Response to the editor

by Sonja van Leeuwen, lead author of manuscript bg-2015-196, on behalf of all co-authors

Dear editor,

we have changed our manuscript bg-2015-196 according to the reviewers comments. This has led to the inclusion of more figures in the site specific graphs (CC + OA LTL + OA HTL). To aid interpretation we have also included these graphs for the single acidification impacts, i.e. climate change effects plus lower trophic level acidification impacts (CC + OA LTL) and climate change effects plus higher trophic level acidification impacts (CC + OA HTL), in the new supplementary materials. This was not specifically asked for, but we feel it significantly adds to the information included in the separate tables and the analysis presented in the separate impact sections (there was some obvious confusion there by both reviewers). We hope you and the reviewers agree with these additions.

yours sincerely,
on behalf of all co-authors,
Sonja van Leeuwen

Response to reviewer 1

by Sonja van Leeuwen, lead author of manuscript bg-2015-196, on behalf of all co-authors

1 General response

The authors are grateful for the detailed comments provided by Dr. Fulton, a well-known expert in end-to-end modelling. As a result the manuscript is now more descriptive of the shortcomings of the method, and contains a better explanation of the applied coupling. Detailed responses are provided below. We hope we have responded to the correct sections but could not find a version of the manuscript with continuous line numbers as used by the referee.

2 Detailed response

1 *Lines 95-103: It would be good to see some reflection on what the expected downsides of not having 2-way coupling are. How do the authors account for consumptive losses in the plankton due to feeding by the fish fauna? Was the level of consumption of the same order as the assumed mortality?*

Regarding 2-way coupling we have added the following line to section 6: "This would also ensure feedback of other predator changes (e.g. increased feeding rates due to increased sea temperature, more pelagic-oriented feeding) on planktonic biomass, which are not included in one-way coupling. ". We expect these impacts to be minor compared to the mortality/feeding feedback.

Regarding the mortality we have added the following lines to section 2.3: "Fish predation mortality in ERSEM-BFM is simulated as cannibalisms of the largest species, ensuring a dynamic mortality dependent on biomass. Thus both lower trophic level mortality and higher trophic level feeding were driven by lower trophic level biomass values, ensuring a proportionate response."

However, these responses do not correspond to the same functional types, as there is some overlap in species representation between the two models. This is being addressed in current development of the coupled model as two-way coupling is being implemented.

2 *Line 118: The fishing pressure that was included, what level was that pressure? Was it based on a particular year? Why was the fishing pressure assumed to be homogeneous spatially? What are the implications of the simplification?*

The applied fishing pressure was that as described in Blanchard et al. (2009), and as such took a value of 1.0 (fishing pressure switched on, pressure proportional to averaged values based on multispecies virtual population analysis ICES (2005) over 1990-2003). This pressure was assumed to be constant over the sites as lack of local observations on the food web scale prevented calibration. Nevertheless, the LTL detritus supply to the HTL model was calibrated to reflect the only available regional detritivore size spectrum observations, representing a fished environment. As such, the different calibration numbers account to some extent for different fishing pressures between the sites. We have changed the text to

"Griffith et al. (2012) showed the importance of including fishing pressure combined with acidification and temperature pressures in an Australian ecosystem. Here it was included in the model as a nominal pressure (based on ICES (2005)), but was not calibrated to represent site-specific mortalities. "

3 *Table 4: It is interesting that few changes are >40%, but still there are many declines in catches despite quite small changes in POC, primary production and biomasses.*

This is mainly due to the limited selection of model state variables in the tables: not all mechanisms and carbon pathways are represented by them. We have now included more analysis of system response (as requested by reviewer 2), including for instance information about near-bed diatom levels: these can be crucial for carbon transport to the benthic system, but are not necessarily proportional to water-column averaged diatom levels. We have also added fish and detritivore predation mortality time series, to better indicate response mechanisms in the higher trophic levels. However, the fact remains that the higher trophic level model is considerably less complex (2 state variables) than the lower trophic level model (60+ state variables), and therefore will be more sensitive to changes in the few drivers.

4 *Line 194: The pelagic and benthic biomasses do decline, but the pelagic ones in particular are small, would they actually be detected in reality?*

As reviewer 2 points out, this study is essentially a sensitivity study into the effects of the different pressures: the main interest is in the trend of the long-term projections of stressor impact. Changes were small for lower trophic level dynamics for acidification impacts, but climatic impacts would certainly be detectable with the larger impacts on benthos (-20 %) and net primary production (+11 %).

5 *Section 3.2: While there are many declines, the changes are typically small. Again are the declines of a magnitude that they would be noticeable in reality, they seem to be potentially negligible relative to likely noise level?*

The OG site is in "transitional waters", meaning it is characterised by large interannual variability in the governing hydrodynamics. As such, it can certainly be expected that the predicted pelagic changes are smaller than interannual variability. Nevertheless, the main objective here is to gauge the future trend due to particular pressures.

6 *Line 266-267: Clarify this sentence, particularly the bit in brackets on food supply it is not clear what you mean here and the logic of the steps.*

We apologise for this confusing sentence, and have now reworded the part in brackets to "increased general increase due to planktonic food supply". There is a difference in the planktonic food supply for small pelagic predators, and the food supply for larger predators (i.e. smaller fish and detritivores). We have now added new figures showing predation mortality rates for the higher trophic level model, both in the manuscript (for combined impacts) and in the new supplementary materials (for separate impacts). Together with the existing figures for planktonic food supply (adjusted figure title to reflect origin of food) we hope we have clarified this matter.

7 *Line 301 (section 5.2 line 24): "Pelagic fish food supply increased slightly due to indirect acidification impacts (figure 4d)". This should be figure 4c in which case it dipped and rebounded ...*

We have corrected the erroneous figure reference. Figure 4c indeed shows a dip and recovery, with the 2069-2098 averaged values just marginally higher than those for 1079-2008 for all scenario's. But the main point here is that acidification impacts caused fish food supply to increase compared to climatic impacts. We have reworded the line to clarify this: "Pelagic fish food supply increased slightly due to indirect acidification impacts (figure 4(c), increased values compared to climate change scenario), ...".

8 *Line 303:"Fishing yield decreases according". I am not sure I would agree based on Figures 4e and 4f. Please be clear about whether you are talking about transients or snapshot end points.*

We have changed the text to better reflect our meaning: i.e. that the decline is for the future conditions under OA and CC pressure relative to the current state (CC simulation 1979-2008 result). The decline therefore does not refer to the temporal development of any one scenario, but to the change between the scenario's. New text included:

"Fisheries yield decreases accordingly (figure 4(e), acidification scenario's vs Temp scenario), with the main decline in the winter period (figure 4(f))."

9 *Line 308 (section 5.3 line 7): "Detritivore growth rates remain more or less equal..." I disagree, please make sure the results match the plot, which indicates an increase.*

We apologise for the confusion. Indeed the corresponding figure shows an increase in detritivore growth rates for all scenario's as a function of time: what we meant was that there is virtually no change in the growth rate between current conditions (climate change run, 1979-2008) and future conditions with both stressors (High scenario run, 2069-2098). We have changed the text to reflect this better: "Detritivore growth rates remained more or less equal when combined effects are applied (figure 5(d), High scenario 2069-2098 result compared to Temp scenario 1979-2008), ..."

10 *Lines 310-311: There is a decline in winter, but there is a big increase in summer, that should not be ignored.*

We have changed the text to reflect this: "Changes to fisheries yield depended strongly on the strength of acidification impacts (figure 5(e)), affecting all seasons (figure 5(f)) and showing a strong decline in winter and strong increase in summer."

11 *Line 331-332: Interaction effects could be explored using the Hedge's d method in Griffith et al 2012. Conservation Biology 26: 1145-1152*

We agree with the reviewer that the Hedge's d method is very useful for exploring interaction effects: it was applied in Griffith et al. (2012) to disentangle effects of fishing pressure, climate change and ocean acidification in Australian marine waters. Unfortunately we do not have a reference simulation without any pressures, so cannot apply the same method here without additional effort (we only consider two pressures, with the climate change simulation acting as the benchmark to measure acidification impacts against). With 3 different sites, 2 different pressures, 2 different trophic impact levels and 3 different reduction rates we do not want to complicate the analysis further by adding an additional reference plane. In this manuscript we want to focus on the underlying processes that effect future fisheries yield in three distinct areas. However, the Hedge's d method would be very useful in future work to include additional pressures like fishing or nutrient stress. Griffith et al. (2012) also notes that variation in interaction response must be taken into account (i.e. combinations of different impact levels to gauge interaction response): this is exactly what this manuscript has tried to do with respect to ocean acidification.

12 *Line 364: What time scale is being considered here? When could monitoring schemes start to check for it?*

As sea surface temperatures are already increasing in the North Sea (**??**), with large scale regional differences (Eastern North Sea vs Western North Sea), the effect is already visible in observations. However, to discern the separate effects of acidification and changing meteorological conditions would require considerable effort, as understanding of species response to OA effects remains limited.

13 *Line 368: Griffith et al 2012 is an example of a paper that has already started to explore this topic.*

We sincerely apologise for not including this highly relevant paper before. We have now included references to this paper were appropriate, and have added the following paragraph to the Discussion:

"When considering multiple stressors like acidification, climate change, nutrient supply and fishing pressure the interactions of different pressures should be studied using statistical techniques such as the Hedges-d method: this was applied in Griffith et al. (2012) with respect to ocean warming, ocean acidification and fishing pressure in Australian marine waters. They showed that interactions between pressures could lead to less than or more than the additive response of the system: for instance, fishing pressure counteracted negative effects from acidification on benthic invertebrates by relieving predation pressure. Similar results were found in this study, as climate-change induced increases in biomass were counteracted by acidification impacts. Together with different impact level studies like the one presented here these methods have the potential to provide a good indication of future marine response to known pressures.".

3 Technical Comments

14 *Line 73: Missing a fullstop after "light climate"*

Corrected.

15 *Figure 2.1: Define ROFI. Explain what the white space in the marine sections of the plot means. Does it mean there is no clear pattern for classification (i.e. transition zone)?*

We have now included a description of the white areas and the ROFI in the caption:

"ROFI stands for Regions of Fresh Water Influence. The white areas represent transitional waters, which experience large variability in duration of mixed and stratified conditions, defying classification."

16 *Table 3: It appears that the second rows is a duplicate*

Yes, and this has now been removed.

17 *Section 3.2 and 3.3. For both of these sections (on Oyster Grounds and Southern Bight) please make it clearer when referring to acidification vs temperature effects, or combined effects.*

We have tried to make this more clear in the relevant sections. Please note that the original text was already structured to this effect: first paragraph on climate impact, second paragraph on acidification impact, third paragraph on combined impact.

18 *Line 283: Should be "... enhanced by the direct acidification..."*

Corrected.

19 *Figure 3 (and Figures 4 and 5): The panels are small and hard to read. The colouring for the bar plots are not friendly for colour blind people. Could a different scale be used (or could the bar plots be broken into multiple panels) so that the temperature results do not obscure what is happening in the other cases.*

We apologise for the use of colours unsuitable for colour blind people, and have now changed the colour scheme to one more suitable. Additionally, hatchings have been applied to the bar plots for easy identification. Temperature effects have been excluded in separate plots where necessary, mainly in the new supplementary materials.

20 *Line 345: This would read more easily as "... aggravate or relieve the impacts of future pressures."*

The text has been changed accordingly.

