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Heterogeneity of impacts of high CO_2 on the North Western European Shelf

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Abstract. The increase in atmospheric CO_2 is a dual threat to the marine environment: from one side it drives climate change, leading to modifications in water temperature, circulation patterns and stratification intensity; on the other side it causes a decrease in marine pH (ocean acidification, or OA) due to the increase in dissolved CO_2. Assessing the combined impact of climate change and OA on marine ecosystems is a challenging task. The response of the ecosystem to a single driver can be highly variable and remains still uncertain; additionally the interaction between these can be either synergistic or antagonistic. In this work we use the coupled oceanographic–ecosystem model POLCOMS-ERSEM driven by climate forcing to study the interaction between climate change and OA. We focus in particular on carbonate chemistry, primary and secondary production. The model has been run in three different configurations in order to assess separately the impacts of climate change on net primary production and of OA on the carbonate chemistry, which have been strongly supported by scientific literature, from the impact of biological feedbacks of OA on the ecosystem, whose uncertainty still has to be well constrained. The global mean of the projected decrease of pH at the end of the century is about 0.27 pH units, but the model shows significant interaction among the drivers and high variability in the temporal and spatial response. As a result of this high variability, critical tipping point can be locally and/or temporally reached: e.g. undersaturation with respect to aragonite is projected to occur in the deeper part of the central North Sea during summer. Impacts of climate change and of OA on primary and secondary production may have similar magnitude, compensating in some area and exacerbating in others.

1 Introduction

Climate change is exerting multiple stresses on marine ecosystems. The increase of temperature modifies the marine habitat, generally encouraging migration of species towards higher latitudes (Beaugrand et al., 2002) with the possible extinction of some cold-adapted species (Hoegh-Guldberg and Bruno, 2010). Temperature further affects organism metabolism (e.g. reducing their thermal tolerance; Pörtner and Farrell, 2008), leading to multiple impacts on the ecosystem like shifts in community composition, e.g. towards smaller sizes (Perry et al., 2005; Morán et al., 2010). The warming of oceanic water will also have significant indirect effects; e.g. increasing of thermal stratification could lead to reduction of surface nutrient and primary production (Sarmiento et al., 2004; Holt et al., 2012a) and to increasing anoxia in the coastal ocean (Diaz and Rosenberg, 2008). Studying the impact of climate change on shelf seas is crucial given their high importance for the global environment – e.g. they are estimated to be a large sink of atmospheric CO_2 despite the small surface (0.4 Pg C yr^{-1}; Thomas et al., 2004)

– and on human society – e.g. up to 30–60 % of reduction in fish catches in shelf seas have been projected to be due to climate change (Blanchard et al., 2012).

At the same time, the ocean has absorbed about half of the anthropogenic emissions of CO$_2$ (Sabine et al., 2004), altering the carbonate equilibrium, thereby causing a reduction of pH and other related parameters, known as ocean acidification (OA) (Caldeira and Wickett, 2003). Several oceanic global circulation models have projected an average reduction of pH between 0.2 and 0.4 pH units by the end of the century (Orr, 2011), with the polar regions being most sensitive. Although the negative trend in large-scale integrated mean pH is defined by atmospheric pCO$_2$ (Ricke et al., 2013), there is much uncertainty regarding the intensity of the OA signal and in particular of its small-scale variability. Global models generally have a coarse spatial resolution and therefore they do not include an adequate representation of shelf and coastal sea processes; hence the uncertainty of these predictions on marginal seas is much higher. In the shelf sea environments, the OA signal can be enhanced or mitigated by many processes. Benthic processes, such as community respiration or biologically mediated redox reactions, are a significant source of dissolved inorganic carbon (DIC) and total alkalinity (TA) and have a significant impact on the carbon budget and the pH (Thomas et al., 2009; Wakelin et al., 2012). The pelagic production–respiration balance, with its effect on DIC and TA, and temperature play a key role in determining the variability of the carbonate system over both the seasonal and diurnal cycles (e.g. Takahashi et al., 2002). Finally, riverine inputs of DIC, TA and nutrients can be at least as significant in determining the carbonate chemistry of coastal areas as the increasing atmospheric pCO2 (Borges and Gypens, 2010; Artioli et al., 2012). The variability of carbonate chemistry in shelf seas and their response to OA is consequently significant; hence specialised shelf sea models are required in order to give reliable estimates of the future state of the carbonate system in these environments.

Over the last five years, the number of studies focusing on the consequences of OA on marine chemistry and in particular on the biota has exponentially increased, but results have shown a high degree of variability and sometimes inconsistency as well. The main complications are the high degree of species-specific responses and the influence of environmental heterogeneity, resource availability and life stage (e.g. Dupont et al., 2010; Melzner et al., 2011; Gobler and Talmage, 2013).

As a result a consensus and comprehensive understanding of the effects of OA on the key biological processes has yet to emerge, although a number of synthesis papers are appearing (e.g. Riebesell et al., 2011; Liu et al., 2010; Kroeker et al., 2010; Kroeker et al., 2013). In particular, even if for the projected pH change at the end of the century the impact on a single function is relatively small (Hendriks et al., 2009), the interaction between multiple affected processes or different levels of the ecosystem or multiple stressors (e.g. Pörtner, 2008) can magnify these effects.

Among all the observed impacts of OA on ecosystem processes, here we focused on the impact of OA on primary production. Riebesell and Tortell (2011) concluded that the majority of experiments investigating the link between photosynthetic rate and CO$_2$ in the water showed an increase of primary production (PP) with CO$_2$, though the null hypothesis has not been totally discarded by rigorous meta-analysis (Doney et al., 2009; Hendriks et al., 2009).

