

# Combined effects of global climate change and regional ecosystem drivers on an exploited marine food web

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## Abstract

Changes in climate, in combination with intensive exploitation of marine resources, have caused large-scale reorganizations in many of the world's marine ecosystems during the past decades. The Baltic Sea in Northern Europe is one of the systems most affected. In addition to being exposed to persistent eutrophication, intensive fishing, and one of the world's fastest rates of warming in the last two decades of the 20th century, accelerated climate change including atmospheric warming and changes in precipitation is projected for this region during the 21st century. Here, we used a new multimodel approach to project how the interaction of climate, nutrient loads, and cod fishing may affect the future of the open Central Baltic Sea food web. Regionally downscaled global climate scenarios were, in combination with three nutrient load scenarios, used to drive an ensemble of three regional biogeochemical models (BGMs). An Ecopath with Ecosim food web model was then forced with the BGM results from different nutrient-climate scenarios in combination with two different cod fishing scenarios. The results showed that regional management is likely to play a major role in determining the future of the Baltic Sea ecosystem. By the end of the 21st century, for example, the combination of intensive cod fishing and high nutrient loads projected a strongly eutrophicated and sprat-dominated ecosystem, whereas low cod fishing in combination with low nutrient loads resulted in a cod-dominated ecosystem with eutrophication levels close to present. Also, nonlinearities were observed in the sensitivity of different trophic groups to nutrient loads or fishing depending on the combination of the two. Finally, many climate variables and species biomasses were projected to levels unseen in the past. Hence, the risk for ecological surprises needs to be addressed, particularly when the results are discussed in the ecosystem-based management context.

**Keywords:** Baltic Sea, climate change, Ecopath with Ecosim, eutrophication, fishing, food web, nutrient loads

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## Introduction

Marine environments have undergone large-scale changes during the past decades, and events such as fish stock collapses, severe hypoxia, and ecosystem reorganizations are documented in increasing numbers worldwide (e.g., Francis *et al.*, 1998; Lees *et al.*, 2006; Beaugrand *et al.*, 2008; Kirby *et al.*, 2009; Alheit & Bakun, 2010). Many of these changes have been observed concomitant to past variations in climate conditions, indicating a close coupling between marine ecosystem processes and the

global climate system (e.g., Francis *et al.*, 1998; Beaugrand *et al.*, 2008; Alheit & Bakun, 2010). The global climate change is considered to already have exceeded a critical threshold for safe operating space (Rockström *et al.*, 2009), and the current climate models project accelerating atmospheric warming toward the end of the 21st century (IPCC, 2007). Thus, it is timely to ask how marine ecosystems that globally provide a wide scope of ecosystem services (Doney *et al.*, 2012) would respond in case such projections became true.

Some more general climate-related ecosystem responses, such as polewards species range expansions due to warming, changes in local species compositions due to physiological intolerance to new conditions (e.g.,

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a shift from marine to brackish or freshwater species with decreasing salinities) and arrival of nonindigenous species, have been observed across a large number of marine ecosystems (Beaugrand *et al.*, 2002; Drinkwater, 2002; Daskalov *et al.*, 2007; Drinkwater *et al.*, 2010). However, more specific changes in climate conditions and consequently in the marine environment are often largely determined by the location and general characteristics of the sea (Philippart *et al.*, 2011). In Europe, for example, higher rates of warming were primarily observed in the Northern or enclosed/semienclosed seas than in the Southern or open ones during 1982–2006 (Belkin, 2009). How a particular marine ecosystem responds to changes in climate is then defined by the interplay of climate and other, often regional or local, drivers. For example, intensive fishing has been suggested to increase the sensitivity of marine ecosystems to changes in climate (Ottersen *et al.*, 2006; Planque *et al.*, 2010; Rouyer *et al.*, 2012). Furthermore, the biological settings, such as the food web structure and biodiversity, can alone or as response to other drivers either enable or buffer climate-induced feedbacks and trophic cascades, i.e., the indirect climate effects (e.g., Drinkwater *et al.*, 2010; Planque *et al.*, 2010; Philippart *et al.*, 2011). Climate change can also alter the local ecosystem function by altering species interactions, particularly if the keystone species are affected (Power *et al.*, 1996; Sanford, 1999).

Modeling studies about the climate change effects on marine ecosystems have recently been carried out in several regions (e.g., Ben Rais Lasram *et al.*, 2010; Brown *et al.*, 2010; Lindegren *et al.*, 2010; Ainsworth *et al.*, 2011). Most of these studies have only concentrated on climate effects, or have not comprehensively accounted for indirect effects via species interactions, even if evaluating the interactive effects of climate and other main drivers would be necessary from the perspective of ecosystem-based management (Brander, 2007; Cury *et al.*, 2008). deYoung *et al.* (2008) found that ecosystem models capable of integrating different management scenarios are increasing in number, but their potential is underused in the adaptive ecosystem management. Recently, Link *et al.* (2012) discussed that new methods need to be developed to present model uncertainties without overriding the usability of ecosystem model results.

For the Baltic Sea region, an accelerated climate change including atmospheric warming and changes in precipitation is projected during the 21st century (The BACC Author Team, 2008). The Baltic Sea ecosystem is also subject to other strong anthropogenic stressors, including intensive fishery that targets, e.g., the main predatory fish cod (*Gadus morhua callarias*), and high nutrient loads that contribute to persistent eutrophication related phenomena (e.g., algal blooms and

hypoxia). In the late 1980s an ecological regime shift in the Central Baltic Sea has been suggested, resulting in a collapse of the cod stock, high increase in the cod prey sprat (*Sprattus sprattus*) and changes in the zooplankton composition (Möllmann *et al.*, 2009). Fishing and climate have been suggested as the main drivers behind this shift (Casini *et al.*, 2009; Möllmann *et al.*, 2009).

How marine ecosystems might respond to future changes in climate in combination with other drivers is of high importance. In the ECOSUPPORT-project, the future climate change effects, in combination with nutrient loads and fishery, were studied in the Baltic Sea ecosystem using a multimodel approach linking information from the global climate models (GCMs) all the way to a regional food web model (Meier *et al.*, 2012a). In addition, the ECOSUPPORT future projections incorporated results from an ensemble of climate scenarios and regional biogeochemical models, making this a unique approach in evaluating climate change effects on a regional marine ecosystem (Wake, 2012). Here, we focus on studying the Central Baltic Sea food web response in relation to different combinations of cod fishing and nutrient load management scenarios under future climate conditions. More specifically, we address (i) the possible climate-related changes in species response to different management scenarios; (ii) the scenario-specific relative effects of nutrient loads and cod fishing on different species and species groups; and (iii) the suitability of applied multimodel approach to study different management scenarios in the context of ecosystem-based management.

## Material and methods

### Study area

The Baltic Sea is one of the world's largest brackish water ecosystems. It has only a narrow connection to the North Sea, from where major inflows of saline and oxygen-rich water intermittently enter the Baltic influencing salinity, stratification, and oxygen concentration (Leppäranta & Myrberg, 2009). Due to the large North–South climatic gradient, high riverine input and semienclosed shape, the environmental conditions, e.g., temperature and salinity, have pronounced spatial gradients. This study focuses on the open areas (minimum depth 20 m) of the Baltic Proper, i.e., the central basin of the Baltic Sea (Fig. 1). At present, the Baltic Proper surface salinity ranges between 6 psu in the North and 10 psu in the South. A permanent halocline at approximately 70 m depth separates the surface water from the more saline bottom water and has, together with eutrophication, contributed to widespread, long-term hypoxia, and loss of benthic fauna at large depths (Hannerz & Destouni, 2006; Conley *et al.*, 2009, 2011; Zillen & Conley, 2010). The Baltic Proper food web has since the late

1980s been dominated by the small pelagic planktivore sprat (Casini *et al.*, 2009). The abundances of cod and herring (*Clupea harengus membras*) are low in comparison. Fishing of these commercial fish species is intensive and has had a particularly negative effect on the Eastern Baltic cod stock in the past. The main mesozooplankton groups present are copepods *Acartia* spp. (mainly *A. bifilosa* and *A. longiremis*, Schmidt, 2006), *Temora longicornis* and *Pseudocalanus acuspes*, which are important prey of sprat, herring and young cod (Möllmann *et al.*, 2000, 2004).

#### Modeling approach

To obtain the species and food web responses to climate and other regional stressors, i.e., nutrient loads and fishing, the results of climate and biogeochemical models (BGMs) were linked with a regional food web model (Meier *et al.*, 2012a;

Fig. 2). First, results from the GCMs were dynamically downscaled using regional climate models (RCMs) and, in combination with three nutrient load scenarios, coupled with an ensemble of three BGMs (Eilola *et al.*, 2011; Meier *et al.*, 2012a). Then, environmental drivers derived from the BGMs were used to force an Ecosim with Ecosim (EwE) food web model of the open Baltic Proper (Tomczak *et al.*, 2012) in combination with two cod fishing scenarios (Fig. 2).