Response to reviewer 2

by Sonja van Leeuwen, lead author of manuscript bg-2015-196, on behalf of all co-authors

4 General response

We thank reviewer two for his detailed and constructive comments on our manuscript. We agree with the reviewer that there are many inherent limitations in this type of modelling, and have reworded our results to reflect this, mainly in the discussions and conclusions sections. We have also reworded our title, taking into account the these considerations as well as the on-line comment left by Dr. Gattuso: "Potential future fisheries yields in shelf waters: a model study of the effects of climate change and ocean acidification". A detailed response to specific comments is given below:

- *First, direct impacts of OA on fishes and invertebrate can be various, interactions among these will be numerous, and uncertainties are still high. Authors' choice to simulate direct impact of OA with a decreased in growth of detritivores is surely a sound assumption, based on several observations and related meta-analysis, but it's "just" one of many possible assumptions. Reduced growth of calcifying detritivores could be compensated by increased growth of non-calcifying detritivores since the reduction of interspecific competition. Many studies also highlight potential direct impact of OA on pelagic fishes (e.g. otolith development, metabolic cost, reproduction success, behavioural response to cues) but authors do not account for these (and not even discuss those) and this could significantly affect the pelagic predator community, and therefore fishery yields.*

  Additional text has been added to the introduction and conclusion section justifying the selection of the processes emulated in this study and recognising the implications of choosing different acidification affects to emulate in the model, as indicated by the reviewer.

- *Secondly, the work is based on the implementation of 1D models that, by nature, do not include lateral advection. Authors are transparent on this limitation (see beginning of section 6), however they just mention this without discussing what are the consequences. The North Sea is indeed heavily influenced by the oceanic input, particularly regarding to nutrient inputs (e.g. Vermaat et al., Estuarine Coastal and Shelf Science, 2008). CC projections from recent IPCC scenarios project an increase in stratification in the North Atlantic with consequent decrease surface nutrients (e.g. Steinacher et al, Biogeosciences, 2010, and more generally AR4 and AR5 reports), and this could impact significantly the North Sea, particularly the central and Northern part (ND and OG – see Holt et al., Biogeosciences, 2012). Given the monodimensionality of the study, authors do not consider such reduction of nutrient input with the oceanic waters and focus only on the local dynamic. This could potentially lead to an overestimation of the temperature effect that could be significantly changed (e.g. change the sign of CC impact) when nutrient reduction is considered.*

  We agree with the reviewer that changes in future nutrient supply could impact heavily on the results discussed here. However, in order to disentangle effects of different pressures with uncertain levels of impact we have elected to restrict the study to two stressors. As we consider three different locations and impacts on both the abiotic and biotic level on three different magnitudes we have performed 33 simulations in total (1 reference run and 10 scenario runs per site). We hope that this work will help interpret future studies which also take into account the effect of nutrients. However, future nutrient scenario's will necessarily be tentative particularly for land-based sources. North Sea circulation patterns cause offshore transport of land-derived nutrients: the peer-reviewed science report by Painting et al. (2013) shows that both the SB site and the OG site are within the influence zone of riverine nutrients (their figure 4). We have therefore added the following line to the discussion: "The bottom-up stressor of nutrient supply should also be considered in future studies, as changes in nutrient availability can change lower trophic level dynamics considerably. However, for the North Sea future changes in nutrient supply should take into account changes in Atlantic sources (Holt et al, 2012) as well as land-based sources (Painting et al,2013, their figure 4).".

Concerning the effect of 3D processes we have added the following lines to the discussion: "Advective processes and oceanic changes have the potential to outweight local response. This applies mainly to ocean acidification impacts, as climatic impacts are mainly a direct response to local meteorology.".

5 Detailed response

Section 2.3 *coupling between ERSEM-BFM and the HTL model is achieved via the biomass of some of the planktonic biomasses (diatoms, flagellates, picophytoplankton, microzooplankton and heterotrophic nanoflagellates). Authors state that ERSEM–BFM has more planktonic groups than these ones (dinoflagellates, phaeocystis, small diatoms and 2 groups of mesozooplankton) but it's not clear why these biomassess are not used to couple the HTL model.*

Dinoflagellates and *Phaeocystis* were not included as these functional groups are predominantly inedible to other species. Mesozooplankton groups were not included as these overlap in size with the start of the pelagic predator size spectrum: this issue is currently being addressed in futher development of the coupled model. Small diatoms were not included initially, as they represented a new functional group within ERSEM-BFM with very limited occurrence (early spring and in small numbers). This group has been included since and comparison studies showed no significant difference due to their small contribution. Subsequent model development on ERSEM-BFM has seen this group transformed into resuspended benthic diatoms with a more defined impact on plankton biomass levels. We have added the following to section 2.3:

"Note that dinoflagellates and *Phaeocystis* were not used as food as these are predominantly inedible. Mesozooplankton was not included as food as it overlaps with the start of the pelagic predator size spectrum."

Section 2.6 *authors assume a decreasing growth of 2, 6 and 10%, with those numbers coming from a combination of impact of OA on growth of calcifying organisms and percentage of calcifiers in the detritivore's community. Even though it would not make any different from a modelling point of view, it would be helpful to disentangle the impact of OA from the community composition effect, in order to better contextualise the study (e.g. is the impact small/large because the simulated community has less/more calcifiers or because of OA?). Furthermore, do the three thresholds have been chosen by authors on the basis of useful range to test model sensitivity, or on the basis of experimental data? To my knowledge the two papers cited do not offer estimates of the decrease of calcifiers' growth.*

Doney et al. (2009) does document studies where decreased calcification has been observed in bivalves (10 to 25 %) so this range could be used to set the sensitivity range to be tested, although somewhat precautionary. A review by Wicks and Roberts (2012) stated –"under short-term experimentally enhanced CO_2 conditions, many organisms have shown trade-offs in their physiological responses, such as reductions in calcification rate and reproductive output", but some of the detritivore/deposit feeder acidification work is not consistent between or within macrofaunal groups as Wicks and Roberts (2012) also discuss. The limits were therefore set in terms of a sensitivity test using the available experimental data, in a conservative fashion and relevant to the detritivores present in the model version. The paper by **?** may be less relevant but has a discussion on infaunal calcification changes and the complexity of this issue, and therefore we included it. We have now added the Wicks and Roberts (2012) reference to this section.

Regarding community structure, we agree with the reviewer that this will be important. But without specific representations of calcifiers in the model it is beyond the scope of this study to quantify this effect. In contrast, the lack of community structure information allows us to make predictions for larger areas. Local community information can then be used together with results presented here to indicate possible local response to future pressures. We have added the following line to section 2.6 to highlight this issue: "Note that community structure observations would be necessary to interpret localised effects of reduced detritivore growth rate.".

Section 3.1 *Authors suggest that organisms adapted to high Ammonium/lower nitrate regime induced by OA: how the model can show organism adaptation? Surely it cannot be evolutionary adaptation, as parameters in ERSEM-BFM are, to my knowledge, static. What is the trait/processes that changed (adapted)? And how? (see also comment on 3.3)*

Indeed adaptation is not possible with the ERSEM-BFM model. But functional groups have the option to use ammonium or nitrate to satisfy their internal nitrogen demand, with each functional group displaying different affinity to the different nutrients. With the reduction of pelagic nitrification the supply of pelagic nitrate decreased while that of pelagic ammonium increased. This led organisms to take up more ammonium compared to nitrate than in the unperturbed scenario. In the text we have changed the word "adapted" to "reverted" to clarify this.

Section 3.2 *authors state that CC will impact more the benthic system (with high increase in benthic detritus and decrease in biomass): why? What are the fluxes simulated by the model that lead to that result? Why growth decreases despite the increase in T?*

The future climatic conditions at the Oyster Grounds location are characterised by a reduction of wind speeds in spring, leading to less suspended particulate matter in the water column. This triggers an earlier start of the spring bloom, but as onset of stratification does not change significantly (a trigger for diatom sinking) there is a strong reduction in diatom levels near the sea bed (Van der Molen et al., 2013). As this is the main food source for filter feeders, and the most important carbon pathway into the benthic system, there is an equivalent reduction in benthic biomass in the lower trophic level model (the more noticeable as benthic biomass is larger than pelagic biomass at this site). With less benthic biomass there is less uptake of benthic POC and thus an increase in benthic POC levels despite a decrease in pelagic POC levels and increased benthic metabolic rates. We have added the following line to this section to clarify this site-specific response:

"Onset of stratification (a trigger for diatom sinking) did not change significantly at this site, leading to a longer period of suspended diatoms and a reduction in near-bed diatom levels during spring. This led to a decline in filter feeder biomass (due to a reduction of the main food supply) and a subsequent reduction in other benthic functional groups (as pelagic-feeding filter feeders form the main carbon pathway into the benthic system in the model), see Van der Molen et al. (2013). As a result, benthic POC levels increased."

Section 3.3 *authors state that reduction in nitrification rate favour plankton with high ammonium preference (picophytoplankton and dinoflagellates). Why this is not seen in the other two test cases? From the paper, it seems that the set of parameter for ERSEM-BFM does not change across the sites, therefore those groups should have higher affinity for ammonium also in the other test cases but in ND the impact is null, while in OG is somehow similar to this case for dinoflagellates (even though authors state that is minor in that case and they do not discuss it – section 3.2). So what's the mechanism behind the increased biomass of picophytoplankton and dinoflagellate? Is difference in nitrogen speciation, or a some other bottom-up process (e.g. less diatoms in the spring blooms could leave more nutrient available for following blooms) or top down control (e.g. change in the spring bloom could change zooplankton community and biomass and therefore relieve later bloom from some grazing pressure). Looking at the nutrient uptake/grazing fluxes and/or nutrient availability estimated by the models could help in supporting either of the hypotheses.*

The author is correct in assuming the parameters are predominantly the same for each site. The response is therefore also visible for the other two sites (see renewed figures for phytoplankton percentage change with adjusted y axis): percentage change for picophytoplankton and dinoflagellates are 2 % and 4 % for the SB site, 2 % and 13 % for the OG site and 2 % and 0 % for the ND site (no dinoflagellates present). The governing mechanisms differ for each site:

At the SB site picophytoplankton benefit in summer from higher ammonium levels and decreased predation (increased levels of omnivorous mesozooplankton cause lower levels of microzooplankton). As the system is nitrate-depleted during this period they outcompete the flagellates due to their ammonium preference. Dinoflagellates also benefit from this in autumn, and experience no grazing pressure as they are inedible.

The OG site also experiences higher ammonium levels but as this site stratifies in summer it does not become nitrate deplete. Grazing pressure for picophytoplankton remains similar and increased levels of picophytoplankton mainly occur during the spring bloom, not in summer. Dinoflagellates increase during the autumn bloom due to less competition from *Phaeocystis* colonies.

The ND site shows a high increase in ammonium levels in early summer, higher than the general increase throughout the year. Picophytoplankton increases during the spring bloom and summer and levels are higher than those for the other two sites, resulting in a smaller percentage change. They also experience increased grazing pressure during this period. Dinoflagellates decrease due to acidification impacts at current conditions but are quickly wiped out by climate change effects in all tested scenario's.

So the reviewer is right in stating that other factors might be important at the different sites. We have added text to each section to highlight this difference.

Section 4.2 *"as fish were more dependent on the detritivore food source" could author provide some comparative estimates of the trophic fluxes across the groups on the different sites? This could help to understand at which level of "connectivity" across groups this mechanism become important.*

To visualise this dependence we have included figures for each site of predation mortality biomass for pelagic predators and detritivores, showing changes in feeding strategy. The new figures are also discussed in the text in the relevant sections. We have now also included the relevant figures for the separate pressure scenario's, i.e. ocean acidification impact only on lower trophic levels (reduction of pelagic nitrification rate), and ocean acidification impact on higher trophic levels only (reduction of detritivore growth rate). these new figures have been included in the supplementary materials.

