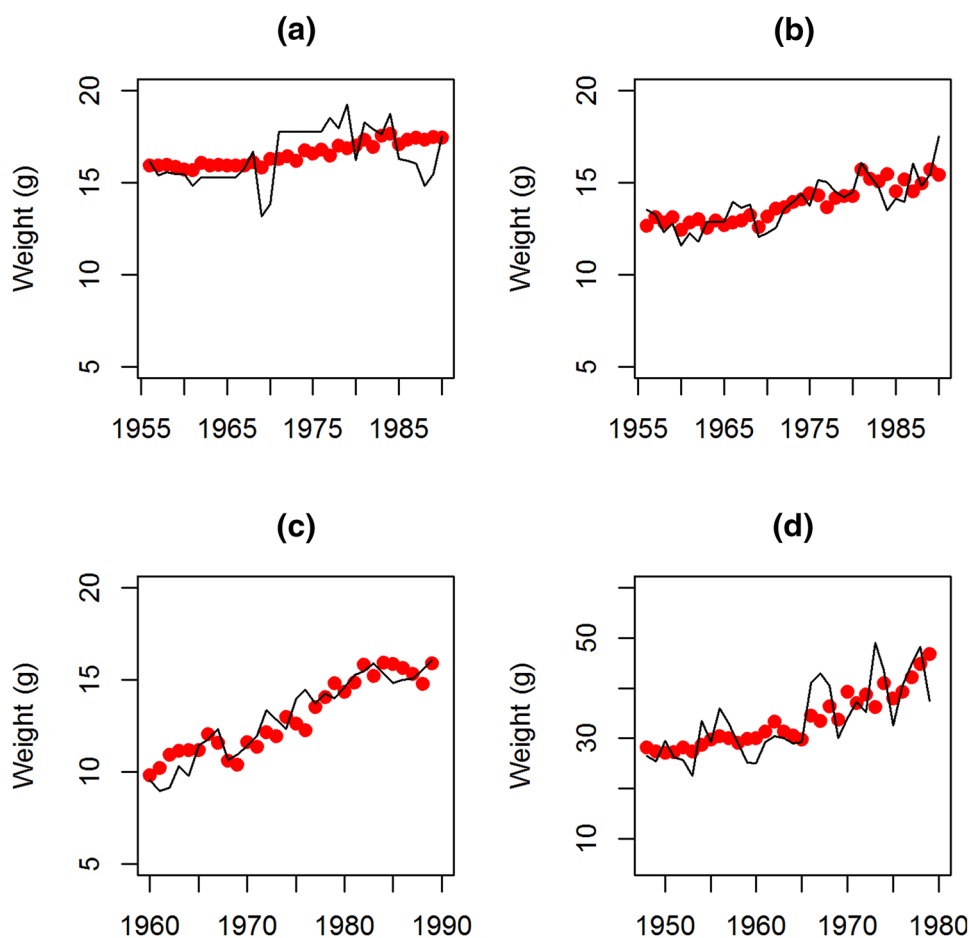
Fig. 3 Mean weight of sprat (**a–c**) and herring (**d**) predicted from regression models (*red dots*) compared to the observed values (*lines*) in southwestern (**a**), southeastern (**b**) and northern (**c, d**) areas in the Baltic Proper

Table 1 The variables significantly (*$p < 0.05$) correlated with mean weight of sprat and herring in southwestern (SW), southeastern (SE) and northern (N) areas of the Baltic Proper in the period from the 1950s to 1990s. The level of significance (*p* value) of nitrogen (Nc) and phosphorus (Pc) concentrations is presented for all regression models

Species	Area	Years	Variables	*p* value
Sprat	SW	1953–1990	Nc	>0.1
			Pc	<0.01*
Sprat	SE	1954–1990	Nc	>0.1
			Pc	<0.01*
			Temperature	0.093
Sprat	N	1960–1989	Sprat abundance	<0.05*
			Nc	>0.1
			Pc	<0.01*
Herring	N	1948–1979	Nc	<0.05*
			Pc	<0.01*

(Fig. 5d, e). In a scale of the entire Baltic Sea, our simulations of sprat dynamics applying constant nutrient concentrations resulted in up to 40 % lower biomass (in the 1980s) compared to the observed level.