#### Climate and biogeochemical models

Transient (1961–2098) regional climate scenarios for the Baltic Sea area were created within the 3-year ECOSUPPORT-project by dynamically downscaling output from a global General Circulation Model (ECHAM5/MPI-OM, Jungclaus *et al.*, 2006; Roeckner *et al.*, 2006) with a RCM (RCMO, Döscher *et al.*, 2002;

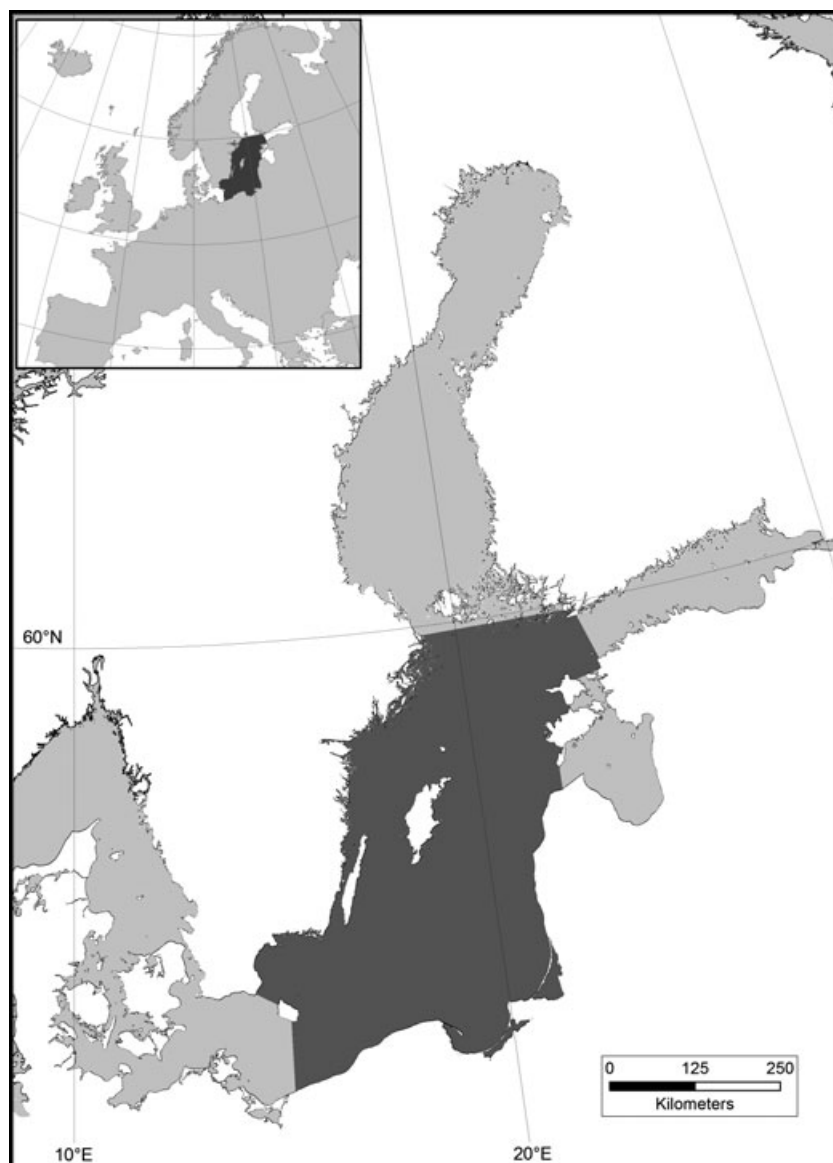
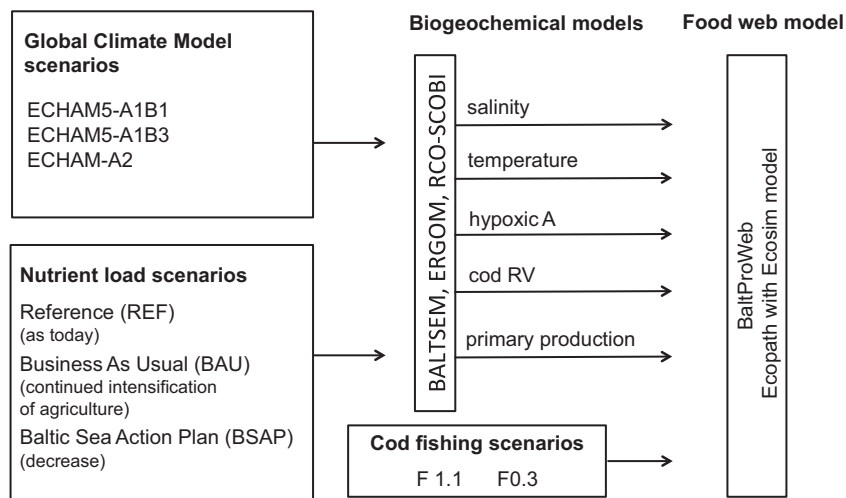


Fig. 1 Map of the Baltic Sea including the Central Baltic Sea study area (shaded dark).



**Fig. 2** A conceptual diagram of linking the global climate, and regional nutrient load and fishing scenarios via an ensemble of biogeochemical models and a food web model.

Meier *et al.*, 2011a). The regional climate scenarios were then used to force three state-of-the-art BGMs of the Baltic Sea in combination with three nutrient load scenarios. The three BGMs used were the BALTic sea Long-Term large-Scale Eutrophication Model (BALTSEM, Gustafsson, 2003), a coupled system of 13 subbasins, all described with high vertical resolution, and the three-dimensional models, the Ecological Regional Ocean Model (ERGOM, Neumann *et al.*, 2002), and the Swedish Coastal Ocean Biogeochemical model coupled to Rossby Centre Ocean circulation model (Meier *et al.*, 2003; Eilola *et al.*, 2009). These three models were used to simulate hydrochemical variables, such as temperature, salinity, and oxygen at different depths, as well as concentrations of nitrogen and phosphorus. They also contain a simplified representation of the lower trophic levels (TLs) of the food web with three groups of autotrophs (diatoms, cyanobacteria, and other phytoplankton) and one group of heterotrophic organisms that graze on phytoplankton.

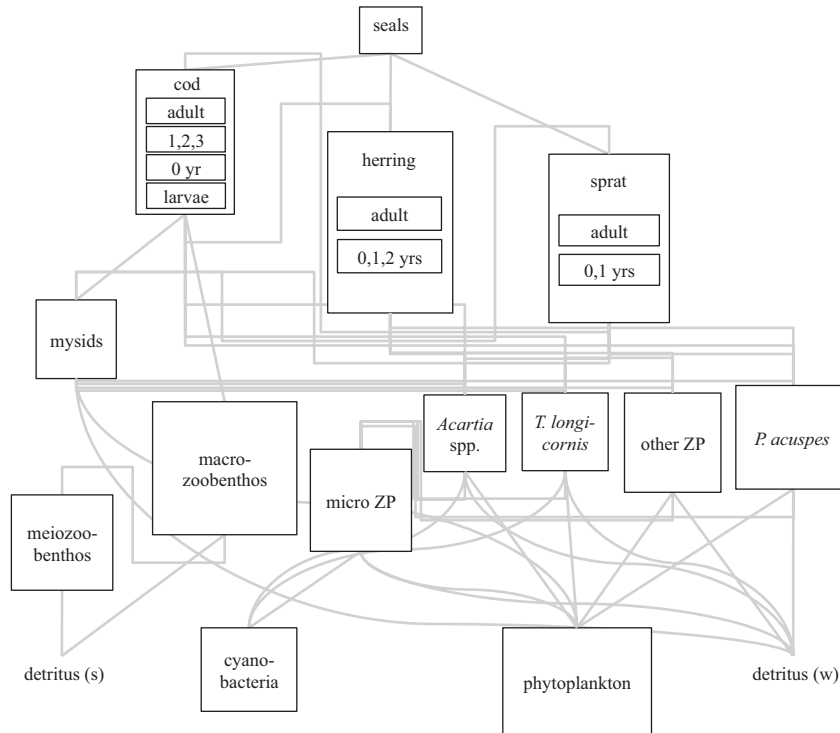
The BGMs were calibrated using atmospheric forcing from the ERA-40 reanalysis data for 1961–2007 (Uppala *et al.*, 2005), dynamically downscaled with the RCA high-resolution regional atmosphere model (Samuelsson *et al.*, 2011), in combination with the observed river nutrient loads from all countries bordering the Baltic Sea for 1970–2007. Simulated nutrient and oxygen concentrations for the time period 1970–2006 were then compared with observations, providing a comprehensive reconstruction of the Baltic nutrient and oxygen conditions for this time period. A detailed description of the calibration of BGMs and their performance is presented in Eilola *et al.* (2011). Model results on the past changes in the biogeochemical and hydrographic properties of the Baltic Sea are also available in Meier *et al.* (2011b, 2012b), MacKenzie *et al.* (2012) and Neumann *et al.* (2012).