Finally *the introduction is not giving an adequate representation of the literature of OA impacts both on biogeochemistry/low trophic levels as well as invertebrate, fish. Although a comprehensive review of OA impact is clearly not the aim of the paper, nor of the introduction, a quick glance of the variety of way on how OA impact on both part of the marine ecosystem citing a series of papers would help those readers not fully aware of the OA topic to put this study in the context and better understand its findings. Here a non-exhaustive and non-compulsory list of suggestions of impact and papers that could help in giving this context:*

- *impacts of OA on Primary producers: Riebesell and Tortell, chapter 6 of Ocean acidification, Gattuso and Hansson eds.; Tagliabue et al., Global Biogeochemical cycles, 2011; Engel et al., Biogeosciences, 2013; Schulz et al., Biogeosciences, 2013; Artioli et al., Biogeosciences, 2014; Taucher et al., L&O, 2015*
- *impacts of OA on benthic detritivores (or more generally benthic fauna): Andersson et al., and Widdicombe et al., chapter 7 and 9 of Ocean acidification, Gattuso and Hansson eds.; Hale et al., Oikos, 2011; Kroeker et al., Global Change Biology, 2013; Wittman and Porter, Nature Climate Change, 2013*
- *impacts of OA on fishes: Porter et al, chapter 8 of Ocean acidification, Gattuso and Hansson eds.; Kroeker et al., Global Change Biology, 2013; Munday et al., Nature Climate Change, 2014; Simpson et al., Biology letters, 2011 C3929*

We thank the reviewer for pointing out more relevant work, not all of which was mentioned previously. Additional text has been added to the introduction to briefly comment on the range of acidification effects that have been identified by the reviewer and references are provided for some of the main reviews that will allow readers to access the ocean acidification literature. There have been many copious reviews of acidification effects: this paper is deliberately seeking to avoid providing yet another review of them.

6 Minor issues

– section 2.4 *which ERSEM-BFM parameters have been calibrated using fish size spectra data? And what is the final value? Why calibrate ERSEM-BFM with fish data instead of calibrating the size spectra model?*

Within the coupled model the ERSEM-BFM lower trophic level model provides detritus time series for the higher trophic level model. This supply was multiplied by a calibration factor before becoming available as food in the size-spectrum model, as detritus supply to the bed was underestimated (Van der Molen et al., 2013). This factor was used to calibrate the higher trophic level model to observations from Maxwell and Jennings (2006) (detritivore observations over the size spectrum). We have changed the text to reflect this: "Here, data from Maxwell and Jennings (2006) were used for calibration of the ERSEM-BFM near-bed detritus levels (indicated to be a problem by Van der Molen et al. (2013)) as supplied to size-spectrum model, while the data from Jennings et al. (2002) was used for validation. Calibration factors were 25, 2.5 and 5 for the ND, OG and SB sites respectively". No parameters within ERSEM-BFM were calibrated for this study.

section 2.4 *authors rightly state that correlation between simulation of fish biomasses and observed data is high, but they don't discuss the high difference in variability (standard deviation): detritivores in all sites have a variability about 60% to 70% higher than the data, while predators about 40% lower. Is that due to higher/lower seasonal cycle? Being so consistent across sites,* *does this suggest a limit of the model?*

We agree with the reviewer that the difference in variability between predators and detritivores can indicate a model limitation. However, it can also relate to the limitations of the observational data used, which was obtained from only 1 study (Maxwell and Jennings, 2006) which did not cover all seasons or all represented detritivore groups. Therefore we think we cannot meaningfully comment on model limitations based on such limited data, but we have highlighted the issue in this section by including the following sentence:

"Note that the large difference in variability between predators and detritivores can indicate both a limitation of the model system (lacking stabilising processes for detritivores or benthic POC supply) or a limitation of the observational data applied (covering only one spring and one autumn cruise and considering only infaunal predators).".

section 2.5 *I suggest to move the description of the sites earlier in the text, so the readers will know the characteristics of the sites before reading details on validation in section 2.4*

Done. The section has been placed after model description but before model validation.

section 2.6 *authors refer to “future conditions” to the period 1958-2089. Clearly this run does not represent only future condition, but it is a transient run forced by climatic forcing (HADRM3) instead that by reanlaysis forcing (ECMWF). Therefore, I would suggest as more appropriate names “reference” (or reanalsyis or hindcast) for the ECMWF forced run, and “climate” or “transient” for the HADRM3 forced one.*

The reviewer is right and we have changed the names of the different simulations, with "reference simulation" now referring to the ECMWF-forced run and "climate change simulation" referring to the HADRM3-forced run in section 2.6. To reflect this we have changed the header in tables 4-6 to have "actual" values rather than "reference" values as these correspond to the climate change simulation and not the ECMWF-forced simulation.

section 6 *authors state that 3D models, contrarily to 1D models, lacks of specific local parameters (e.g. bed composition or sediments properties). Although I generally agree with the authors that medium-coarse resolution models can neglect local specificity, and that high resolution 3D models are costly, it’s not clear which specific local parameters in this 1D implementation that couldn’t be included in a 3D model and that improved the results.*

There are no parameters or processes included in the 1DV model that are not included in the 3D version of the same code, and we apologize for suggesting this in the text. What we meant was that local parameter calibration is possible in a 1DV setting whereas the same parameter can have a spatially constant value in a 3D model. We have changed the text here to better reflect our meaning:

"The use of 3D models adds advective processes and far-field influences, but generally lacks specific local parameter settings (here bed porosity and increased vertical resolution). As such, the two approaches are complementary. The less computationally expensive water column model also allows for many scenario simulations to be performed within a reasonable time frame, and is therefore very suitable for scenario studies including different pressures."

table 3 *I assume that the repetition of the first row is a mistake*

Indeed, and this has now been corrected.

tables 4-6 *it would be interesting to highlight which changes are statistically significant (any simple significance test would do, t-test or Kurskal-Wallis). Furthermore, I would suggest authors to write in the caption that changes shown here are 2069-2098 vs 1979-2009*

We have added the requested time indication to the captions. We have not added any statistical tests to show significance as we only present a subset of variables here from a very complex model system. We also feel it would distract from the overall goal of presenting long-term change as any statistical analysis would have to be performed on the original time series (or at the least annual time series), including seasonal, interannual and decadal effects.

figure 2 *there is no legend for the white areas in the domain*

We apologise for this omission and have added the following line to the caption:

"The white areas represent transitional waters, which experience large variability in duration of mixed and stratified conditions, defying classification."

figure 3,4,5 *similarly to table 4,5,6, I would specify in the caption the two time horizons used to calculate the data shown in the bar plot. More importantly, why outputs from ERSEM-BFM are shown with bar plot while outputs from the size spectra models are shown by time series? My understanding is that both models have been run for the same period 1958-2089, so the results could be shown in the same way to better understand the dynamics. Furthermore, since authors have run the models for the full period, why showing the outcome averaged by 30 years? In my opinion, such a way authors reduce significantly the power of their work, flattening all variability, masking non-linearities and limiting the ability to highlight and understand interacting mechanisms. If authors decide to keep the 4 timeslices approach to show their results, I would suggest to remove the lines among the dots (or maybe choose bar plots) to avoid suggesting (unlikely) linear trends across 30 years average.*

We agree with the reviewer that the 30-year averages reduce variability, but this was precisely the aim: with such complex models we wanted to focus on the long-term changes which can be obscured by interannual and decadal variability within the system. The full results were used in the analysis of the work when necessary, but with the large number of state variables and the many different scenario's we have opted to focus on the long-term changes only.

Concerning the type of plots used we have elected to present the majority of the work in line plots, as they contain more information. Bar plots showing percentage change were only applied to functional groups as actual values can vary widely between groups and thus obscure change if presented in one graph. Thus we have decided to stick with the current graph styles: the new figures added which relate to the higher trophic level model are therefore also line plots. We have adjusted the scale on some of the bar plots to better show change.

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Potential future fisheries yields in shelf waters: a model study of the effects of climate change and ocean acidification

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Abstract. We applied a coupled, marine water column model to three sites in the North Sea. The three sites represent different hydrodynamic regimes and are thus representative of a wider area. The model consists of a hydro-biogeochemical model (GOTM-ERSEM-BFM) coupled one way upwards to a size-structured model representing pelagic predators and detritivores (Blanchard et al., 2009). Thus, bottom-up pressures like changing abiotic environment (climate change, chemical cycling) impact on fish biomass across the size spectrum. Here, we studied three different impacts of future conditions on fish yield: climatic impacts (medium emission scenario), abiotic ocean acidification impacts (reduced pelagic nitrification) and biotic ocean acidification impacts (reduced detritivore growth rate). The three impacts were studied separately and combined, and showed that sites within different hydrodynamic regimes responded very differently. The seasonally stratified site showed an increase in fish yields (occuring in winter and spring), with acidification effects of the same order of magnitude as climatic effects. The permanently mixed site also showed an increase in fish yield (increase in summer, decrease in winter), due to climatic effects moderated by acidification impacts. The third site, which is characterised by large interannual variability in thermal stratification duration, showed a decline in fish yields (occuring in winter) due to decline of the benthic system which forms an important carbon pathway at this site. All sites displayed a shift towards a more pelagic oriented system.

7 Introduction

Responsible management of marine resources has to take into account the different pressures operating on the marine system, like fishing pressures, changing climatic conditions and eutrophication issues. Ocean acidification, the increased uptake of CO_2 by the marine environment due to elevated levels of atmospheric CO_2 (Doney et al., 2009; Gattuso et al., 2011), has been a recent addition to this list, but has the potential for wide-spread impact on the marine food web (see e.g. Fabry et al. (2008); Kroeker et al. (2010)). Research into ocean acidification effects have focussed largely on individual species and changes to their local environment, without considering the wider ecosystem and possible societal impact ~~(Doney et al., 2009; ?) . Contradictory results from laboratory experiments complicate the overall picture (Ries et al., 2009; Kroeker et al., 2010; Liu et al., 2010) , reducing confidence in the up-scaling ability of single-species experimental results.~~ (Doney et al., 2009; Le Quesne and Pinnegar, 20 The combined effects of direct (species level) and indirect (abiotic environment level) changes due to ocean acidification across the food web remain unknown. However, these relative impacts need to be understood in order to support effective ~~marine management, and to make best use of scant management resources~~and targeted environmental management. This study applies a modelling approach to examine the potential higher-level effects of the impacts of climate change and ocean acidification on marine ecosystems.

There is a growing body of evidence that ocean acidification can have a range of direct effects on marine organisms and processes (Fabry et al., 2008; Kroeker et al., 2010, 2013) . However evidence of a physiological response to ocean acidification does not necessarily imply an ecological or system level response to ocean acidification (Le Quesne and Pinnegar, 2012) . Potential system level responses of ocean acidification are most likely to occur where there is a clear relationship between the effect of ocean acidification and a system level process such as nutrient recycling or energy fluxes.

In this study we examine potential higher- and lower-trophic level effects of ocean acidification with the potential to affect ecosystem-wide dynamics by emulating two effects that have been demonstrated to occur in multiple independent studies. These effects that are examined are a decrease in microbial nitrification (Beman et al., 2011; Huesemann et al., 2002; Hutchins et al., 2009) and decline in growth efficiency in benthic calcifiers due to the increased energetic cost of calcification (Andersson et al., 2011) . A decline in nitrification could reduce the supply of oxidised nitrogen; the nitrogen substrates that supports new primary production, leading to a shift in the phytoplankton community. An increase in the energetic cost of calcification could reduce growth efficiency and hence reduce trophic transfer efficiency of benthic calcifiers.

