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REVIEW

Warming up, turning sour, losing breath: ocean biogeochemistry under global change

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In the coming decades and centuries, the ocean's biogeochemical cycles and ecosystems will become increasingly stressed by at least three independent factors. Rising temperatures, ocean acidification and ocean deoxygenation will cause substantial changes in the physical, chemical and biological environment, which will then affect the ocean's biogeochemical cycles and ecosystems in ways that we are only beginning to fathom. Ocean warming will not only affect organisms and biogeochemical cycles directly, but will also increase upper ocean stratification. The changes in the ocean's carbonate chemistry induced by the uptake of anthropogenic carbon dioxide (CO_2) (i.e. ocean acidification) will probably affect many organisms and processes, although in ways that are currently not well understood. Ocean deoxygenation, i.e. the loss of dissolved oxygen (O_2) from the ocean, is bound to occur in a warming and more stratified ocean, causing stress to macro-organisms that critically depend on sufficient levels of oxygen. These three stressors—warming, acidification and deoxygenation—will tend to operate globally, although with distinct regional differences. The impacts of ocean acidification tend to be strongest in the high latitudes, whereas the low-oxygen regions of the low latitudes are most vulnerable to ocean deoxygenation. Specific regions, such as the eastern boundary upwelling systems, will be strongly affected by all three stressors, making them potential hotspots for change. Of additional concern are synergistic effects, such as ocean acidification-induced changes in the type and magnitude of the organic matter exported to the ocean's interior, which then might cause substantial changes in the oxygen concentration there. Ocean warming, acidification and deoxygenation are essentially irreversible on centennial time scales, i.e. once these changes have occurred, it will take centuries for the ocean to recover. With the emission of CO_2 being the primary driver behind all three stressors, the primary mitigation strategy is to reduce these emissions.

Keywords: climate change; deoxygenation; ocean warming; ocean acidification; ocean carbon cycle; ocean oxygen cycle

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1. Introduction

In 2006, the German Advisory Council on Global Change (WBGU) published an influential report in which it summarized what was known at that time with regard to how the ocean might respond to global change, primarily induced by the increases in greenhouse gases and the resulting warming [1]. It pointedly named this report 'The future oceans: warming up, rising high, turning sour'. As the title suggests, the Council highlighted three important stressors for marine systems: ocean warming, sea-level rise and ocean acidification. Since then, it has become increasingly clear that the Council missed an important additional stressor—ocean deoxygenation [2], i.e. the loss of oxygen from the ocean as a result of global climate change. Leaving out sea-level rise, as its direct impact on open ocean biogeochemistry and ecosystems is probably small, this paper aims to take a unified, broad-level look at the other three stressors, i.e. ocean warming, acidification and deoxygenation. Each of them, unless strong climate mitigation measures are implemented, is bound to have profound effects on marine biogeochemistry and ecosystems. The situation may be aggravated by these three stressors acting not in isolation but simultaneously, and even in part synergistically. It thus behoves us to improve our understanding of how large these stressors will be, where they will be most strongly expressed and how quickly, and how ocean biogeochemistry and ecosystems will respond to them. By adapting and updating the title of the WBGU report to 'Warming up, turning sour, losing breath: ocean biogeochemistry under change', this paper pays homage to the important foundation laid by that report, but also recognizes the developments since then.

The three stressors are the flip-side of the invaluable services that the ocean has provided to mankind since the onset of the industrial revolution. Ocean warming is the consequence of the ocean having taken up much of the extra heat accumulating in the Earth system as a result of the enhanced greenhouse effect. Between 1955 and 1998 alone, the ocean was responsible for more than 80 per cent of the total increase in the heat content of the Earth system (e.g. [3,4]). Most of this extra heat has accumulated in the near-surface ocean, causing a surface ocean warming of about 0.7°C over the last 100 years [5]. In contrast, the deep ocean changes are minuscule so far, so that the global mean ocean temperature has increased by less than 0.04°C between 1955 and 1998. This differential heating of the water column has increased the density gradient between the near-surface waters and the deep ocean, increasing the upper ocean stratification (figure 1*a*). Upper ocean stratification may be further modified by the expected acceleration of the hydrological cycle in response to global warming. Particularly in the high latitudes, the expected decrease in salinity in response to enhanced rainfall, melting of sea ice and river run-off may substantially enhance the warming-induced stratification (e.g. [8]). Stronger stratification tends to decrease upper ocean mixing and transport, thereby more strongly separating the upper ocean, which is in ready exchange with the atmosphere from the intermediate and deep ocean that contains the nutrients required for ocean productivity. Thus, the rising temperatures of the ocean will lead to at least two types of effects with regard to ocean biogeochemistry and ocean ecosystems. First, there will be direct effects as a result of most rates of biogeochemical and biological processes being temperature dependent. Second, ocean warming-induced stratification and other