#### Food web model

Ecopath with Ecosim is a widely used (Fulton, 2010) modeling approach to describe trophic flows in aquatic ecosystems

(Christensen & Pauly, 1992). A previously published EwE model of the open Baltic Proper food web (BaltProWeb, Tomczak *et al.*, 2012) was applied after some modifications (Fig. 3; Tables S1–S3). This model comprises an Ecopath mass-balance module (Polovina, 1984) for 1974, and the time-dynamic Ecosim simulation module that was calibrated for 1974–2006 (Eqn 1 and 2 in Table 1). In Ecosim, changes in the biomass of each functional group are described by coupled differential equations (Eqn 2 in Table 1) that are derived from the Ecopath equation for mass balance (Eqn 1 in Table 1). The description of time-dynamic trophic interactions between the functional groups is based on a foraging arena theory, so that each prey population is split into a component that is vulnerable and a component that is invulnerable to predation (Walters *et al.*, 1997; Ahrens *et al.*, 2012). The rate at which the prey can move between these two components determines the predation pressure on a particular prey population and is determined by vulnerability constant ( $v$ , Eqn 3 in Table 1).

Six environmental time series, produced by the BGMs described above, were used to force the Ecosim model based on existing literature on the most important environmental drivers affecting the Baltic Sea food web (see references in Table 2). All environmental forcing chosen improved the model fit (also in Tomczak *et al.*, 2012), with the exception of salinity effects on *P. acuspes*. However, as the negative effects of decreasing salinities on *P. acuspes* are well documented (Casini *et al.*, 2009; Möllmann *et al.*, 2009), salinity forcing on *P. acuspes* was included in this study. All environmental forcing were applied as anomalies from the Ecopath base year (1974) values as in EwE, the environmental forcing is applied as a multiplier of Ecopath base rates. Environmental forcing functions, directly derived from temperature, salinity, and oxygen content, were either used to force the egg production of fish or predator search rates ( $a_{ij}$  in Eqn 3 in Table 1). The annual production per biomass ( $P/B$ ) of phytoplankton projected by the BGMs was used to force the phytoplankton production in the food



**Fig. 3** Structure of the open Baltic Proper food web model (ZP, zooplankton; detritus (s), sediment detritus; detritus (w), water-column detritus).

**Table 1** The core formula of the Ecopath with Ecosim food web model

| Equation no. | Equation  | Variables  |
|--------------|---|--|
| Eqn. 1       | $B_i \cdot \left(\frac{P}{B}\right)_i = F_i \cdot B_i + M2_i \cdot B_i + B_i \cdot \left(\frac{P}{B}\right)_i \cdot (1 - EE_i)$ | $B_i$ is the biomass, $(P/B)_i$ the annual production per biomass ratio, $F_i$ the fishing mortality and $M2_i$ the predation mortality rate of group $i$ . Other mortality equals $B_i \cdot \left(\frac{P}{B}\right)_i \cdot (1 - EE_i)$ in which $EE_i$ is the ecotrophic efficiency of group $i$ (i.e., the proportion of group $i$ production that is consumed by predators included in the model and extracted by the fishery) |
| Eqn. 2       | $\frac{dB_i}{dt} = g_i \sum_j C_{ji} - \sum_j C_{ij} - (MO_i + F_i)B_i$   | $\sum_j C_{ji}$ is the total annual consumption per biomass, $g_i$ is the net growth efficiency and $MO_i$ other mortality rate of group $i$ . Term $\sum_j C_{ij}$ is the biomass of group $i$ eaten by predators $j$ .   |
| Eqn. 3       | $C_{ij} = \frac{a_{ij} \cdot v_{ij} \cdot B_i \cdot B_j}{2v_{ij} + a_{ij} \cdot B_j}$   | $C_{ij}$ is the total consumption of $i$ by $j$ , $a_{ij}$ the effective search rate of $i$ and $v_{ij}$ vulnerability of $i$ to predation by $j$ . $B_i$ and $B_j$ as in the Eqn 1.   |

web model (Table 2) and it corresponds to the specific phytoplankton growth rate determined by light and nutrient availability. P/B therefore reflects the influence of biogeochemical processes on phytoplankton growth on an annual timescale. In addition, forcing of fishing mortality ( $F$ ) was applied on adult and small (2–3 years) cod, adult, and juvenile (<3 years) herring, as well as adult and juvenile (<2 years) sprat.

*Food web model calibration*

The food web model was calibrated with monitoring and assessment biomass time series (1974–2006) on cod (adult, small), herring (adult, juvenile), sprat (adult, juvenile), mysids, macrozoobenthos, *P. acuspes*, *Acartia* spp., and *T. longicornis*, and catch time series of cod (adult, small), herring (adult, juvenile), and sprat (adult, juvenile). The same calibration data

**Table 2** Environmental time series used to force the Ecosim model. The effect type defines if the relationship between the forcing and target variable is positive (+) or negative (–)

| Environmental variable  | Target group                                      | Target variable (effect type) | Reference  |
|---|---|-------------------------------|--|
| Sea-surface (0–10 m) temperature in August (August <i>T</i> )                               | Sprat   | Egg production (+)            | MacKenzie & Köster (2004), Nissling (2004)                   |
| Reproductive volume (RV, >11 psu and >2 mg l <sup>-1</sup> O <sub>2</sub> ), annual average | Cod   | Egg production (+)            | Plikshs <i>et al.</i> (1993), MacKenzie <i>et al.</i> (2000) |
| Hypoxic area, annual average  | Macrozoobenthos, mysids                           | Predator search rate (–)      | Laine <i>et al.</i> (1997)                                   |
| Lower water-column (80–100 m) salinity, annual average                                      | <i>Pseudocalanus acuspes</i>                      | Predator search rate (+)      | Möllmann <i>et al.</i> (2009), Casini <i>et al.</i> (2009)   |
| Upper water-column (0–50 m) temperature in March–May (spring <i>T</i> )                     | <i>Acartia</i> spp.,<br><i>Temora longicornis</i> | Predator search rate (+)      | Möllmann <i>et al.</i> (2000), Möllmann <i>et al.</i> (2008) |
| Phytoplankton production per biomass (P/B), annual*   | Phytoplankton                                     | Production per biomass (+)    |  |

\*P/B was calculated based on the total annual phytoplankton production (*P*) and average standing stock biomass (*B*), so that  $P/B = P_t/B_{t-1}$ , where  $B_{t-1}$  is the previous year's biomass. The approach accounts for the interannual changes of total phytoplankton production and is in line with the Ecosim calculation of total phytoplankton production  $P_t = B_{t-1} \cdot (P/B)_t$ .

and approach were used as in Tomczak *et al.* (2012) (Table S4). Environmental forcing from BGMs driven by the ERA-40 reanalysis data was used in model calibration instead of monitoring data. This was mainly because no comprehensive monitoring data on phytoplankton production were available that would have covered the entire calibration period. Fishing mortalities were recalculated from ICES (2011) assessment data as described in Tomczak *et al.* (2012). No one BGM performed over the others for all variables projected, but some models performed better for some variables, locations, and scalings (see Eilola *et al.*, 2011; MacKenzie *et al.*, 2012). Hence, we assumed the data from each BGM equally valid, and calibrated the food web model three times, using environmental forcing from only one BGM at a time. This resulted in three differently fitted models that all reproduced the main temporal dynamics of fish biomass in the period from 1974 to 2006 (Fig. S1g–l). The models calibrated with the environmental forcing from ERGOM and RCO-SCOBI captured also the changes in the *P. acuspes* (Fig. S1d). All models simulated only moderate increases in the biomass of *Acartia* spp., (Fig. S1c) and there was in general a large temporal variation, both, in the observed and modeled biomasses of *T. longicornis* (Fig. S1b). Mysids and macrozoobenthos, which are groups with high data uncertainties due to issues in sampling and discontinuous monitoring (Niiranen *et al.*, 2012), were not modeled accurately (Fig. S1e and f). Hence, our analysis was foremost focused on the pelagic groups.