Here, modelling tools are used to provide a first indication of single and combined effects of direct and indirect impacts ~~on the~~ of climate change and ocean acidification on a marine food web. The main objective is to estimate the relative impact of both changing climatic conditions and ocean acidification effects (direct and indirect effects) across ~~the~~ a marine food web. To this end, a coupled ecosystem model was applied in selected locations around the North Sea (north-western European continental shelf), which described the abiotic and biotic environment up to commercial-size fish level. Impacts of future climatic conditions are compared with ~~impacts due to altered~~ ocean acidification driven impacts on pelagic nitrogen cycling and growth ~~alterations of seabed~~ efficiency of benthic organisms.

8 The applied ecosystem model

The model simulating the physical processes, chemical cycling and lower trophic level biological communities is GOTM-ERSEM-BFM. This water column model was developed in a joint effort by the Cefas (UK) and NIOZ (Netherlands) institutes with the specific aim to represent shallow shelf seas in detail. Higher trophic levels are simulated using a size-structured model.

8.1 Lower trophic levels

Water column hydrodynamics were simulated using the GOTM model (General Ocean Turbulence Model, see www.gotm.net and Burchard et al. (1999)). This model simulates the most important hydrodynamic and thermodynamic processes related to vertical mixing in natural waters, including different parametrisations for turbulent processes. The ERSEM-BFM model was used to simulate chemical cycling and lower trophic level communities: this model was jointly developed by Cefas and NIOZ from the original ERSEM and BFM codes. The ERSEM model (Baretta et al., 1995; Ruardij and Raaphorst, 1995; Ruardij et al., 1997; Ebenhöh et al., 1997) was developed in the 1990's to represent marine biogeochemical processes with the specific aim to model functional types (rather than species) and allow for internally varying nutrient ratio's within its organisms. It incorporates four phytoplankton types (diatoms, flagellates, picophytoplankton, dinoflagellates), four zooplankton types (microzooplankton, heterotrophic nanoflagellates, omnivorous and carnivorous mesozooplankton), 5 benthic types (megabenthos, deposit feeders, filter feeders, meiobenthos, infaunal predators) and pelagic and benthic (aerobic and anaerobic) bacteria. The dynamic cycles for nitrogen, phosphorous, silicate, oxygen and carbon are included. The sediment is divided in three layers of varying depth: the oxic layer, denitrification layer and anoxic layer.

Subsequent reprogramming of ERSEM in Fortran 95 led to the formation of the more modular BFM model (Biological Flux Model, see http://bfm-community.eu) in the early 20th century. This code was applied in oceanic form (Vichi et al., 2003, 2004, 2007) but also in shelf seas applications (Ruardij et al., 2005). The ERSEM-BFM code applied here stems from further development by Cefas and NIOZ of the shelf seas BFM code: it therefore includes specific processes to represent shelf seas dynamics not found in ERSEM or BFM codes. Additional functional types include: small diatoms and *Phaeocystis* colonies in phytoplankton, pelagic filter feeder larvae in zooplankton and young filter feeders in benthos. Thus the ERSEM-BFM model includes benthic larvae with a distinct pelagic phase. Further additions include production of transparent exopolymer particles (TEP) by nutrient-stressed diatoms and *Phaeocystsis*, leading to macro-aggregate formation and increased sinking rates. A simple SPM parameterisation, assuming proportionality to bed-shear stress induced by surface waves, has been included as described in Van der Molen et al. (2014) to improve representation of the underwater light climate. Improvements in benthic-pelagic coupling have led to a benthic module comprising 53 state variables, see Van der Molen et al. (2013) for more details including validation for benthic-pelagic exchange. For other applications of the ERSEM-BFM model see van Leeuwen et al. (2013, 2015). A closed nitrogen budget was obtained for 1DV set-ups (watercolumn set-up) by re-introducing all lost nitrogen (N_2 escape to the atmosphere) as atmospheric deposition.

8.2 Higher trophic levels

A size-structured model was used to represent the higher trophic levels of the marine food web. This model (see Blanchard et al. (2009) for more details) incorporates the two main marine carbon pathways: via size-based predation (by pelagic or benthic predators) or via unstructured feeding based on a common food source (by detritivores, autotrophs and herbivores). The two modelled size-spectra (referred to here as fish/predators and detritivores) are linked via size-selective feeding of predators on detritivores. Fisheries yield is calculated as the mortality due to fishing pressure on commercial-sized fish (i.e. predators $>$ 10 gram wet weight [gWW]).

Key processes as food assimilation, growth, mortality and fishing pressure are included, with ambient temperature effects on feeding rates (and thus growth) incorporated. The size-structured approach is a strong simplification of the complex marine food web, but has been shown effective in simulating marine biomass and abundance across the marine system (Blanchard et al., 2009, 2010). Without species representation the model is flexible enough to apply to different sites for long-term simulations, and allows for a qualitative description of the studied effects.

8.3 Coupling

Coupling of the lower and higher trophic level models was achieved one way upwards, with GOTM-ERSEM-BFM simulated, time-varying, plankton biomass (for diatoms, flagellates, picophytoplankton, microzooplankton and heterotrophic nanoflagellates) inserted in their respective size class of the higher trophic level predator size-spectrum (see ~~table~~ Table 1). Benthic detritus from ERSEM-BFM was used as a time-varying food source for detritivores, while simulated sea surface and near-bed temperatures were used to control feeding rates for predators and detritivores respectively. There was no influence of higher trophic level biomass on lower trophic level dynamics. Fish predation mortality in ERSEM-BFM is simulated as cannibalism of the largest species, ensuring a dynamic mortality dependent on biomass. Thus both lower trophic level mortality and higher trophic level feeding were driven by lower trophic level biomass values, ensuring a proportionate response. Note that dinoflagellates and *Phaeocystis* were not used as food as these are predominantly inedible. Mesozooplankton was not included as food as it overlaps with the start of the pelagic predator size spectrum. The applied coupling allows bottom up pressures like indirect impacts on the abiotic environment to travel up the marine food web, with consequences for e.g. commercial fisheries yield.

8.4 Locations

Table 1. Distribution of planktonic food supply for pelagic predators

size range [g]	food source
10^{-12}-10^{-9}	picophytoplankton, heterotrophic nanoflagellates
10^{-9}-10^{-6}	diatoms, flagellates, microzooplankton
10^{-6}-10^{-3}	diatoms, flagellates

Table 2. Overview of locations used. See also Fig. 1.

site	location	depth	hydrodynamic regime	substrate
North Dogger (ND)	[55.68 °N, 2.28 °E]	85 m	seasonally stratified	muddy sands
Oyster Grounds (OG)	[54.4 °N, 4.02 °E]	45 m	transitional waters	muddy sands
Southern Bight (SB)	[53.17 °N, 2.81 °E]	31 m	permanently mixed	mobile sands

Three locations have been chosen in the North Sea, a shallow shelf sea located on the European shelf (Fig. 1). The North Dogger (ND) site is located at [55.68 °N, 2.28 °E]. This site is characterised by seasonal, thermal stratification, a depth of 85 m and a muddy, sandy bed type. The Oyster Grounds (OG) site, at [54.4 °N, 4.02 °E], represents transitional waters with frequent seasonal thermal stratification of varying duration (i.e. large inter-annual variability), a medium depth of 45 m and typically a muddy-sandy substrate. The Southern Bight site (SB, also known as Sean Gas Field) is located at [53.17 °N, 2.81 °E] in the well-mixed area of the southern North Sea, and has a depth of 31 m and a mobile sandy bed. Together, the three sites represent two of the major stratification regimes in the North Sea area and transitional waters (which can vary between regimes), as shown in Fig. 1. For more details on the different regimes see van Leeuwen et al. (2015) .

8.5 Model validation

Extensive validation of the GOTM-ERSEM-BFM model for the three sites has been published in Van der Molen et al. (2013). In general most variables were within the correct order of magnitude compared to observations. The model underestimated benthic detritus at ND and OG sites (due to underestimation of pelagic detritus supply and bioturbation) and general validation for bed and near-bed processes was poor for the SB site (due to lack of pore water exchange). Additional spatial validation results (showing representation of vertical distribution of phytoplankton) are available in van Leeuwen et al. (2013).

The lack of observations aggregated on the size-spectra scale hinders validation of the size-structured model representing the upper layers of the marine food web. Observations presented in Jennings et al. (2002) and Maxwell and Jennings (2006) (for predators and detritivores respectively) have shown good validation results in Blanchard et al. (2009) for the size-structured model

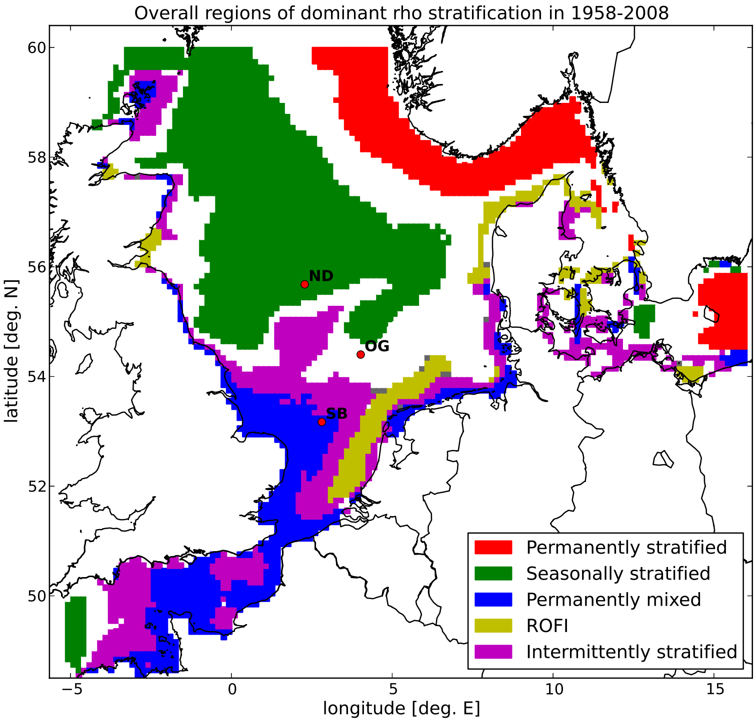

Figure 1. Location of the three sites in the North Sea, imposed on a map of dominant vertical density stratification regimes. ROFI stands for Regions of Fresh Water Influence. The white areas represent transitional waters, which experience large variability in duration of mixed and stratified conditions, defying classification. From van Leeuwen et al. (2015) .

alone. Here, data from Maxwell and Jennings (2006) were used for calibration of the ERSEM-BFM ~~detritus supply to the bed~~ near-bed detritus levels (indicated to be ~~a problem~~ underestimated by Van der Molen et al. (2013)) as supplied to size-spectrum model, while the data from Jennings et al. (2002) was used for validation. ~~Fishing pressure~~ Calibration factors were 25, 2.5 and 5 for the ND, OG and SB sites respectively. Griffith et al. (2012) showed the importance of including fishing pressure combined with acidification and temperature pressures in an Australian ecosystem. Here fishing pressure was included in the model as a nominal pressure (based on ICES (2005)), but was not calibrated to represent site-specific mortalities. ~~Here, as in Van der Molen et al. (2013) , a~~

A reference run with ECMWF meteorological forcing covering 1958-2008 was used for validation (European Centre for Medium-range Weather Forecasts, ERA-40 and ERA-15 data, UK Met Office). The selected validation period was 1979-2008 to allow for model spin up of the benthic system. Figure 2 shows the validation results for the resulting higher trophic levels in a normalised

Taylor diagram (Jolliff et al., 2009). This diagram shows the correlation coefficient (information regarding phase agreement, shown on the radial axis) and the normalised standard deviation (information regarding amplitude comparison, shown on polar axis) between modelled and observed data.