In this paper we use a coupled hydrodynamic ecosystem model to study the impact of climate change and OA on the carbonate chemistry, primary and secondary production in the North Western European Shelf. In particular we focus on assessing the temporal and spatial variability of these impacts and we will test the hypothesis that the feedbacks of OA on PP can exacerbate/hinder the changes in production and/or biomass at low trophic levels (phytoplankton and zooplankton) due to climate change.

2 Material and methods

2.1 Model and study area description

This study is focused on the eastern North Atlantic, bounded by latitude 40° N to 65° N and longitude 20° W to 13° E (Fig. 1), and in particular in the North Western European Shelf. This shelf sea is largely influenced by the exchanges with the open ocean (Gomez-Gesteira et al., 2011; Holt et al., 2009), which provides the largest source of nutrients (Vermaat et al., 2008). The coastal areas are also influenced by some large rivers (e.g. Rhine, Elbe, Thames), particularly along the margins of continental Europe.

The physical model is the Proudman Oceanographic Laboratory Coastal Ocean Modelling System (POLCOMS), a finite difference model able to resolve the fundamental hydrodynamic processes important in shelf seas. The model grid has resolution of 1 / 9° latitude and 1 / 6° longitude with 42 s levels in the vertical (Wakelin et al., 2009).

The ecosystem model coupled to POLCOMS is the European Regional Sea Ecosystem Model (ERSEM; Blackford et al., 2004), an ecosystem model based on plankton functional types (PFTs) describing the lower trophic levels. It is a model of medium–high complexity, specifically designed for shelf seas, with independent cycling of the different nutrients (C, N, P, Si), variable stoichiometry for phytoplankton, bacteria, small zooplankton and a benthic submodel. The model is able to simulate OA thanks to its carbonate system module (Blackford and Gilbert, 2007), recently developed to take into account the biological feedback and riverine influences on TA (Artioli et al., 2012). The coupled model has already proved to give good to acceptable simulations of many variables and ecosystem properties (Allen et al., 2007; Allen and Somerfield, 2009; Shutler et al., 2011). More details on the

Fig. 1. Map of the study area with location of the major toponyms.

model and the validation of this particular set-up are provided by Artioli et al. (2012) and Holt et al. (2012a)

2.2 Parameterisation of OA impact on primary production

In the Pelagic Ecosystem CO_2 Enrichment Study III (PeECE III) mesocosm experiments (Bellerby et al., 2008) a clear increase in carbon uptake relative to nutrient uptake was observed, and this relationship was tightly dependent on the CO_2 treatment values. This was used to derive a carbon enhancement factor (C_{enh}) to describe the observed overconsumption of carbon. This factor has been parameterised dependent on atmospheric pCO_2 (Eq. 1), as this is the closer proxy to the pCO_2 levels used to treat the mesocosms.

This factor has been applied to the specific gross primary production and consequently to the activity respiration that in the model is tightly correlated with primary productivity (see Eq. 10 in Blackford et al., 2004):

$$C_{enh} = 0.0005 \cdot \left(pCO_{2,a} - pCO_{2,a}\big|_{2005} \right) \tag{1}$$

$$gPP_{enh} = gPP \cdot (1 + C_{enh}) \tag{2}$$

$$act.resp._{enh} = act.resp. \cdot (1 + C_{enh}), \tag{3}$$

where $pCO_{2,a}\big|_{2005}$ is the atmospheric partial pressure of CO_2 in the year 2005, gPP is the gross PP rate and act.resp. is the activity respiration.

A similar relationship has been used previously to assess the response to carbon overconsumption on global primary production (Riebesell et al., 2007) and ensuing modifications to global oxygen distributions (Oschlies et al., 2008).

The sensitivity of this parameterisation to the empirically derived value of the slope ($= 0.0005$) has been analysed using a 1-D set-up of ERSEM coupled to the turbulence model GOTM (Burchard et al., 1999) located in the middle of the North Sea ($56°$ N; $3°$ E) and using the same atmospheric forcing as in the IPCC AR4 A1B scenario (corresponding to a business as usual emissions scenarios; see IPCC, 2000).. The slope of the empirical relation varied uniformly between 0.00025 and 0.00075, and changes in net PP and zooplankton biomass were used to assess the sensitivity of the ecosystem response to this parameter. This analysis highlighted that the uncertainty on the slope of the parameterisation has an important effect on net PP: this indeed varied in a range of $\pm 20\%$ as a consequence of the change in the parameter of $\pm 50\%$, while the zooplankton biomass is only slightly sensitive ($< 2\%$ of variation).

2.3 Model experiments

Three sensitivity simulations have been run in this work, each using atmospheric forcing and oceanic boundary conditions derived from the IPSL-CM4 climate model (Marti et al., 2006). The baseline scenario (named PD) is driven by contemporary historical (1981–2000) output from the climate model, while the two projections (named A1B and A1B$_{PP}$) are both driven by outputs from the period 2080–2099 under the IPCC AR4 A1B scenario. We used a single member of the ensemble that is representative of the ensemble's average response (Laurent Bopp, CNRS, personal communication). The A1B$_{PP}$ simulation includes the primary production response detailed above. Table 1 summarises the different simulations.

The diagnostic variables used are the monthly means over the simulation period of pH, aragonite saturation state (Ω), net PP (calculated as particulate primary production), and zooplankton biomass. Net PP and zooplankton biomass are depth integrated over the whole water column, while all the other variables refer to surface values where not differently specified. Seasonal means have been calculated as means of three consecutive months starting from January (winter $=$ JFM; spring $=$ AMJ; summer $=$ JAS; autumn $=$ OND).