Model uncertainty arising from the initial parameterization of the functional group biomasses in Ecopath was estimated using the simplified approach by Niiranen *et al.* (2012). In this approach keystone groups, i.e., groups that had a large effect on the entire food web if their biomass was changed, were identified. Then the model sensitivity to changes in the initial biomasses of the keystone groups was tested for within the boundaries of data uncertainty. Here, three biomass changes that the future food web projections were potentially most

sensitive to (based on Niiranen *et al.*, 2012), i.e., increase in the biomass of cod and decreases in the biomasses of sprat and other zooplankton, were tested to capture the maximum potential spread of future projections.

#### Future scenarios

In future projections, the food web model was run for all combinations of three transient climate scenarios, three nutrient load scenarios, and two fishing scenarios for the period 2010–2098. The climate scenarios were based on the dynamically downscaled output of the ECHAM5/MPI-OM GCM (Meier *et al.*, 2012a), corresponding to the IPCC emission scenarios A1B and A2 (Nakićenović, 2000), the latter causing in general warmer climate than the former. ECHAM5/MPI-OM was chosen because its biases in atmospheric circulation over the Baltic Sea region are smaller than in other investigated GCMs (Meier *et al.*, 2011a). The scenarios A1B and A2 were chosen to represent the uncertainty in future greenhouse gas emissions, i.e., a medium and an extreme projection. To investigate the impact of natural climate variability in the A1B scenario two initial realizations, i.e., ECHAM5-r1-A1B (A1B1) and ECHAM5-r3-A1B (A1B3), of the GCM were used. Nutrient loads from rivers were calculated from the products of riverine nutrient concentrations and water discharges following, e.g., Stålnacke *et al.* (1999). Future runoff changes were calculated from the RCM results (Meier *et al.*, 2011c). Future nutrient concentrations based on three nutrient loading scenarios: reference (REF) – future nutrient concentrations in rivers remain at their present level; business as usual (BAU) – exponential growth of agriculture and therefore increasing riverine nutrient concentrations; or Baltic Sea Action Plan (BSAP) – reduction in nutrient loads following the implementation of the BSAP (described in Gustafsson *et al.*, 2011). The atmospheric nitrogen deposition was kept at its current level in the REF and BAU scenarios and decreased by 50% in the BSAP

scenario. In general, water temperatures, primary productivity, and the extent of hypoxic area increased across scenarios, whereas salinity decreased and oxygen conditions worsened, causing a decreased trend in the cod reproductive volume (cod RV). In the nutrient load scenarios, REF and BAU primary production and hypoxic area increased, whereas cod RV decreased. All environmental forcing are presented in Figs S2 and S3. Each BGM-specific food web model calibration was run for every future scenario with the respective BGM forcing variables. When comparing the monitoring data and environmental forcing (e.g., salinity and cod RV) resulting from the ERA-40 and RCM driven BGMs for 1974–2006, rather large differences were observed (Fig. S4). Hence, the future food web model results were always compared with the past values from the respective model run, i.e., forced with environmental forcing from the corresponding RCM also for 1974–2006, instead of the ERA-40 data.

The two cod fishing scenarios applied were a) high fishing mortality ( $F_{1.1}$ ) – the future constant cod  $F$  of 1.1, corresponding to the average  $F$  of the years 2002–2006, and b) cod recovery plan ( $F_{0.3}$ ) – the future constant cod  $F$  of 0.3, following the EU Council recovery plan (EC, 2007). In both scenarios, the  $F$ s for sprat and herring were constantly 0.32 and 0.16 for 2011–2100, respectively. This corresponds to the maximum sustainable yield ( $F_{msy}$ ) estimations for these species by ICES (2011).

### Analysis of results

For each food web group, the projected biomasses were averaged across all three BGMs and two greenhouse gas emission scenarios (including two initial realizations of the A1B scenario) for each cod fishing – nutrient load scenario. Climate projections were not studied separately as this study primarily aims to analyze the effects of regionally manageable drivers, i.e., fishing and nutrient loads. Moreover, e.g., Meier *et al.* (2006) have earlier observed that the choice of GCM can result in greater differences and uncertainties in the RCM results than those between climate scenarios. The focus was on analyzing the response of cod, herring and sprat, as well as zooplankton *P. acuspes*, *Acartia* spp., and ‘other zooplankton’ (mainly cladocerans, BIOR database) in the food web context to different climate, nutrient load, and fishery scenarios. Results from scenario runs were analyzed as 30-year averages to take the considerable natural climate variability in atmospheric variables into account (e.g., Meier *et al.*, 2012b) and the future projections were compared with the past (1974–2006) conditions. To ensure comparability between the future and past projections, the average biomasses for 1974–2006 from the simulations analyzed were used as reference conditions. The minimum and maximum biomass projections, resulting from the different climate scenarios and BGMs used, were presented to define the species-specific ranges of response to different nutrient load – cod fishing scenarios.

In total, 18 future scenarios were run as different combinations of three nutrient load, three climate and two cod fishing scenarios for all three BGMs totaling in 54 model runs. As results were averaged across the BGMs and climate scenarios,

differences between six scenarios (REF- $F_{1.1}$ , REF- $F_{0.3}$ , BAU- $F_{1.1}$ , BAU- $F_{0.3}$ , BSAP- $F_{1.1}$ , and BSAP- $F_{0.3}$ ) were analyzed under future climate. Of these, the low nutrient load – cod recovery plan (BSAP- $F_{0.3}$ ) represented the best-case, and the high nutrient load – intensive cod fishing (BAU- $F_{1.1}$ ) represented the worst-case management scenario.

## Results

### Common trends under future climate

Even if the different nutrient load and cod fishing scenarios resulted in a range of futures for the Baltic Sea ecosystem, a few general trends were present. In all scenarios, the biomasses of copepods *Acartia* spp. and *T. longicornis* (not shown, but responded alike *Acartia* spp.), mysids, zoobenthos, and phytoplankton were on average projected higher than the reference conditions (i.e., average biomass for 1974–2006), in both near (2020–2049) and far (2070–2098) future (Fig. 4e and g; Table 3; Figs S5 and S6). In addition, in five of six scenarios, the sprat biomass increased until 2098 (Fig. 4c; Table 3; Fig. S5c). For herring all scenarios resulted in a biomass decrease in near future, but the responses became more variable after the 2050s (Fig. 4b; Table 3; Fig. S5b). The lowest future biomasses of *P. acuspes* were projected for 2080–2098 (Fig. 4d and Fig. S5d). A decreasing trend was also observed in the adult cod biomass from 2040s onwards across all scenarios (Fig. 4a; Fig. S5a). Yet, all low cod fishing scenarios ( $F_{0.3}$ ) resulted in higher cod biomasses at the end of the model run compared with the reference conditions.

The scenario-specific ranges of species response, i.e., the range between the minimum and maximum biomasses simulated across all BGMs and climate scenarios used, changed over time along with changing climate conditions, but were in general large at all times (Fig. 4; Figs S5 and S6). This resulted in situations where several scenarios could project a similar outcome. The highest and lowest biomass trajectories were, however, in most cases projected only by some scenarios. The most contrasting paths for the food web response, but still displaying the common attributes mentioned above, were projected in the best-case, i.e., BSAP- $F_{0.3}$ , and worst-case, i.e., BAU- $F_{1.1}$  management scenarios. In the best-case scenario, cod biomass increased, biomasses of clupeids decreased (herring), or remained close to reference conditions (sprat), and phytoplankton biomass showed only a weak increasing trend (Fig. 4a–c and g; Figs S5–S6). In the worst-case scenario, on the other hand, cod biomass decreased to very low levels, clupeid biomasses increased rapidly and a twofold increase in phytoplankton was projected by the end of the 21st century.