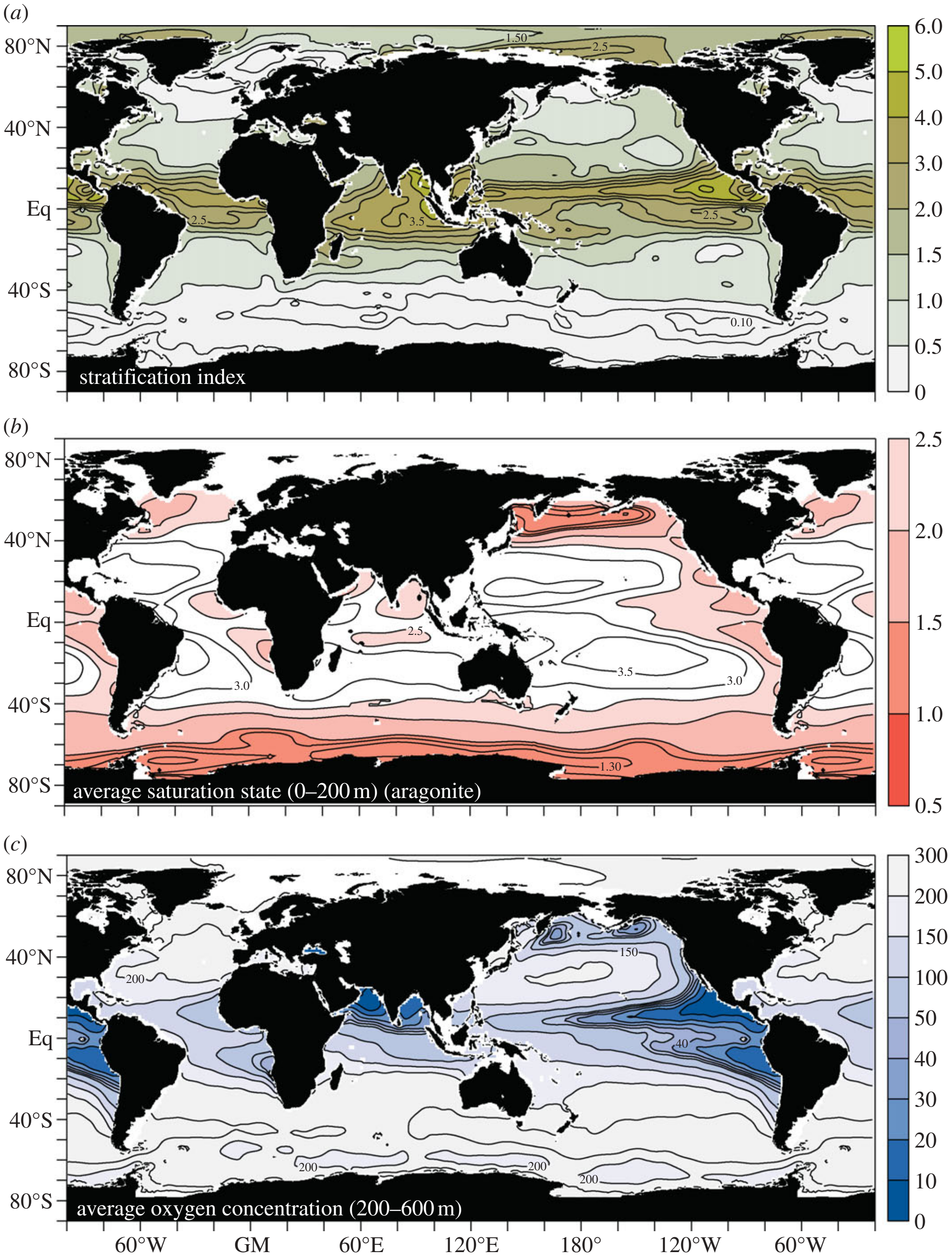

Figure 1. Global maps of present-day oceanic distributions. (*a*) Annual mean upper ocean stratification, expressed as the potential density difference (kg m^{-3}) between the upper ocean (0–50 m) and the upper thermocline (100–200 m). (*b*) Annual mean aragonite saturation state in the upper 200 m (computed from GLODAP [6]). (*c*) Mean oxygen concentration (µmol kg^{-1}) in the thermocline between 200 and 600 m depth (based on WOA05 [7]).

changes in upper ocean mixing and transport will cause a range of indirect effects. Among those, one can expect a more favourable light regime for phytoplankton in the high latitudes, more nutrient stress for phytoplankton in the low latitudes (e.g. [9,10]) and a generally reduced transport of gases (anthropogenic CO_2, chlorofluorocarbons (CFCs) and dissolved oxygen) from the near surface into the ocean's interior [11].

Ocean acidification is a direct consequence of the ocean absorbing large amounts of the anthropogenic CO_2 emitted into the atmosphere as a result of human activities [12,13]. Over the last 250 years, the ocean has removed about 30 per cent of the total anthropogenic emissions of CO_2 [14], thereby slowing down the increase in atmospheric CO_2 considerably. Without this sink, atmospheric CO_2 would have already surpassed 450 ppm, a level above which the chances to exceed the 2°C warming target are very substantial [15]. This uptake increases the concentration of dissolved CO_2 in sea water, but, because CO_2 is also a (weak) acid, a fraction of it dissociates and releases protons, which reduces the pH of seawater. The anthropogenic CO_2 that the ocean has taken up so far has led to a drop of about 0.1 pH units since pre-industrial times, but much larger changes are likely to loom in the future.

Most of the CO_2 taken up reacts with the carbonate ion (CO_3^{2-}) in seawater to form two bicarbonate ions (HCO_3^-) [16]. This decreases the concentration of CO_3^{2-} and thus lowers the saturation state with regard to the mineral phases of $CaCO_3$. Of particular relevance is the saturation concentration itself, i.e. the critical concentration of CO_3^{2-}, above which seawater is supersaturated with regard to mineral phases of $CaCO_3$, and