

BGD

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**Climate and
acidification impacts
on future fisheries
yield**

S. M. van Leeuwen et al.

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Future fisheries yield in shelf waters: a model study into effects of a warmer and more acidic marine environment

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Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



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 (occurring 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 (occurring 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.

1 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 CO₂ by the marine environment due to elevated levels of atmospheric CO₂ (Doney et al., 2009; Gattuso et al., 2011), has been a recent addition to this list, but has the potential

BGD

12, 9695–9727, 2015

Climate and acidification impacts on future fisheries yield

S. M. van Leeuwen et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Climate and acidification impacts on future fisheries yield

S. M. van Leeuwen et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



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; Le Quesne and Pinnegar, 2012). 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. 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.

Here, modelling tools are used to provide a first indication of single and combined effects of direct and indirect impacts on the 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 marine food web. To this end, a coupled ecosystem model was applied in selected locations around the North Sea, 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 pelagic nitrogen cycling and growth alterations of seabed organisms.

2 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.

2.1 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 1990s 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 21st 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 ex-

BGD

12, 9695–9727, 2015

Climate and acidification impacts on future fisheries yield

S. M. van Leeuwen et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Climate and acidification impacts on future fisheries yield

S. M. van Leeuwen et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



opolymer particles (TEP) by nutrient-stressed diatoms and *Phaeocystis*, 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.

2.2 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 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).

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.

et al. (2002) was used for validation. Fishing pressure was included in the model as a nominal pressure, but was not calibrated to represent site-specific mortalities. Here, as in Van der Molen et al. (2013), 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 1 shows the validation results 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.

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.

2.5 Locations

Three locations have been chosen in the North Sea, a shallow shelf sea located on the European shelf (Fig. 2). 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. 2. For more details on the different regimes see van Leeuwen et al. (2015).

BGD

12, 9695–9727, 2015

Climate and acidification impacts on future fisheries yield

S. M. van Leeuwen et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



2.6 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 Fig. 2). Hydro-biogeochemical conditions at these sites were simulated for the period 1958–2008, using ECMWF forcing data (UK Met Office), for validation purposes. Future conditions were simulated for the period 1958–2089, 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 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:

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

BGD

12, 9695–9727, 2015

Climate and acidification impacts on future fisheries yield

S. M. van Leeuwen et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



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.

3.1 North Dogger

The seasonally stratified site was characterised by a negative impact of future climate conditions on pelagic and benthic biomass levels (see also Fig. 3a and b). Net primary production increased due to increased metabolic processes (resulting in higher pelagic turn-over 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 (Fig. 3a) but this was relative to originally very low biomass values ($6 \text{ mg C m}^{-2} \text{ d}^{-1}$). 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, resulting in higher biomass for both fish and detritivores despite the minor decrease in food supply.

Ocean acidification effects on the abiotic environment 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 biomass decline was due to decreased levels of filter feeders: all other benthic functional groups increased their biomass levels (see Fig. 3b). 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. As a result, 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).

BGD

12, 9695–9727, 2015

Climate and acidification impacts on future fisheries yield

S. M. van Leeuwen et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



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).

3.2 Oyster Grounds

Climatic impact reduced pelagic biomass slightly at this site, with a larger impact on benthic functional groups (Fig. 4b), 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: Fig. 9). The overall reduction in phytoplankton (see also Fig. 4a) and zooplankton biomass reduced the 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. Fisheries yield showed negligible change as fish biomass decrease was limited mainly to non-commercial size fish.

Impacts of reduced nitrification at this site were minor. With virtually no impact on the benthic system, 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. Impact on fisheries yield was negligible.

3.3 Southern Bight

The well-mixed site in the southern bight showed a large increase in net primary production under future climate conditions. 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 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

BGD

12, 9695–9727, 2015

Climate and acidification impacts on future fisheries yield

S. M. van Leeuwen et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



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 loss of benthos biomass (see also Fig. 5b) 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.

