

Modelling marine ecosystem response to climate change and trawling in the North Sea

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Abstract The marine ecosystem response to climate change and demersal trawling was investigated using the coupled hydrodynamic-biogeochemical water column model GOTM-ERSEM-BFM for three contrasting sites in the North Sea. Climate change forcing was derived from the HadRM3-PPE-UK regional climate model for the UK for the period 1950–2100 using historical emissions and a medium emissions scenario (SRESA1B). Effects of demersal trawling were implemented as an additional mortality on benthic fauna, and changes in the benthic–pelagic nutrient and carbon fluxes. The main impacts of climate change were (i) a temperature-driven increase in pelagic metabolic rates and nutrient cycling, (ii) an increase in primary production fuelled by recycled nutrients, (iii) a decrease in benthic biomass due to increased benthic metabolic rates and decreased food supply as a result of the increased pelagic cycling, and (iv) a decrease in near-bed oxygen concentrations. The main impacts of trawling were (i) reduced benthic biomass due to the

increased mortality, and (ii) the increased benthic–pelagic nutrient fluxes, with these effects counteracting each other, and relatively small changes in other variables. One important consequence was a large decrease in the de-nitrification flux predicted at the two summer-stratified sites because less benthic nitrate was available. The effects of trawling scaled linearly with fishing effort, with greatest sensitivity to fishing in summer compared to fishing in winter. The impacts of climate change and trawling were additive, suggesting little or no non-linear interactions between these disturbances.

Keywords Biogeochemistry · Climate change · Trawling · Anthropogenic impact · North Sea

Introduction

Background

The responses of planktonic and benthic food webs in northwest European shelf seas to anthropogenic impacts are relatively poorly understood in terms of standing stocks, productivity and carbon and nutrient conversion processes. Significant work has been carried out on assessing the impact of (reductions in) anthropogenic riverine nutrient sources (Lenhart et al. 2010), but little is known about the impacts of

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greenhouse-gas driven climate change or of demersal fishing (trawling), or of interactions between these processes. Any changes in primary or secondary production resulting from such anthropogenic impacts may well influence the availability of food to higher trophic levels and, through that, commercial and non-commercial fish stocks. Also, changes in production, oxygen and rates and pathways of carbon and nutrient cycling between the pelagic and benthic systems may lead to variations in carbon fate and storage (Doney 2010). It is important to better understand these processes in order to plan and manage our marine resources in a sustainable way.

In situ observational studies of planktonic and benthic processes and how they are impacted by anthropogenic influences, though indispensable, are hampered by the long time scales at which marine shelf sea ecosystems respond, and by inter-annual and spatial variability in forcing factors and biological processes. Moreover, it is often difficult to disentangle the results of the interactions between various disturbances. Numerical models can help to better understand these interactions, as disturbances can be applied in isolation or in combinations. Also, models can provide scenario projections into the future. Here, an intermediate trophic level ecosystem model is used to assess the impacts of climate variability and trawling on productivity and carbon and nutrient fluxes. The work was part of the Marine Ecosystems Connections project, which addressed the source, cycling and fate of carbon, nutrients (nitrate, ammonium, silicate, phosphate) and oxygen in UK Shelf Seas, specifically the North Sea. Further results of the project can be found in the other publications in this special issue, and references therein.

Study sites

The work focused on three sites, selected within the Marine Ecosystems Connections project to be representative of larger areas with similar water column and seabed characteristics (Fig. 1). The distribution of the regions represented by each site was derived using k-means clustering based on water depth, percentage of silt and clay in the seabed sediment and degree of water column stratification. The site in the southern Bight represented region R4, and is characterised by a shallow (30 m), well mixed water column and a mobile, sandy sea-bed that results in a greater oxic

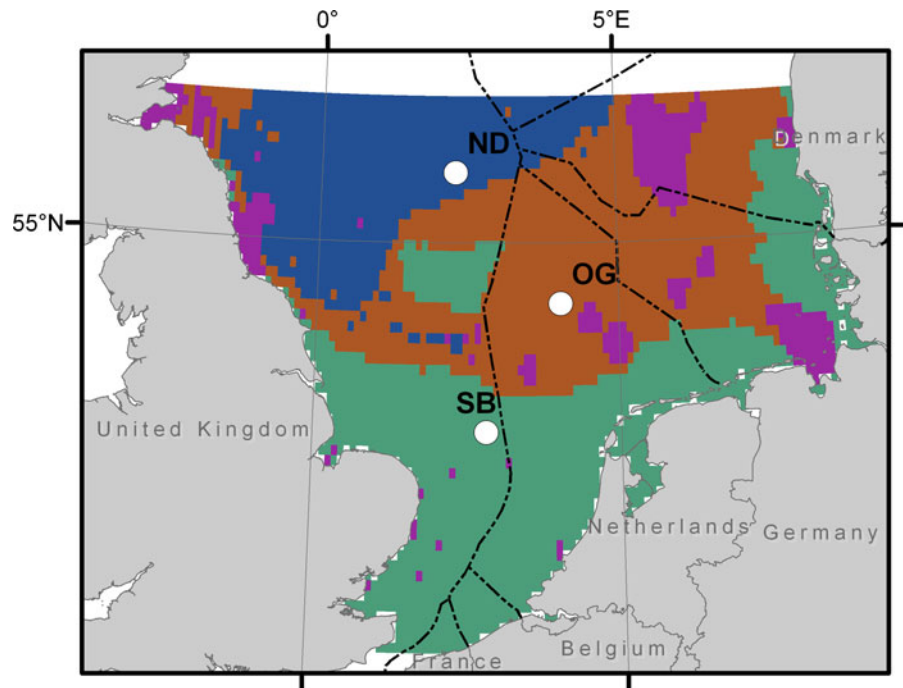
layer depth (~ 2 to 6 cm) and depth of pore-water nutrient generation than at the other sites. The Oyster Grounds site represented region R2, has intermediate water depth (45 m), and is characterised by a muddy-sand sediment, is seasonally stratified with a shallower oxic layer (~ 1 cm) than region R4 allowing nutrient regeneration closer to the sediment–water interface and potentially making it more susceptible to disturbance. Macrofaunal bioturbation is significant within this region and controls oxic and suboxic layer depths and nutrient cycling. The site north of the Dogger Bank represented region R1, is much deeper (80 m), and has a bottom mixed layer that remains cool throughout the stratified period (7–8 °C). Furthermore, the sea-bed consists of muddy sand and has sparse fauna, resulting in a very shallow oxic layer and apparent redox potential discontinuity (aRPD, also referred to here as anoxic layer), and high sea-bed nutrient content close to the sediment–water interface. Due to its depth and weak tidal currents, this area is rarely disturbed by hydrodynamical processes. Region type R3 was identified by the clustering method as well-mixed, muddy, non-continuous and geographically restricted, but did not coincide with any of the sites. For more information about the benthic assemblages, sea-bed characteristics and carbon/nutrient cycling processes at the two stratified sites, see Birchenough et al. 2012 (this issue). The under-water light regime at the three sites was studied by Capuzzo et al. 2012 (this issue), and seasonal changes in zooplankton trophodynamics was studied by Painting et al. 2012 (this issue), Kürten et al. 2011 (this issue a) and Kürten et al. 2012 (this issue b).

Materials and methods

Model description

The coupled physical-biogeochemical model GOTM-ERSEM-BFM was used for the simulations. GOTM (General Ocean Turbulence Model) is a public domain, one-dimensional Finite Difference hydrodynamical water column model designed initially for testing turbulence closure models (Burchard et al. 1999; www.gotm.net). It solves the 1DV partial differential equations for conservation of mass, momentum, salt and heat. The ERSEM-BFM (European Regional Seas Ecosystem Model-Biogeochemical Flux Model)

Fig. 1 Study sites and regions. *Blue* region R1, *brown*: region R2, *purple*: region R3, *green*: region R4



version used here is a development of the model ER-SEM III (see Baretta et al. 1995; Ruurdij and van Raaphorst 1995; Ruurdij et al. 1997, 2005; Vichi et al. 2003, 2004, 2007; www.nioz.nl/northsea_model), and describes the dynamics of the biogeochemical fluxes within the pelagic and benthic environment. The ER-SEM-BFM model simulates the cycles of carbon, nitrogen, phosphorus, silicate and oxygen and allows for variable internal nutrient ratios inside organisms, based on external availability and physiological status. The model applies a functional group approach and contains four phytoplankton groups, four zooplankton groups and five benthic groups, the latter comprising four macrofauna and one meiofauna groups. Pelagic and benthic aerobic and anaerobic bacteria are also included. The pelagic module includes additional processes over the oceanic version presented by Vichi et al. (2007) to make it suitable for temperate shelf seas: (i) a parameterisation for diatoms allowing growth in spring, (ii) enhanced transparent exopolymer particles (TEP) excretion by diatoms under nutrient stress, (iii) the associated formation of macro-aggregates consisting of TEP and diatoms, leading to enhanced sinking rates and a sufficient food supply to the benthic system especially in the deeper offshore areas (Engel 2000), (iv) a *Phaeocystis* functional group for improved simulation of primary production in coastal

areas (Peperzak et al. 1998), and (v) a suspended particulate matter (SPM) resuspension module that responds to surface waves for improved simulation of the under-water light climate. The ERSEM-BFM model used here includes a 3-layer benthic module comprising 53 state variables, which enables it to resolve substantially more benthic processes and more detailed benthic–pelagic coupling than other biogeochemical models recently applied to the North Sea (Radach and Moll 2006; Lenhart et al. 2010), and making it suitable for the present study. To avoid nitrogen depletion in the one-dimensional model used here, the nitrogen budget was closed artificially by re-introducing nitrogen lost by denitrification as nitrate through atmospheric deposition.

Physical forcing is a major influence in determining the results of ecological models (e.g., Skogen and Moll 2005). Such forcing includes components that have local dominance (e.g., air temperature, irradiation, sediment resuspension and effects on light climate, and anthropogenic disturbance), and components that include regional and gradient effects (advection of properties). Although 1D models such as the one used here cannot represent advection and gradient effects unless forced by gradient terms (Verspecht et al. 2009), which was not done here, they can represent the effects of changes in local forcings. Hence they can be

used to provide first estimates of such effects in a much more efficient way than could be done using full 3D models, subject to the assumption that conditions in the vicinity of the study sites under consideration are reasonably homogeneous in the horizontal direction. As such, the result presented here should not be considered as final or highly accurate, but rather as a step along the way, which is nevertheless instructive.

