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# Ocean acidification with (de)eutrophication will alter future phytoplankton growth and succession

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Human activity causes ocean acidification (OA) through the dissolution of anthropogenically generated CO<sub>2</sub> into seawater, and eutrophication through the addition of inorganic nutrients. Eutrophication increases the phytoplankton biomass that can be supported during a bloom, and the resultant uptake of dissolved inorganic carbon during photosynthesis increases water-column pH (bloom-induced basification). This increased pH can adversely affect plankton growth. With OA, basification commences at a lower pH. Using experimental analyses of the growth of three contrasting phytoplankton under different pH scenarios, coupled with mathematical models describing growth and death as functions of pH and nutrient status, we show how different conditions of pH modify the scope for competitive interactions between phytoplankton species. We then use the models previously configured against experimental data to explore how the commencement of bloom-induced basification at lower pH with OA, and operating against a background of changing patterns in nutrient loads, may modify phytoplankton growth and competition. We conclude that OA and changed nutrient supply into shelf seas with eutrophication or de-eutrophication (the latter owing to pollution control) has clear scope to alter phytoplankton succession, thus affecting future trophic dynamics and impacting both biogeochemical cycling and fisheries.

## 1. Introduction

Effects of ocean acidification (OA), and specifically the impacts of higher  $p\text{CO}_2$  and a lower pH (higher  $[\text{H}^+]$ ) on marine life are subjects of much research. Taken together with other climate change events, notably changes in temperature and water-column stability, OA has the potential for various impacts upon marine plankton communities and production [1–9]. The removal of CO<sub>2</sub> by primary production leads to seawater basification (increase in pH), and the tendency towards this event is enhanced by increased nutrient availability. Indeed, in coastal waters subjected to eutrophication by addition of inorganic nutrients that support large algal blooms, the increase in pH can be highly significant and can override any signal from OA [10]. On the contrary, when organic eutrophication promotes increased system respiration (net addition of CO<sub>2</sub>), then acidification is increased [11]. Events can also run in series, with inorganic eutrophication promoting first primary production and then respiration during decay of the bloom biomass. Either way, the system pH displays variations

that may affect ecology, and these events will be affected with OA by commencement at a lower pH. Such transients are of most consequence in the highly dynamic coastal zones which contain elevated nutrient loadings in comparison with the relatively stable and low nutrient oligotrophic oceans.

Significant basification during bloom development directly influences phytoplankton species growth rates and succession [12–14], selecting species most capable of growth as pH increases [13–16]. Further, the major grazers of phytoplankton, the microzooplankton, can be sensitive to elevated pH [17], just as copepods can show sensitivity to lower pH [8]. Such selective pressures affect the extent of biomass production and also its fate. These pH-sensitive events in future oceans will be affected by the long-term decrease in ocean pH with OA overlain by short-term changes in seawater pH such as basification during phytoplankton blooms. Because of climate change (including changes in terrestrial runoff), human population growth and allied changes in land use, enhanced nutrient release from the land is also expected over the coming decades. There are expected to be particularly severe regional impacts affecting coastal marine ecosystems [18,19], though some areas may see reversal of eutrophication under policies to decrease pollution. Any changes in nutrient loading that affect primary production will also affect the degree of basification.

The implications of the potentially synergistic effects of (de)eutrophication and OA, inducing modifications to phytoplankton growth and species succession, have not previously been explored. With OA, bloom-induced basification will commence at a lower pH. This will fundamentally shift the conditions for competitive interactions between bloom-forming species over a different range of  $H^+$  concentrations, with potentially unanticipated impacts on predator–prey dynamics through to higher trophic levels. Any significant changes to plankton growth in estuarine, coastal and shelf sea systems will have profound implications owing to the substantial contribution these systems make to global productivity [18,19] and marine ecosystem services [20].

This paper explores how these contrasting drivers on seawater pH (pH declining with OA versus basification with inorganic nutrient eutrophication) may affect growth and interactions of different types of phytoplankton. We show, using a combination of experiments and models, that future changes in ocean carbonate chemistry, coupled with changes in the availability of nutrients, will have an important influence on competitive interactions between phytoplankton taxa during bloom development.