Reduction of pelagic nitrification rates resulted in higher pelagic ammonium concentrations and lower nitrate levels, favouring phytoplankton species with high ammonium preference like picophytoplankton and dinoflagellates (Fig. 5a). 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 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.

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 and detritivore biomass decreasing. Fisheries yield was predicted to increase under future conditions.

4 Effects on higher trophic levels

Reduced growth of calcifying organisms was represented by reductions in the size-based model of the net growth conversion efficiency for organisms in the detritivore size-spectrum (parameter K_v). Modelled growth rates therefore depend on ambient

BGD

12, 9695–9727, 2015

Climate and acidification impacts on future fisheries yield

S. M. van Leeuwen et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



food supply due to climatic changes) displaying a downward trend due to a reduced detritivore food source.

Climatic impacts dominated over species-level ocean acidification impacts at this site, with temperature-induced decline of detritivore biomass significantly enhanced by direct acidification impact. Fisheries yield was predicted to increase due to climatic impacts (increased food supply, increased fish growth rates).

5 Combined effects: indications of future fisheries trends

Results for combined impacts from climate and direct and indirect ocean acidification are listed in Table 6.

5.1 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 to increases in ambient water temperature, despite species-level acidification impacts (Fig. 3d). Fish food supply declined due to climatic impacts, but the decline was moderated by positive impacts from acidification effects on the abiotic environment (Fig. 3c). Fish yield increased (Fig. 3e), mainly during the spring bloom and winter periods (Fig. 3f).

5.2 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. Detritivore growth rates increased over time (Fig. 4d), but increases were heavily modified due to direct acidification impacts. Pelagic fish food supply increased slightly due to indirect acidification impacts (Fig. 4d),

BGD

12, 9695–9727, 2015

Climate and acidification impacts on future fisheries yield

S. M. van Leeuwen et al.

[Title Page](#)
[Abstract](#)
[Introduction](#)
[Conclusions](#)
[References](#)
[Tables](#)
[Figures](#)
[Back](#)
[Close](#)
[Full Screen / Esc](#)
[Printer-friendly Version](#)
[Interactive Discussion](#)


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, 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. 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. 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 CO₂ 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.

7 Conclusions

This article has provided an 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 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 the potential to severely mediate this positive impact on fisheries harvest for permanently mixed areas.

The three sites also showed local responses 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,

Climate and acidification impacts on future fisheries yield

S. M. van Leeuwen et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



with fisheries yield expected to increase. Both impacts contributed 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 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 predicted to decline, particularly in winter months.

– Well-mixed areas

Climatic impacts were of the same order of magnitude as acidification impacts. Increases in fisheries yield can be expected due to more pelagic recycling and increased primary production, but any quantitative increase will depend heavily on the strength of acidification effects on both the abiotic environment and the species level. Changes in fish yield are equally distributed over the seasons when impacts are of similar strength, with reduced yield in winter and increased yield in summer.

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BGD

12, 9695–9727, 2015

Climate and acidification impacts on future fisheries yield

S. M. van Leeuwen et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Climate and acidification impacts on future fisheries yield

S. M. van Leeuwen et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



- Baretta, J. W., Ebenh oh, W., and Ruardij, P.: The European regional seas ecosystem model: a complex marine ecosystem model, *J. Mar. Res.*, 33, 233–246, 1995. 9698
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Climate and acidification impacts on future fisheries yield

S. M. van Leeuwen et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



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Climate and acidification impacts on future fisheries yield

S. M. van Leeuwen et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



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BGD

12, 9695–9727, 2015

Climate and acidification impacts on future fisheries yield

S. M. van Leeuwen et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



BGD

12, 9695–9727, 2015

**Climate and
acidification impacts
on future fisheries
yield**

S. M. van Leeuwen et al.

[Title Page](#)[Abstract](#)[Introduction](#)[Conclusions](#)[References](#)[Tables](#)[Figures](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)**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

BGD

12, 9695–9727, 2015

Climate and acidification impacts on future fisheries yield

S. M. van Leeuwen et al.

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

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

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

I◀

▶I

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Climate and acidification impacts on future fisheries yield

S. M. van Leeuwen et al.

Table 3. Simulated scenarios. p_{sN4N3} is the pelagic specific nitrification rate (in 1 d^{-1}) 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 to the higher trophic level model (size-based model).