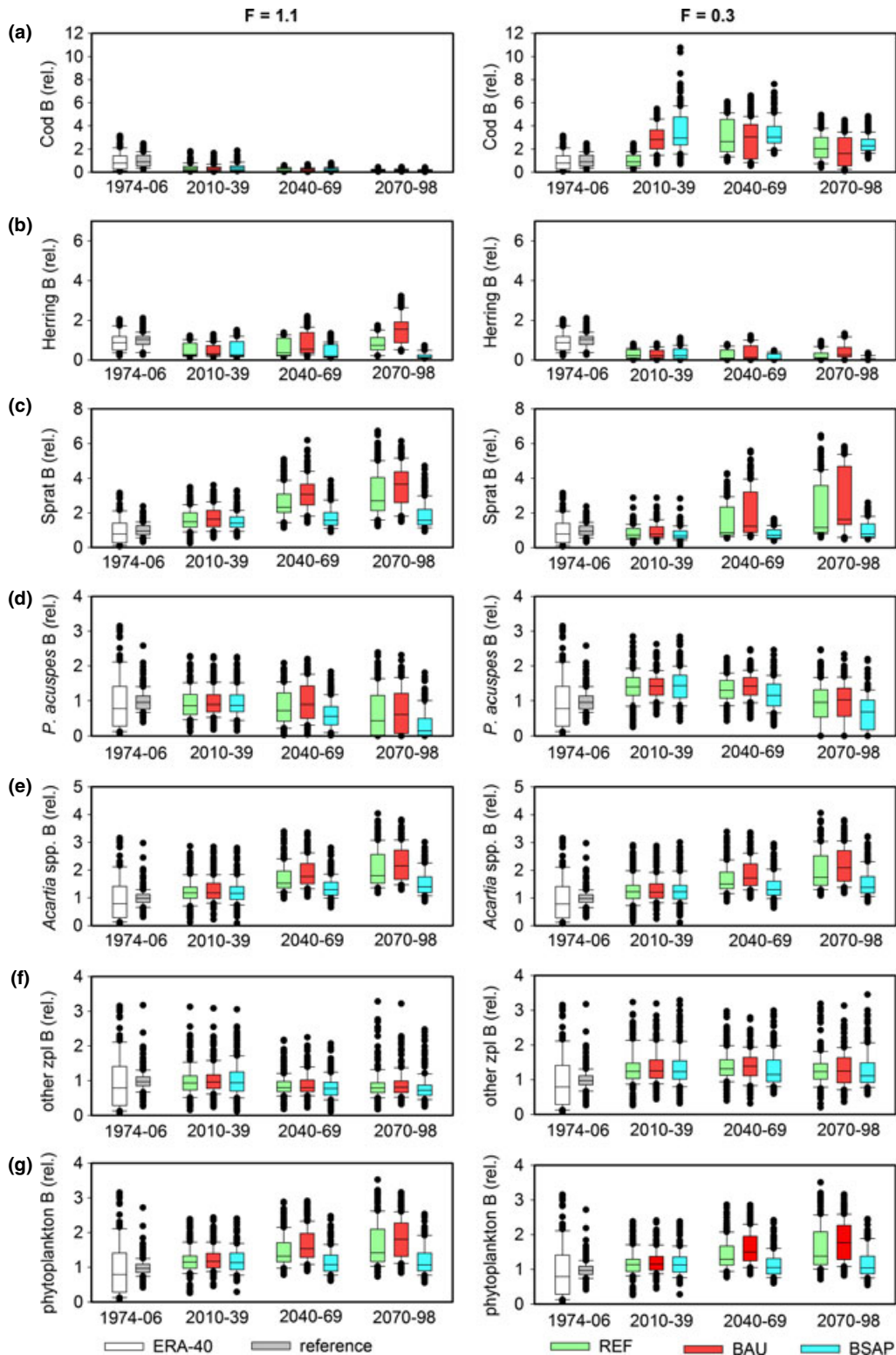


Fig. 4 Future (2010–2098) biomass (B) projections of (a) cod, (b) herring, (c) sprat, (d) *Pseudocalanus acuspes*, (e) *Acartia* spp., (f) other zooplankton (zpl), and (g) phytoplankton in different nutrient load – cod fishing scenarios across all climate scenarios and biogeochemical models. In addition, projections using ERA-40 and scenario data (i.e., reference data) are shown for 1974–2006. The changes in biomass, i.e., relative (rel.) change in comparison to the reference (1974–2006) conditions, are presented as box and whisker plots with 50% (median), 25% and 75% quartiles.



**Table 3** The average biomass trends of selected groups for near (2020–2049) and far (2070–2098) future in different management scenarios for nutrient loads

| Group                        | 2020–2049 |           |           |           |           |           | 2070–2098 |           |           |           |           |           |
|------------------------------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|
|                              | REF       |           | BAU       |           | BSAP      |           | REF       |           | BAU       |           | BSAP      |           |
|                              | $F_{1.1}$ | $F_{0.3}$ | $F_{1.1}$ | $F_{0.3}$ | $F_{1.1}$ | $F_{0.3}$ | $F_{1.1}$ | $F_{0.3}$ | $F_{1.1}$ | $F_{0.3}$ | $F_{1.1}$ | $F_{0.3}$ |
| Adult cod                    | ↓         | ↑         | ↓         | ↑         | ↓         | ↑         | ↓         | ↑         | ↓         | ↑         | ↓         | ↑         |
| Adult herring                | ↓         | ↓         | ↓         | ↓         | ↓         | ↓         | ↓         | ↓         | ↑         | ↓         | ↓         | ↓         |
| Adult sprat                  | ↑         | –         | ↑         | ↑         | ↑         | ↓         | ↑         | ↑         | ↑         | ↑         | ↑         | –         |
| <i>Pseudocalanus acuspes</i> | –         | ↑         | –         | ↑         | ↓         | ↑         | ↓         | –         | ↓         | –         | ↓         | –         |
| <i>Acartia</i> spp.          | ↑         | ↑         | ↑         | ↑         | ↑         | ↑         | ↑         | ↑         | ↑         | ↑         | ↑         | ↑         |
| Other mesozooplankton        | –         | ↑         | –         | ↑         | –         | ↑         | ↓         | ↑         | ↓         | ↑         | ↓         | ↑         |
| Phytoplankton                | ↑         | ↑         | ↑         | ↑         | ↑         | ↑         | ↑         | ↑         | ↑         | ↑         | ↑         | ↑         |

REF, reference; BAU, business as usual; BSAP, Baltic Sea Action Plan; for cod fishing:  $F_{1.1}$  = intensive fishing,  $F_{0.3}$  = recovery plan. Arrows indicate a decrease or increase in biomass from 1974–2006 (black arrow =  $\pm 10$ –49%, red arrow =  $\pm \geq 50\%$ ) and ‘–’ indicates no change in biomass (max  $\pm 10\%$ ).

### Effects of nutrient loads and cod fishing

Groups at the bottom and top of the food web responded differently to changes in nutrient loads and cod fishing. Phytoplankton was almost solely affected by nutrient load induced changes in productivity. In the BAU scenarios, the phytoplankton biomass increased on average twofold from the past reference conditions to the end of the 21st century, whereas only a minor increase was projected in the BSAP scenarios, both independent of the cod fishing scenario (Fig. 4g; Fig. S6d). Also, both, the maximum and minimum phytoplankton biomasses projected increased with time. The top predatory fish, cod, on the other hand, responded primarily to changes in fishing mortality (Fig. 4a; Fig. S5a). The lowest cod biomasses were simulated in the BAU- $F_{1.1}$  scenario and in all  $F_{1.1}$  scenarios, the adult cod biomass on average decreased close to extinction levels. Reduction in cod fishing ( $F_{0.3}$  scenario) was followed by fast increases in adult cod biomass, on average resulting in fourfold higher biomasses in near future and more than twofold higher biomasses in far future compared with reference conditions (Fig. 4a; Fig. S5a). The highest biomasses were projected when both the nutrient loads and cod fishing were low (BSAP- $F_{0.3}$ ). When the entire range of response, i.e., all scenarios and model runs, was studied, a maximum 11-fold higher cod biomass was projected in comparison to the reference conditions. In the best-case scenario (BSAP- $F_{0.3}$ ), the range of response decreased by half from near to far future following the decrease in salinity.