Model confirmation

For the purpose of model confirmation, the GOTM-ERSEM-BFM model was run using meteorological hind cast forcing obtained from the European Centre for Medium-Range Weather Forecasts (ECMWF) ERA-40 and Operational Analysis Hindcasts (see http://badc.nerc.ac.uk/data/dataset_index/?source=data for details). Together, these data sets provide a realistic representation of the weather for the period 1958 to the present.

The observational programme of the Marine Ecosystems Connections project collected a large amount of data with which to compare the model output (Greenwood et al. 2010; Birchenough et al., this issue; Capuzzo et al., this issue; Johnson et al. 2012, this issue; Painting et al., this issue). Based on the observed macrofaunal data in terms of numbers of individuals, carbon values were derived using conversion metrics from biomass to carbon (Brey 2001).

For confirmation, the model was run for the years 1958–2008. The results for the years 1978–2008 were compared with the available observations in terms of RMS difference and model-observation bias, and as time series plots and vertical profiles (for reasons of space, a few typical examples are given here).

The RMS difference E_{RMS} was defined as:

$$E_{RMS} = \sqrt{\frac{1}{I} \sum_{i=1}^I (x_{m,i} - x_{o,i})^2} \quad (1)$$

where I is the number of observations, i a counter, and x_m and x_o are the model and observational results, respectively.

The model-observation percentage bias B was defined as:

$$B = 100 \frac{\sum_{i=1}^I (x_{m,i} - x_{o,i})}{\sum_{i=1}^I x_{o,i}} \quad (2)$$

Climate change scenario forcing

The scenarios were run with the Met Office Hadley Centre Regional Model Perturbed Physics Ensemble simulations for the twenty-first century for the UK domain experiment (HadRM3-PPE-UK, Met Office 2008, see also Murphy et al. 2007a; Pope et al. 2007; Collins 2007), which was designed to simulate the regional climate for the UK in the period 1950–2100 for a historical and medium (SRESA1B) emissions scenario. The results for the unperturbed member of the ensemble were obtained through the British Atmospheric Data Centre (BADC). The simulation was driven by historical and SRESA1B green-house gas emissions, including methane, sulphur and sulphur dioxide background emissions, anthropogenic sulphur dioxide emissions, and tropospheric/stratospheric ozone. The data has daily resolution in time, approximately 25 km resolution in space, and has 12 standard months of 30 days in a year. The HadRM3 model does not include an interactive ocean component.

Forcing from the nearest model grid cell in the HadRM3 model was used for each of the study sites. For the forcing parameters (10 m wind, air pressure, air temperature, relative humidity and cloud cover), the 360 day General Circulation Model (GCM) year was extended to a full calendar year by interpolation, taking account of leap years and applying a global correction to ensure annual average values were preserved. The daily data were then interpolated to six-hourly values and for wind speeds sub-daily variability was added to obtain more realistic simulations of the timing of the autumn break up of stratification and in situ concentrations of suspended particulate material (SPM). The added variability took the maximum daily wind speed as stored by the GCM into account. Thirty-year moving averages of the forcing parameters (Fig. 2), using the classical meteorological definition of climate, indicated that the dominant predicted change was in temperature, with some effects on wind speed, and minor changes in the other forcing parameters. Thirty-year averaged, 30 day moving averaged seasonal cycles of the wind speed indicate quieter projected conditions in late winter and spring by the end of the century, in particular for the Oyster Grounds site (Fig. 3). Note that the averaged results of this scenario retain considerable variability, which is inherent to the climate system (e.g. Hawkins 2010).

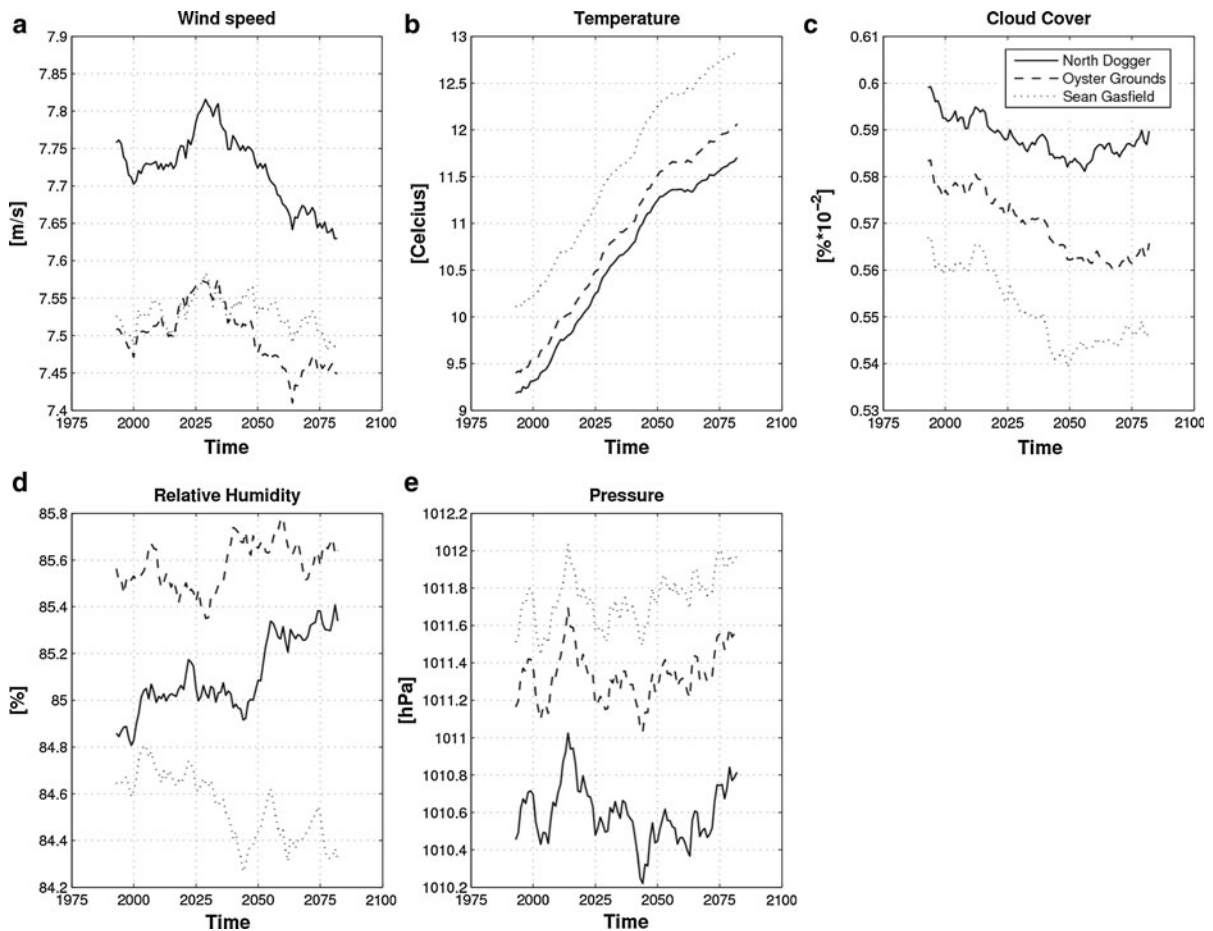


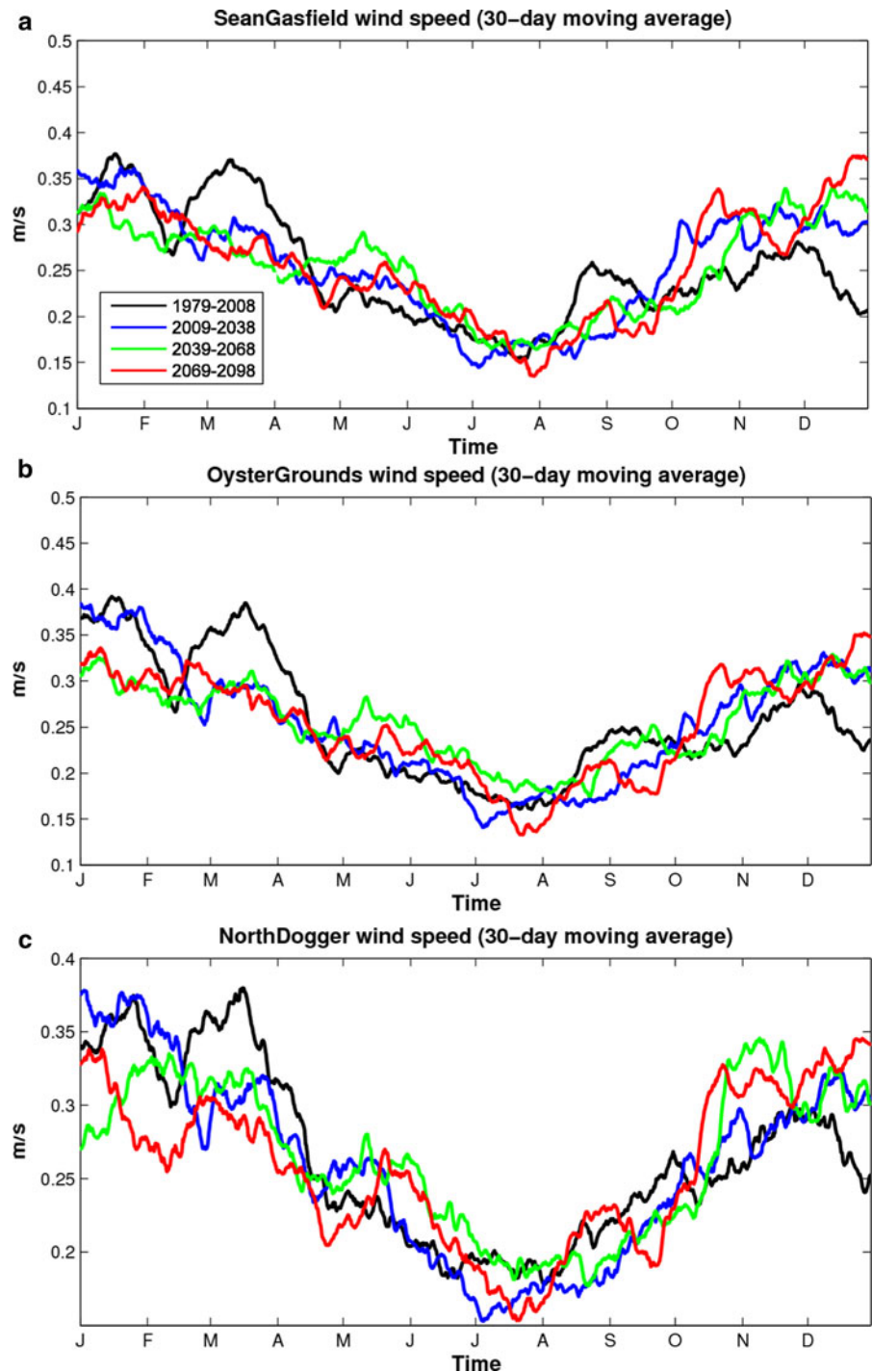
Fig. 2 Thirty-year moving averages of atmospheric forcing for the three sites, HadRM3-PPE-UK. **a** Wind speed, **b** air temperature, **c** cloud cover, **d** relative humidity, and **e** air pressure