## 2. Material and methods

A brief overview is provided here; detailed methods are described in [21] and in the electronic supplementary material. Three taxonomically contrasting phytoplankton, a weakly calcifying strain of the non-motile prymnesiophyte (*Emiliania huxleyi*), a motile cryptophyte (*Rhodomonas* sp.), and a silicifying diatom (*Thalassiosira weissflogii*), were grown in nitrogen-limiting cultures. Initial pH treatments were set as typical of present day seawater (extant: pH 8.2), future OA (acidic: pH 7.6) or within dense blooms (basic: pH 8.8). pH was then allowed to drift with phytoplankton growth with no  $CO_2$  entry to counter dissolved inorganic carbon (DIC) removal through primary production. (In the oceans, gas exchange to equilibrium is very slow, especially into a mixing depth of many metres.) These pH treatments are henceforth termed ED (start at extant pH with drift), AD (start at acidic pH with drift) and BD

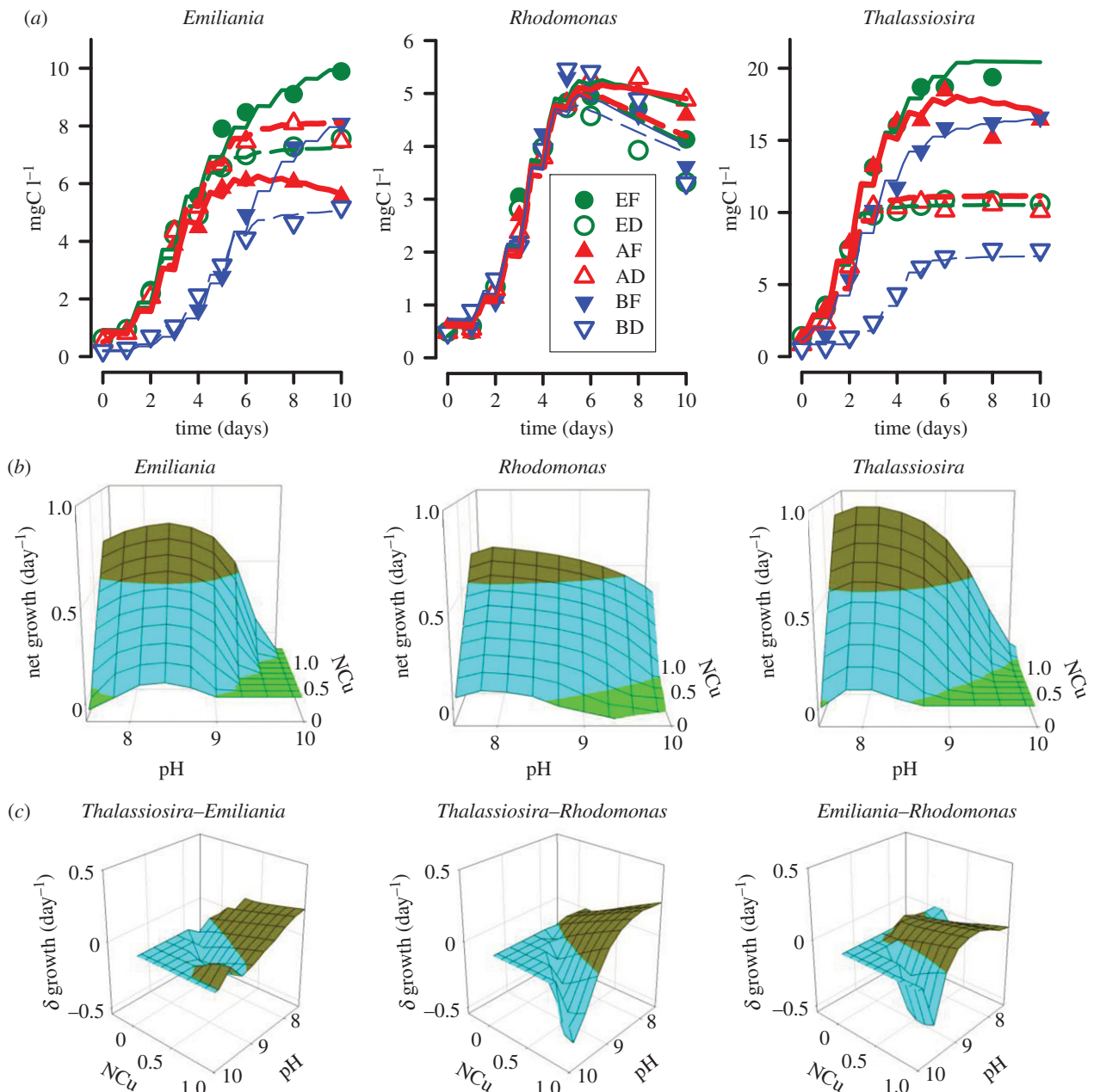
(start at basic pH with drift). In addition, comparative treatments were run with pH held fixed at the initial values by addition of HCl or NaOH; these conditions are termed EF (extant pH fixed), AF (acidic pH fixed) and BF (basic pH fixed). Data from experiments (nutrients, biomass C, N and P) were used to configure multi-nutrient, photoacclimative, variable stoichiometry models of phytoplankton growth dynamics, which were coupled to a carbonate chemistry submodel, as described in [22]. These models were then run under different scenarios of nutrient and  $pCO_2$  (OA), and of mixing depth, to simulate growth of single or multi-species phytoplankton communities.