At intermediate TLs, responses to external forcing were group specific. Benthic related trophospecies, i.e., macrozoobenthos and mysids, were almost solely

positively affected by changes in nutrient loads and their biomasses were projected to increase on average twofold from the reference conditions to far future (2070–2098) in the REF/BAU scenarios, but only less than half of this in the BSAP scenarios (Fig. S6b and c). The small pelagics, herring, and sprat, were also strongly affected by nutrient loads, but in addition responded to changes in cod fishing (Fig. 4b and c; Fig. S5b and c). The highest increases in herring biomass, i.e., on average 1.6-fold in far future in comparison to reference, were projected in the BAU- $F_{1.1}$  scenario. When the entire range of response to management scenarios was studied, a maximum 3.2-fold increase in biomass was projected (in 2070–2098) compared with reference conditions. The second highest biomasses were projected in the BAU- $F_{0.3}$  scenario. This range also increased with time, mainly due to increasing maximum biomass values. The minimum trajectory was constantly very low. Nutrient load effects on herring were relatively low before 2030–2040, such that in near future the herring biomass was projected on average 0.3 ( $F_{0.3}$ )- to 0.6 ( $F_{1.1}$ )-fold in the BAU/REF scenarios and 0.2 ( $F_{0.3}$ )- to 0.6 ( $F_{1.1}$ )-fold in the BSAP scenarios (Fig. 4b; Fig. S5b). In far future, however, the simulated herring biomass was on average 0.3 ( $F_{0.3}$ )- to 1.2 ( $F_{1.1}$ )-fold in the BAU/REF scenarios, but only 0.1 ( $F_{0.3}$ )- to 0.2 ( $F_{1.1}$ )-fold in the BSAP scenarios, the nutrient effects being more pronounced when herring was under low ( $F_{1.1}$  scenario) than high cod predation pressure. Increase in predation pressure had a negative effect on herring biomass, particularly in far future and when nutrient loads were high, i.e., BAU scenario. As in the case of herring, the highest increases of adult sprat biomass, i.e., on average 3.5-fold and a maximum 7-fold (Fig. 4c; Fig. S5c) in comparison to the reference, were

projected in the BAU-F<sub>1.1</sub> scenario. The maximum sprat biomasses projected for far future in the REF/BAU scenarios were so high that they were hardly affected by changes in the predation by cod. However, changes in cod biomass affected the lowest biomasses of sprat at any time. Both, the minimum and maximum biomass projections of sprat increased with time. The adult sprat biomass was projected on average 1.3 (F<sub>0.3</sub>)- to 2.2 (F<sub>1.1</sub>)-fold in the REF/BAU scenarios and 0.9 (F<sub>0.3</sub>)- to 1.8 (F<sub>1.1</sub>)-fold in the BSAP scenarios in near future. In far future, the corresponding values were higher, i.e., 2.7- to 3.3-fold and 1.1- to 1.8-fold. As in the case of herring, the differences in nutrient loads had little effect on sprat prior to 2030–2040s. Increased predation pressure by cod resulted in lower sprat biomasses, in both near and far future. In far future, the trophic cascade effects of cod fishing on sprat were greater in the BSAP than REF/BAU scenarios.

The responses to external forcing were more varied between the zooplankton groups. *P. acuspes* was affected by nutrient loads and cod fishing, both, such that the lowest biomasses were simulated in the BSAP-F<sub>1.1</sub>, and the highest in the BAU-F<sub>0.3</sub> scenario (Fig. 4d; Fig. S5d). Changes in predation pressure by clupeids dominated over the different nutrient load scenarios until around 2040, but after this, nutrients became increasingly important in defining the biomass trajectories of *P. acuspes*. The strength of trophic control varied between nutrient load scenarios. In near future, the *P. acuspes* biomass was 0.9-fold in F<sub>1.1</sub> scenarios and 1.5-fold in F<sub>0.3</sub> scenarios, such that no great difference was observed between nutrient load scenarios. In far future, the *P. acuspes* biomass was projected 0.7 (F<sub>1.1</sub>)–0.9 (F<sub>0.3</sub>) in BAU/REF scenarios and 0.3 (F<sub>1.1</sub>)–0.7 (F<sub>0.3</sub>) in BSAP scenarios. Hence, lowering the cod fishing had a greater positive impact on *P. acuspes* in the BSAP than REF/BAU scenarios, and in near than far future. Furthermore, the nutrient reduction effects were more pronounced in the F<sub>1.1</sub> than F<sub>0.3</sub> scenarios. *Acartia* spp., on the other hand, was almost solely affected by nutrient loads. On average, a twofold increase in *Acartia* spp. was projected in the BAU/REF scenarios in far future compared with the reference conditions, but only a 1.5-fold increase in the BSAP scenario (Fig. 4e; Fig. S5e). As for phytoplankton, the response range was shifted upward, such that both the minimum and maximum biomasses projected increased with time. Also, in the case of *Acartia* spp. results from different nutrient load scenarios deviated only after 2040.

The total biomass of the system was twice as high in the BAU than BSAP scenarios or during the reference period (Fig. 5a–e). Macrozoobenthos had the highest biomass in all scenarios, forming the highest proportion of system biomass in the BSAP-F<sub>1.1</sub> (41.0%) and lowest

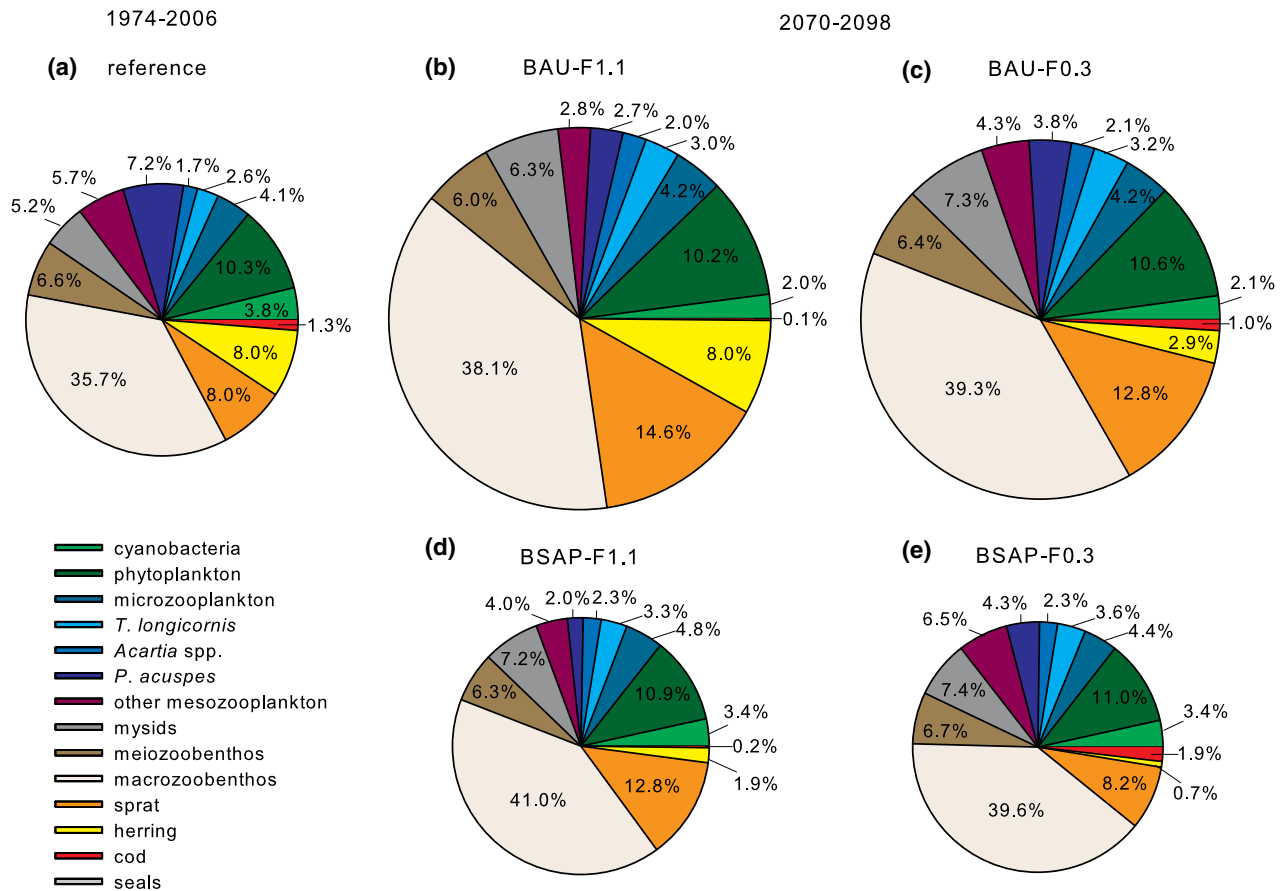
in the BAU-F<sub>1.1</sub> (38.1%) scenario. The proportions of herring and sprat were higher in the BAU than BSAP scenarios, and F<sub>1.1</sub> than F<sub>0.3</sub> scenarios. At the same time the proportions of nearly all other groups were higher in the BSAP than BAU scenarios. In the F<sub>0.3</sub> scenarios, the proportions of cod and *P. acuspes*, in particular, were higher than in the F<sub>1.1</sub> scenario.