3 Results

The results of all simulations have been analysed as follows in order to highlight the response of the ecosystem to different stressors and processes:

Table 1. Main characteristics of the set-up of the three scenarios.

| Scenario	Forcing	Enhanced PP
PD	1981–2000	No
A1B	SRES A1B 2080–2099	No
A1B$_{PP}$	SRES A1B 2080–2099	Yes

– Scenario A1B vs. scenario PD (Sect. 3.1): they differ only in the forcing (present day compared with future); hence comparing their outputs determines the potential impact of climate change on the whole ecosystem, and the impact of OA on the carbonate chemistry.

– Scenario A1B$_{PP}$ vs. scenario A1B (Sect. 3.2): these differ only in the inclusion of the PP response to high CO_2, enabling quantification of the impact of the potential enhancement of PP on the ecosystem.

Here we will focus in detail only on impacts on the carbonate chemistry and the primary and secondary production. Climate change will also induce an increase in temperature (larger in summer and autumn than in winter and spring, potentially ranging from $\sim 4\,°C$ in the North Sea to $\sim 0.5\,°C$ in the Bay of Biscay) and in stratification (particularly off-shelf and during winter) and a consequent decrease in nitrate availability in most of the domain (except the more coastal area where the temperature increase fosters the recycling of organic matter). All of these impacts are discussed in detail in Holt et al. (2012a).

## 3.1 Impacts of high CO_2 on the ecosystem properties

The model projects a mean decrease of surface pH of about 0.27 units over the whole domain by 2080–2099, with significant spatial and temporal variability (Fig. 2a). Winter shows a clear difference between the shelf and the oceanic waters, with the former being more "acidified" by about 0.1 units. In spring the decrease in pH reaches its minimum across most of the entire domain, and the spatial heterogeneity is lower. Acidification reaches its maximum in summer and autumn, with a pH decrease exceeding 0.4 units (equivalent to an approximate 2.5 times increase in hydrogen ion concentration). The shelf–ocean gradient is also evident when looking at the future Ω (Fig. 2b): here the difference between the shelf and the open ocean is even more critical as the shelf sea surface waters are close to undersaturation ($\Omega < 1$) during winter and autumn, with localised undersaturation in the German Bight. In spring and summer surface waters are fully saturated, even though these are the seasons where the decrease in Ω is maximum (up to 2 units during summer). The decoupling between the maximum decrease of Ω occurring in summer and a simultaneous less important decrease in pH is due to the different effect of temperature in influencing pH and Ω.

The vertical gradients on the shelf are also significant (Fig. 3). During warm seasons, the water column in the
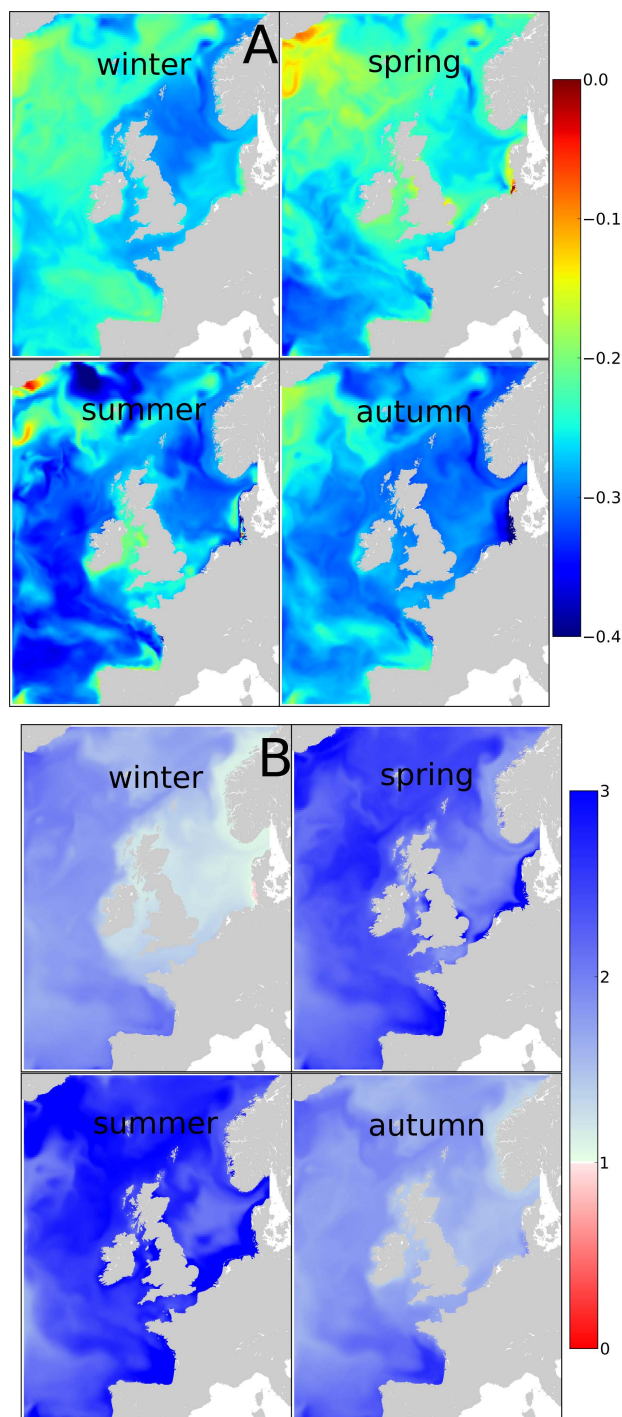
Fig. 2. Impacts of climate change and OA on the carbonate system as projected by the A1B scenario: **(a)** absolute difference in surface pH compared to the present-day scenario, and **(b)** future surface saturation state of aragonite.