Demersal trawling impacts

Two potential consequences of the physical disturbance of the bed caused by beam and otter trawling were modelled: (1) increased nutrient flux between the seabed and water column due to bed resuspension, (2) enhanced mortality of benthic organisms. Trawling intensity was set to represent the entire bed trawled once per year distributed through the year with three separate runs assuming effort was distributed uniformly through the year, concentrated entirely in summer, or entirely in winter. This fishing intensity represents a reasonable upper bound as estimates for the study sites based on Vessel Monitoring System (VMS) data (Lee et al. 2010) lie in the range 0.2–0.5 times per year. An average gear penetration depth of 5 cm was assumed (Van

Santbrink and Bergman 1994). The proportion of biomass removed after the passage of a single trawl for each benthic functional group was based on an earlier modelling study (Forryan et al. 2012, submitted) that made an ensemble of model runs using a range of observed trawling mortality (e.g. Kaiser and de Groot 2006). The values chosen (Table 1) best reproduced the mean of the ensemble. Mortality was represented as a flux from the zoobenthos functional group to benthic detritus (Allen and Clarke 2007). This assumption neglects fishing removal and scavenging by fish species (not included in the model) and assumes no production of pelagic detritus. However it was considered reasonable for an initial assessment of the magnitude of trawling impact. Trawling intensity r , expressed as the proportion of area trawled per day, was used

Fig. 3 Thirty-year average seasonal cycles of wind speed, filtered with a 30-day moving average filter, for the four time slices. **a** At the site in the southern Bight, **b** at the Oyster Grounds site, and **c** at the site north of the Dogger Bank



to scale the daily overall mortality rate. If the proportion of biomass removed by a single trawl was γ , the additional mortality due to trawling λ , for a given benthic group with biomass Y (g C m^{-2}), was calculated as

$$\lambda = r\gamma Y \quad (3)$$

The additional nutrient flux from the bed to the water column ($\text{mmol m}^{-2} \text{ day}^{-1}$) due to beam trawling f was calculated from the assumed gear penetration

Table 1 Percentage of biomass killed within each benthic group due to the impact of a single trawl track

Benthic group	Epibenthos (%)	Deposit feeder (%)	Suspension feeder (%)	Meiofauna (%)	Infaunal predator (%)
Trawling mortality	49	22	32	0	29

depth d (m), the specified proportion of area trawled per day r (day^{-1}) and the difference between pore-water concentration K and overlying water concentrations N (mmol m^{-3}) via

$$f = rd(K - N) \quad (4)$$

Note, if the pore water concentration is less than the bottom water concentration this can lead to a flux into the bed.

Modelling approach

A model setup was created for each of the three sites. The setups were different in terms of water depth, geographic location (Coriolis parameter), sea-bed porosity, atmospheric forcing (from the appropriate locations in the GCM output), and initial conditions for nutrient concentrations. The latter were tuned to ensure that each setup had the appropriate total nutrient content for the site it represented such that after spinup the winter nutrient concentrations compared with the observations. Salinity was set to a constant value representing average conditions at the sites. All other model settings, such as those for physical and biological parameterisations, were the same. No lateral restoration of vertical profiles was included.

Model runs were undertaken covering the period 1958–2098. To separate genuine effects of climate change from changes due to potential long-term

equilibration of the model, reference runs were also carried out with three subsequent repetitions of the last 30 years (1978–2008) of the current climate atmospheric forcing extended into the future (i.e. a forcing data set with no climate change present). Model results were analysed in terms of 30-year moving averages and 30-year averaged, 30-day moving averaged seasonal cycles for the periods 2009–2038, 2039–2068 and 2069–2098, resulting in climatological time series of relevant variables. Changes in ecosystem dynamics as a response to climate change and trawling were analysed, in particular in relation to primary production, benthic–pelagic coupling (nutrient fluxes from bed to water column) and sea-bed integrity (seabed state and processes).

Results

Model confirmation

The model results compared most favourably with the observations (bias within 10 %, Tables 2, 3, 4) for (i) surface chlorophyll concentrations at the Oyster Grounds (slight under-estimate), (ii) surface and bottom temperature (slight under-estimate of typically 1 °C), (iii) near-bed ammonium at the site in the southern Bight (slight underestimate), (iv) near-bed silicate at the Oyster Grounds (slight underestimate), (v) near-bed oxygen at the site in the southern Bight

Table 2 Model confirmation results for SmartBuoy surface observations

Variable	Code	Units	Site	Number obs.	RMS difference	Model bias (%)
Chlorophylla	Chla	mg Chl/m^3	OG	500	1.22	−4.9
			ND	278	0.84	−43.9
Suspended sediment	ESS	mg/m^3	OG	624	1529.03	−30.1
			ND	379	805.09	−10.4
Temperature	temp	Celsius	OG	743	0.77	−1.9
			ND	568	0.61	0.4

No surface observations were available for the site in the southern Bight

OG Oyster Grounds, ND site north of the Dogger Bank

Table 3 Model confirmation results for bottom lander observations

Variable	Code	Units	Site	Number obs.	RMS difference	Model bias (%)
Chlorophylla	Chla	mg Chl/m ³	SB	162	2.34	−74.6
			OG	284	1.65	11.3
			ND	468	1.45	62
Suspended sediment	ESS	mg/m ³	SB	220	51480.28	−69
			OG	349	56178	−69.6
			ND	492	10929.97	17
Temperature	temp	Celsius	SB	363	0.91	0.6
			OG	475	0.96	−3.6
			ND	567	0.54	−3.9

SB site in the southern Bight, *OG* Oyster Grounds, *ND* site north of the Dogger Bank

(slight underestimate), and (vi) benthic predators at the Oyster Grounds (slight underestimate).

The model results were of a different order of magnitude compared with the observations (bias >1000 % over-estimate, Tables 2, 3, 4) for ammonium in the anoxic layer (aRPD) at all sites and for suspension feeders at the site in the southern Bight. Similarly, under-estimates exceeding −90 % occurred for omnivorous mesozooplankton the site in the southern Bight and the site north of the Dogger Bank, and particulate organic carbon and deposit feeders at the site north of the Dogger Bank.

The model results over-estimated the observations substantially (bias >100 %, Tables 2, 3, 4) for (i) near-bed ammonium at the Oyster Grounds and the site north of the Dogger Bank (up to 200 %), (ii) near-bed phosphate at the Oyster Grounds (135 %), (iii) denitrification layer depth at the site north of the Dogger Bank (288 %), (iv) ammonium in the denitrification layer at all sites (up to 550 %) and (v) the flux of nitrate at the bottom at all sites (up to 125 %). Similarly, substantial under-estimates (<−50 %) occurred for (i) near-bed chlorophyll concentrations at the site in the southern Bight, (ii) near-bed suspended sediment concentrations at the site in the southern Bight and the Oyster Grounds, (iii) near-bed nitrate concentrations and oxygen penetration depth at the site in the southern Bight, (iv) reduction equivalents (mmol S^{2−}/m²) in the oxic layer, ammonium in the oxic layer, labile organic carbon, epibenthos and suspension feeders at the site north of the Dogger Bank, (v) deposit feeders at the site in the southern Bight and the Oyster Grounds, and (vi) total benthic oxic respiration and denitrification flux at all sites.

For all other variables, the bias was in the range of 10–100 % over-estimate or −10 to −50 % under-estimate (Tables 2, 3, 4), i.e. within a factor of 2 of the observed values.

Graphical representation of e.g. surface chlorophyll concentration (Fig. 4) illustrates that within these statistics, further qualification is possible, e.g. good spring bloom and summer concentrations, but under-estimating winter concentrations, and a late start of the spring bloom at the site north of the Dogger Bank. Similarly, example profiles of nitrate at the stratified sites after the spring bloom and the onset of stratification (Fig. 5) show a good representation of the nutrient depletion in the surface-mixed layer, as well as of the depth of stratification, but model results over-estimated concentrations in the bottom mixed layer at the site north of the Dogger Bank. Example time series of variables that were sampled during the cruises (Fig. 6) illustrate the often substantial uncertainty in the observations (not taken into account in the RMS error and the bias calculations), and the sparsity of the observations compared with the potential time dependence suggested by the model results.

Carbon budgets for 2007

Annual average standing stocks, fluxes and residence times of carbon from the model confirmation run with ECMWF forcing for 2007 were calculated for the main functional compartments (phytoplankton, zooplankton, detritus, bacteria, benthos, etc.) in the model, and compared with available values derived from the field observations (Table 5). Model results were within the observational error for phytoplankton,

Table 4 Model confirmation results for data from the cruise programme

Variable	Code	Units	Site	Number obs.	RMS difference	Model bias (%)
Nitrate	N3n	mmol N/m ³	SB	5	4.95	−59.8
			OG	5	4.51	75.1
			ND	5	5.22	65.4
Ammonium	N4n	mmol N/m ³	SB	5	0.39	−1.2
			OG	5	1.16	207.8
			ND	5	0.72	155.5
Phosphate	N1p	mmol P/m ³	SB	5	0.39	23.5
			OG	5	0.73	135
			ND	5	0.65	40.1
Silicate	N5s	mmol Si/m ³	SB	5	4.32	73.3
			OG	5	1.68	−3.9
			ND	5	3.09	69.2
Omnivorous mesozooplankton	Z4c	mg C/m ³	SB	5	34.56	−91.3
			OG	5	12.02	−79.9
			ND	5	25.71	−99.5
Oxygen	O2o	mmol O ₂ /m ³	SB	5	27.82	−5.1
			OG	5	46.37	−13.9
			ND	5	75.02	−21.9
Temperature	ETW	C	SB	5	1	−1.4
			OG	5	1.36	−7.9
			ND	5	0.27	−3.1
Oxygen penetration depth	D1m	m	SB	4	0.04	−75.9
			OG	5	0	40.5
			ND	5	0.01	97.7
Denitrification layer depth	D2m	m	SB	1	0.02	53.6
			OG	5	0.02	47.8
			ND	5	0.06	287.6
Reduction equivalents in oxic layer	K6r	mmol S [−] /m ²	SB	5	0.98	32.8
			OG	5	0.79	−36.2
			ND	5	0.99	−71.7
Ammonium in anoxic layer	K24n	mmol N/m ²	SB	2	21.26	4166.4
			OG	4	46.29	5348.7
			ND	2	11.84	1478.3
Ammonium in denitrification layer	K14n	mmol N/m ²	SB	4	2.04	546.2
			OG	4	3.43	297.6
			ND	2	1.63	249.3
Ammonium in oxic layer	K4n	mmol N/m ²	SB	4	0.18	−21.6
			OG	4	0.43	−39
			ND	2	1.09	−70.8
Labile organic carbon	Q1c	mg C/m ²	SB	5	1.09	56.7
			OG	5	3.41	−33.1
			ND	5	2.6	−64
Particulate organic carbon	Q6c	mg C/m ²	SB	5	5190.8	35.3
			OG	5	15164.32	−48.9
			ND	5	47911.74	−93.7