#### *Future projections exceeding the reference conditions*

In case of most species, some future biomass projections were beyond the minimum and maximum values simulated for reference conditions (1974–2006). In near future, the maximum projections of adult cod and sprat clearly exceeded the maximum reference conditions (1974–2006) (Fig. 4a and c; Fig. S5a and c). In the case of cod, all F<sub>0.3</sub> fishing scenarios could result in values above the reference conditions. For sprat, several combinations of cod fishing and nutrient loads, projected higher biomasses compared with the reference maximum (Fig. 4c and S5c). In addition, lower biomasses than the reference minimum were projected by some scenarios or model runs for all groups. For cod and *P. acuspes*, this was the case in the F<sub>1.1</sub> scenarios regardless the nutrient load (Fig. 4a and d; Fig. S5a and d). Sprat biomasses lower than the reference minimum were projected in all nutrient load scenarios, but only when the cod fishing was low (F<sub>0.3</sub>). Any scenario tested could at some time result in herring, *Acartia* spp., and other zooplankton biomasses lower than the reference conditions (Fig. 4b, e and f; Figs S5b, e and S6a). The BSAP scenarios resulted in the lowest phytoplankton biomasses, rather independent of the cod fishing. In far future, the maximum reference biomasses of *Acartia* spp., phytoplankton, and herring were exceeded, in addition to cod and sprat, given that the nutrient loads were high. In the case of herring, also high fishing mortality of cod, i.e., F<sub>1.1</sub>, was required. Biomasses below the reference minimum were no longer projected for *Acartia* spp., other zooplankton, and phytoplankton. For herring and sprat, fewer scenarios (BSAP-F<sub>1.1</sub> and BAU/BSAP-F<sub>0.3</sub> for herring, and BSAP-F<sub>0.3</sub> for sprat) resulted in biomasses below the reference minimum in far than near future. The opposite was true for cod and *P. acuspes*. Furthermore, in the case of cod also the BAU-F<sub>0.3</sub> scenario, and in the case of *P. acuspes* all scenarios resulted in biomasses below the reference minimums in far future.

#### *Food web model uncertainties*

The simplified uncertainty analysis indicated that uncertainties originating from the parameterization of the Ecopath food web model are potentially large



**Fig. 5** The mean proportional biomass of each functional group modeled for (a) the reference period (1974–2006) and for far future (2070–98) in scenarios (b) BAU-F<sub>1.1</sub> (business as usual-intensive fishing), (c) BAU-F<sub>0.3</sub> (cod recovery plan), (d) BSAP (Baltic Sea Action Plan)-F<sub>1.1</sub> and (e) BSAP-F<sub>0.3</sub>. The sizes of the pie charts (a)–(e) are proportional to the mean total biomass of the system.

(Figs S7–S8). The simulations of sprat and cod were particularly sensitive to uncertainties in the Ecopath biomass data. In general, the spread in cod projections was higher in the F<sub>0.3</sub> (Fig. S8) than the F<sub>1.1</sub> (Fig. S7) cod fishing scenario. However, also in the F<sub>0.3</sub> scenario the spread in general increased toward the end of the modeled period. For sprat, a higher spread was observed in the F<sub>1.1</sub> cod fishing scenario, when sprat was under lower predation pressure. Across groups, the spread was in general lower in the BSAP than in the REF and BAU scenarios. In some occasions, the model also behaved chaotically due to very low cod biomass projections.

## Discussion

### Climate-induced changes in food web response

The main aim was to analyze the combined potential effects of future climate, nutrient loads, and cod fishing on the Baltic Sea food web. The applied modeling approach comprehensively linked regionally downscaled

climate projections to a food web model to study how global events affect regional ecosystem response, as called after by, e.g., Lubchenco *et al.* (1991) and Philippart *et al.* (2011). The results show that regional drivers can have a large impact on defining Baltic Sea future (Fig. 4), but that climate-induced changes in hydrodynamic conditions still set boundaries for food web structure and function.

Direct climate-induced effects that were not fully compensated by food web response to nutrient loads and fishing were found in phytoplankton, *Acartia* spp., *T. longicornis*, *P. acuspes*, sprat, and cod (Fig. 4). Phytoplankton production was favored by increasing temperatures (Marañón *et al.*, 2012), compensating for the nutrient load reductions (BSAP scenario, also in Meier *et al.*, 2012a). The thermophile zooplankton species *Acartia* spp. and *T. longicornis* increased with spring temperature. *P. acuspes* was negatively affected by the freshening of the Baltic Sea, particularly at salinities below 8 psu, independent of nutrient loads and predation. Sprat increased with summer temperatures (see also MacKenzie *et al.*, 2012) and decreasing

salinities, the exception being the BSAP-F<sub>1.1</sub> scenario with limited food resources in relation to sprat biomass. As the reproduction conditions for Baltic cod are negatively affected by low salinities (MacKenzie *et al.*, 2000), all cod trajectories declined during the second half of the 21st century (see also Lindegren *et al.*, 2010; MacKenzie *et al.*, 2011). Based on our results future climate-induced changes will greatly affect the Baltic Sea food web dynamics, as also found for other regions (Stenseth *et al.*, 2002; Richardson & Schoeman, 2004; Beaugrand *et al.*, 2008).

#### *Trophic control and nonadditive nature of multiple drivers*

The multiple driver interactions had a large effect on most groups, and the responses varied between and within TLs. Fishing was the main driver affecting cod, whereas phytoplankton, *Acartia* spp., and *T. longicornis* were mainly controlled by resource availability and climate. The intermediate TL groups, sprat, herring, and *P. acuspes*, were more clearly affected by the combination of drivers. For example, the lowest biomass of sprat, the major prey item of cod, was simulated in the BSAP-F<sub>0.3</sub> scenario (Fig. 4c) with the highest trajectory of cod (Fig. 4a). Hence, the increased predation by cod may partly offset the positive effects of temperature on sprat reproduction, and eventually lead to growth limitation in cod. However, the high maximum biomasses of cod projected imply that other density-dependent effects could be important to describe before food limitation. These interpretations need to be taken carefully as for example no fishery related changes to the fish population structure, e.g., increased turnover rates and higher allocation of resources to reproduction, possibly causing a higher vulnerability to climate (Myers & Worm, 2005), were explicitly modeled. Furthermore, the high cod biomass projections may be overestimates as our model comprises the entire Central Baltic Sea and some spatial effects, such as the recent spatial mismatch between increasing cod stock and its prey fish resulting in decrease in cod weight at age (Eero *et al.*, 2012a), cannot be represented. For *P. acuspes*, the negative salinity effects were amplified via increased predation by sprat, but could be partly compensated by increases in phytoplankton (Fig. 4d). As sprat and *P. acuspes* have an ecosystem structuring role in the Baltic Sea (e.g., Möllmann *et al.*, 2009; Niiranen *et al.*, 2012), it seems particularly important to evaluate the interplay of multiple drivers when projecting the ecosystem future (see also Daskalov *et al.* (2007), Llope *et al.* (2011), and Fauchald *et al.* (2011) for examples from other regions).

Primary production constrains fishery production in several marine ecosystems (Ware & Thomson, 2005;

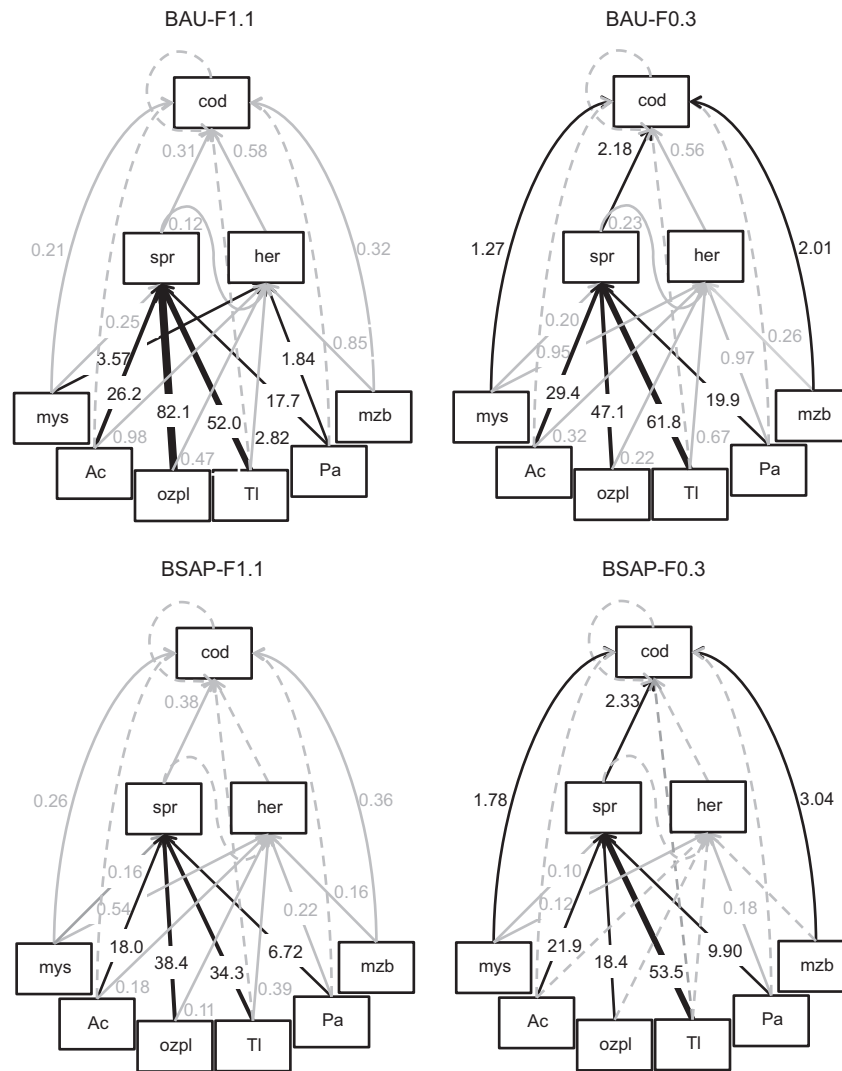
Frank *et al.*, 2007; Chassot *et al.*, 2010), and climate change induced increases in phytoplankton have been suggested to cascade to small pelagic fish (Brown *et al.*, 2010). We found a strong positive indirect nutrient response in, both, sprat and herring (Figs 4 and 5). Also, macrozoobenthos and mysids were positively affected by increasing nutrient loads regardless the negative effects of eutrophication-related hypoxia (Laine *et al.*, 1997). However, the calibration data for both groups were sparse (Tomczak *et al.*, 2012). In contrast to Casini *et al.* (2008, 2009), no top-down trophic cascades to phytoplankton were found, probably due to our one-way coupling between the food web model and BGMs.