DISCUSSION

Marine fish species in the Baltic Sea are living at conditions close to their tolerance boundaries and their

Table 2 The variables explaining significant (*$p < 0.05$) amount of variability in sprat and herring recruitment in southwestern (SW), south-eastern (SE) and northern (N) areas of the Baltic Proper (spawning stock biomass (SSB), seas surface temperature (SST), Baltic Sea environmental index (BSE)). The level of significance (p value) of nitrogen (Nc) and phosphorus (Pc) concentrations is presented for all recruitment models

Species	Area	Years	Variables	P value
Sprat	SW	1957–2010	SSB, SST	<0.01*
		1957–2010	Nc	>0.1
		1957–2010	Pc	>0.1
Sprat	SE	1957–2010	SSB, SST	<0.01*
		1957–2010	Nc	>0.1
		1957–2010	Pc	>0.1
Sprat	N	1957–2010	SSB	0.041*
		1957–2010	SST	<0.01*
		1957–2010	BSE	0.019*
		1957–2010	Nc	>0.1
		1957–2010	Pc	>0.1
Herring	N	1949–1998	SSB, BSE	<0.01*
		1949–1998	Nc	>0.1
		1949–1998	Pc	>0.1

productivity is influenced by a number of hydrographic and ecosystem drivers (e.g. MacKenzie et al. 2007). Separating out the cause and effect may be possible under controlled experiments, for example in lakes, but is generally extremely difficult in open sea ecosystems. Therefore, large enough contrast in time series is essential to possibly be able to identify an ecosystem response to a change in driver, which would not be detectable at small-scale variability. For this reason, we focus this study on the years from the 1950s to 1980s when the most pronounced increase in nutrient concentrations took place, expecting that if nutrient enrichment has enhanced fish production in the Baltic Sea, this would likely be best detectable in this period. After that, nutrient concentrations stabilized (Fig. 1), while the hydrographic status of the Baltic Sea changed due to lack of frequent major inflows since the late 1980s, which in combination with high nutrient concentrations led to increased hypoxic areas (Meier 2007; Conley et al. 2009). Thus, from this period onwards the negative effects of high nutrient concentrations likely dominate. This is another reason why we focus on the period from the 1950s to 1980s, as we are interested in elucidating whether positive effects of nutrient increase on forage fish production potentially occurred.

There is strong evidence that a massive increase in anthropogenic nutrient load to the Baltic Sea has led to increased spread of hypoxia, decreased water transparency and increased summer cyanobacteria blooms (Andersen et al. 2015 and references therein). The biological effects associated with the onset of increased nutrient discharges are also well documented for coastal zone (Cederwall and

Elmgren 1990 and references therein). However, it has been surprisingly difficult to convincingly demonstrate the biological changes, for example in phytoplankton and zooplankton biomasses, resulting from increased nutrient availability in the open Baltic Proper, in the period from the 1950s to 1980s (see Elmgren 1989; Cederwall and Elmgren 1990 and references therein for a review). This is because few observational series exist that have used identical methods with a sufficient sampling intensity. A few studies have demonstrated an increase in primary production resulting from eutrophication, though the dataseries often started only from the 1970s (Kononen and Niemi 1984; Wulff et al. 1986). Polish data show an increase in zooplankton biomass from the 1950s to 1970s (Cederwall and Elmgren 1990). However, several shorter zooplankton series from other parts of the Baltic Sea have failed to show significant trends, and a reconstruction of mesozooplankton dynamics in different basins of the open Baltic Proper from the 1960s onwards did not reveal increasing trends in zooplankton biomasses until the 1980s (Möllmann et al. 2000). This is probably because zooplankton biomass is greatly influenced by other factors, e.g. variations in water temperature and salinity (Möllmann et al. 2000). A clearly demonstrated biological effect of the increased nutrients was the 3- to 5-fold increase in macrobenthic biomass between 1920/1923 and 1976/1977 in shallower waters not impacted by anoxia (Cederwall and Elmgren 1980).