Table 4 continued

Variable	Code	Units	Site	Number obs.	RMS difference	Model bias (%)
Epibenthos	Y1c	mg C/m ²	SB	5	151.53	39.4
			OG	5	96.72	61.1
			ND	5	97.95	−57.6
Deposit feeders	Y2c	mg C/m ²	SB	5	1086.87	−84.6
			OG	5	985.43	−79.7
			ND	5	719.77	−92.7
Suspension feeders	Y3c	mg C/m ²	SB	5	1873.72	1653
			OG	5	458.48	−13.4
			ND	5	2723.16	−51.3
Benthic predators	Y5c	mg C/m ²	SB	5	50.32	−38.9
			OG	5	52.07	−7.9
			ND	5	220.1	−87
Total benthic oxic respiration	rrBTo	mmol O ₂ /m ² /day	SB	4	5.73	−68.1
			OG	5	8.65	−80.1
			ND	5	5.46	−89.2
Denitrification flux	jK3G4n	mmol/m ² /day	SB	4	0.12	−88
			OG	5	0.35	−82
			ND	5	0.19	−83.6
Flux of ammonium at bottom	jbotN4n	mmol N/m ² /day	SB	1	0.11	124
			OG	1	0.21	565
			ND	1	0.01	−13.9
Flux of nitrate at bottom	jbotN3n	mmol N/m ² /day	SB	4	0.09	−104
			OG	4	0.11	−105.6
			ND	4	0.1	−125.2

SB site in the southern Bight, *OG* Oyster Grounds, *ND* site north of the Dogger Bank

zooplankton and zoobenthos. Model values for benthic dissolved organic carbon and detritus were too low at the Oyster Grounds and north of the Dogger Bank sites. Fluxes were generally high compared to standing stocks, indicating high turnover rates with typical residence times of up to a few days. The exceptions at all sites were zoobenthos and pelagic and benthic detritus, all of which had residence times ranging from a month to almost a year.

Climate change

The largest effects of climate change seen in the model run (Fig. 7) were (1) an increase in surface and bottom water temperature, (2) an increase in gross primary production, (3) a decrease in zoobenthos biomass and (4) a reduction in near-bed oxygen levels. Other state variables showed relatively little response. Carbon budgets were derived for climate change conditions as

in Table 5, and directions of change compared to present-day conditions were derived (Table 6). The carbon fluxes through the main sets of functional groups in the pelagic system increased, while the changes in the benthic fluxes were site-dependent, with the site north of the Dogger Bank showing a decrease, the Oyster Grounds an increase, and the site in the southern Bight very little change.

Trawling

Given the assumption that the bed is trawled once per year (an upper bound), changes to variables directly affected by trawling were quite large. For example, compared to the climate-only run an additional 25.8 % decline in epibenthos was predicted by 2098 at the site north of the Dogger Bank, with similar results at the other sites (Table 7). The effects on nutrient fluxes could also be rather substantial (Fig. 8). Thus at the

Fig. 4 Chlorophyll concentration at surface. *Lines* model results, *crosses* observations from fluorometer on surface SmartBuoy. Surface observations were not available at the site in the southern Bight

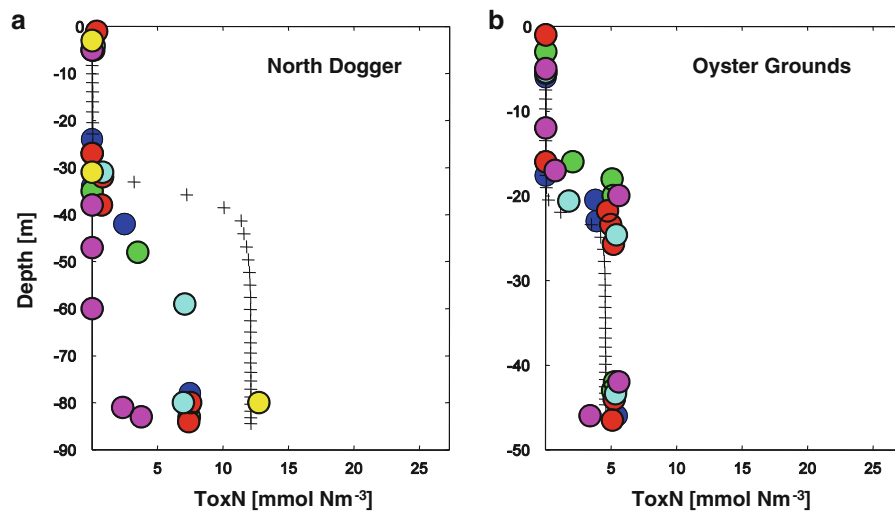
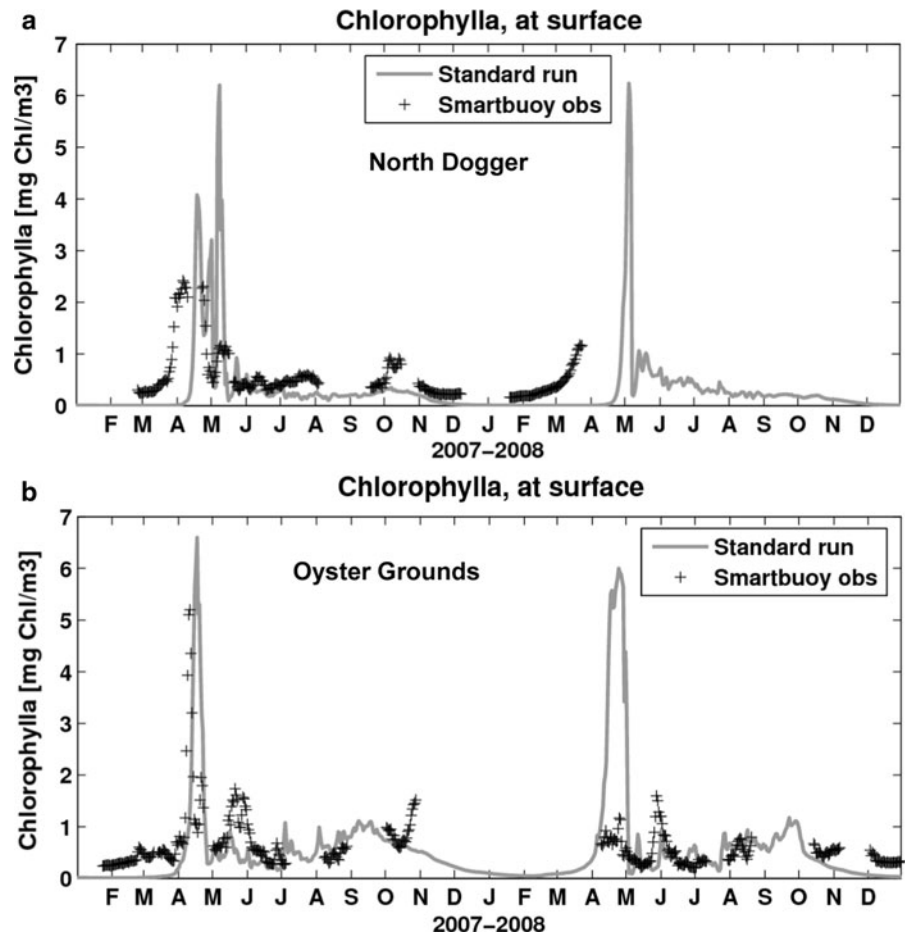


Fig. 5 Vertical profiles of nitrate from water samples for stratified conditions, May 2007, **a** site north of the Dogger Bank, **b** Oyster Grounds. Crosses: model results. *Coloured dots* water samples, each colour indicates results from a separate CTD cast

taken within a period of 1–2 days. The site in the southern Bight does not stratify, and nitrate concentrations were near zero throughout the water column in both the model and the observations