## 3. Results

In comparison with growth in the extant drift (ED) pH systems, growth of *Thalassiosira* and *Emiliania* was almost halved in the basic drift (BD) systems, and was similar or slightly enhanced in the acidic drift (AD) systems (figure 1a). There was little difference between *Rhodomonas* grown in drift systems of different initial pH, at least during the nutrient-replete phase. Typically, growth of these single species cultures was greater under fixed-pH rather than under drift-pH conditions (figure 1a), with DIC draw-down continuing until concentrations of substrates for photosynthesis ( $H_2CO_3$  and  $HCO_3^-$ ) were very low (electronic supplementary material, figures S1, S3–S5). Cessation of growth at high pH in drift systems was thus not a simple consequence of the exhaustion of DIC. Only for *Emiliania* was growth under AF pH conditions poorer than under AD pH conditions (figure 1a). Within multi-species cultures, *Emiliania* biomass declined following nutrient exhaustion; this could not be explained simply through reference to the results from single species cultures (figure 1 and the electronic supplementary material, figure S1 versus S6), but appears to be related to the extent of growth of total biomass (which was greater in fixed-pH systems), perhaps associated with a lack of DIC and/or an allelopathic (or other cell–cell) interaction.

Fits of the model to experimental data (figures 1a and the electronic supplementary material, figures S1 and S2) were achieved by inclusion of functions relating both phytoplankton growth and death to pH and cellular nutrient status (electronic supplementary material, table S1). The optimal pH, and form of the interaction between pH with nutrient stress, differed between species (figure 1b). When emergent relationships were compared for pairs of species (figure 1c), potential windows of opportunity for each competing species became apparent. Thus, *Emiliania* growth is favoured under extant pH, with more acidic and basic conditions being unfavourable. *Rhodomonas*, which had the lowest maximum growth rate, has its highest competitive scope at elevated pH but only when nutrient-replete; these are conditions likely associated with eutrophic areas during blooms.

Dynamic sensitivity analyses, conducted on simulations for the multi-species cultures under the fixed- and drift-pH regimes (electronic supplementary material, figures S7–S9), indicated that phytoplankton succession is most predictable (i.e. least variable) under extant pH, and least predictable under the acidic (OA) scenarios. This reflects the form of the relationship between pH–nutrient status–growth/death for each species (figure 1b), tracking consumption of DIC and nutrients during growth of the total algal community. Variability in response was further enhanced by the decreased buffering capacity of seawater at lower pH [22], which affects growth under the acidic scenarios. Even within a narrow pH