central North Sea stratifies, creating two contrasting environments: while the surface is oversaturated, bottom waters reach significant undersaturation ($\Omega \sim 0.7$) over a large area.
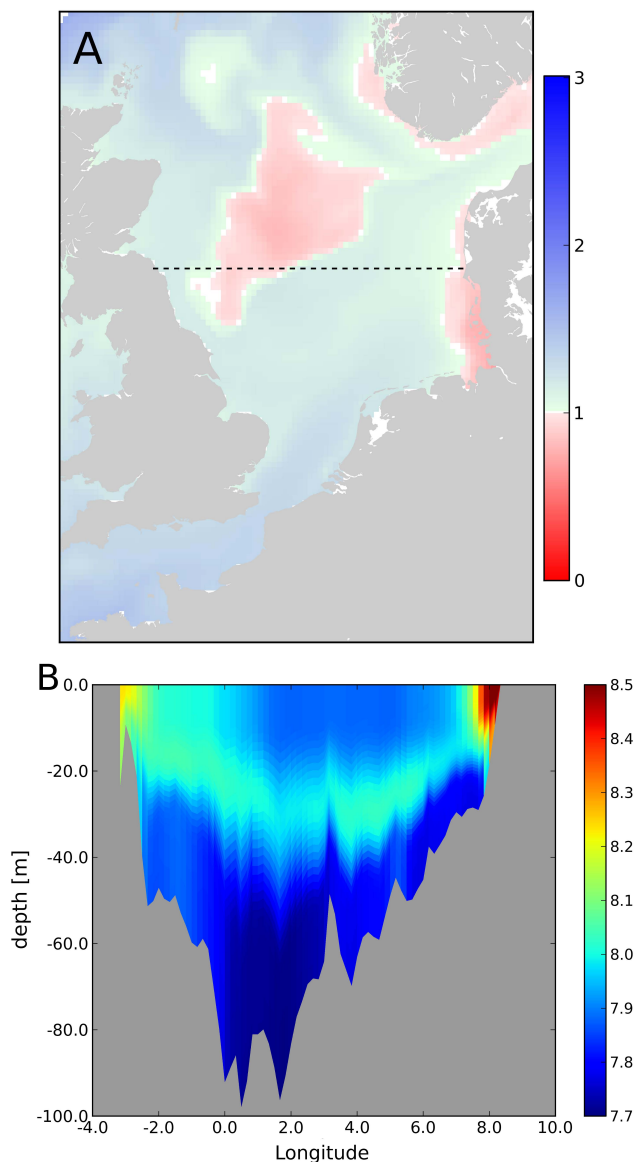
Fig. 3. Importance of the vertical variability of the carbonate system. **(a)** Mean values over the 20 yr simulation period of the annual minimum of saturation state of aragonite in the bottom waters in the A1B scenario. Red areas highlight undersaturation. Dashed black line indicates the location of the transect shown in the right figure. **(b)** Mean summer pH on a W–E transect along 56° N in the A1B scenario.

pH has a similar vertical gradient, with surface pH up to 0.3 units higher than in the bottom waters.

Figure 4a shows the difference in net PP driven by changes in temperature and physically mediated nutrient availability: the largest differences occur during the productive seasons, when a general decrease in net PP is observed (up to $-150\,\text{mg C m}^{-2}\,\text{d}^{-1}$ in the northern oceanic regions in summer and $-300\,\text{mg C m}^{-2}\,\text{d}^{-1}$ in the southern oceanic region in spring). Contrarily, the model forecasts an increase of net PP in the Irish Sea, the Celtic Sea and the Icelandic waters, with the latter experiencing the larger increase in spring (up to $+150\,\text{mg C m}^{-2}\,\text{d}^{-1}$). In winter and autumn the differences are smaller with a tendency for small increase on the shelf and in the Bay of Biscay. Figure 5a summarises the relative changes in the net PP for the different PFTs in each sub-domain. A similar pattern can be observed between the shallower and more enclosed basins (English Channel and the Irish Sea) with a small increase in diatom production all over the year, an increase in flagellate and dinoflagellate net PP in the second half of the year (with no change/decrease in the first half) and a larger increase in net PP of picophytoplankton during winter and autumn. At the same time, the Celtic Sea, the North Sea and the open ocean exhibit similar distribution of net PP, which is generally higher in winter and autumn and lower in spring and summer.

Changes in total zooplankton biomass are generally consistent with those of net PP (Fig. 4b) with one notable exception: in spring, in the Western Approaches (the oceanic areas west of UK and Ireland) a strong increase in zooplankton biomass (more than $+500\,\text{mg C m}^{-2}$) is observed despite the decrease in net PP occurring in the same season. Zooplankton community composition is also projected to change, with a shift towards mesozooplankton (Fig. 5b).

3.2 Impacts of enhanced PP

The major consequence of the assumption of enhanced PP due to OA is a general increase in net PP in most of the domain, particularly in spring, with an increase ranging between $+50$ and $+250\,\text{mg C m}^{-2}\,\text{d}^{-1}$, and in summer, when the increase is limited to the coastal area of the shelf, with a peak of more than $+200\,\text{mg C m}^{-2}\,\text{d}^{-1}$ (Fig. 6a). This latter pattern is generally associated with high nutrient availability in the more coastal area, mostly due to riverine input and faster mineralisation in the shallow water. The presence of highly nutrient-enriched water allows the phytoplankton to fully express the enhanced potential productivity. In contrast, most of the open ocean experiences a reduction of net PP of about $-50\,\text{mg C m}^{-2}\,\text{d}^{-1}$ during summer.

Again, not all phytoplankton groups respond in the same way, with diatoms exhibiting a lower increase in production (Fig. 5c). Changes in zooplankton biomass are tightly coupled to net PP changes (Fig. 6b).