Scenario	Reference		Low		Medium		High	
Parameter Reduction	p_{sN4N3}	K_v	p_{sN4N3} 10%	K_v 2%	p_{sN4N3} 30%	K_v 6%	p_{sN4N3} 50%	K_v 10%
Parameter Reduction	p_{sN4N3}	K_v	p_{sN4N3} 10%	K_v 2%	p_{sN4N3} 30%	K_v 6%	p_{sN4N3} 50%	K_v 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

[Title Page](#)
[Abstract](#)
[Introduction](#)
[Conclusions](#)
[References](#)
[Tables](#)
[Figures](#)
[⏪](#)
[⏩](#)
[◀](#)
[▶](#)
[Back](#)
[Close](#)
[Full Screen / Esc](#)
[Printer-friendly Version](#)
[Interactive Discussion](#)


Climate and acidification impacts on future fisheries yield

S. M. van Leeuwen et al.

Table 4. Simulated results for lower trophic level impacts: percentage change for all sites and scenarios [%] and actual reference values ($\text{gC m}^{-2} \text{d}^{-1}$ for lower trophic level results and $\text{g wet weight m}^{-2}$ for fisheries results) of depth-integrated, 30 year averages. The reference values refer to the period 1979–2009 of the climate change scenario simulation. POC refers to Particulate Organic Carbon.

variable		Low	Med.	ND High	T	Ref.	Low	Med.	OG High	T	Ref.	Low	Med.	SB High	T	Ref.
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 <i>a</i>	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

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Climate and acidification impacts on future fisheries yield

S. M. van Leeuwen et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Table 5. Simulated results for higher trophic level impacts only: percentage change for all sites % and actual reference values g wet weight m^{-2} of depth-integrated, 30 year average values.

variable		ND				OG					SB					
		Low	Med.	High	T	Ref.	Low	Med.	High	T	Ref.	Low	Med.	High	T	Ref.
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

Climate and acidification impacts on future fisheries yield

S. M. van Leeuwen et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Table 6. Simulated results for combined lower and higher trophic level impacts: percentage change % and actual reference values g wet weight m^{-2} for all sites of depth-integrated, 30 year average values.

variable		ND				OG				SB						
		Low	Med.	High	T	Ref.	Low	Med.	High	T	Ref.	Low	Med.	High	T	Ref.
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