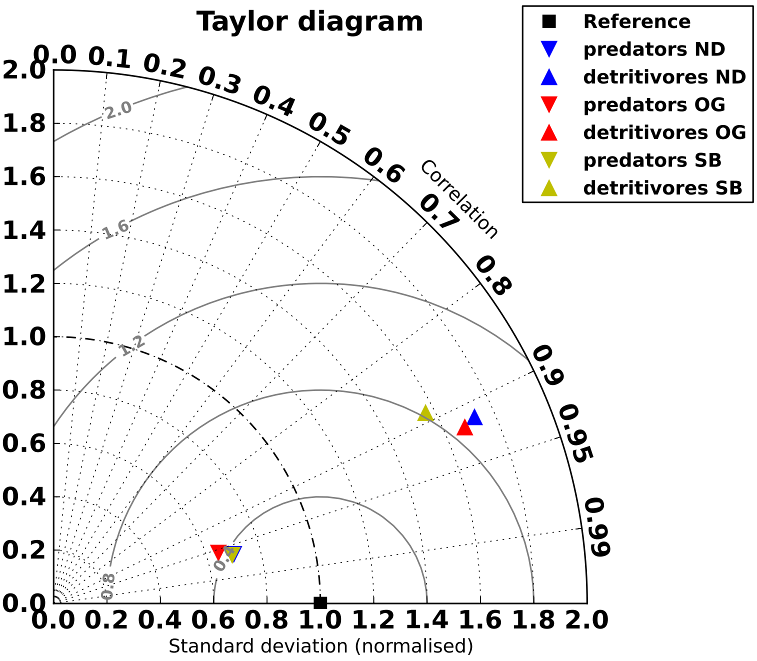

Figure 2. Taylor diagram for predator and detritivore abundance from the coupled model. Note that observations for detritivores were used for calibration purposes, so that predator observations provide the only validation of the higher trophic levels here. Predator abundance results for the North Dogger site overlap with those of the Southern Bight site. The internal grey arcs represent the root-mean-square-error.

Validation results for the three sites are very similar, with high correlation factors, reflecting the general size-based structure of the marine ecosystem and the small geographic area. More observations on a size spectrum scale are necessary to allow for any quantitative application of the size-based model.

8.6 ~~Locations~~

~~Three locations have been chosen in the North Sea, a shallow shelf sea located on the European shelf (figure 1). The North Dogger (ND) site is located at 55.68 °N, 2.28 °E. This site is characterised by seasonal, thermal stratification, a depth of 85 and a muddy, sandy bed type. The Oyster Grounds (OG) site, at 54.4 °N, 4.02 °E, represents transitional waters with frequent seasonal thermal stratification of varying duration (i.e. large~~ Note that the large difference in variability between predators and detritivores can indicate both a limitation of the model system (lacking stabilising processes for detritivores or benthic POC supply) or a limitation of the observational data applied (covering only one spring and one autumn cruise, therefore lacking a full seasonal signal and inter-annual ~~variability) , a medium depth of 45 and typically a muddy-sandy substrate. The Southern Bight site (SB, also known as Sean Gas Field) is located at 53.17 °N, 2.81 °Ein the well-mixed area of the southern North Sea, and has a depth of 31 and a mobile sandy bed. Together, the three sites represent two of the major stratification regimes in the North Sea area and transitional waters (which can vary between regimes), as shown in figure 1. For more details on the different regimes see van Leeuwen et al. (2015) . Location of the three sites in the North Sea, imposed on a map of dominant vertical density stratification regimes. From van Leeuwen et al. (2015) .~~ variability between seasons).

~~Overview of locations used. See also figure 1. site location depth hydrodynamic regime substrate North Dogger (ND) 55.68 °N, 2.28 °E85 m seasonally stratified muddy sands Oyster Grounds (OG) 54.4 °N, 4.02 °E45 m transitional waters muddy sands Southern Bight (SB) 53.17 °N, 2.81 °E31 m permanently mixed mobile sands~~

8.6 Scenario setup

The objective of this paper is to provide a first qualitative estimate of effects of ocean acidification on the marine food web across trophic levels relative to climate change effects. To this end, we use a water column model in three separate sites which together are representative of a large part of the North Sea (see ~~figure~~Fig. 1). Hydro-biogeochemical conditions at these sites were simulated for the period 1958-2008, using ECMWF forcing data (UK Met Office), for validation purposes ~~.~~ ~~Future~~ (reference simulation). Future and past conditions were simulated for the period 1958-2089 (climate change simulation), using meteorological forcing from the Met Office Hadley Centre Regional Model Perturbed Physics Ensemble simulations (HadRM3-PPE-UK, see Met Office (2008-); Murphy et al. (2007)), as supplied by BADC (British Atmospheric Data Centre). These simulations focus on regional UK climate (1950-2100) and represent a historical and medium emissions scenario (SRESA1B). Only the unperturbed member of the ensemble was applied here as forcing, and data from the nearest HadRM3 grid cell (25 km resolution) for each site was used. For a detailed overview of climatological changes during the simulated period see Van der Molen et al. (2013), especially their ~~figure~~ Fig. 5. In general, the applied forcing is characterised by increasing air temperatures and decreasing cloud cover at all three sites. Pressure increases at all sites but with considerable inter-annual variability. Wind speeds show an increase in the period up to 2030, followed by a strong decrease at all sites. Relative humidity exhibits an increase at the ND and OG sites, but a decline at the SB site.

Three main impacts on the marine environment were studied:

Table 3. Simulated scenarios. p_sN4N3 is the pelagic specific nitrification rate (in $1/\mathrm{d}$) in ERSEM-BFM, while K_v represents the net growth conversion efficiency $(-)$ for detritivores in the size-structured model. LTL refers to the lower trophic level model (ERSEM-BFM), HTL top the higher trophic level model (size-based code)

Scenario	Reference		Low		Medium		High	
Parameter	p_sN4N3	K_v	p_sN4N3	K_v	p_sN4N3	K_v	p_sN4N3	K_v
Reduction			10%	2%	30%	6%	50%	10%
Reference	0.16	0.2						
LTL			0.144	0.2	0.112	0.2	0.08	0.2
HTL			0.16	0.196	0.16	0.188	0.16	0.18
LTL+HTL			0.144	0.196	0.112	0.188	0.08	0.18

1. climate change, acting on the abiotic environment, lower trophic levels and higher trophic levels,
2. decreased pelagic nitrification (indirect effect of ocean acidification, see Huesemann et al. (2002); Hutchins et al. (2009); Beman et al. (2011)), acting on the lower trophic levels and
3. reduced detritivore growth rate (direct effect, i.e. reduced growth of calcifying organisms, ~~Doney et al. (2009); ?~~ Doney et al. (2009); Andersson and Mackenzie (2011); Wicks and Roberts (2012) and references therein), acting on higher trophic levels.

Low, medium and high reduction rates were applied to allow for uncertainties in future emission predictions and acidification impact on different species. Table 3 lists the different scenario's and the parameter values used in each. For pelagic nitrification reductions of 10, 30 and 50% were applied, while for reduced detritivore growth rate reductions of 2,6 and 10 % were imposed. The latter values reflect not just observed reductions in calcifying capacity but also the percentage of simulated detritivores representing calcifying organisms. ~~Both climatic effects and reduced growth efficiency affect~~ Note that community structure observations would be necessary to interpret localised effects of reduced detritivore growth rate. Climatic effects thus affect both fish and detritivore growth rates, while reduced growth efficiency is applied solely to detritivores.

Simulations covered the period 1958-2098, of which the first 20 years are considered model spin up time. To estimate temperature impacts we calculated the relative difference in a variable between the 30-year averaged value for the period 1979-2009 (current state) and 2069-2098 (future state) of the ~~reference~~ climate change simulation. To estimate acidification effects we considered the relative difference in a variable in the period 2069-2098 (30 year averaged value) between the ~~reference simulation (climate change)~~ climate change simulation and the scenario simulation (climate change and ocean acidification). This approach differs from that used by Van der Molen et al. (2013), which compared results to a reference simulation (1958-2098) with repeated current climate conditions. A comparison study showed minor changes between the two approaches.

9 Effects on lower trophic levels

Published effects of ~~more acidic conditions~~ ocean acidification impacts on pelagic nutrient supply include a predicted decline in water-column nitrification (Hutchins et al., 2009). The lower trophic level experiments mimic this effect by reducing the pelagic nitrification rate in the ERSEM-BFM model (parameter p_sN4N3). ERSEM-BFM does not explicitly model NH_3 or NO_2^-, so the nitrification rate relates to the transformation of NH_4^+ to NO_3^-. Note that processes related to NH_3 (NO_2^-) will be included via direct effects on the internal NH_4^+ (NO_3^-) pools. Urea is explicitly modelled in ERSEM-BFM, and forms an integral part of the models' nitrogen cycle.

Simulation results for biomass showed site-specific response, see ~~table 4~~ Table 4 and Figs. S1, S2, S3.

9.1 North Dogger

The seasonally stratified site was characterised by a negative impact of future climate conditions on lower trophic level pelagic and benthic biomass levels (see also ~~figure~~Figs. 3(a~~) and (~~,b)). Net primary production increased due to increased metabolic processes (resulting in higher pelagic turnover rates) and a lengthening of the growing season due to an earlier start of the spring bloom (Van der Molen et al., 2013). A strong increase in *Phaeocystis* was observed (~~figure~~Figs. 3(a)) but this was relative to originally very low biomass values (6 mgC/m^2/d). Benthic biomass declined due to a decline in the (main) diatom food source, as a result of increased zooplankton grazing on diatoms~~(Van der Molen et al., 2013)~~. The rise in ambient water temperatures caused higher trophic level growth rates to increase (favouring fish as stratification limited near-bed temperature increases), resulting in higher biomass for both fish and detritivores despite the minor decrease in planktonic food supply. Fish yield increased accordingly.

Ocean acidification effects on the abiotic environment (Fig. S1) showed only a minor impact on lower trophic level dynamics at this site~~, as organisms easily adapted to more ammonium uptake to satisfy internal nitrogen demands. Benthos~~. Percentage change for picophytoplankton (Figs. 3 (a), Fig. S1 (a)) was small due to high original biomass levels (highest of all the three sites) but increases were observed both in spring and summer accompanied by reduced grazing. Benthic biomass decline was due to decreased levels of filter feeders (the dominant functional group): all other benthic functional groups increased their biomass levels (see ~~figure~~Figs. 3(b), S1 (b)). Benthic bacteria biomass levels increased slightly as the benthic system became more bacterial orientated. Increased plankton biomass led to increased levels of particulate organic carbon (POC), causing increased levels of both fish and detritivore biomass due to increased food supply ~~.~~ (Figs. S1 (c,d,i,j)). As a result,

Table 4. Simulated results for lower trophic level impacts: percentage change for all sites and scenarios $[\%]$ (2069-2098 vs 1979-2009) and actual ~~reference~~ values ($\mathrm{gC}/\mathrm{m}^2/\mathrm{d}$ for lower trophic level results and $\mathrm{gwetweight}/\mathrm{m}^2$ for fisheries results) of depth-integrated, 30-year averages. The ~~reference~~ actual values refer to the period 1979-2009 of the climate change scenario simulation. POC ~~refders~~ refers to Particulate Organic Carbon.

variable		ND					OG					SB				
		Low	Med.	High	T	**~~Ref~~Act.**	Low	Med.	High	T	**~~Ref~~Act.**	Low	Med.	High	T	**~~Ref~~Act.**
Biomass	phytoplankton	0	1	2	-6	**1.3**	-0	-0	-1	-2	**1.5**	-0	-1	-1	11	**1.5**
	zooplankton	1	2	3	-2	**0.5**	-0	0	0	-2	**0.5**	-0	-0	-1	6	**0.3**
	pelagic bacteria	0	0	1	-1	**0.5**	-0	-1	-1	-3	**0.3**	-0	-1	-1	13	**0.3**
	benthos	0	-2	-5	-20	**1.6**	-0	0	-0	-17	**3.5**	-1	-4	-8	-19	**1.6**
	benthic bact.	1	2	4	-13	**0.05**	-0	-0	-0	-7	**0.15**	-0	-2	-4	-14	**0.07**
Primary production	net	1	2	3	11	**0.3**	0	-1	-1	10	**0.4**	-1	-2	-2	50	**0.5**
	Chlorophyll-a	1	0	3	-2	**0.03**	-0	-1	-1	2	**0.03**	-0	-1	-1	20	**0.03**
POC	pelagic	2	3	3	-10	**16.2**	0	-1	-1	-15	**7.5**	-0	-0	-1	0	**15.8**
	benthic	2	3	8	-4	**4.1**	-0	-0	-1	5	**25.8**	-1	-3	-7	0	**11.3**
Fisheries biomass	fish	24	24	30	20	**3.1**	-6	-8	-9	-6	**2.7**	25	21	17	27	**1.8**
	detritivores	13	13	30	6	**2.4**	10	12	14	10	**4.2**	-33	-38	-46	-32	**2.6**
	fish yield	33	33	42	27	**2.0**	0	-1	-1	1	**1.9**	16	11	5	18	**1.2**

fisheries yield increased (note that increased food supply and higher ambient temperatures caused a non-linear increase in higher trophic level biomass, resulting in large percentage differences for the separated acidification effects).