**Figure 1.** Experimental data and model outputs. (a) Experimental data (symbols) for the prymnesiophyte *Emiliania huxleyi*, the cryptophyte *Rhodomonas* sp. and the diatom *Thalassiosira weissflogii* grown under conditions of pH that were extant fixed at pH 8.2 (EF), extant drifting from pH 8.2 (ED), acidic fixed at pH 7.6 (AF), acidic drifting from pH 7.6 (AD), basic fixed at pH 8.8 (BF) or basic drifting from pH 8.8 (BD). Experimental data are averages from duplicate experiments, with the range of those values typically within the symbol size. Lines are model fits to the data. (b) Emergent relationships between growth rate, pH and nutrient status (NCu; where 0 is nutrient-starved and 1 is replete). Measured pH ranged between 7.5 and 10; simulation outputs are shown within these values. Darkest zones (brown in online colour plot) indicate zones with growth rates  $>0.5$  day<sup>-1</sup>. (c) Differences in net growth potential ( $\delta$  growth) between pairs of algae, with pH and nutrient status. In each plot, the light zones (blue in online colour plot) indicate where the second named species would outgrow the first named species; a value of  $\delta$  growth = zero indicates where neither species exhibited positive net growth. (Online version in colour.)

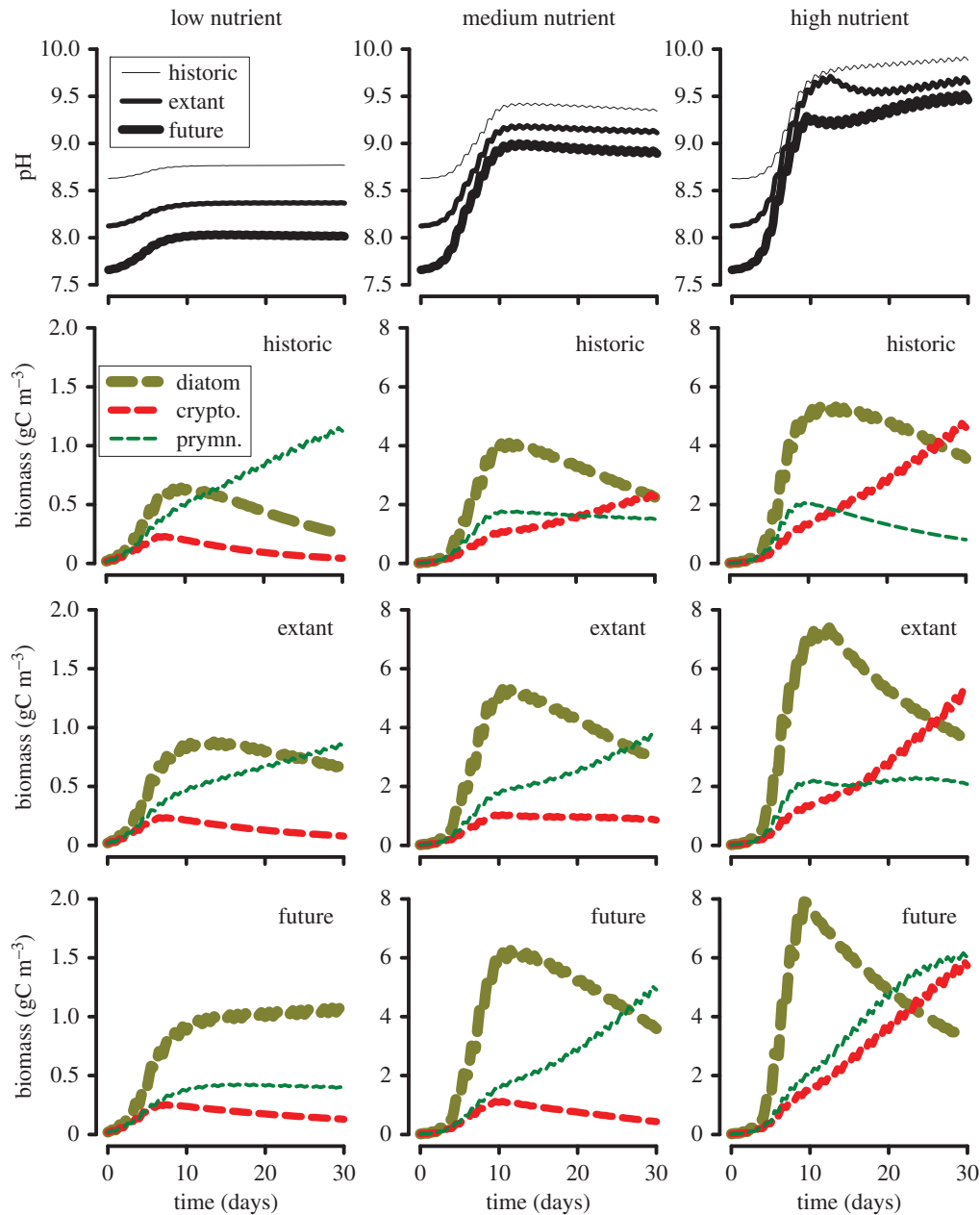
range, the additional impact of nutrient stress can be significant (figure 1c); the prymnesiophyte *Emiliania* showed greater sensitivity and relatively lower competitive advantage in the acidic fixed-pH (AF) simulations.