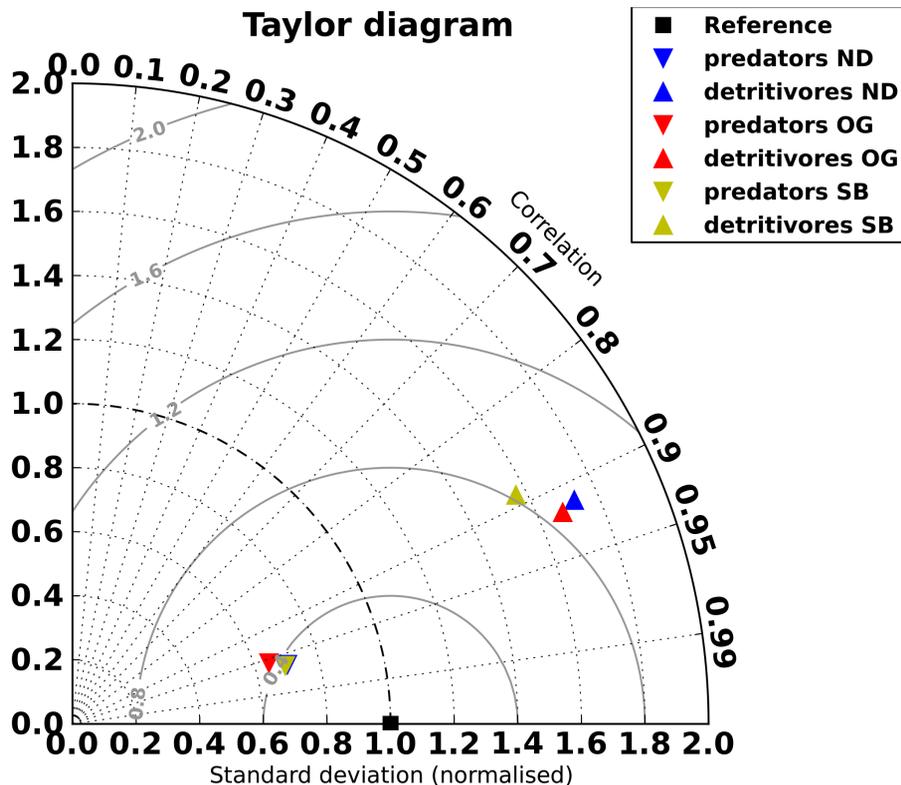


Figure 1. Taylor diagram for predator and detritivore abundance from the coupled model. Note that observations for detritivores were used for calibration purposes, so that predator observations provide the only validation of the higher trophic levels here. Predator abundance results for the North Dogger site overlap with those of the Southern Bight site. The internal grey arcs represent the root-mean-square-error.