Overall, climatic changes and acidification impact on the abiotic environment both had a positive impact on future fisheries yield at this site, and were of a similar order of magnitude~~with the exception of detritivore impact (OA effect dominant)~~.

9.2 Oyster Grounds

~~Climatic impact~~ Climate change impacts only reduced pelagic biomass slightly at this site, with a larger impact on benthic functional groups (~~figure~~ Fig. 4(b)), indicating again a shift towards a more pelagic orientated system. Net primary production increased at this site, due to faster recycling of nutrients and a longer growing season (characterised by an earlier spring bloom due to reduced wind speeds, see Van der Molen et al. (2013): ~~figure~~ Fig. 9). ~~The overall reduction in phytoplankton (see also figure 4(a)) and zooplankton biomass reduced the~~ Onset of stratification (a trigger for diatom sinking) did not change significantly at this site, leading to a longer period of suspended diatoms and a reduction in near-bed diatom levels during spring (longer grazing period for zooplankton). This led to a decline in filter feeder biomass (due to a reduction of the main food supply) and a subsequent reduction in other benthic functional groups as pelagic-feeding filter feeders form the main carbon pathway into the benthic system in the model (Van der Molen et al., 2013) . As a result, benthic POC levels increased. The overall reduction in phytoplankton and zooplankton biomass did not significantly change the planktonic food supply for fish ~~, which showed a minor decline in biomass despite higher growth rates.Increased levels of benthic detritus (plus decreased predation and higher growth rates)led to more detritivore biomass.~~ (Fig. 4(a), S2 (c), diatom increase compensated for loss of other functional groups). Predation on detritivores increased (Fig. S2(j), reflecting increased detritivore biomass) but fish predation declined (Fig. S2(i), reflecting decreased fish biomass), showing a change in feeding behaviour for pelagic predators. Fisheries yield showed ~~negligible change as~~ a negligible, positive change (Fig. S2 (g,h)), indicating that fish biomass decrease was limited mainly to non-commercial size fish. The decline in fish biomass may therefore be due to increased predator growth rates causing increased predation pressure on smaller size fish.

Impacts of reduced nitrification (acidification impact) at this site were minor~~. With virtually no impact on the benthic system,fisheries~~ , as climate change effects countered acidification impacts with increasing sea temperatures. Decreased nitrification favoured organisms with a high ammonium affinity, like picophytoplankton (spring bloom increase) and dinoflagellates (autumn bloom increase at the expense of *Phaeocystis*). Fish biomass was negatively impacted while detritivores were marginally positively impacted (Figs. S2 (d,e)). Fisheries impacts were negligible~~as well~~.

In all, climatic effects dominated at this site over abiotic environmental effects of ocean acidification for lower trophic levels, but were of the same order of magnitude for higher trophic levels

~~.~~ (except for detritivore levels, where the main driver was climate). Acidification effects showed a reduced signal strength with increasing climate impact on higher trophic levels, indicating a non-additive effect of the combined stressors. Impact on fisheries yield was ~~negligible~~positive (climate change) but became negligible in combination with the high acidification scenario.

9.3 Southern Bight

The well-mixed site in the southern bight showed a large increase in net primary production under future climate conditions (no OA effects included). Higher sea temperatures led to faster recycling of nutrients, and an associated increase in regenerated production. With a closed nutrient budget the main driver for the large productivity increase ~~is~~ was likely the improved light conditions, as suggested by decreased cloud cover at this site and episodic reductions in SPM concentrations in summer (Van der Molen et al., 2013). Contrary to the other two sites the growing season did not lengthen here (Van der Molen et al., 2013). ~~Increased levels of pelagic recycling (by both phytoplankton and bacteria) led to a reduction of benthic detritus input, leading to~~ The large decline in diatoms resulted in a loss of benthos biomass (~~see also figure 5~~Fig. 5 (b)) and a shift towards a more pelagic orientated system. Increased planktonic biomass led to ~~more fish biomass, with detritivores suffering from both decreased detritus input and increased predation. Growth rates increased for both fish and detritivores, but as the water column is well mixed at this site temperature effects did not favour one carbon pathway over the other~~a decrease in planktonic food supply for fish (Fig. S3(c)) as the increases were limited to inedible functional groups (dinoflagellates and *Phaeocystis* colonies). Therefore increased growth rates for fish are deemed responsible for the large increase in fish biomass and associated fisheries yield (Figs. S3(d,g)). Predation mortality biomass for detritivores remained constant (Fig. S3(j)) , indicating increased predation on lower biomass levels.

Reduction of pelagic nitrification rates (acidification impact) resulted in higher pelagic ammonium concentrations and lower nitrate levels, favouring phytoplankton species with high ammonium preference like picophytoplankton (also experiencing decreased predation) and dinoflagellates (~~figure~~Fig. 5(a), S3(a)). Accompanying loss of diatom and *Phaeocystis* biomass led to virtually no effect on overall plankton biomass and net primary production levels. Benthic biomass decreased due to decreased diatom levels (a main food source for suspension feeders) and decreased pelagic detritus generation, resulting in less benthic detritus (both labile and particulate) and associated loss of benthic bacteria (also a food source for benthos). ~~The overall, small, decrease in both pelagic and benthic biomass led to a decrease in both fish and detritivore population.~~Planktonic food supply for fish decreased more with increased climate pressure, again displaying a non-additive response. Fish and detritivore levels were negatively impacted by indirect acidification impacts (Fig. S3(d,e)).

Here, climate effects dominated over acidification effects on the abiotic environment for lower trophic levels, showing a strong shift towards a more pelagic oriented system. Impacts on higher trophic level biomass were of the same order of magnitude ~~and trend , with fish biomass increasing~~ but of opposing trend for fish (same negative trend for detritivores). Fish biomass increased and detritivore biomass ~~decreasing. Fisheries yield was predicted to increase under future conditions~~decreased, but fisheries yield (trend) depended strongly on acidification impact strength.

10 Effects on higher trophic levels

Reduced growth of calcifying organisms was represented by reductions in the sizebased model of the net growth conversion efficiency for organisms in the detritivore size-spectrum (parameter K_v). Modelled growth rates therefore depend on ambient temperature, growth conversion efficiencies and food availability, see Blanchard et al. (2009). Results are presented in ~~table 5~~ Table 5 and Fig. S4, S5, S6.

10.1 North Dogger

The deeper, seasonally stratified site showed that impact of ocean acidification effects on species level could be of the same order of magnitude as climatic impacts ~~.~~ (Fig. S4), with dominant impact on parts of the ecosystem (here detritivore levels). The negative impact of reduced detritivore growth rates was initially offset by increased food supply (POC), but showed a strong negative effect for the medium and high impact scenario's, resulting in lower detritivore biomass than current conditions. This reduction in part of the food supply for fish led to lower fish biomass with strengthening of the acidification impact (general increase due to increased ~~food supply~~planktonic food supply and increased growth rates).

Combined effects indicated increased biomass for fish (climatic impact modified by species-level acidification impact) and decreased levels of detritivore biomass (species-level acidification impact), resulting in increased fisheries yield during the spring bloom under future conditions ~~.~~ (Fig. S4(h)).

10.2 Oyster Grounds

At the mid-depth, seasonally stratified site the benthic system forms an integral part of the local ecosystem (Van der Molen et al., 2013). As such, a reduction in detritivore growth efficiency led to a stronger ~~reduction in~~ effect on fish biomass than at the other two sites, as fish were more dependent on the detritivore food source ~~.~~ (see Fig. S5 (d,e,i,j)). The larger impact on fisheries shows that the pelagic impact mainly ~~affects~~ affected commercial size species.

With only a limited climatic impact at this site the species-level acidification impact dominated fish dynamics, resulting in biomass loss and declined fisheries yield. Both impacts were of similar order for detritivores, with climate impacts resulting in increased growth rates (Fig. S5 (f)) despite the reduction applied for calcifying organisms.

Table 5. Simulated results for higher trophic level impacts only: percentage change for all sites ~~%~~ and scenarios [%] (2069-2098 vs 1979-2009) and actual ~~reference~~ values $(\mathrm{gwetweight}/\mathrm{m}^2)$ of depth-integrated, 30-year ~~average~~ averages. The actual values refer to the period 1979-2009 of the climate change scenario simulation.

variable		ND					OG					SB				
		Low	Med.	High	T	~~Ref~~Act.	Low	Med.	High	T	~~Ref~~Act.	Low	Med.	High	T	~~Ref~~Act.
Fisheries	predator biomass	18	15	12	20	**3.1**	-9	-13	-18	-6	**2.7**	25	21	17	27	**1.8**
	detritivore biomass	1	-8	-17	6	**2.4**	6	-2	-11	10	**4.2**	-35	-42	-48	-32	**2.6**
	fish yield	25	20	15	27	**2.0**	-3	-10	-17	1	**1.9**	15	9	4	18	**1.2**

10.3 Southern Bight

Reduced growth efficiency for detritivores also led to decreased detritivore biomass at the well mixed site (see also Fig. S6), with fish biomass increases (~~originally buoyed by increased food supply due to climatic changes) displaying a downward trend~~ buoyed by climate-induced increased growth rates) modified due to a reduced detritivore food source ~~.~~(Fig. S6(e,i,j): predated detritivore biomass nearly equaled predated fish biomass under combined stressors).

Climatic impacts dominated over species-level ocean acidification impacts at this site ~~,~~ for fish, but were of the same order for detritivores, with temperature-induced decline of detritivore biomass significantly enhanced by the direct acidification impact. Fisheries yield was predicted to increase due to climatic impacts (~~increased food supply, increased fish growth rates~~summer increase, winter decrease).

11 Combined effects: indications of future fisheries trends

Results for combined impacts from climate and direct and indirect ocean acidification are listed in ~~table 6 .~~Table 6 and visualised in Fig. 3,4,5.

11.1 North Dogger

Climatic effects and acidification impacts (both abiotic and biotic) were of the same order of magnitude at the seasonally stratified site, with positive results for future fish yields. Indirect ocean acidification impacts compensated for losses due to reduced growth efficiency of detritivores~~. Detritivore growth rates increased due~~ , leading to increases in ~~ambient water temperature, despite species-level acidification impacts (figure~~fish and detritivore biomass driven by climate change (Fig. 3(d~~)). Fish~~,e), S1(d,e), S4(d,e)). Planktonic fish food supply declined due to climatic impacts, but the decline was moderated by positive impacts from acidification effects on the abiotic environment (~~figure~~Fig. 3(c)). The pelagic food source for predators increased accordingly (climate impact, including increased growth rates, Fig. 3(i)), while the detritivore food source increased due to climatic impacts (Fig. 3(j)). Fish yield increased (~~figure~~Fig. 3(~~e~~g)), mainly during the spring bloom and ~~winter periods (figure~~pre-spring bloom periods (Fig. 3(~~f~~h)).