Simulations were also made under different conditions of gas exchange equilibration to historic, extant or future atmospheric  $p\text{CO}_2$ , low medium and high nutrient loadings, and mixing depths (figure 2). These plots should be viewed as being indicative of the potential for different successions, and not necessarily that one or other plankton group (diatom versus cryptophyte versus prymnesiophyte) will dominate in nature under a given set of conditions. Simulated future scenarios generally gave rise to faster and more extensive growth

(figure 2), and more extreme elemental stoichiometry (electronic supplementary material, figure S10) when light or Si was not limiting. Simulated bloom composition varied between  $p\text{CO}_2$  scenarios, because the deleterious conditions at elevated pH were encountered later during bloom development under future scenarios (the starting pH being lower with OA).

## 4. Discussion

Our study shows species variability within the pH-growth relationship and how this is affected by nutrient stress (figure 1b). Predicted under different OA and



**Figure 2.** Simulations of competitive growth between three phytoplankton types under different  $p\text{CO}_2$  scenarios and physico-chemical characteristics. The plankton type models conform to the cryptophyte (crypto.), diatom (diatom) and prymnesiophyte (prymn.) types, as configured against experimental data (figure 1a). Initial algal-C biomass values were the same for each type; biomass has units of  $\text{gC m}^{-3}$ . Scenarios conformed to historic (preindustrial,  $p\text{CO}_2$  280 ppm), extant ( $p\text{CO}_2$  390 ppm) and future (prediction for 2100,  $p\text{CO}_2$  1000 ppm) conditions. Nutrients (N, P, Si) were supplied at Redfield ratios; the low nutrient regime contained  $5 \mu\text{mol N l}^{-1}$  with mixing depth of 40 m; the medium nutrient regime contained  $40 \mu\text{mol N l}^{-1}$  with mixing depth of 10 m; the high nutrient regime contained  $200 \mu\text{mol N l}^{-1}$  but with only  $40 \mu\text{mol Si l}^{-1}$  with mixing depth of 5 m. In all instances wind speed was set at  $10 \text{ m s}^{-1}$ , maximum day time surface irradiance at  $2000 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$  in a 12 : 12 h light : dark cycle, mixing rate between upper and lower layers of  $0.05 \text{ day}^{-1}$ , temperature of  $16^\circ\text{C}$  and salinity of 35. (Online version in colour.)

(de)eutrophication scenarios (figure 2), the implications of our results for shifting plankton successions in shelf seas are numerous and far reaching. Over time, some waters (e.g. North Sea) will have seen changes from conditions akin to historic  $p\text{CO}_2$  with mesotrophy, to extant  $p\text{CO}_2$  with eutrophy, to future  $p\text{CO}_2$  with mesotrophy, with corresponding scope for significant changes in plankton dominance (figure 2). More broadly, with greater inorganic eutrophy (an increasingly likely event [18,19,23]) coupled with elevated  $p\text{CO}_2$ , there is potential for an increase in total bloom size and/or of the rate of growth in coastal and shelf seas. The nutrient balance in shallow waters is also affected by basification during blooms leading to the release of bound nutrients

[23], and decreased coupling of nitrification–denitrification [24]. With OA, initiation of all these events will occur at a lower average pH, but additional differences in bloom extent and composition as a consequence of other impacts, including temperature changes and pollution control measures may be expected [10,25].