below which seawater is undersaturated. In the present ocean, nearly all surface waters are substantially supersaturated, although to strongly varying degrees (figure 1*b*). In contrast, most of the deep ocean is undersaturated, creating conditions under which mineral forms of $CaCO_3$ are chemically dissolved. While the chemical changes resulting from the uptake of anthropogenic CO_2 by the ocean are well understood, the impact of these changes on marine biology, ecosystems and biogeochemical cycles are largely unclear.

The third and most recently recognized stressor, i.e. ocean deoxygenation, is primarily a consequence of the ocean's heat uptake [2,17,18], with the total effect being the sum of two generally reinforcing, but independent, processes. The first process is associated with the ocean's capacity to hold dissolved oxygen, i.e. O_2, which decreases with increasing temperatures as a result of the reduced O_2 solubility. The second process is associated with the kinetics of the resupply of O_2 to the ocean's interior. Given the demand for O_2 in the ocean interior away from the light-illuminated near-surface ocean owing to the oxidation of reduced organic matter, the O_2 concentration of the ocean's interior is determined by the balance between this demand and the supply of oxygen from the surface ocean. Many thermocline regions of the low latitudes have relatively high O_2 demands and low supply rates, leading to extended zones with low and even near-zero O_2 concentrations (figure 1*c*). Since the ocean warming-induced increased stratification tends to reduce mixing and transport, the supply of oxygen will tend to go down, causing interior O_2 levels to drop. Particular regions of the ocean have indeed been subject to substantial long-term loss trends [19], but current observations are insufficient to determine with great confidence whether the ocean's oxygen levels have indeed gone down on a global basis and by how much [2]. However, atmospheric O_2 measurements, when interpreted together with independent estimates of the oceanic uptake of anthropogenic CO_2 (e.g. [20]), suggest the presence of a considerable amount of 'excess' O_2 in the atmosphere that most likely stems from ocean outgassing (see also [21]).