Changes in pH following from increased biological uptake of CO_2 (Fig. 6c) mimic the pattern of changes in net PP. During spring a small increase of 0.016 pH unit on average is simulated compared to the non-PP enhancement scenario in most of the domain (Fig. 2a), with a maximum in river-influenced regions of up to 0.1 units. In summer the coastal areas are still projected to have a higher pH than in the non-PP-enhanced scenario, while the rest of the domain is experiencing a small decrease. Changes in saturation state follow the same pattern, but they are statistically not separable from the one predicted by the non-PP-enhanced scenario.
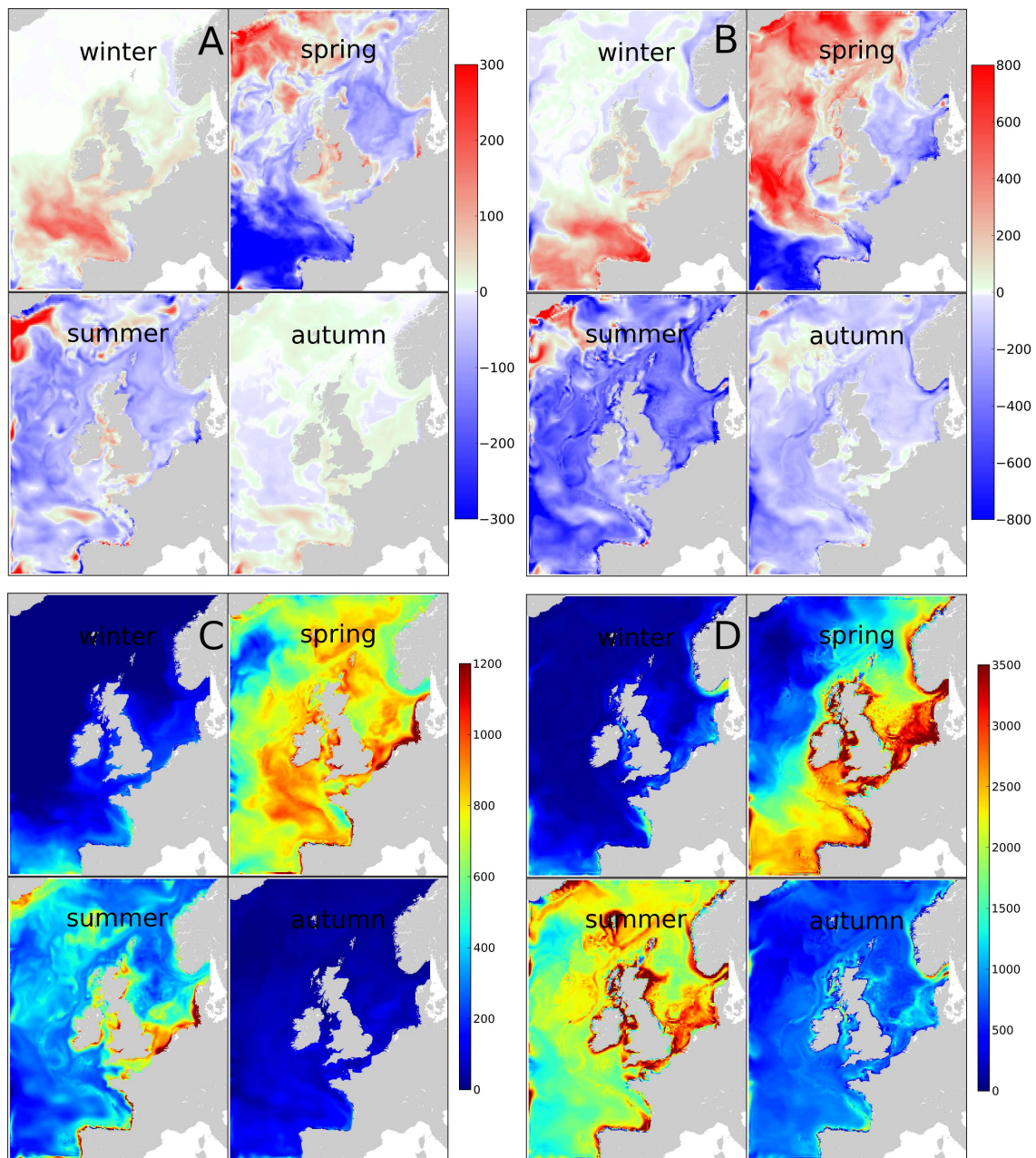
Fig. 4. Impacts of climate change and OA in the ecosystem as projected by the A1B scenario (A1B minus PD scenarios). **(a)** difference in net primary production (depth integrated, $mg\,C\,m^{-2}\,d^{-1}$), **(b)** difference in zooplankton biomass (depth integrated, $mg\,C\,m^{-2}$). Reference values of the seasonal mean of net primary production **(c)** and zooplankton biomass **(d)** are also shown.