The responses of our coupled experimental–model systems, with respect to growth dynamics and C:N:P, are consistent with empirical studies [1,2,9,26], providing confidence in the behaviour of the models. However, dominance of different taxa in nature will also be affected by other factors, including responses of the zooplankton. Blooms develop only in the absence of effective grazing pressure [27]. The activity of

grazers will have several points of interaction. More extreme stoichiometry (electronic supplementary material, figure S10) may be detrimental to grazers [27,28], and also promote toxicity in some phototrophic species [29]. High pH may decrease net growth of grazer populations [17] and hence decrease feeding on phytoplankton, whereas low pH has been seen to affect vertical migration of flagellates [30] and copepod growth [8]. Nonetheless, all these interactions are ultimately secondary to the auto-ecological responses of individual primary producers to nutrients, pH and light.

The fate of this changed primary production, depending on local conditions and bloom composition, when coupled with impacts on grazers, will likely be associated with increased frequency of deleterious events such as harmful and ecosystem-disruptive algal blooms [31,32], and increases in hypoxic and anoxic zones, affecting fisheries [33] and thence food security. For blooms of calcifying phototrophs, and any plankton growing within these blooms, the situation is complicated further as calcification with primary production mitigates pH increases [22]. If coccolithophore growth is adversely affected by lower pH (as seen here), then there is opportunity for enhanced variability in their bloom development; this will depend on how preceding non-coccolithophorid primary production conditions affect the water column (figures 1*b,c* and 2).

Our work shows variation in the sensitivity of phytoplankton commencing growth under different initial conditions to changes in pH (figure 2 and the electronic supplementary

material, figures S7–S9). While there has always been variability in seawater pH, with OA, the variability in  $[H^+]$  will be greater, starting from a less buffered state at a higher  $[H^+]$  [22,34]. Studies on OA, therefore, need to consider the dynamic interplay between primary and secondary producers grown under variable pH, and their physiological mechanisms to cope with these dynamics. While one may expect organisms growing with OA to adapt to lower pH [35], it is uncertain whether such adaptations would then adversely affect scope for growth over the broader pH range with bloom-induced basification. Further, as nutrient stress impacts negatively on the ability to cope with pH-induced stress (figure 1*b*), the potential for mixotrophs, with their ability to derive nutrients from different sources [36,37], to be favoured under OA scenarios also warrants research. Taken together, we have every reason to expect a more variable and less predictable future for primary production in coastal and shelf seas.

**Data accessibility.** Raw experimental data used in this work are available from the corresponding author; these are graphically displayed in this work and its allied electronic supplementary material. Model code is available in, and is described in, the electronic supplementary material; code may also be obtained in the form used for this work (i.e. as a Powersim Constructor file) from the corresponding author.