Title Page

Abstract	Introduction
Conclusions	References
Tables	Figures

⏪

⏩

◀

▶

Back	Close
------	-------

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

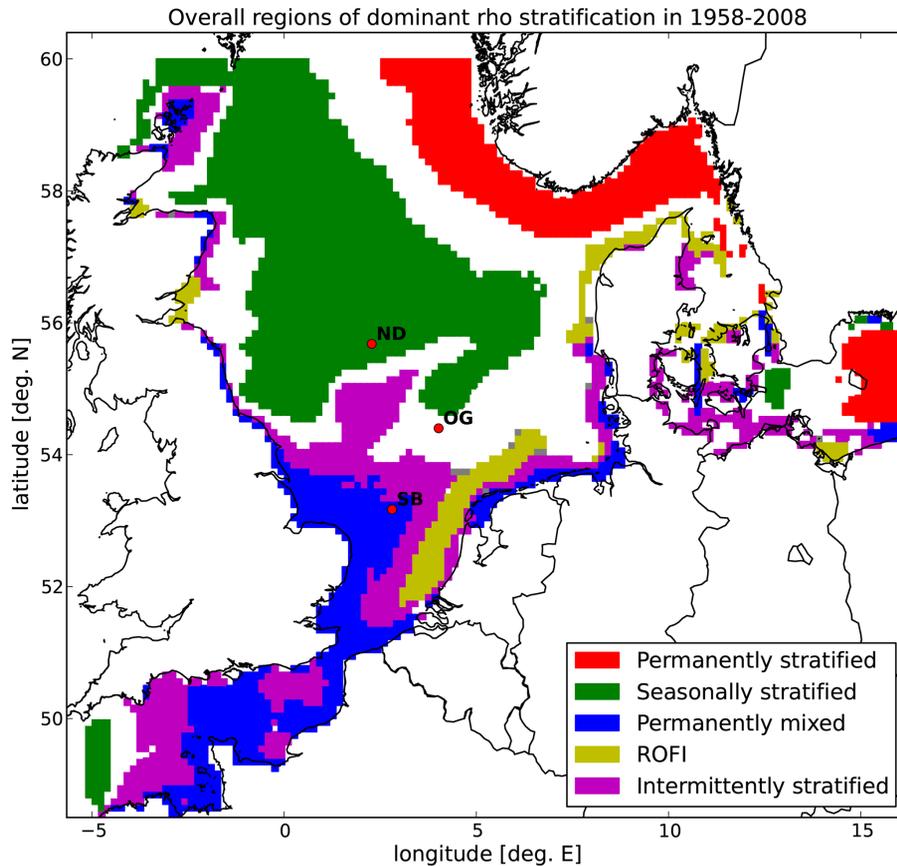


Figure 2. Location of the three sites in the North Sea, imposed on a map of dominant vertical density stratification regimes. From van Leeuwen et al. (2015).

Climate and acidification impacts on future fisheries yield

S. M. van Leeuwen et al.

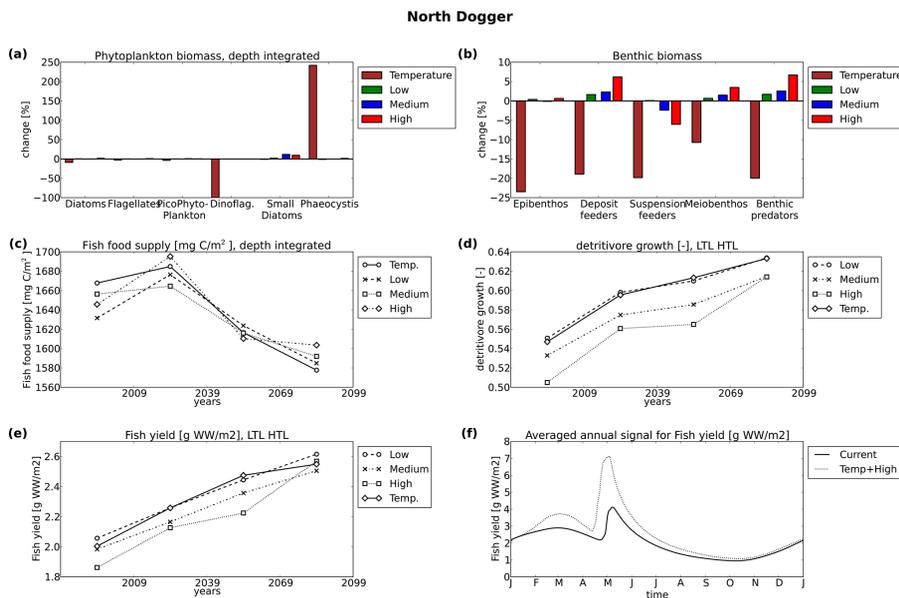


Figure 3. North Dogger: 30 year averaged values, climatic plus high ocean acidification (LTL + HTL) effects: **(a)** phytoplankton changes [%], **(b)** benthos changes [%], **(c)** fish food, **(d)** detritivore growth rates, **(e)** fish yield and **(f)** annual fish yield signal for the current time (1979–2008 climate scenario) and the high impact scenario (2069–2098 climatic plus LTL + HTL acidification effects) signal.