In addition to this primarily climate change-driven deoxygenation in the open ocean, oxygen levels are also declining in many near-shore coastal regions and enclosed bays [22]. The primary driver for these near-shore changes is coastal eutrophication, however, caused by the increasing levels of nutrients added to the ocean from run-off and atmospheric deposition (see [23]). The loss of oxygen from the ocean will cause a myriad of effects, including a reduction in the habitable range for higher organisms that require a certain minimum level of oxygen for survival, and possibly major biogeochemical shifts.

The aim of this paper is not to provide a full in-depth review of all three stressors—interested readers are referred to more detailed studies—but to undertake a comparative analysis providing a unified view, highlighting the fact that all of these stressors are acting simultaneously and partially synergistically. Given the limited understanding of many effects and the rapid progress that is being made to improve this situation, this is by necessity only a snapshot. Although many details are uncertain, there is no doubt that ocean biogeochemistry and ocean ecosystems will be facing a period of rapid and substantial change (see [24]).

2. The three stressors—future changes and impacts

(*a*) *Ocean warming*

The magnitude of surface ocean warming during this century will be largely determined by the amount of greenhouse gases that will be emitted in the coming decades [25]. To first order, surface ocean temperatures will be warming at a slightly slower rate than the global mean surface air temperatures, which are predicted to increase between less than 2°C for the B1 scenario (1.1–2.9°C) and about 4°C for the high-emission scenario A1FI (2.4–6.4°C) [25]. In order to illustrate the magnitude and spatial distribution of the ocean changes in more detail, we turn to the results from one particular model (the National Center for Atmospheric Research Community Climate Model (NCAR CSM) v. 1.4) that was run using the SRES A2 scenario [26]. In this 'business-as-usual'-type scenario, the ocean warms by about 2°C relative to the pre-industrial type (figure 2*a*), about 0.6°C less than the lower parts of the atmosphere. Note that, because of its modest climate sensitivity, this model warms considerably less than the majority of climate models, which simulated a warming of 3.1°C for the end of this century under the A2 scenario (see [25]).

Surface ocean warming is not uniform, though, with stronger warming in the tropics and in the higher latitudes of the Northern Hemisphere (figure 2*a*). The largest warming is predicted to occur in regions where sea ice disappears, as the change from a highly reflectant ice surface (high albedo) to a low-reflectance ocean surface (low albedo) leads to a much stronger absorption of the incoming shortwave radiation from the sun. Little surface ocean warming is predicted in the Southern Ocean, as sea ice is simulated to remain largely unchanged there.