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## References

- Riebesell U *et al.* 2007 Enhanced biological carbon consumption in a high CO<sub>2</sub> ocean. *Nature* **450**, 545–548. (doi:10.1038/nature06267)
- Bellerby RG, Schultz KG, Riebesell U, Neill C, Nondal G, Heegaard E, Johannessen T, Brown KR. 2008 Marine ecosystem community carbon and nutrient uptake stoichiometry under varying ocean acidification during the PeECE III experiment. *Biogeoscience* **5**, 1517–1527. (doi:10.5194/bg-5-1517-2008)
- Doney SC, Fabry VJ, Feely RA, Kleypas JA. 2009 Ocean acidification: the other CO<sub>2</sub> problem. *Annu. Rev. Mar. Sci.* **1**, 169–192. (doi:10.1146/annurev.marine.010908.163834)
- Artioli Y, Blackford JC, Nondal G, Bellerby RGJ, Wakelin SL, Holt JT, Butenschön M, Allen JI. 2013 Heterogeneity of impacts of high CO<sub>2</sub> on the North Western European Shelf. *Biogeoscience* **10**, 9389–9413. (doi:10.5194/bgd-10-9389-2013)
- Connell SD, Kroeker KJ, Fabricius KE, Kline DI, Russell BD. 2013 The other ocean acidification problem: CO<sub>2</sub> as a resource among competitors for ecosystem dominance. *Phil. Trans. R. Soc. B* **368**, 20120442. (doi:10.1098/rstb.2012.0442)
- Duarte CM, Hendriks IE, Moore TS, Olsen YS, Steckbauer A, Ramajo L, Carstensen J, Trotter JA, McCulloch M. 2013 Is ocean acidification an open-ocean syndrome? Understanding anthropogenic impacts on seawater pH. *Estuar. Coast.* **36**, 221–236. (doi:10.1007/s12237-013-9594-3)
- Schulz KG *et al.* 2013 Temporal biomass dynamics of an Arctic plankton bloom in response to increasing levels of atmospheric carbon dioxide. *Biogeoscience* **10**, 161–180. (doi:10.5194/bg-10-161-2013)
- Cripps G, Lindeque P, Flynn KJ. 2014 Have we been underestimating the effects of ocean acidification in zooplankton? *Glob. Change Biol.* **20**, 3377–3385. (doi:10.1111/gcb.12582)
- Schoo KL, Malzahn AM, Krause E, Boersma M. 2013 Increased carbon dioxide availability alters phytoplankton stoichiometry and affects carbon cycling and growth of marine planktonic herbivore. *Mar. Biol.* **160**, 2145–2155. (doi:10.1007/s00227-012-2121-4)
- Borges AV, Gypens N. 2010 Carbonate chemistry in the coastal zone responds more strongly to eutrophication than to ocean acidification. *Limnol. Oceanogr.* **55**, 346–353. (doi:10.4319/lo.2010.55.1.0346)
- Cai W-J *et al.* 2011 Acidification of subsurface coastal waters enhanced by eutrophication. *Nat. Geosci.* **4**, 766–770. (doi:10.1038/ngeo1297)
- Macedo MF, Duarte P, Mendes P, Ferreira JG. 2001 Annual variation of environmental variables, phytoplankton species composition and photosynthetic parameters in a coastal lagoon. *J. Plankt. Res.* **23**, 719–732. (doi:10.1093/plankt/23.7.719)
- Hansen PJ. 2002 The effect of high pH on the growth and survival of marine phytoplankton: implications for species succession. *Aquat. Microb. Ecol.* **28**, 279–288. (doi:10.3354/ame028279)
- Hinga KR. 2002 Effect of high pH on coastal marine phytoplankton. *Mar. Ecol. Prog. Ser.* **238**, 281–300. (doi:10.3354/meps238281)
- Lundholm N, Hansen PJ, Kotaki Y. 2004 Effect of pH on growth and domoic acid production by potentially toxic diatoms of the genera *Pseudo-nitzschia* and *Nitzschia*. *Mar. Ecol. Prog. Ser.* **273**, 1–15. (doi:10.3354/meps273001)
- Hansen PJ, Lundholm N, Rost B. 2007 Growth limitation in marine red-tide dinoflagellates: effects of pH versus inorganic carbon availability. *Mar. Ecol. Prog. Ser.* **334**, 63–71. (doi:10.3354/meps334063)
- Pedersen MF, Hansen PJ. 2003 Effects of high pH on the growth and survival of six marine heterotrophic protists. *Mar. Ecol. Prog. Ser.* **260**, 33–41. (doi:10.3354/meps260033)
- Howarth RW. 2008 Coastal nitrogen pollution: a review of sources and trends globally and regionally. *Harmful Algae* **8**, 14–20. (doi:10.1016/j.hal.2008.08.015)
- Doney SC. 2010 The growing human footprint on coastal and open-ocean biogeochemistry. *Science* **328**, 1512–1516. (doi:10.1126/science.1185198)
- Coolley SR, Kite-Powell HL, Doney SC. 2009 Ocean acidification's potential to alter global marine ecosystem services. *Oceanography* **22**, 172–181. (doi:10.5670/oceanog.2009.106)
- Clark DR, Flynn KJ, Fabian H. 2014 Variation in elemental stoichiometry of the marine diatom