We recognize that nutrients are not directly influencing secondary production but via food web interactions at lower tropic levels (Sommer et al. 2002). Thus, ideally, the
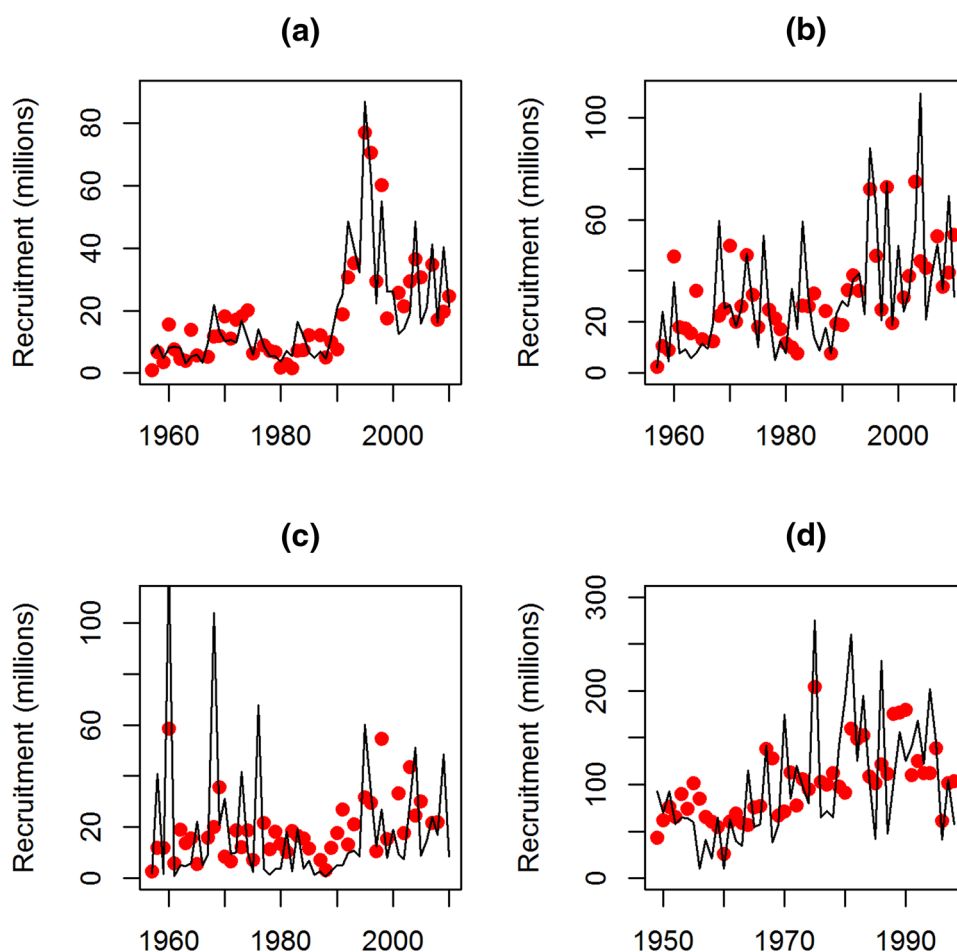
Fig. 4 Recruitment of sprat (**a–c**) and herring (**d**) predicted from stock-recruitment models (*red dots*) compared to the estimates from stock assessment (*lines*) in southwestern (**a**), southeastern (**b**) and northern (**c, d**) areas in the Baltic Proper

investigations of how nutrients have affected fish production should follow the signals of nutrient increase through the entire food web. Due to lack of consistent time series on lower trophic levels covering the period of major nutrient increase, we have chosen an alternative approach in this study. In our approach, we took into account the drivers that have been shown in the literature to have most explanatory power in describing variations in mean weight and recruitment of sprat and herring, and explored whether the remaining unexplained variability could be ascribed to a process with a strong positive trend over time, possibly associated with the observed increase in nutrient concentrations. We evaluated the potential effects of nutrient increase separately on recruitment and mean body weight of fish, which, to our knowledge, has not been done earlier for the open Baltic Sea. Furthermore, in several earlier analyses addressing eutrophication effect on fish stocks (e.g. Österblom et al. 2007), the perception of fish stock dynamics before the 1970s has largely been based on landings that increased in parallel with intensified

eutrophication (Fig. S4). However, changes in fishing intensity and fishing methods that coincided with the onset of eutrophication in the Baltic Sea make the use of landings data as an indicator for changes in fish production difficult (Hansson et al. 2007).