4 Discussion

4.1 Impacts on carbonate chemistry

The average decrease of pH is consistent with the mean estimate provided by global modelling approaches, but it is highly heterogeneous in time and space (Figs. 2a and 3a). Atmospheric CO_2 concentration is clearly the driver of OA, but this is not the only factor regulating the carbonate system in

the shelf seas. Biological processes are particularly important in defining the seasonality of the impact: in the areas where an increase in net PP is projected, a relatively lower acidification is simulated by the model (e.g. in spring in the North Atlantic or in the southern North Sea in summer). Similarly the undersaturation of aragonite projected in bottom waters in the central North Sea (Fig. 3a) is caused by the accumulation of DIC during summer and early autumn: in this season increases in pelagic community respiration (average in
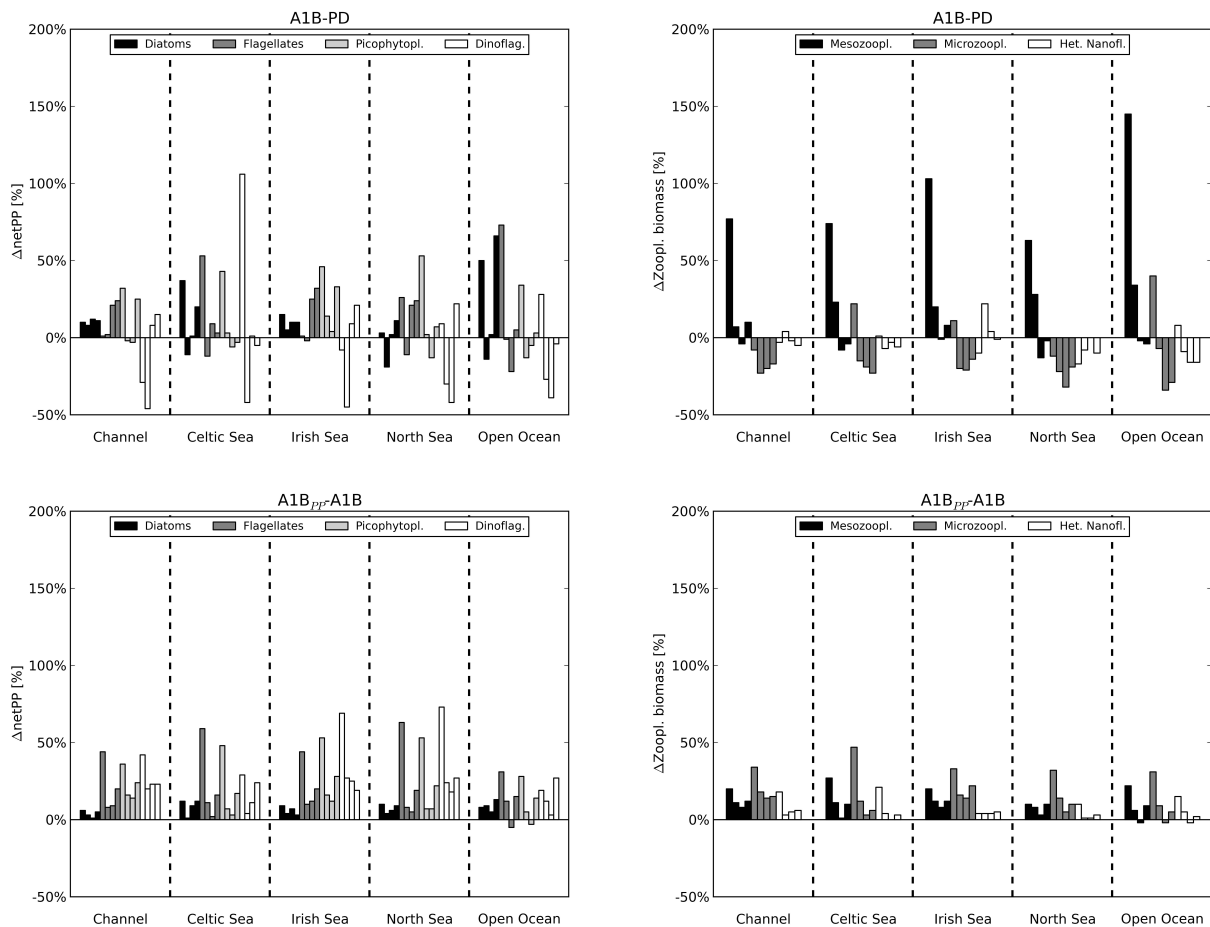
Fig. 5. Relative difference between the seasonal mean of net primary production **(a, c)** and zooplankton biomass **(b, d)**, shown for different sub-regions. **(a, b)** show the difference between the A1B (future climate) scenario and the PD (present day) scenario (A1B-PD); **(c, d)** show the difference between the enhanced production run and the A1B scenario (A1Bpp − A1B). Colour of the bars denotes the plankton functional type. The four adjacent bars for each functional type, within each region, represent the seasons, in the order winter, spring, summer, autumn.

the deep waters goes from about 2.2 mg C m^{-3} d^{-1} in winter to 3.9 mg C m^{-3} d^{-1} in summer) and in DIC fluxes from the benthic system (from an average value of 4 mg C m^{-2} d^{-1} to 9 mg C m^{-2} d^{-1}, again due to increased benthic community respiration) are estimated by the model. This excess of DIC is then trapped in the lower part of the water column because of the concurring stratification that prevents ventilation.

The increase in temperature plays two contrasting roles. From one side it decreases the solubility of CO$_2$ in water, promoting the outgassing and therefore preventing further acidification. At the same time rising temperature increases the values of the dissociation constants of the carbonic acid system, leading to an increase in the more dissociated forms and a consequent decrease in pH. This effect is partially responsible for the shelf–ocean gradient in the OA signal: the shelf warms up more than the ocean, seen in both historical observations (Holt et al., 2012b) and these simulations, (Holt et al., 2012a) with differences in temperature varying

between 1 °C and 4 °C depending on season and a relative difference in pH of up to 0.05 units.