- Thalassiosira weissflogii* (Bacillariophyceae) in response to combined nutrient stress and changes in carbonate chemistry. *J. Phycol.* **50**, 640–651. (doi:10.1111/jpy.12208)
22. Flynn KJ, Blackford JC, Baird ME, Raven JA, Clark DR, Beardall J, Brownlee C, Fabian H, Wheeler GL. 2012 Changes in pH at the exterior surface of plankton with ocean acidification. *Nat. Clim. Change* **2**, 510–513. (doi:10.1038/nclimate1696)
  23. Glibert PM, Fullerton D, Burkholder JM, Cornwell J, Kana TM. 2011 Ecological stoichiometry, biogeochemical cycling, invasive species and aquatic food webs: San Francisco Estuary and comparative systems. *Rev. Fish. Sci.* **19**, 358–417. (doi:10.1080/10641262.2011.611916)
  24. Gao Y, Cornwell JC, Stoecker DK, Owens MS. 2012 Effects of cyanobacterial-driven pH increases on sediment nutrient fluxes and coupled nitrification-denitrification in a shallow fresh water estuary. *Biogeoscience* **9**, 2697–2710. (doi:10.5194/bg-9-2697-2012)
  25. Rabalais NN, Turner RE, Diaz RJ, Justić D. 2009 Global change and eutrophication in coastal waters. *ICES J. Mar. Sci.* **66**, 1528–1537. (doi:10.1093/icesjms/fsp047)
  26. Egge JK, Thingstad TF, Engel A, Bellerby RGJ, Riebesell U. 2009 Primary production during nutrient-induced blooms at elevated CO<sub>2</sub> concentrations. *Biogeoscience* **6**, 877–885. (doi:10.5194/bg-6-877-2009)
  27. Mitra A, Flynn KJ. 2006 Promotion of harmful algal blooms by zooplankton predatory activity. *Biol. Lett.* **2**, 194–197. (doi:10.1098/rsbl.2006.0447)
  28. Mitra A, Flynn KJ. 2005 Predator–prey interactions: is ‘ecological stoichiometry’ sufficient when good food goes bad? *J. Plankt. Res.* **27**, 393–399. (doi:10.1093/plankt/fbi022)
  29. Granéli E, Flynn KJ. 2006 Chemical and physical factors influencing toxin production. In *Ecology of harmful algae, Ecological studies*, vol. 189 (eds E Granéli, JT Turner), pp. 229–241. Berlin, Germany: Springer.
  30. Kim H, Spivack AJ, Menden-Deuer S. 2013 pH alters the swimming behaviors of the raphidophyte *Heterosigma akashiwo*: implications for bloom formation in an acidified ocean. *Harmful Algae* **26**, 1–11. (doi:10.1016/j.hal.2013.03.004)
  31. Anderson DA, Glibert PM, Burkholder JM. 2002 Harmful algal blooms and eutrophication: nutrient sources, composition, and consequences. *Estuaries* **25**, 562–584. (doi:10.1007/BF02804901)
  32. Heisler J *et al.* 2008 Eutrophication and harmful algal blooms: a scientific consensus. *Harmful Algae* **8**, 3–13. (doi:10.1016/j.hal.2008.08.006)
  33. Stramma L, Prince ED, Schmidtko S, Luo J, Hoolihan JP, Visbeck M, Wallace DWR, Brandt P, Körtzinger A. 2012 Expansion of oxygen minimum zones may reduce available habitat for tropical pelagic fishes. *Nat. Clim. Change* **2**, 33–37. (doi:10.1038/nclimate1304)
  34. Thomas H *et al.* 2007 Rapid decline of the CO<sub>2</sub> buffering capacity in the North Sea and implications for the North Atlantic Ocean. *Glob. Biogeochem. Cycle* **21**, GB4001. (doi:10.1029/2006GB002825)
  35. Lohbeck KT, Riebesell U, Reusch T. 2012 Adaptive evolution of a key phytoplankton species to ocean acidification. *Nat. Geosci.* **5**, 346–351. (doi:10.1038/ngeo1441)
  36. Flynn KJ, Stoecker DK, Mitra A, Raven JA, Glibert PM, Hansen PJ, Granéli E, Burkholder JM. 2013 Misuse of the phytoplankton–zooplankton dichotomy: the need to assign organisms as mixotrophs within plankton functional types. *J. Plankt. Res.* **35**, 3–11. (doi:10.1093/plankt/fbs062)
  37. Mitra A *et al.* 2014 The role of mixotrophic protists in the biological carbon pump. *Biogeoscience* **11**, 995–1005. (doi:10.5194/bg-11-995-2014)