The effect of nutrient concentrations on fish abundances is likely species specific and the effects mediated by recruitment (Massol et al. 2007). In our analyses, recruitment variations of sprat and herring were not associated with the strong increase in nutrient concentrations. Complex processes and interactions involved in regulating food availability and thereby survival of early life stages, such as temporal mismatch between fish larvae and their prey organisms and/or inter-specific competition for prey (Voss et al. 2012) can have contributed to the lack of direct coupling between nutrient increase and recruitment success. In recent decades, most of the variability in especially sprat recruitment has been explained by climatic variables, such as temperature (e.g. Margonski et al. 2010). Our results suggest that climate variability was a dominating
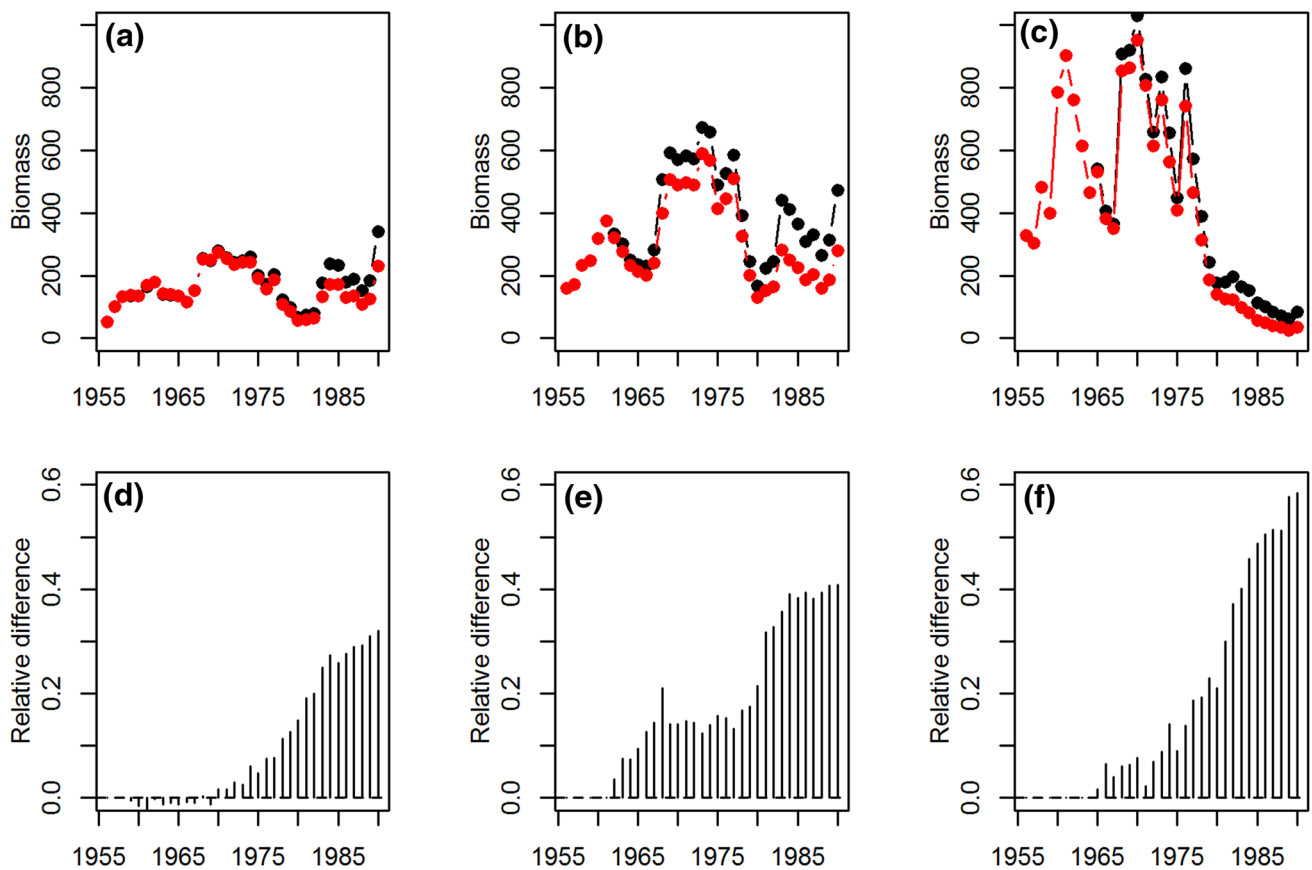
Fig. 5 *Upper panels* simulated sprat biomass (*red line*) applying constant nutrient concentrations from the 1950s compared to the observed biomass (*black line*) as estimated from stock assessment (Eero 2012). *Lower panels* proportional difference between the observed and simulated sprat biomass. The results are shown separately for southwestern (**a**, **d**), southeastern (**b**, **e**) and northern (**c**, **f**) areas of the Baltic Proper