Climate and acidification impacts on future fisheries yield

S. M. van Leeuwen et al.

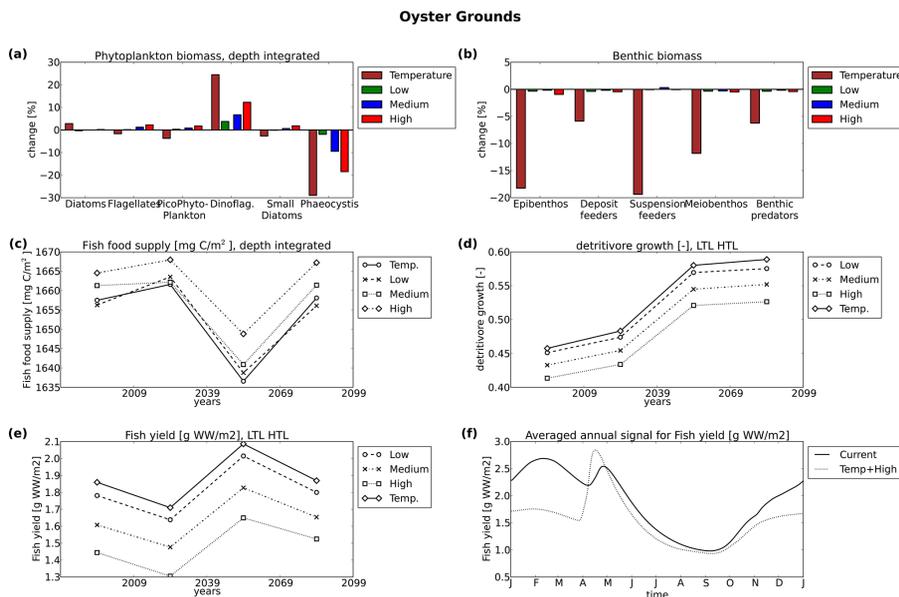


Figure 4. Oyster Grounds: 30 year averaged values, climatic plus high ocean acidification (LTL + HTL) effects: **(a)** phytoplankton changes [%], **(b)** benthos changes [%], **(c)** fish food, **(d)** detritivore growth rates, **(e)** fish yield and **(f)** annual fish yield signal for the current time (1979–2008 climate scenario) and the high impact scenario (2069–2098 climatic plus LTL + HTL acidification effects) signal.

Climate and acidification impacts on future fisheries yield

S. M. van Leeuwen et al.

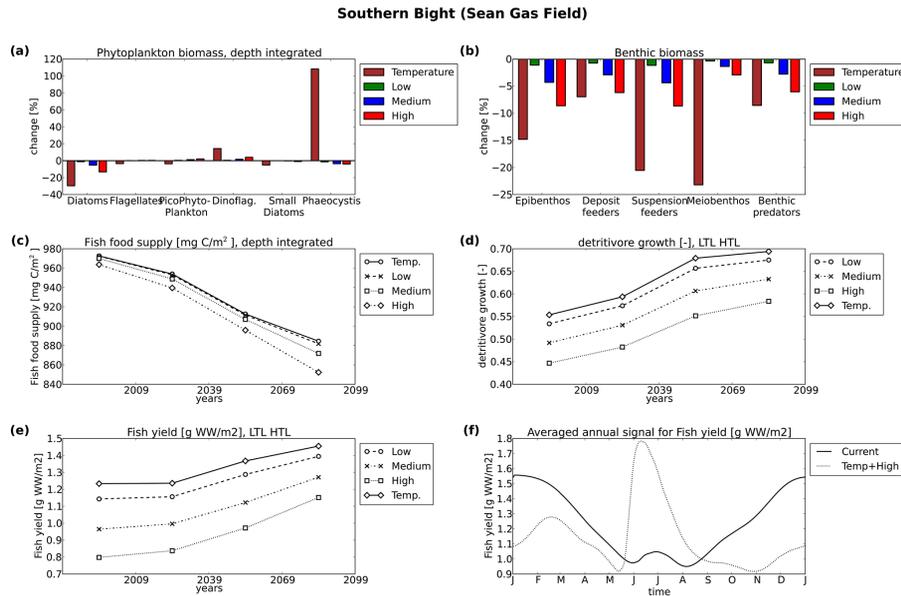


Figure 5. Southern Bight: 30 year averaged values, climatic plus high ocean acidification (LTL + HTL) effects: **(a)** phytoplankton changes [%], **(b)** benthos changes [%], **(c)** fish food, **(d)** detritivore growth rates, **(e)** fish yield and **(f)** annual fish yield signal for the current time (1979–2008 climate scenario) and the high impact scenario (2069–2098 climatic plus LTL + HTL acidification effects) signal.