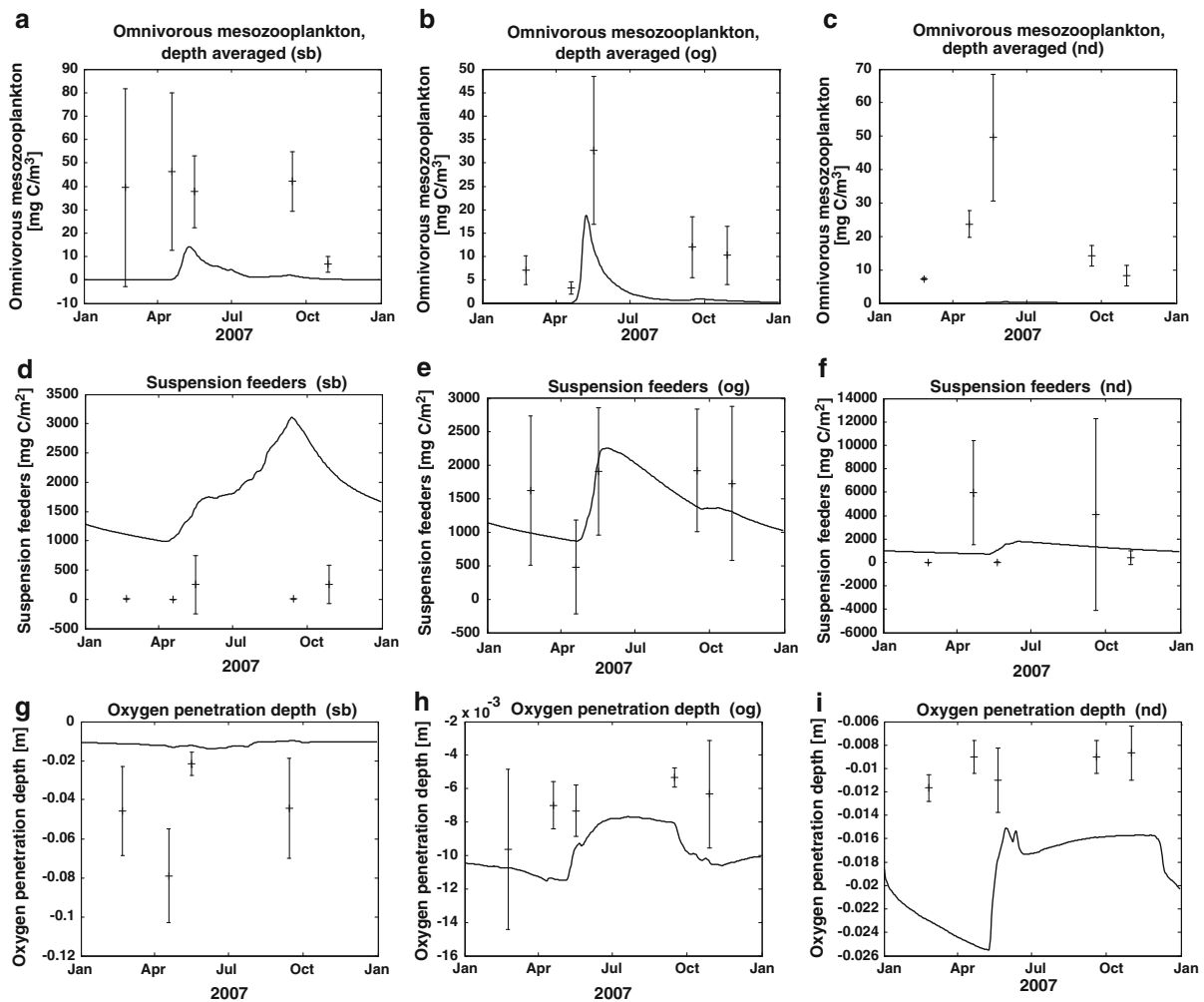


Fig. 6 Comparison of model results with samples for 2007. **a, c, e** Oyster Grounds, **b, d, f** site north of the Dogger Bank. **a, b** Zooplankton biomass. Model results for the omnivorous mesozooplankton functional group for 2007 (*line*), and observations derived from vertical net hauls. Biomass was measured

using a chitin assay. **(c, d)** Suspension feeder biomass. Model results for 2007 (*line*), and observations derived from NIOZ core samples. **(e, f)** Oxygen penetration depth. Model results for 2007 (*line*), and observations derived from oxygen microelectrode profiles

site north of the Dogger Bank a 13.2 % reduction (2069–2098 average) in benthic silicate flux out of the bed due to climate forcing became a 25.6 % reduction when trawling was included (Table 7) and a 19.1 % climate reduction in phosphorous flux at the same site became a 35.6 % reduction with trawling. More representative, however, were the 5.4 % increase in average ammonium flux at the Oyster Grounds, and 5.5 % decrease of phosphorous flux to the bed at the site in the southern Bight. Generally the relative change to the nutrient flux due to trawling was less than 10 % (Table 7). Noteworthy was the change to

the nitrate flux at the Oyster Grounds and the site in the southern Bight where trawling was predicted to reverse the average net flux from out of the bed to one directed into the bed. A large decrease in the nitrification flux was predicted at these two sites (20 % at the Oyster Grounds, 40 % at the site in the Southern Bight). Changes to fluxes and variables other than those directly affected by trawling were found to be small. A sensitivity analysis (results not shown here) indicated that variables that showed a clearly discernable trawling impact scaled approximately linearly with the applied fishing intensity, and that seasonality

Table 5 Budgets, gross fluxes and residence times of carbon for the main pools in the pelagic and benthic systems for the three sites for the validation run for 2007

	Southern Bight			Oyster Grounds			North Dogger		
	Standing stock (gC/m ²)	Annual flux (gC/m ² /year)	Residence time (day)	Standing stock (gC/m ²)	Annual flux (gC/m ² /year)	Residence time (day)	Standing stock (gC/m ²)	Annual flux (gC/m ² /year)	Residence time (day)
Phyto-plankton	0.83 (2.9 ± 2.7)	261	1.2	1.1 (2.5 ± 1.3)	208.5	1.9	0.47 (1.7 ± 1.3)	162	1.1
Zoo-plankton	0.2 (1.0 ± 0.5)	92	0.8	0.36 (0.6 ± 0.5)	101.5	1.3	0.22 (1.6 ± 1.6)	82	1.0
Bacteria	0.21	178	0.4	0.29	105.0	1.0	0.24	103	0.9
Pelagic dissolved organic carbon and detritus	16.6	201	30.2	10.4	129.5	29.3	9.4	106	32.5
Zoo-benthos	2.0 (1 ± 1)	12	63.5	2 (3 ± 1)	13.0	56.4	1.3 (1.0 ± 0.2)	3	137.5
Benthic bacteria	0.08	16	1.8	0.12	24.0	1.8	0.046	5	3.7
Benthic dissolved organic carbon and detritus	15 (10 ± 4)	18	303.4	16 (29 ± 3)	25.2	232.2	3.3 (51 ± 1)	4	273.8
Pelagic to benthic flux (in/out)		20 17			23.5 21			4.6 4.8	

Values between brackets were derived from the field observations at each of the sites for 2007

in trawling had only a minor effect with a tendency for a slightly higher benthic mortality when all fishing effort occurred in summer (e.g. a 45 vs. a 38 % decrease in suspension feeder biomass at the site north of Dogger Bank for summer and winter trawling respectively).

Discussion and conclusions

Model confirmation

Compared with observations, the model performed least well for the sandy site in the southern Bight. One reason for this was the relatively poor representation of benthic processes for sandy substrates, in particular the advective exchange of pore water with the overlying water, which was not included in the model. These physical processes cannot be accounted for by increasing porosity alone, as was attempted here. The model performed reasonably well for the site north of the Dogger Bank, and at the Oyster Grounds, although the organic matter supply or incorporation into the bed by macrofauna was too low. This led to over-estimation of the oxygen penetration depth and apparent redox potential depth, low particulate organic carbon levels, lowoxic respiration, and increased rates of nutrient turnover.

For most of the variables for which observations were available, model results were of the right order of magnitude. Exceptions were: ammonium in the anoxic layer, suspension feeders at the site in the southern Bight, omnivorous mesozooplankton at the site in the southern Bight and the site north of the Dogger Bank, and particulate organic carbon and deposit feeders at the site north of the Dogger Bank. These are obvious candidates for improvement. For many variables, observed values were reproduced within a factor of two. As such, the model setups were considered suitable to carry out climate change and trawling simulations, and to investigate the effects of changes in model forcing, if not in an absolute, then at least in a relative sense.

Carbon budgets for 2007

At all sites there were small living pools of carbon and big pools of detritus, in both the pelagic and benthic systems (Table 5). Living pools had lower residence

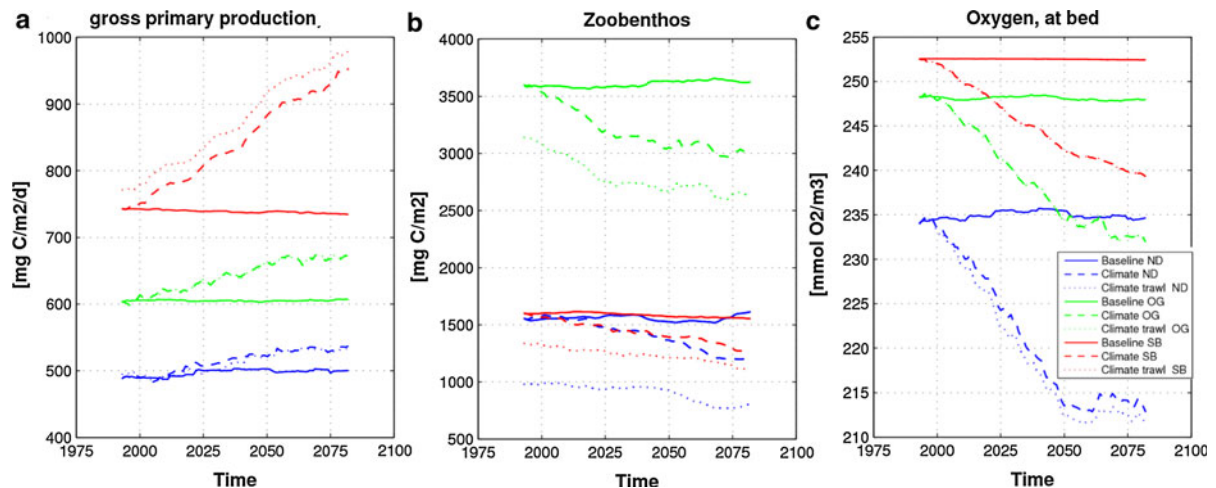


Fig. 7 Thirty-year moving averages for the three sites (*colours*), for the base-line run without climate change (*solid line*), for the climate-change run (*dashed line*), and for combined

climate change and trawling (*dotted line*). **a** Gross primary production, **b** zoobenthos biomass, and **c** near-bed oxygen concentration

Table 6 Schematic generalisation of the effects of climate change and trawling on carbon biomasses and carbon fluxes averaged over the last 30 years of the projections, and compared with present-day climate

Site	Pelagic stock		Pelagic fluxes		Benthic stock		Benthic fluxes		Benthic–pelagic fluxes	
	Climate	Trawling	Climate	Trawling	Climate	Trawling	Climate	Trawling	Climate	Trawling
ND	0	0	+	0	–	–	–	±	–	–
OG	0	0	+	0	–	–	+	±	+	0
SB	0	0	+	+	–	–	0	0	0	0

0: limited change; +: increase; –: decrease; ±: variable

SB site in the southern Bight, OG Oyster Grounds, ND site north of the Dogger Bank

times than detrital pools, and pelagic pools had lower residence times than their benthic equivalents. This was illustrated by the comparative residence times of carbon within living pools which ranged from days for bacteria, phytoplankton and zooplankton up to several months for zoobenthos.