11.2 Oyster Grounds

Dynamics at the Oyster Grounds site changed mainly due to direct acidification impacts, as benthic communities form an important part of the local ecosystem. Fish ~~and detritivore~~ biomass declined over time ~~.~~ due to acidification impacts on species level (Fig. 4(d)) while the trend for detritivore levels was strongly dependent on the strength of the acidification impact on species level (Fig. 4(e)). Detritivore growth rates increased over time (~~figure~~Fig. 4(~~d~~f)), but increases were heavily modified due to direct acidification impacts. ~~Pelagic~~ The larger direct acidification impact on pelagic

Table 6. Simulated results for combined lower and higher trophic level impacts: percentage change ~~%~~ for all sites and scenarios [%] (2069-2098 vs 1979-2009) and actual ~~reference~~ values ($\mathrm{gwetweight}/\mathrm{m}^2$ ~~for all sites~~) of depth-integrated, 30-year ~~average~~ averages. The actual values refer to the period 1979-2009 of the climate change scenario simulation.

variable		ND					OG					SB				
		Low	Med.	High	T	~~Ref~~Act.	Low	Med.	High	T	~~Ref~~Act.	Low	Med.	High	T	~~Ref~~Act.
Fisheries	predator biomass	22	19	22	20	**3.1**	-9	-15	-20	-6	**2.7**	23	16	9	27	**1.8**
	detritivore biomass	8	-2	2	6	**2.4**	6	-0	-8	10	**4.2**	-37	-47	-60	-32	**2.6**
	fish yield	31	25	28	27	**2.0**	-3	-11	-18	1	**1.9**	13	3	-7	18	**1.23**

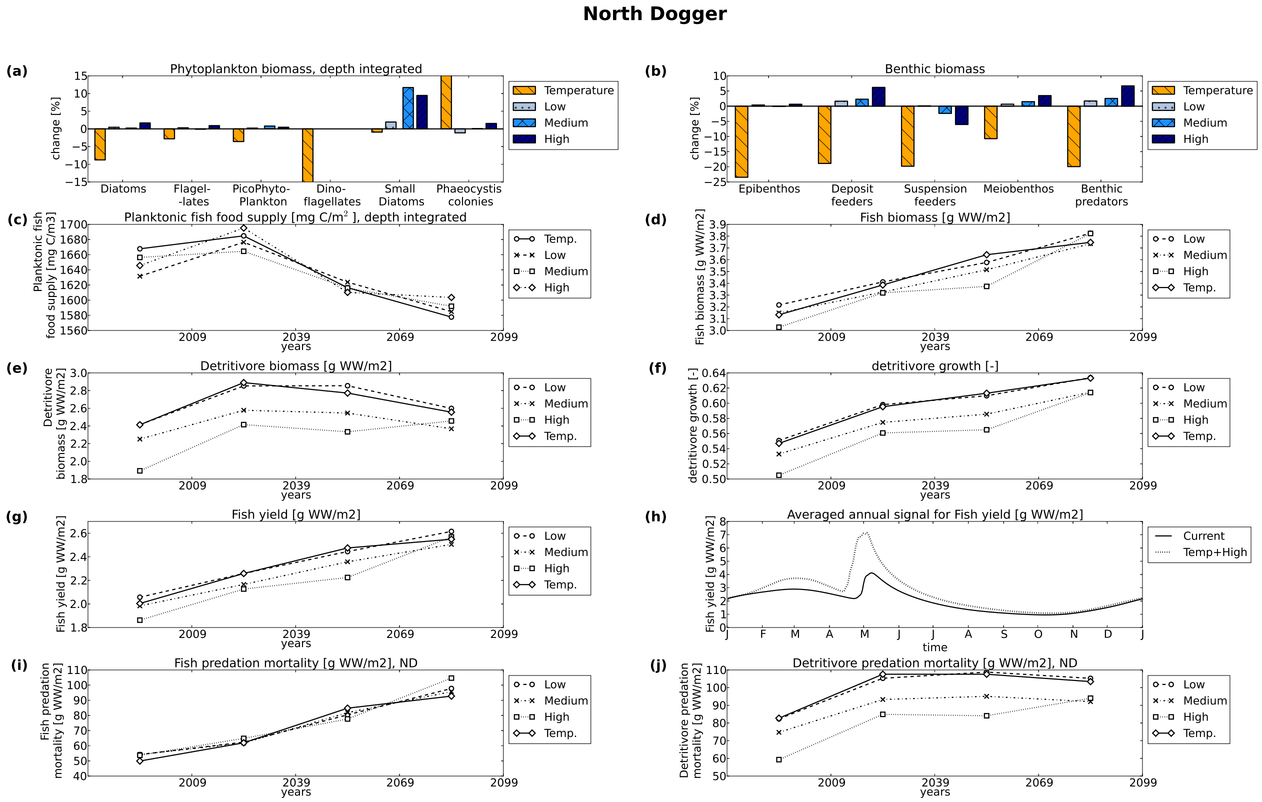

Figure 3. North Dogger: 30-year averaged values, climatic plus high ocean acidification (LTL+HTL) effects: (a) phytoplankton changes [%], (b) benthos changes [%], (c) planktonic fish food, (d) fish or pelagic predator biomass, (e) detritivore biomass, (f) detritivore growth rates, (~~e~~g) fish yield~~and~~, (~~f~~h) annual fish yield, signal for the current time (1979-2008 climate scenario) and the high impact scenario (2069-2098 climatic plus LTL+HTL acidification effects) signal, (i) predated biomass for pelagic predators and (j) predated biomass for detritivores. Maximum values outside of axis range for phytoplankton changes are -100 % for dinoflagellates (small levels were wiped out) and +241 % for *Phaeocystis* (small original biomass).

predators compared to detritivores (Fig. S5(d,e)) suggests a strong resilience of the comparatively large benthic system at this site. Planktonic fish food supply increased slightly due to indirect acidification impacts (~~figure~~Fig. 4(~~d)~~c), increased values compared to climate change scenario), but could not counteract the ~~large decline in the detritivore food source~~decline in pelagic predators due to all stressors (climate change, indirect and direct acidification impact). Fisheries yield decreases accordingly (~~figure~~Fig. 4(~~e)~~g), acidification scenario's vs Temp scenario), with the main decline in the winter period (~~figure~~Fig. 4(~~f~~h)).

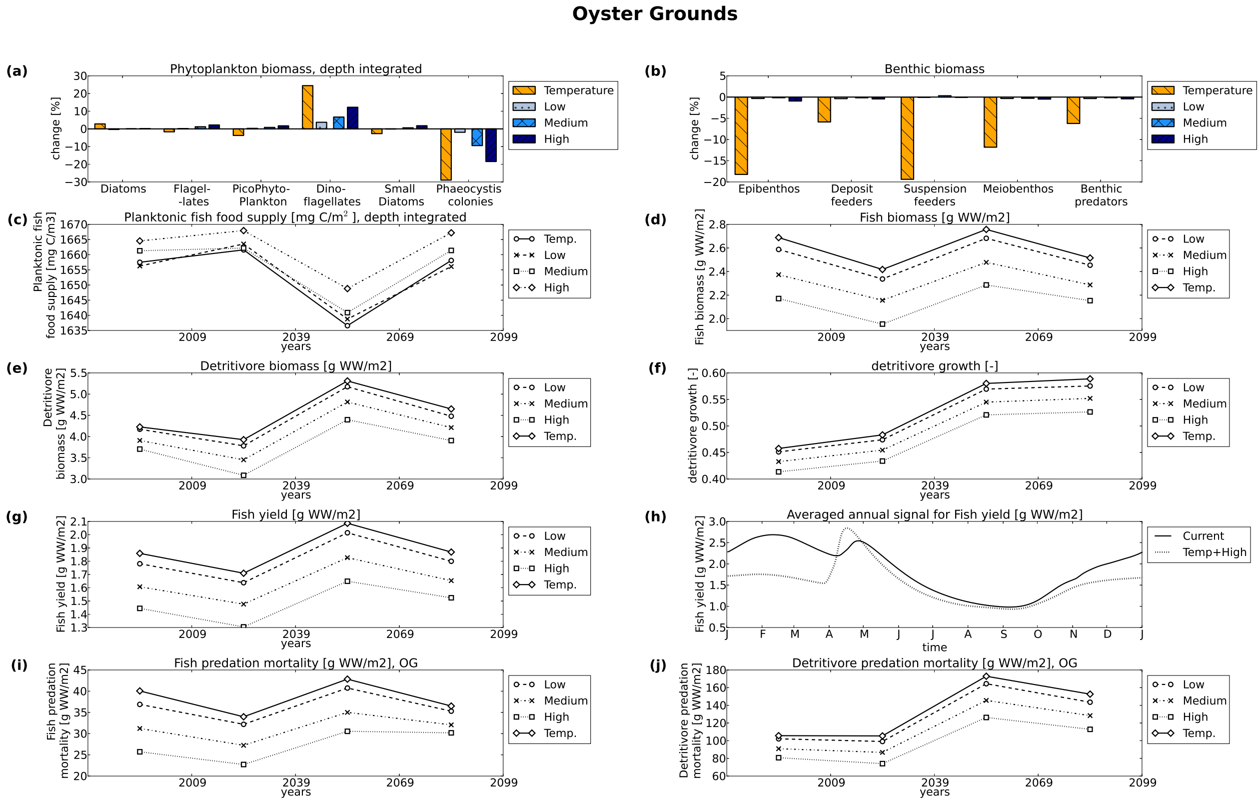

Figure 4. Oyster Grounds: 30-year averaged values, climatic plus high ocean acidification (LTL+HTL) effects: (a) phytoplankton changes [%], (b) benthos changes [%], (c) planktonic fish food, (d) fish or pelagic predator biomass, (e) detritivore biomass, (f) detritivore growth rates, (~~e~~g) fish yield~~and~~, (~~f~~h) annual fish yield, signal for the current time (1979-2008 climate scenario) and the high impact scenario (2069-2098 climatic plus LTL+HTL acidification effects) signal, (i) predated biomass for pelagic predators and (j) predated biomass for detritivores.