factor in regulating major variations in year-class strength also historically. We recognize that a number of other processes affect fish recruitment that were not taken into account in our analyses, for example intra-specific competition for zooplankton. These unaccounted processes likely constitute the unexplained part of recruitment variability in our analyses. The residuals from recruitment models did not indicate that these unaccounted processes could be associated with nutrient increase. Earlier investigations on cod showed that nutrient increase possibly had a minor positive contribution to cod recruitment in the 1980s (Eero et al. 2011), which suggests that nutrient concentrations may impact different parts of the food web differently.

For adult fish, nutrient enrichment likely improved feeding conditions evidenced by the increased mean body weight of both sprat and herring from the 1950s to 1980s. This is in line with increased fat content in sprat in the southeastern Baltic Sea (Elwertowski et al. 1974). The weights of both sprat and herring in the Baltic Sea have undergone large variations over time, including a substantial decline in the 1990s (Casini et al. 2011 and

references therein). The reasons for this are not fully understood, but the processes likely involved include climate variability affecting the abundance of favoured prey items and competition (Casini et al. 2011). Due to complexity of the processes affecting fish growth, it cannot be excluded that the increase in body weight from the 1950s to 1980s coincidentally occurred in parallel with increased nutrients without being a direct effect of it. This would imply that the contribution of nutrient enrichment to mean weight and thereby to biomass of forage fish may be less than suggested by our analyses. For example, competition for food is represented only by sprat abundance in our analyses, while total clupeid abundance may as well be important. However, long time series of herring abundance are not available for all parts of the Baltic Sea and previous studies have identified significant effect of sprat abundance on growth of both sprat and herring (Möllmann et al. 2005; Casini et al. 2010).

The almost twofold increase of mean body weight of fish in some areas led to up to 40 % higher sprat biomass in the entire Baltic Sea in the 1980s than would have been the case at mean weight values corresponding to constant

nutrient levels from the 1950s (Fig. 5). This supports the findings, for example, from Black Sea where a dramatic increase in nutrient loads in the 1970s appeared to benefit the anchovy (Knowler 2007). Furthermore, positive relations between nutrients and fish biomasses have been found in lakes and semi-enclosed seas (Hanson and Leggett 1982; Bernotas 2002). In contrast, a meta-analysis of experimental and field data concluded that the effects of changes in nutrient availability and primary productivity rarely cascaded upward to affect biomasses of marine pelagic consumers (Micheli 1999). Our results also provide support to the latter hypothesis, as the nearly linear increase in mean weight of fish in parallel with the increase in nutrient concentrations did not translate into a similar trend in biomass. In fact, the sprat biomass declined substantially from the late 1960s–1980s, especially in the northern Baltic Sea, reaching record low levels in the 1980s when the nutrient concentrations were highest (Fig. 1). This is because growth is just one of the processes regulating fish biomasses that additionally are modified by recruitment variability and removals due to predation and fishing (Fig. 6). The decline in sprat biomass in the 1970s was mainly due to a combination of unfavourable climatic conditions for recruitment and high predation pressure from cod (Köster et al. 2003).

In summary, although our analyses suggest that the nutrient increase enhanced the level of sprat biomass via mean weight, this effect appears relatively minor compared to the more than fivefold fluctuations in sprat biomass that have occurred over time due to other drivers (Fig. 1). This makes it difficult to predict future trajectories of fish biomasses resulting from nutrient reduction, as these will probably largely depend on combinations of other drivers. However, nutrient concentrations will likely modify the biomass levels possible to reach under given ecosystem and environmental conditions.