Detrital particulate pools in the bed turned over much more slowly with residence times of 230–300 days. The sites in the southern Bight and the Oyster Grounds had faster detrital carbon turnover due to increased aerobic processes, temperature and biological processes.

Carbon budgets at the Oyster Grounds and the site in the southern Bight budgets were largely similar, as would be expected from the observations, but the model over-predicts the detrital pool at the site in the southern Bight due to the omission of advective bed processes. In reality, carbon turnover at this site is

much faster than in the model as it is mediated by advective aerobic bacterial processes, resulting in a smaller detrital pool than in the model.

The modelled supply of detritus to the bed is likely to be too low for both the Oyster Grounds and the site north of the Dogger Bank, which resulted in under-predicted benthic detritus concentrations (Table 5) and over-predicted anoxic layer depth (denitrification layer depth in the model) (Table 4). This is particularly evident at the site north of the Dogger Bank, where zoobenthos biomass is lower and anoxic layer depth deeper. During this work, observations have illustrated the significance of the surface deposit feeders and other active bioturbators in moving carbon from the sediment water interface into the bed, often on timescales of days (Teal 2009). The model is as yet unable to reproduce this process and this is likely to be the reason for the lack of benthic detritus in the bed,

Table 7 Relative change in quantity. Model results from the climate and climate + trawling runs, averaged over the last 30 years of the projections (2069–2098), compared with the reference run. For fluxes, the direction is out of the bed unless stated otherwise

Quantity	Site	Climate (2069–2098)— reference	Climate + trawling— reference	Difference (i.e. only trawling change)
Epibenthos	ND	−28.1 %	−53.9 %	−25.8 %
	OG	−18.3 %	−33.4 %	−15.1 %
	SB	−15.1 %	−31.3 %	−16.2 %
Deposit feeders	ND	−22.5 %	−24.4 %	−1.9 %
	OG	−7.1 %	−5.8 %	1.3 %
	SB	−2.4 %	−7.1 %	−4.7 %
Suspension feeders	ND	−25.3 %	−53 %	−27.7 %
	OG	−20.8 %	−33.3 %	−12.5 %
	SB	−21.7 %	−32.2 %	−10.5 %
Meiofuana	ND	−12.7 %	−12.7 %	0 %
	OG	−12.4 %	−8.3 %	4.1 %
	SB	−21 %	−20.6 %	0.4 %
Infaunal predators	ND	−23.5 %	−26.7 %	−3.2 %
	OG	−7.4 %	−6.6 %	0.8 %
	SB	−3.3 %	−9.3 %	−5 %
Benthic–pelagic P flux	ND	−19.1 %	−35.6 %	−17.4 %
	OG	1.1 %	0.0 %	−1.1 %
	SB	−4.4 %	−9.9 %	−5.5 %
Benthic–pelagic NO ₃ flux	ND	53 % (into bed)	136 % (into bed)	83 %
	OG	−6.7 %	−179 % (into bed)	−172 %
	SB	−85 %	−193 % (into bed)	−108 %
Benthic–pelagic NH ₄ flux	ND	−9.4 %	−14.6 %	−5.2 %
	OG	6.8 %	12.2 %	5.4 %
	SB	3.6 %	4.3 %	0.7 %
Benthic–pelagic Si flux	ND	−13.2 %	−25.6 %	−12.4 %
	OG	17.2 %	20.5 %	3.3 %
	SB	−3.0 %	−3.5 %	−0.5 %
O ₂ (bottom)	ND	−9.4 %	−9.9 %	−0.5 %
	OG	−6.5 %	−6.5 %	0.0 %
	SB	−5.3 %	−5.3 %	0.0 %
Oxygen penetration depth	ND	5.6 %	10.2 %	4.6 %
	OG	−1.1 %	3.7 %	4.8 %
	SB	1.1 %	7.7 %	6.6 %
Denitrification depth	ND	9.6 %	4.3 %	−5.30 %
	OG	4.4 %	4.6 %	0.2 %
	SB	4.4 %	4.9 %	0.3 %
Gross PP	ND	7.7 %	6.9 %	0.8 %
	OG	10.2 %	10.4 %	0.2 %
	SB	30.3 %	33.8 %	3.5 %

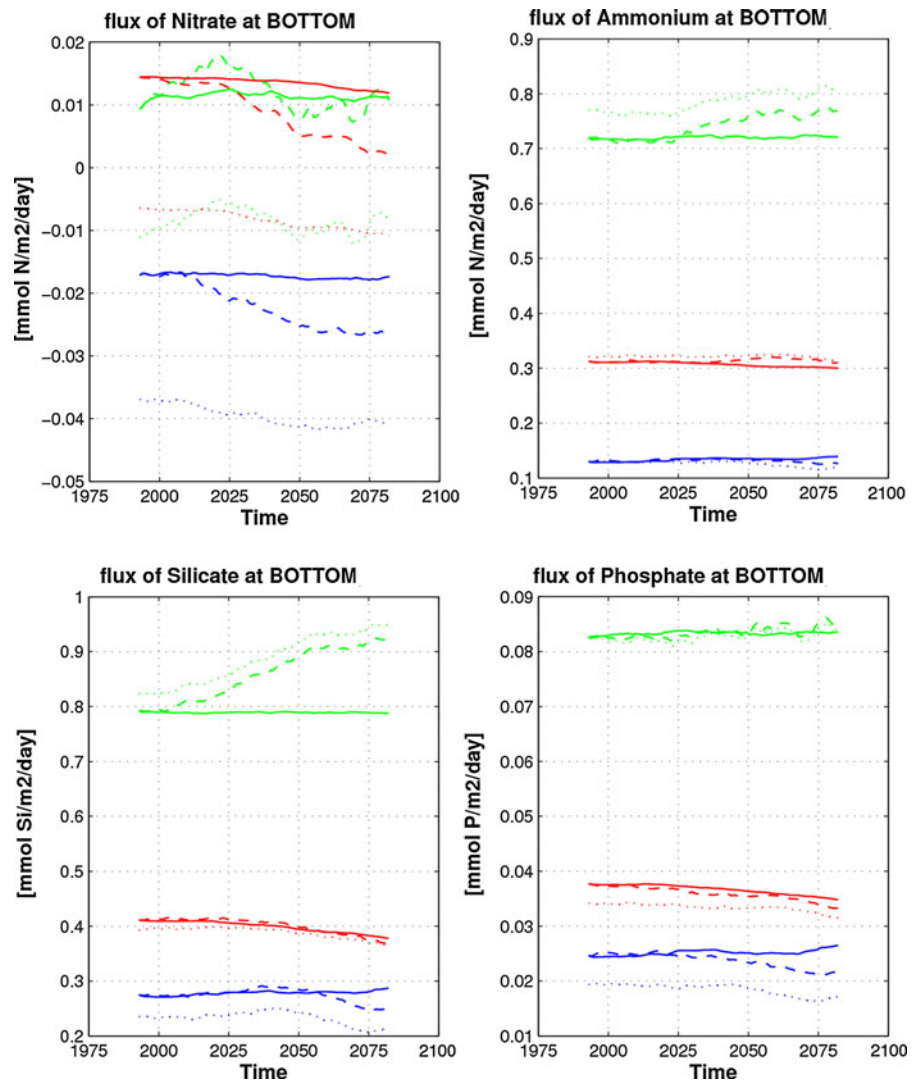
Table 7 continued

Quantity	Site	Climate (2069–2098)— reference	Climate + trawling— reference	Difference (i.e. only trawling change)
Net PP	ND	5.1 %	3.4 %	−1.7 %
	OG	10.0 %	10.1 %	0.1 %
	SB	26.2 %	29.3 %	3.1 %

Unless stated differently, the quantities refer to carbon content

SB site in the southern Bight, *OG* Oyster Grounds, *ND* site north of the Dogger Bank

Fig. 8 Thirty-year moving averaged benthic–pelagic nutrient fluxes for the three sites for the ambient, climate change and trawling scenarios. Positive fluxes are from the benthos to the pelagic



which has an impact on anoxic layer depth and respiration rates. In reality, these sites (especially the site north of the Dogger Bank) are not carbon limited

(Neubacher 2009), so respiration processes do not utilise all the carbon available to them within a year. Hence, unless carbon is removed by horizontal

transport processes, the sites act as effective carbon stores (North Dogger > Oyster Grounds > Southern Bight) as reflected by the detrital pools at each site (50, 30 and 10 g C m⁻², Table 5).

As a result of the low rate at which detritus is incorporated in the sea bed, substantial amounts remain in the pelagic system, where they are turned over much more quickly, leading to high summer nutrient concentrations in the bottom mixed layer, which contributed to the positive model bias for near-bed nutrients (Table 4).

Climate change

The reduction in near-bed oxygen concentrations with climate change forcing (Fig. 7) must be due to a combination of changes in the balance of production and consumption, changes in vertical mixing and changes in solubility. The detailed mechanisms were not investigated as part of this study.

The increased pelagic carbon fluxes in the model (Table 6) are associated with the average increase in water temperature, which is a strong driver of biogeochemical metabolic processes, and is explicitly expressed in the model formulations.

Understanding the increase in primary production with climate change also requires a consideration of the seasonal variations. Thirty-year average seasonal signals were computed for key model variables for the four adjacent 30-year periods in the simulation. At the site north of the Dogger Bank and at the Oyster Grounds, the start of the growing season as seen from the gross primary production occurred earlier with climate change (Figs. 9, 10), while the remainder of the season showed relatively little change, thus increasing total growth. The earlier start of growth was mainly due to lower wind speeds leading to reduced SPM concentrations in early spring, at the start of the spring bloom. On the other hand, at the site in the southern Bight (Fig. 11), the length of the growing season did not show a change with climate because the start of the spring bloom coincided with a period of minor changes in wind conditions. However, the gross primary production during the growing season was larger, in part corresponding to episodic reductions in SPM concentrations during the summer.

Reductions in zoobenthos biomass were related to reduced, temperature-related metabolic efficiency of the filter feeders, and slightly reduced food availability

(in particular diatoms). The mechanisms for the reductions in food availability were different at each site. At the site north of the Dogger Bank, near-bed diatom concentrations reduced with climate change, mainly because of an increase in the duration of grazing by zooplankton during the spring bloom (Fig. 10). A similar but less well understood reduction in diatom concentrations occurred at the site in the southern Bight (Fig. 11). At the Oyster Grounds (Fig. 9), part of the spring bloom occurred before the onset of stratification (determined from the temperature graphs as the point where the surface and bottom temperature start to diverge), which, through a combination of biological processes, is the trigger for diatom sinking to the sea bed. The spring bloom occurred earlier with climate change, but the onset of stratification remained more or less the same, reducing the proportion of the diatoms that reached the bed and acted as food for filter feeders.