Another concurring reason for the winter shelf/off-shelf gradient of the decrease in pH is linked to circulation and the freshwater balance. The IPSL model projects a general increase in precipitation at the end of the century over the domain considered here, particularly over the shelf sea and ocean (up to +13 %). Furthermore, the influx of surface oceanic water from the south and western boundary of the domain has mostly lower salinity in the future compared to present day (generally between 0.5 and 1.0 units lower, with only the northern part of the boundary having no changes in salinity or a slight increase). Finally river discharge in the future scenario has been parameterised using changes in regional precipitation projected by the IPSL model: globally the total river discharge decreases by about 7 %, mostly due to the decrease in precipitation over central Europe projected by the climate model. The net result is a general decrease
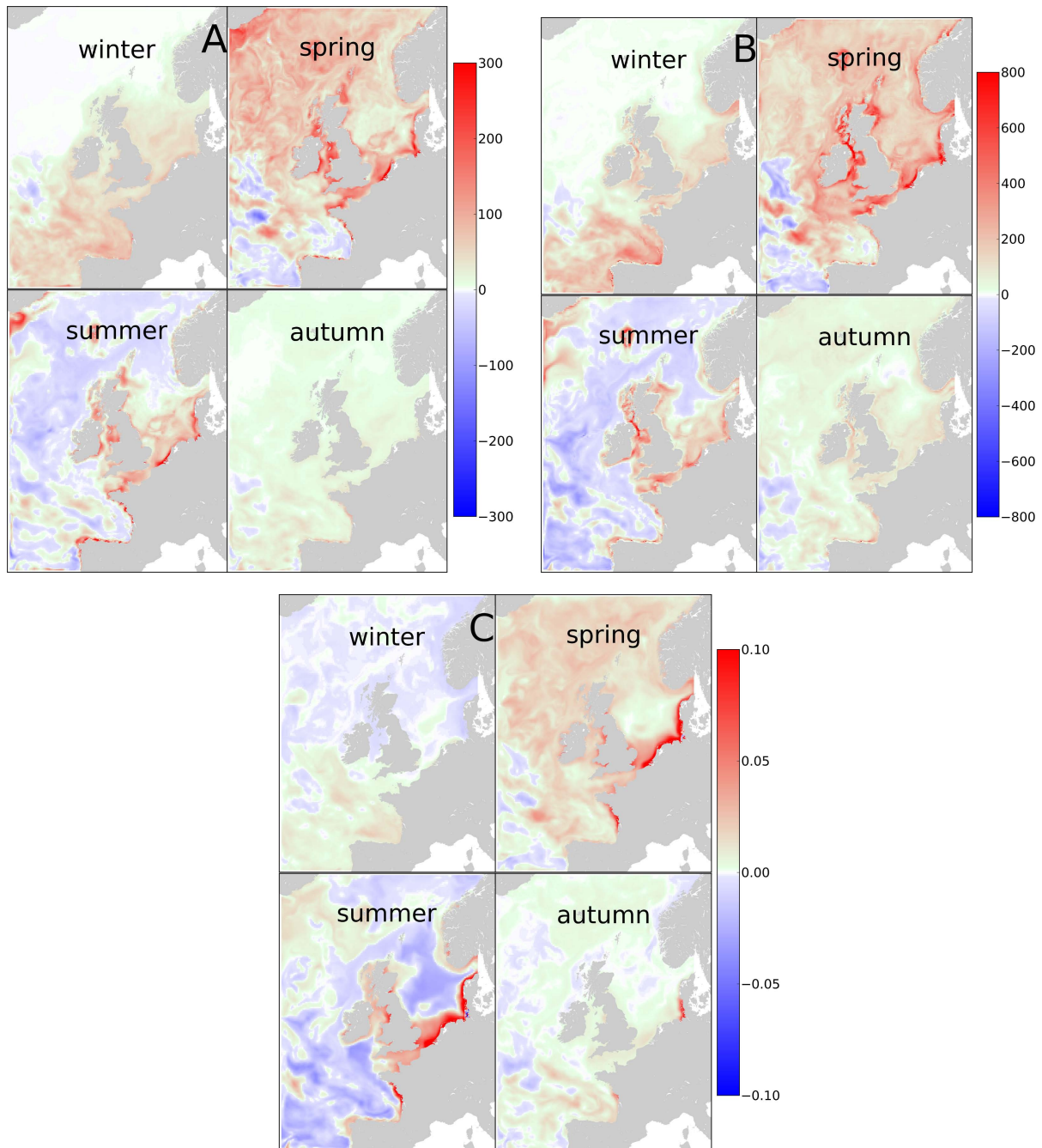
Fig. 6. Impacts of the enhanced primary production due to OA (A1B$_{PP}$ minus A1B scenarios). **(a)** absolute difference in net primary production (depth integrated, $mg\,C\,m^{-2}\,d^{-1}$), **(b)** difference in zooplankton biomass (depth integrated, $mg\,C\,m^{-2}$), **(c)** difference in pH in the surface waters.

in salinity over the whole domain, with bigger changes on the shelf sea than in the surface open ocean. Given that TA is mostly parameterised as a linear correlation of salinity following Millero (1995) (see Artioli et al. (2012) for further details on the parameterisation), this gradient leads to a stronger decrease of TA on the shelf and therefore lowers the buffer capacity of the shelf system.

Changes in riverine nutrient inputs are another important source of variability in the more coastal areas because they largely determine the intensity of PP and therefore the seasonal cycle of DIC in those regions. It is also important to note that in all the scenarios only the freshwater discharge has been changed, but all concentrations (nutrients, DIC and TA) have been kept as in the present day, due to a lack

of information. Clearly a change in riverine concentrations could also significantly modify the near-coastal results presented here.

The impact of enhanced PP on the carbonate system is relatively small, generally lower than the model uncertainty (0.04 units for pH and 64.7 μatm for pCO$_2$; see Artioli et al., 2012). However in the coastal areas of the southern North Sea pH can increase up to 0.1 units because of the enhanced PP, almost halving the impact of OA in this region

The high variability in the OA signal on marine carbonate chemistry increases the uncertainty in the estimates of OA impacts on biota. Shaw et al. (2013) showed how natural variability of the carbonate system can have a significant impact on determining the impact of OA on biota. Adding on top of the diel/seasonal natural variability a variable change in pH, and more generally in the entire carbonate system, makes the quantitative estimates of impacts of OA really challenging.