Several studies imply that eradicating top-predators may make ecosystems more vulnerable to bottom-up forcing, via reduced top-down control, reduced biodiversity, or accelerating life-histories (e.g., Worm *et al.*, 2006; Casini *et al.*, 2009; Perry *et al.*, 2010; Planque *et al.*, 2010). Cod was more sensitive to changes in nutrient loads and decreasing salinities in the F<sub>0.3</sub> scenario. Consequently, the negative response of sprat to decrease in nutrients was also greater in that scenario, due to increased predation by cod. Opposite dynamics were observed for herring, with lower biomasses than sprat and hence under higher predation control. The maximum sprat trajectories were projected in the BAU/REF scenarios independent of cod predation, indicating that sprat is controlled by bottom-up forces when sprat/cod ratio is large.

#### *Management implications and need to prepare for ecological surprises*

The two most extreme management scenarios indicated very different futures for the Baltic Sea: a eutrophied and strongly sprat-dominated ecosystem with increased total production in the worst-case scenario, or a cod-dominated ecosystem with eutrophication and total production levels close to present in the best-case scenario (Fig. 5 and 6). Furthermore, in the BSAP-F<sub>0.3</sub> scenario benthos formed an important energy supply to cod, as was observed also during the cod peak around the early 1980s (Uzars, 1994; Tomczak *et al.*, 2012), whereas the energy pathway via pelagic fish was more important in the BAU-F<sub>1.1</sub> scenario (Fig. 6). The response time of the Baltic Sea ecosystem to nutrient reductions was projected as 30–40 years (see also Vahtera *et al.*, 2007; Meier *et al.*, 2012b), whereas changes in cod fishing had more immediate (<10 years) effect (see Eero *et al.*, 2012b for recent cod recovery).

The future projections of several Baltic Sea climate variables (see Meier *et al.*, 2012a) and species biomass exceed those measured in the past indicating that the



**Fig. 6** Average biomass flows to and between cod, herring and sprat in BAU-F1.1 (business as usual-intensive fishing), BAU-F0.3 (cod recovery plan), BSAP (Baltic Sea Action Plan)-F1.1, and BSAP-F0.3 scenarios as projected for 2070–2098. All values are in  $t\ km^{-2}$ , and the strength and color of arrows are indicative of the magnitude of the biomass flow. Values below  $0.1\ t\ km^{-2}$  are not shown, but are indicated by a dashed line (spr, sprat; her, herring; mys, mysids; Ac, *Acartia* spp.; ozpl, other zooplankton; TI, *Temora longicornis*; Pa, *Pseudocalanus acuspes*, and mzb, macrozoobenthos).

ecosystem conditions are moving out of the current space (Williams & Jackson, 2007). Hence, unseen threshold values in species response to changing drivers may exist possibly causing sudden ecosystem surprises. Furthermore, there is a risk of nonindigenous species invasions, resulting in novel assemblages of organisms (Daskalov *et al.*, 2007; Williams & Jackson, 2007). Linking several models can also accumulate uncertainties in model parameterization and structure (MacKenzie *et al.*, 2012; Meier *et al.*, 2012a; Neumann *et al.*, 2012). Some uncertainties were addressed by using BGM and climate scenario ensembles, leading to large ranges of species-specific responses but also to some general conclusions (Fig. 4; Table 3). Unpredict-

ability and uncertainties should be accommodated by applying precautionary management options (Brander, 2007; Hoegh-Guldberg & Bruno, 2010) identified, e.g., by ecosystem model ensembles (Smith *et al.*, 2011; Gårdmark *et al.*, 2013). In addition, the management actions should be fast and flexible to avoid long-term costs of, e.g., suboptimal harvesting (Brander, 2007; Kirby *et al.*, 2009; Brown *et al.*, 2012) calling after a closer coupling between human behavior and ecosystem modeling (Österblom *et al.*, 2010). Such coupling could result in more detailed and consistent ecosystem scenarios, and hence provide valuable input to the assessments of potential future conditions of regional marine ecosystems (see, e.g., Halpern *et al.*, 2012).

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Figure S1.** Observed data and model estimates, using ERA-40 output from BALTSEM, ERGOM, and SCOB1 as environmental forcing, of the calibration period (1974–2006): (a) phytoplankton, (b) *Temora longicornis*, (c) *Acartia* spp., (d) *Pseudocalanus Acuspes*, (e) macrozoobenthos, (f) mysids, (g) juvenile sprat, (h) juvenile herring, (i) small cod, (j) adult sprat, (k) adult herring, and (l) adult cod (B, biomass).

**Figure S2.** Oceanographical forcing under climate scenarios A1B1, A1B3, and A2 for a) annual salinity 80–100 m, b) spring 0–50 m temperature, c) August 0–10 m temperature.

**Figure S3.** Biogeochemical forcing in climate scenarios A1B1, A1B3, and A2 for (a) cod reproductive volume (RV), (b) reversed hypoxic area (A), and (c) primary production (as used in model forcing, i.e.,  $P/B = P_t/B_{t-1}$ , where P, production; B, biomass; and  $B_{t-1}$  is the previous year's biomass).

**Figure S4.** Comparisons between the observations and ERA-40 and scenario model estimates of environmental drivers: (a) spring temperature (May T), (b) summer temperature (Aug T), (c) salinity (Sal), (d) cod reproductive value (cod RV), and (e) reversed hypoxic area (Rev. hypoxic A), as well as the biomasses of selected groups: (f) phytoplankton, (g) *Acartia* spp., (h) *Temora longicornis*, (i) *Pseudocalanus acuspes*, (j) adult sprat, (k) adult herring, and (l) adult cod for the model calibration period (1974–2006) (obs, observations; scen, scenarios).

**Figure S5.** Future biomasses of selected organism groups a) cod, b) herring, c) sprat, d) *Pseudocalanus acuspes*, and e) *Acartia* spp. in all nutrient load – fishing scenarios.

**Figure S6.** Future biomasses of selected trophospecies groups (a) other mesozooplankton (other zpl), (b) mysids, (c) macrozoobenthos, and (d) phytoplankton in all nutrient load – fishing scenarios.

**Figure S7.** Results from the simplified uncertainty analysis of the food web model for (a) cod, (b) sprat, (c) *Pseudocalanus acuspes*, (d) *Acartia* spp., and (e) phytoplankton (phytopl.) in the intensive cod fishing scenarios ( $F_{1.1}$ ).

**Figure S8.** Results from the simplified uncertainty analysis of the food web model for (a) cod, (b) sprat, (c) *Pseudocalanus acuspes*, (d) *Acartia* spp., and (e) phytoplankton (phytopl.) in the low cod fishing scenarios ( $F_{0.3}$ ).

**Table S1.** Changes in the food web model input data in comparison to the BaltProWeb model.

**Table S2.** Changes in the food web model parameterization of multistanza groups in comparison to the BaltProWeb model.

**Table S3.** The food web model diet composition input table (spr, spring; values as proportions of the total diet).

**Table S4.** Data sources used in building the Ecopath model and calibration of the Ecosim model.