It is note-worthy that the ecosystem variables in the model contained different levels of the variability present in the climate forcing scenario. This was evident both in the seasonally averaged results (Figs. 7, 8) and in the climate-averaged seasonal cycles (Figs. 9, 10, 11). These differences in variability could be caused by a combination of differences in response time, or by specific sensitivity to climate variables with a different level of inherent variability (e.g. temperature versus wind). This topic should be investigated further, and is relevant to the definition of, results for, and interpretation of marine indicators of climate change.

There is substantial uncertainty in the model response related to seasonality of the wind climate, mainly because future projections of the wind climate are more difficult to achieve by atmospheric circulation models than projections of temperature change. Moreover, the mechanism by which the wind climate influences the ecosystem model results includes calculation of suspended sediment concentrations, which also had a fairly large degree of uncertainty.

In summary, the following general picture presents itself of the system's response to climate change. With climate change, increased water temperature led to higher metabolic and biogeochemical rates. Hence, more material was recycled in the pelagic system. As the model system was closed in terms of nutrients, the same, growth limiting amount of nutrients was available for primary production, so the increase in

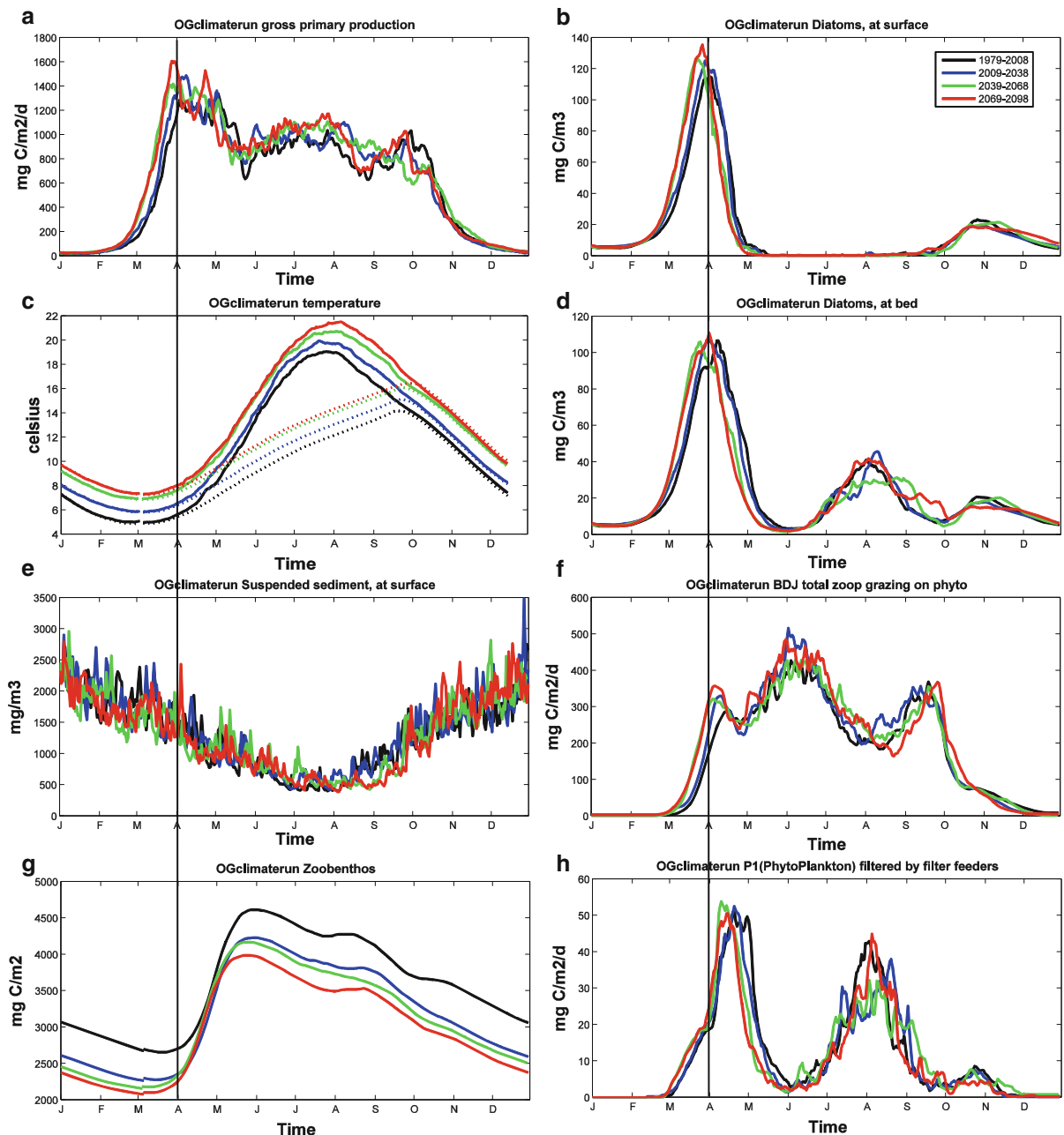


Fig. 9 Thirty-year average seasonal cycles for the four time slices at the Oyster Grounds for **a** gross primary production, **b** surface diatom concentration, **c** surface (solid lines) and bottom (dashed lines) temperature, **d** bed diatom concentration,

e surface suspended sediment concentration, **f** zooplankton grazing on phytoplankton, **g** zoobenthos biomass and **h** phytoplankton ingested by filter feeders

production was fuelled by nutrients recycled within the growing season. This increased pelagic recycling led to (slightly) reduced food supply to the benthic system, leading to reduced zoobenthos biomass. A

further reduction in biomass was related to an increased food requirement due to the temperature driven increase in metabolic rates. As a result, the system was more pelagic oriented than at present, in

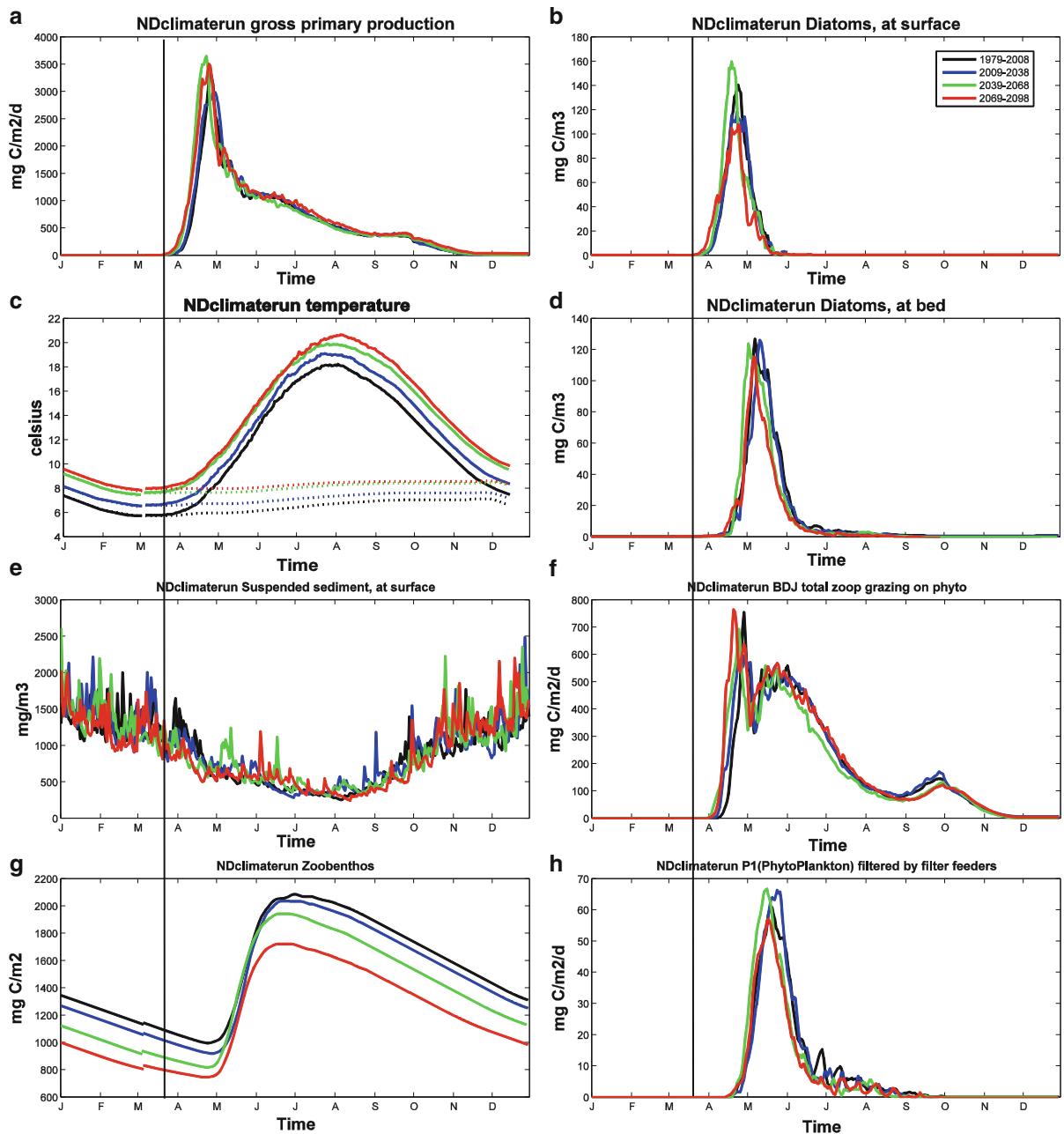


Fig. 10 Thirty-year average seasonal cycles for the four time slices at the site north of the Dogger Bank for **a** gross primary production, **b** surface diatom concentration, **c** surface (*solid lines*) and bottom (*dashed lines*) temperature, **d** bed diatom

concentration, **e** surface suspended sediment concentration, **f** zooplankton grazing on phytoplankton, **g** zoobenthos biomass and **h** phytoplankton ingested by filter feeders

terms of both biomass and relative biogeochemical fluxes.