4.2 Impacts on primary and secondary production

As highlighted by Holt et al. (2012a) climate change will potentially induce a general decrease of net PP (Fig. 4a) in most of the domain due to the increased stratification and a subsequent decrease in nutrient availability. Within this general trend, here we have shown that the PFTs may respond differently to climate change (Fig. 5a). In all areas winter production may be more favoured, thanks to the increased temperature and the nutrient-replete environment. The pattern in the more open basins, showing a potential decrease in PP in the central part of the year, is mostly due to the lack of nutrients: these areas are more influenced by the ocean and therefore impacted by the increased stratification (Holt et al., 2012a). However in the English Channel and the Irish Sea only the dinoflagellates are showing a consistent and marked decrease in production: here, indeed, PFTs with a higher turnover (i.e. flagellates and picophytoplankton) can take advantage of the high mineralisation of organic matter fostered by the increase in temperature, while dinoflagellates, characterised by slower dynamics, are outcompeted. This could cause changes in phytoplankton community composition, with subsequent impact on the higher trophic levels. Figure 5b shows how mesozooplankton is projected to increase (particularly in winter and spring) while microzooplankton will decrease throughout almost the entire year. This is a direct consequence of changes in primary production: the increased early blooms of diatoms fuel the large zooplankton pathways, resulting in a net increase in mesozooplankton biomass. Microzooplankton biomass then decreases due to increased grazing pressure from larger zooplankton and decreased prey availability in the small size spectrum of phytoplankton. This mechanism also explains the apparently contradictory results in the Western Approaches during spring; the increase in net PP occurring in late winter–early spring in the region is transferred first to the small zooplankton, and

then to mesozooplankton that reach a peak in late spring, when the net PP is curtailed by the strongest nutrient limitation.

These changes in community composition could then transfer even further to higher trophic levels.

The potential variation in net PP due to OA alone (Fig. 6a) is of the same order of magnitude as that due to climate change. The heterogeneity indicates that sometimes these may have the opposite sign and tend to cancel out (e.g. in the central North Sea in spring or in the southern North Sea in summer), whilst sometimes they have the same sign and OA magnifies the climate change impact. This is in agreement with work from Tagliabue et al. (2011), who tested similar hypotheses at a global scale. This impact is transferred up into trophic network to zooplankton (Fig. 6b) and potentially to higher trophic levels.

In this initial study we assumed that all phytoplankton functional groups (diatoms, flagellates, picophytoplankton and dinoflagellates) respond similarly to high CO_2 by increasing productivity with the same rate. Despite this, the phytoplankton community composition changed (Fig. 5c): diatoms indeed are not able to fully exploit the increased primary productivity due to silicon limitation as highlighted by the value of the N : Si ratio (not shown) being higher than the optimal value of 1 (Brzezinski, 1985; Cloern, 2001). The other groups respond qualitatively similar in all the domains, with a lower increase in the open ocean due to the lower nutrient availability. Here we also observed a decrease in net PP for some PFTs during summer even though the parameterisation would imply an increase. The enhanced production due to CO_2 enrichment will exacerbate the effect due to climate change described above; spring blooms remove a larger proportion of available nutrients from the off-shelf water columns, leaving a more nutrient-depleted environment for summer production.

The simulated shift in community composition could change even further if we considered that there is some evidence that smaller species are more likely to respond to OA than the larger ones (Egge et al., 2009).

The change in phytoplankton community composition causes changes in the zooplankton community composition (Fig. 5d), with a general increase of the two larger groups. The magnitude of the change is generally of the same order of magnitude as the one induced by climate change, but with the opposite sign.

5 Conclusions

In this paper, we have shown how the impacts of OA and climate change are likely to be strongly interlinked even when simple parameterisations are implemented and the combination of the effects can lead to complex results. OA could either exacerbate or compensate climate change impacts depending on season, area and process; this could occur either

via direct interference of the two drivers (e.g. enhanced production due to OA could mitigate reduction of PP due to climate change) but also via indirect feedback (e.g. the increased PP in coastal area due to OA will lead to a reduced acidification in the same area).

Furthermore, the effects of these global drivers can magnify along the trophic network, as shown here for zooplankton: in particular changes in community composition could have important impacts on the whole trophic network, favouring one trophic pathway over others. The non-linear complex interactions among the different components of the ecosystem can also trigger unexpected responses (e.g. the local increase of zooplankton biomass despite a decrease in PP).

This underlines that an ecosystem and multi-driver approach to study global changes is necessary (Blackford 2010), because we demonstrated that single driver-process responses can be negated or exacerbated by feedbacks from another driver-process response or ecosystem feedback.

Finally, this complexity enhances the heterogeneity of the system and of the impacts. Even considering a relatively simple chemical process like the carbonate equilibrium in the seawater, the variability of pH decrease is significant despite a homogeneous increase in atmospheric $p\mathrm{CO_2}$ due to the interaction with physical and biological processes. It is therefore crucial to highlight this variability when impacts of OA and climate change are assessed in order to identify which are the more (or the less) vulnerable regions. This should be also taken into account in future experiments in order to expose organisms to treatments that are more realistic approximations to their future environment. Similarly, marine ecosystem models should consider more deeply the variability of the biological part of the ecosystem ,including improved physiological realism (Allen and Polimene, 2011), in order to be able to better represent the ecosystem response to global change and to better interface with experimental science.

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