CONCLUSIONS

The state of the Baltic Sea similar to that before the onset of major industrialization in the 1950s is used as a basis for defining targets for nutrient reductions to restore the good ecological status of the Baltic Sea (HELCOM 2007). Empirical evidence suggests that nutrient increase from the 1950s to 1980s enhanced the level of forage fish biomass (up to 40 % in our analyses) in the Baltic Sea via increased body weight of the fish. Thus, nutrient reduction likely will affect the level of lows and peaks in future biomasses. However, major trends in sprat biomass in past decades have occurred independently of nutrient dynamics, largely driven by climate and top-down control (predation, fishing). This suggests that future biomass trajectories may not follow changes in nutrient dynamics, but will probably largely depend on other prevailing ecosystem and climate conditions. Furthermore, future nutrient levels and availability for biological production are difficult to predict due to long response times to reduced nutrient loads (e.g. Conley et al. 2009), combined effects of changing climate and nutrient loads (Hägg et al. 2014) and the uncertainty of whether the nutrient loading objectives themselves can be achieved by all Baltic countries.
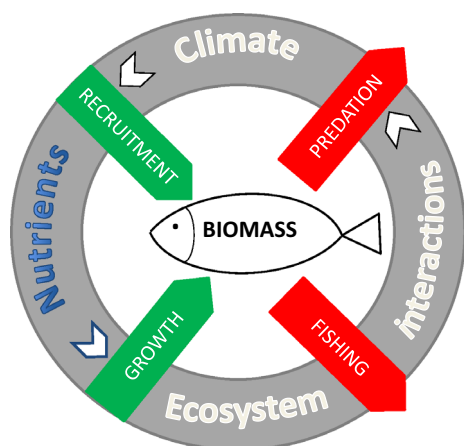
Fig. 6 Schematic illustration of the main processes impacting on fish biomass (growth, recruitment, predation, fishing) and the pathway through which nutrients increase may have impacted on forage fish biomasses in the Baltic Sea (i.e. via growth), based on the results of this study

REFERENCES

Andersen, J.H., J. Carstensen, D.J. Conley, K. Dromph, V. Fleming-Lehtinen, B.G. Gustafsson, A.B. Josefson, A. Norkko, et al. 2015. Long-term temporal and spatial trends in eutrophication status of the Baltic Sea. *Biological Reviews*. doi:10.1111/brv. 12221.

Anderson, D.M., J.M. Burkholder, W.P. Cochlan, P.M. Glibert, C.J. Gobler, C.A. Heil, R.M. Kudela, M.L. Parsons, et al. 2008. Harmful algal blooms and eutrophication: Examining linkages from selected coastal regions of the United States. *Harmful Algae* 8: 39–53.

Bernotas, E. 2002. Changes in fish biomass under impact of a thermal effluent and eutrophication in Lake Druksiai. *Acta Zoologica Lituanica* 12: 242–253.

Cardinale, M., M. Casini, and F. Arrhenius. 2002. The influence of biotic and abiotic factors on the growth of sprat (*Sprattus sprattus*) in the Baltic Sea. *Aquatic Living Resources* 15: 273–281.

Carpenter, S.R., N.F. Caraco, D.L. Correll, R.W. Howarth, A.N. Sharpley, and V.H. Smith. 1998. Nonpoint pollution of surface waters with phosphorus and nitrogen. *Ecological Applications* 8: 559–568.

Casini, M., V. Bartolino, J.C. Molinero, and G. Kornilovs. 2010. Linking fisheries, trophic interactions and climate: Threshold dynamics drive herring *Clupea harengus* growth in the central Baltic Sea. *Marine Ecology Progress Series* 413: 241–252.

Casini, M., G. Kornilovs, M. Cardinale, C. Möllmann, W. Grygiel, P. Jonsson, T. Raid, J. Flinkman, and V. Feldman. 2011. Spatial and temporal density dependence regulates the condition of central Baltic Sea clupeids: Compelling evidence using an extensive international acoustic survey. *Population Ecology* 53: 511–523.

Cederwall, H., and R. Elmgren. 1980. Biomass increase of benthic macrofauna demonstrates eutrophication of the Baltic Sea. *Ophelia* 1: 287–304.

Cederwall, H., and R. Elmgren. 1990. Biological effects of eutrophication in the Baltic Sea, particularly the coastal zone. *Ambio* 19: 109–112.

Chassot, E., F. Mélin, O. Le Pape, and D. Gascuel. 2007. Bottom-up control regulates fisheries production at the scale of eco-regions in European seas. *Marine Ecology Progress Series* 343: 45–55.