11.3 Southern Bight

Climatic and acidification effects were equally important at the well-mixed site. Fish biomass increased due to climatic impacts, ~~while detritivore biomass declines due to both climatic and direct and indirect acidification impacts . Detritivore growth rates remain~~ but was heavily modified by indirect and direct acidification impacts (Fig. 5(d), S3(d), S6(d)). Detritivore biomass declined due all stressors (Fig. 5(e), S3(e), S6(e)), with a dominant role for acidification effects (abiotic environment and species level). Detritivore growth rates remained more or less equal when combined effects ~~are applied (figure~~were applied (Fig. 5(~~d)~~f), High scenario 2069-2098 result compared to Temp scenario 1979-2008), while ~~pelagic~~ planktonic food supply for fish was reduced mainly due to climatic effects ~~.~~ (Fig. 5(c)). Changes to fisheries yield depended strongly on the strength of acidification im-

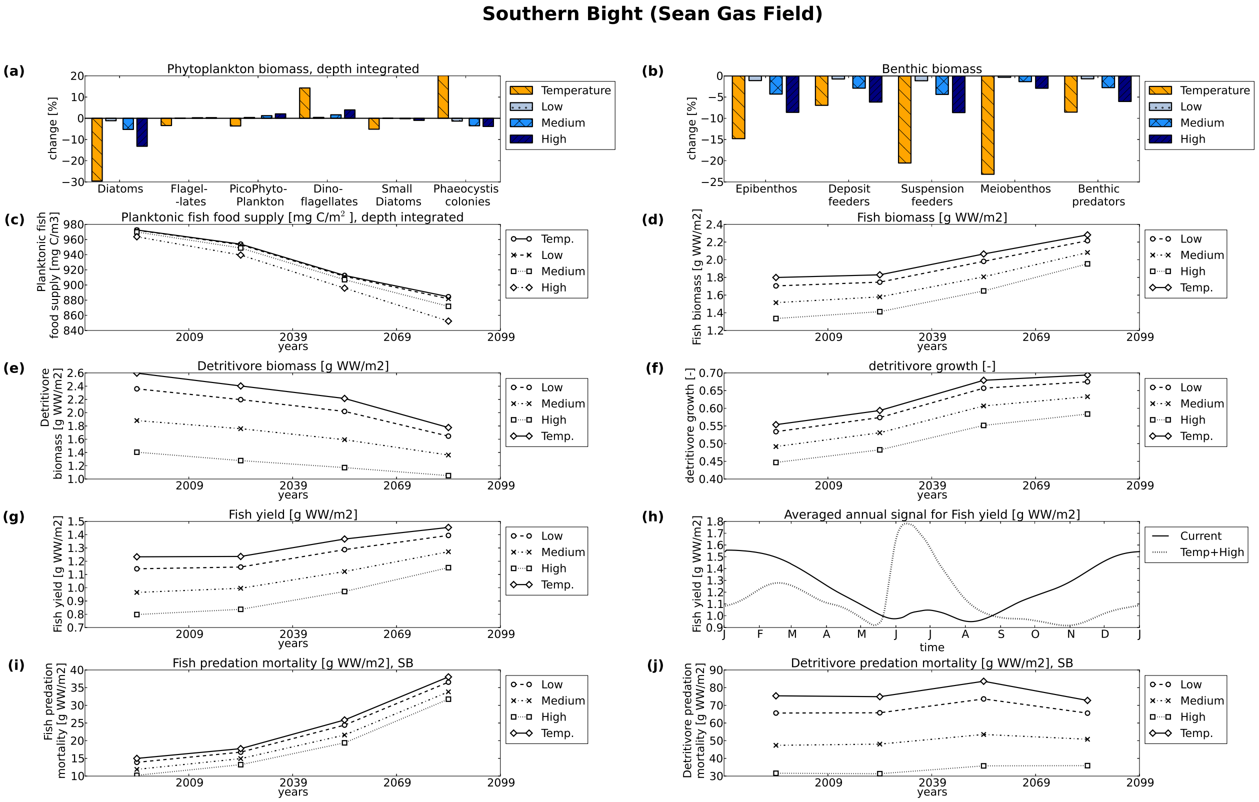

Figure 5. Southern Bight: 30-year averaged values, climatic plus high ocean acidification (LTL+HTL) effects: (a) phytoplankton changes [%], (b) benthos changes [%], (c) planktonic fish food, (d) fish or pelagic predator biomass, (e) detritivore biomass, (f) detritivore growth rates, (~~e~~g) fish yield~~and~~, (~~f~~h) annual fish yield, signal for the current time (1979-2008 climate scenario) and the high impact scenario (2069-2098 climatic plus LTL+HTL acidification effects) signal, (i) predated biomass for pelagic predators and (j) predated biomass for detritivores. Maximum values outside of axis range for phytoplankton changes are 108 % for *Phaeocystis*.

pacts~~(figure~~, affecting all seasons and showing a strong decline in winter and strong increase in summer (Fig. 5(~~e)), affecting all seasons (figure~~g,h)). Feeding behaviour showed a strong increase in the reliance on the pelagic food source for fish as detritivore biomass levels decreased (Fig. 5(~~f))but with the stongest effect in winter~~i,j)).

12 Discussion

Results presented in the last section show regionally differing responses to future pressures. This high spatial variability was also reported by Artioli et al. (2013) using a fully three dimensional shelf seas model, and can be seen in Skogen et al. (2014) for the Arctic region and in Blanchard et al.

(2012) for 11 regional seas. The use of 3D models adds advective processes and far-field influences, but generally lacks specific local ~~parameters (e.g. bed composition, sediment properties~~parameter settings (here bed porosity and increased vertical resolution). As such, the two approaches are complementary. Advective processes and oceanic changes have the potential to outweight local response. This applies mainly to ocean acidification impacts, as climatic impacts are predominantly a direct response to local meteorology (unless large scale circulation patterns are altered). The less computationally expensive water column model also allows for many scenario simulations to be performed within a reasonable time frame, and is therefore very suitable for scenario studies including different pressures at different impact levels.

Here, the use of ~~3~~ three separate sites within one shelf sea, each calibrated and validated independently (Van der Molen et al., 2013), allows for these regional differences to be investigated. Results for sites located in stable hydrodynamic regimes (North Dogger, Southern Bight) can be indicative for the system stressor response in the associated regime areas (see ~~figure~~Fig. 1). However, results for the Oyster Grounds (located in transitional waters) should be interpreted as relating to areas of thermal stratification of varying duration during summer (1-6 months), with medium depths (40-50 m).

~~Model~~ The study only emulated the potential impact of two different mechanisms of ocean acidification impacts on marine organisms and marine ecosystem functioning. The outcomes of the study will be sensitive to the assumption regarding the nature of the direct impact of ocean acidification. However when looking at whole-system level effects emulating acidification effects is challenging based on current understanding of ocean acidification and ecological processes. Where there is no clear effect on a system level process, individual species level effects may just lead to changes in community composition with little impact at a whole-system level. Similarly model limitations should also be considered. ERSEM-BFM is one of the most advanced lower trophic level models available, incorporating (besides multiple functional groups with internally varying nutrient ratio's): nitrifying bacteria, urea, TEP, benthic diatoms, pelagic filter feeder larvae and an extensive benthic module (including pore water processes, bio-irrigation and bio-turbation). Nevertheless, it remains a simplification of the marine ecosystem. Temperature controls virtually every biological process, and as such any temperature change can be expected to have a large impact on simulated results. The main conclusions therefore cannot identify whether climate impacts are dominant (if they are, this might be the results of the model's extensive implementation of temperature), but can indicate if simplified ocean acidification impacts are of comparable order to fully included climatic effects. The results showed that this is the case for both the seasonally stratified site and the permanently mixed site, with the site located in transitional waters exhibiting a dominant impact due to ocean acidification. This aligns with the conclusion from Griffith et al. (2012) that ocean acidification was the main driver in a study considering the separate and combined impacts of fishing, acidification and ocean warming. With respect to the applied size-structured model, both temperature and acidification impacts have been included in limited form. Other environmental consequences (e.g. low oxygen levels, see Van der Molen et al. (2013) for future predictions at these sites) have not been included directly in the higher trophic level model. It assumes a size distribution of biomass, neglecting species characteristics, seasonal reproduction and life stages. As such, it can provide qualitative information about future trends in marine biomass and fish yield, but cannot predict effects on specific commercial species (cold-water species may be replaced by warmer-water ones, see e.g. Cheung et al. (2010) for related impacts on fish yield) or the associated fisheries-landings value. Only a nominal fishing pressure was applied: changes in fishing pressure have the potential to aggravate or relieve ~~future pressures impact~~the impacts of future pressures. This also applies to the usage of the medium emissions scenario, which is dependent on future management of carbon emissions. Note that the interaction of ambient temperature and abiotic and/or species-level acidification impacts is non-linear: the presented values for acidification impacts alone are indicative of the trend due to acidification effects under future climate conditions, but should not be interpreted as percentage changes likely to occur under current climate conditions and increased CO_2 levels.

Finally, the linkage between the lower and higher trophic level model allowed for impact assessment of bottom-up pressures like climate change and acidification throughout the food web. However, top-down pressures like fishing effort only impacted the higher end of the food chain, with no mechanism included to allow for top-down pressures to impact on lower trophic level dynamics. Thus, if fishing pressure is to be included in future studies comparing marine pressures a 2-way coupled approach is necessary, with fish biomasses impacting on planktonic-level organisms and associated nutrient cycling. This would also ensure feedback of other predator changes (e.g. increased feeding rates due to increased sea temperature, more pelagic-oriented feeding) on planktonic biomass, which are not included in one-way coupling. The bottom-up stressor of nutrient supply should also be considered in future studies, as changes in nutrient availability can change lower trophic level dynamics considerably. However, for the North Sea future changes in nutrient supply should take into account changes in Atlantic sources (Holt et al., 2012) as well as land-based sources (Painting et al. (2013) , their Fig. 4). When considering multiple stressors like acidification, climate change, nutrient supply and fishing pressure the interactions of different pressures should be studied using statistical techniques such as the Hedges-d method: this was applied in Griffith et al. (2012) with respect to ocean warming, ocean acidification and fishing pressure in Australian marine waters. They showed that interactions between pressures could lead to less than or more than the additive response of the system: for instance, fishing pressure counteracted negative effects from acidification on benthic invertebrates by relieving predation pressure. Similar results were found in this study, as climate-change induced increases in biomass were counteracted by acidification impacts, with non-additive response. Together with different impact level studies like the one presented here these methods have the potential to provide a good indication of future marine response to known pressures.

13 Conclusions

This article has provided ~~an~~ a first indication of future trends in fisheries harvests, based on predicted impacts from both climatic changes and ocean acidification (abiotic and biotic) effects in an economically important shelf sea. To this end we applied a coupled ecosystem model (simulating the hydrodynamics, nutrient cycling, plankton, benthos, fish and detritivore biomass) to three hydrodynamically different sites in the North Sea. Results showed high regional variability and an overall shift towards more pelagic oriented systems (due to temperature-induced increased pelagic recycling and acidification impacts on benthic organisms). Fisheries yield ~~is expected~~ displayed an inclination to increase in large parts of the North Sea due to climate change effects, as reported by Blanchard et al. (2012). However, the strength of ocean acidification impacts on both the abiotic and biotic level ~~have~~ has the potential to severely mediate this positive impact on fisheries harvest for permanently mixed areas.

The three sites also showed local repsonses depending on the governing hydrodynamic regime and relative importance of the benthic system:

- **Seasonally stratified areas**

  Acidification impacts were of the same order of magnitude as climatic impacts, with ~~fisheries yield expected to increase. Both impacts contributed to increased yields ,~~ indirect and direct acidification effects exhibiting opposing trends. Fisheries yield indicated a positive trend, with both stressors contributing to increased yields which mainly occurred in winter and spring.

- **Transitional areas**

  Ocean acidification impacts dominated over climatic effects, reflecting the ~~existing, large , variability in abiotic environment that the local ecosystem already copes with. Fisheries are expected~~ large benthic system at this site and its importance in transporting carbon to higher trophic levels. Fisheries were predicted to be negatively impacted, mainly due to ocean acidification impacts on species level (due to the relatively large importance of the benthic system). Fish yield ~~is~~ under the projected circumstances was predicted to decline, particularly in winter months.

- **Well-mixed areas**

  Climatic impacts were of the same order of magnitude as acidification impacts, with a dominant acidification impact on detritivore levels. Increases in fisheries yield ~~can be expected~~ were predicted due to more pelagic recycling and increased primary production, but any quantitative ~~increase~~ change will depend heavily on the strength of acidification effects on both the abiotic environment and the species level (assuming no change in nutrient supply). Changes in fish yield ~~are~~ were equally distributed over the seasons when impacts ~~are~~ were of similar strength, with predicted reduced yield in winter and increased yield in summer.

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