Climate models have considerable uncertainty associated with the results, so ideally, an ensemble of a number of regional models downscaled from

different global models should be used as forcing for the ecosystem model (e.g., Meier et al. 2006). However, such an approach requires a major (international) effort, which was far beyond the resource available for the present study. Having said that, the

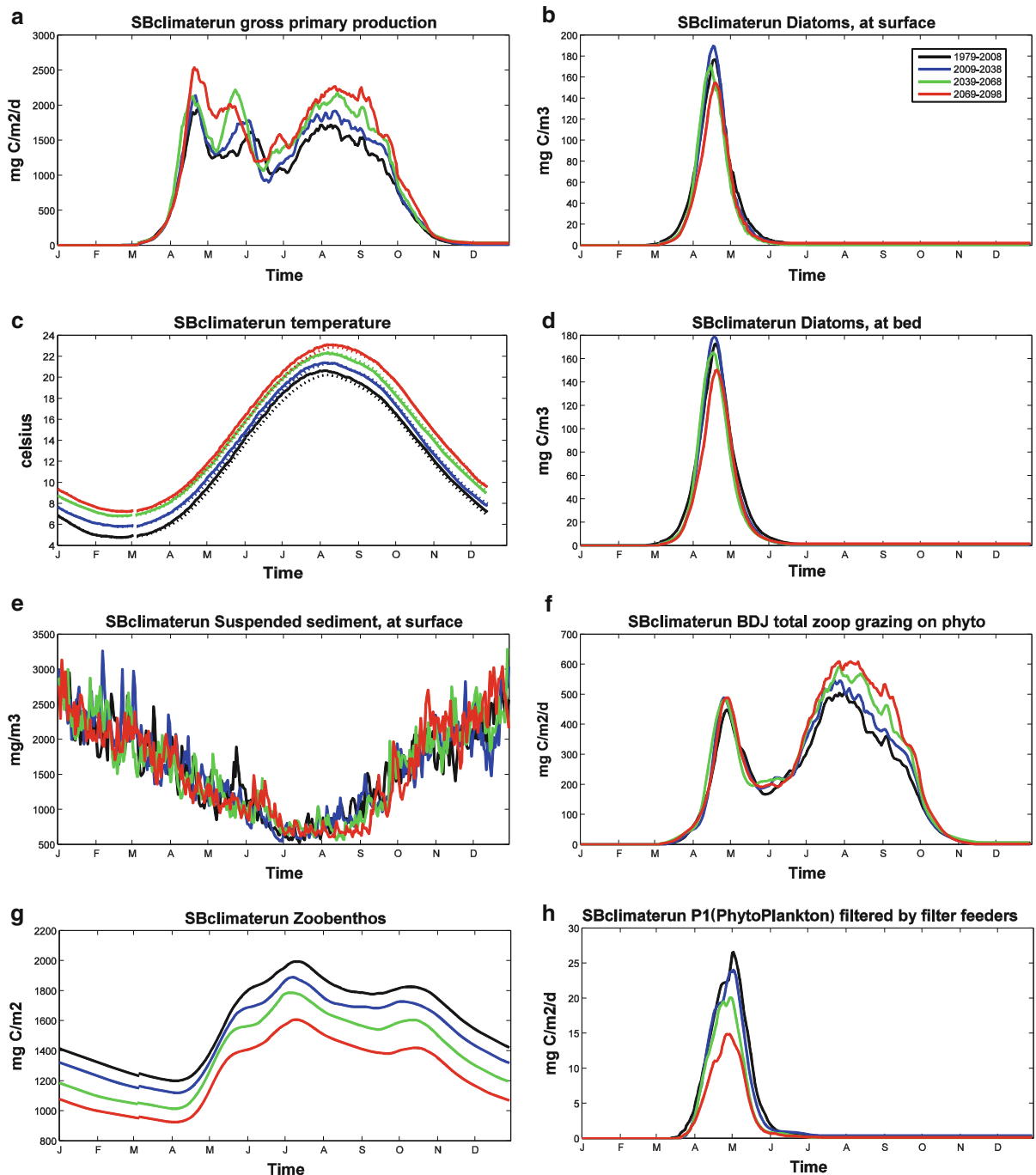


Fig. 11 Thirty-year average seasonal cycles for the four time slices at the site in the Southern Bight for **a** gross primary production, **b** surface diatom concentration, **c** surface (*solid lines*) and bottom (*dashed lines*) temperature, **d** bed diatom

concentration, **e** surface suspended sediment concentration, **f** zooplankton grazing on phytoplankton, **g** zoobenthos biomass and **h** phytoplankton ingested by filter feeders

increase in air temperature in the HadRM3-PPE-UK model is a robust result, which is in line with observations, and shared with other climate models

(e.g., IPCC 2007), if not in magnitude then in the very least in direction. This temperature increase is by far the largest climate effect evident in the results, and is

the dominant factor determining changes in the results of the ecosystem model, lending credibility to the results presented here. A similar argument cannot be made for the changes in the wind climatology (to which the ecosystem model results at Oyster Grounds were sensitive through changes in the SPM concentrations), so these results need to be treated with caution, and should be investigated further.

Trawling

Trawling had the obvious direct effect of decreasing benthic biomass through enhanced mortality. For some benthic groups, however, the effect was offset by the greater quantities of detritus available due to mortality of other groups. Thus, deposit feeder biomass at the Oyster Grounds increased slightly (especially under summer trawling scenarios) and only small decreases were seen at the other sites for this functional group. Overall there was a reduction in the total amount of food entering the benthic system because trawling strongly impacted filter feeders, one of the main food pathways into the benthos. A corresponding increase in water column diatom biomass occurred because of less grazing pressure due to reduced filter feeder biomass. The interplay of these effects led to a range of site-dependent outcomes for how the balance of organisms responded to trawling pressure. Overall, a general shift in favour of the pelagic system was predicted due to demersal trawling. A similar trend was noted in the modelling study of Petihakis et al. (2007). As discussed in the previous section, climate change is predicted to lead independently to a similar shift in productivity away from the benthic system.

On balance, trawling during the summer months had a slightly greater impact, especially on benthic biomass, than annual or winter trawling. This is not unexpected as benthic biomass is greatest at this time so the absolute value of trawling induced mortality and associated feedbacks will be greatest. However, the effect was not uniform between sites and benthic groups. The model does not take account of complex species specific behaviour, or size. Hence, work is required, using a more realistic model of benthic organisms and a more realistic incorporation of trawling impacts, to see if the results concerning seasonality of trawling hold generally.

It should be noted that the way denitrification is handled in this set of model runs may play a role in the model response. In order to close the system, the denitrification flux is returned immediately to the water column to prevent a run-down in nitrogen over time. However, this has the effect of making the model less sensitive to the effect of a reduced denitrification flux. We believe this effect will be small, but nevertheless it represents a limitation in using a closed 1D water column model. Three dimensional modelling with realistic boundary and nutrient inputs would remove this limitation. In general, the model simulation greatly underestimated denitrification flux, being on average only 15 % of the observed values (Table 4). Nevertheless, the relative changes due to the effect of trawling are of interest. The change in direction of the nitrate flux to one directed into the bed at the Oyster Grounds and the site in the Southern Bight was linked to the increased ammonium flux out of the bed due to trawling. Increased ammonium flux to the water column decreases the amount available for benthic nitrate production. The resulting decrease in nitrate pore water concentration in the model was sufficient to make it, on average, smaller than the bottom water and hence reverse the net flux direction. One important consequence of this appeared to be the large decrease in the denitrification flux predicted at the two sites (20 % at the Oyster Grounds, 40 % at the site in the Southern Bight) as less benthic nitrate was available for denitrification. Demersal trawling was thus predicted to cause a reduction in nitrogen removal and an increase in bio-available ammonium. At the large scale, demersal trawling may therefore have a negative impact on natural processes that remove nitrogen and hence on eutrophication related issues.

It is perhaps surprising that the changes in benthic–pelagic fluxes were predicted to have such a small effect on primary productivity (gross and net). First it should be noted that enhanced benthic mortality and enhanced benthic flux were often found to operate in opposite directions leading to a small net effect. In addition, nutrient recycling occurs in the pelagic as well as in the benthic system so the benthic flux is not the only, or even the dominant, source of regenerated nutrients. Also, at stratified sites released nutrients have to diffuse through the pycnocline or are only available after breakdown of stratification, so the effect on productivity is weakened. The largest effect on primary productivity was at the mixed site where

changes in nutrient supply can immediately affect the entire water column. More subtly, and assuming that nitrogen is the limiting nutrient, an increased ammonium flux is compensated by the decreased or even reversed nitrate flux leading to little net change in available nitrogen.

A key factor in predicting nutrient flux is the dynamics of dissolved nutrient and particle redox reactions following sediment resuspension, a process that is currently not included in the model. Increased desorption of nutrients, especially silicate, can increase the net nutrient release into the water column (Couceiro et al. 2012). The process of carbon and nutrient release by trawling, including desorption, oxidation and scavenging reactions is complex and would be need to be included to simulate the full effects of demersal trawling on benthic–pelagic nutrient exchange.

Finally, the possible interaction between climate and trawling was considered. To a good approximation, there was only a fixed relative offset between the results for trawling plus climate and those for climate only (Fig. 7). This suggests that any interaction between the two forcing mechanisms was weak and that the responses of the two impacts are approximately additive. This, in turn, suggests that climate change impacts on the benthic system might be mitigated to some extent by reducing the benthic impact of demersal trawling.

Nature and capability of the model

It is important to be aware of limitations in the methods used and in the capabilities of the model itself. Although ERSEM-BFM is one of the most complex ecosystem models currently in use, the representation of some processes is nevertheless simple and constrained by our lack of knowledge of the processes and feedbacks between processes. The field work and validation procedure carried out within this project has highlighted some of these and suggested elements for improvement: ammonium in the benthic system, advective processes in coarse sediments, omnivorous mesozooplankton, particulate organic carbon (burial, degradation, resuspension), and functional-group specific and size impacts of trawling. Also, predicted changes may be constrained by the fact that the water column model represents a closed system with respect to nutrients. Calculations

with a 3D model including horizontal transport may show additional effects.

The analysis in terms of 30 year (moving) averages is a powerful and necessary way of summarising and comprehending the overall effect of many complex interactions but may nevertheless miss important or interesting details. In particular, the increasing frequency of extreme events that leave the mean unchanged will be hidden.

A further consideration is the representation of trawling within the model. The 1D model represents a horizontally uniform region of unspecified area. Conceptually, however, it might be imagined as of the order of ten to twenty square kilometres. Trawling is acting at any one time on a small fraction of this area. The impact at the spatial scale of the trawl is clearly large. In the model, this large impact at a small spatial scale is represented by a smaller impact over a larger area. Although this correctly represents the overall levels of nutrient release and/or benthic mortality, the scale effect may mean that the model response does not capture local detail.

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