Chassot, E., S. Bonhommeau, N.K. Dulvy, F. Mélin, R. Watson, D. Gascuel, and O. Le Pape. 2010. Global marine primary production constrains fisheries catches. *Ecology Letters* 13: 495–505.

Conley, D.J., S. Björck, E. Bonsdorff, J. Carstensen, G. Destouni, B.G. Gustafsson, S. Hietanen, M. Kortekaas, et al. 2009. Hypoxia-related processes in the Baltic Sea. *Environmental Science and Technology* 43: 3412–3420.

Díaz, R.J., and R. Rosenberg. 2008. Spreading dead zones and consequences for marine ecosystems. *Science* 321: 926–929.

Dippner, J.W., G. Kornilovs, and K. Junker. 2012. A multivariate Baltic Sea environmental index. *Ambio* 41: 699–708.

Eero, M., B.R. MacKenzie, F.W. Köster, and H. Gislason. 2011. Multi-decadal responses of a cod (*Gadus morhua*) population to human-induced trophic changes, exploitation and climate variability. *Ecological Applications* 21: 214–226.

Eero, M. 2012. Reconstructing the population dynamics of sprat (*Sprattus sprattus balticus*) in the Baltic Sea in the 20th century. *ICES Journal of Marine Science* 69: 1010–1018.

Eilola, K., H.E.M. Meier, and E. Almroth. 2009. On the dynamics of oxygen, phosphorus and cyanobacteria in the Baltic Sea: A model study. *Journal of Marine Systems* 75: 163–184.

Elmgren, R. 1989. Man's impact on the ecosystem of the Baltic Sea: Energy flows today and at the turn of the century. *Ambio* 18: 326–331.

Elmgren, R. 2001. Understanding human impact on the Baltic Sea ecosystem: changing views in recent decades. *Ambio* 30: 222–231.

Elwertowski, J., M. Giedz, and J. Maciejczyk, 1974. Changes of fat content in Baltic sprat during the past 25 years. *ICES CM Document H*: 14.

Haddon, M. 2001. *Modelling and quantitative methods in fisheries*. Florida: Chapman & Hall/CRC.

Hanson, J.M., and W.C. Leggett. 1982. Empirical prediction of fish biomass and yield. *Canadian Journal of Fisheries and Aquatic Sciences* 39: 257–263.

Hansson, S., O. Hjerne, C. Harvey, J.F. Kitchell, S.P. Cox, and T.E. Essington. 2007. Managing Baltic Sea fisheries under contrasting production and predation regimes: Ecosystem model analyses. *Ambio* 36: 265–271.

Hägg, H.E., S.W. Lyon, T. Wällstedt, C.-M. Mörth, B. Claremar, and C. Humborg. 2014. Future nutrient load scenarios for the Baltic Sea due to climate and lifestyle changes. *Ambio* 43: 337–351.

HELCOM. 2007. *Baltic Sea action plan*. Helsinki: HELCOM.

Jansson, B.O., and K. Dahlberg. 1999. The environmental status of the Baltic Sea in the 1940s, today and in the future. *Ambio* 28: 312–319.

Kemp, W.M., W.R. Boynton, J.E. Adolf, D.F. Boesch, W.C. Boicourt, G. Brush, J.C. Cornwell, T.R. Fisher, et al. 2005. Eutrophication of Chesapeake Bay: Historical trends and ecological interaction. *Marine Ecology Progress Series* 303: 1–29.

Kerr, S.R., and R.A. Ryder. 1992. Effects of cultural eutrophication on coastal marine fisheries: A comparative approach. In *Marine coastal eutrophication: The response of marine transitional systems to human impact: Problems and perspectives for restoration: Proceedings of an international conference*, ed. R.A. Vollenweider, R. Marchetti, and R. Viviani, 599–614. Amsterdam: Elsevier Science Publishers B.V.

Knowler, D. 2007. Estimation of a stock–recruitment relationship for Black Sea anchovy (*Engraulis encrasicolus*) under the influence of nutrient enrichment and the invasive comb-jelly, *Mnemiopsis leidyi*. *Fisheries Research* 84: 275–281.

Kononen, K., and Å. Niemi. 1984. Long-term variation in the phytoplankton composition at the entrance to the Gulf of Finland. *Ophelia* 3: 101–110.

Köster, F.W., C. Möllmann, S. Neuenfeldt, M. Vinther, M.A.S. John, J. Tomkiewicz, R. Voss, H.-H. Hinrichsen, et al. 2003. Fish stock development in the central Baltic Sea (1974–1999) in relation to variability in the environment. *ICES Marine Science Symposia* 219: 294–306.

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

MacKenzie, B.R., H. Gislason, C. Möllmann, and F.W. Köster. 2007. Impact of 21st century climate change on the Baltic Sea fish community and fisheries. *Global Change Biology* 13: 1348–1367.

Margonski, P., S. Hansson, M.T. Tomczak, and R. Grzebielec. 2010. Climate influence on Baltic cod, sprat, and herring stock–recruitment relationships. *Progress in Oceanography* 87: 277–288.

Massol, F., P. David, D. Gerdeaux, and P. Jarne. 2007. The influence of trophic status and large-scale climatic change on the structure of fish communities in Perialpine lakes. *Journal of Animal Ecology* 76: 538–551.

Mcowen, C.J., W.W.L. Cheung, R.R. Rykaczewski, R.A. Watson, and L.J. Wood. 2015. Is fisheries production within Large Marine Ecosystems determined by bottom-up or top-down forcing? *Fish and Fisheries* 16: 623–632.

Meier, H.E.M., R. Döscher, and T. Faxén. 2003. A multiprocessor coupled ice-ocean model for the Baltic Sea: Application to salt inflow. *Journal of Geophysical Research* 108: 3273.

Meier, H.E.M. 2007. Modeling the pathways and ages of inflowing salt- and freshwater in the Baltic Sea. *Estuarine, Coastal and Shelf Science* 74: 610–627.

Micheli, F. 1999. Eutrophication, fisheries, and consumer-resource dynamics in marine pelagic ecosystems. *Science* 285: 1396–1399.

Möllmann, C., G. Kornilovs, M. Fetter, and F.W. Köster. 2005. Climate, zooplankton, and pelagic fish growth in the central Baltic Sea. *ICES Journal of Marine Science* 62: 1270–1280.

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

Nixon, S.W., and B.A. Buckley. 2002. "A strikingly rich zone"—Nutrient enrichment and secondary production in coastal marine ecosystems. *Estuaries* 25: 782–796.

Ojaveer, E. 2003. Baltic herring. In *Fishes of Estonia*, ed. E. Ojaveer, E. Pihu, and T. Saat, 58–79. Tallinn: Estonian Academy Publishers (in Estonian).

Österblom, H., S. Hansson, U. Larsson, O. Hjerne, F. Wulff, R. Elmgren, and C. Folke. 2007. Human-induced trophic cascades and ecological regime shifts in the Baltic Sea. *Ecosystems* 10: 887–889.

Ricker, W.E. 1954. Stock and recruitment. *Journal of the Fisheries Research Board of Canada* 11: 559–623.

Smith, V.H., G.D. Tilman, and J.C. Nekola. 1999. Eutrophication: Impacts of excess nutrient inputs on freshwater, marine, and terrestrial ecosystems. *Environmental Pollution* 100: 179–196.

Sommer, U., H. Stibor, A. Katechakis, F. Sommer, and T. Hansen. 2002. Pelagic food web configurations at different levels of nutrient richness and their implications for the ratio fish production: Primary production. *Hydrobiologia* 484: 11–20.

Voss, R., M.A. Peck, H.-H. Hinrichsen, C. Clemmesen, H. Baumann, D. Stepputtis, M. Bernreuther, J.O. Schmidt, et al. 2012. Recruitment processes in Baltic sprat—A re-evaluation of GLOBEC Germany hypotheses. *Progress in Oceanography* 107: 61–79.

Ware, D.M., and R.E. Thomson. 2005. Bottom-up ecosystem trophic dynamics determine fish production in the northeast Pacific. *Science* 308: 1280–1284.

Wulff, F., G. Aertebjerg, G. Nicolaus, Å. Niemi, P. Ciszewski, S. Sculz, and W. Kaiser. 1986. The changing pelagic ecosystem of the Baltic Sea. *Ophelia* 4: 299–319.

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