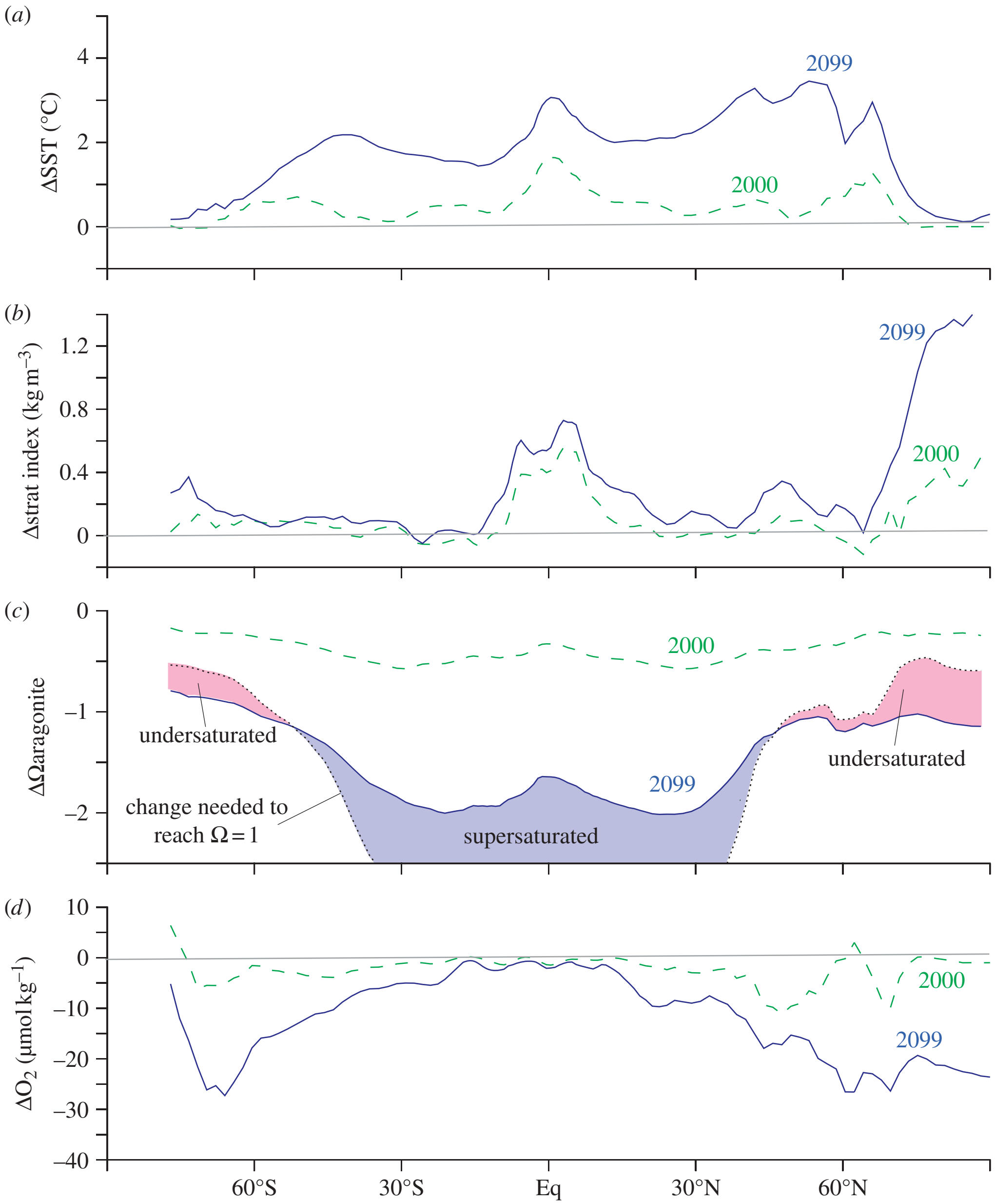

Figure 2. Zonal mean profiles of model-simulated changes in ocean properties for 2099 (under the IPCC SRES A2 scenario) and 2000 relative to the year 1850 (atmospheric CO_2 increased from 280 ppm in 1850 to 370 ppm in 2000 and to 840 ppm in 2099). (*a*) Change in sea-surface temperature; (*b*) change in upper ocean stratification, expressed as the density gradient between the upper ocean (0–50 m) and the upper thermocline (100–200 m); (*c*) change in the surface ocean saturation state with respect to aragonite; (*d*) change in the mean concentration of oxygen in the thermocline (200–600 m). Results are from the NCAR CSM 1.4 model and were kindly provided by Thomas Frölicher and Marco Steinacher, University of Bern [26,27].

Ocean warming will affect ocean ecosystems and biogeochemical processes directly, as most physiological and biogeochemical processes are strongly temperature dependent. For most physiological processes, typical Q10 factors, i.e. a measure of how much a rate increases per 10°C temperature increase, are in the range between 1.5 and 4 [28–30]. This means that the 2°C warming predicted by the A2 scenario for the end of this century would cause an acceleration of most physiological processes by about 7–30%. While it is virtually certain that these accelerated rates will lead to a faster turnover of matter in the ocean, it is substantially less clear whether this will also lead to a change in net productivity and export, as there are many other factors limiting these rates. Model simulations suggest that, with the exception of the Arctic, the direct influence of temperature changes on productivity is relatively small [9]. In contrast, the strong apparent temperature dependence of the fraction of production that is exported from the near-surface ocean [29] would suggest that a warming of a few degrees would substantially reduce export. Furthermore, a faster decomposition of the sinking organic matter would lead to reduced downward transport of organic carbon in the thermocline, causing a weaker biological pump and consequently a net loss of carbon from the ocean to the atmosphere. The magnitude of this positive feedback on global climate could be substantial (see [31]). Many other biogeochemical processes such as denitrification and $CaCO_3$ dissolution might be affected by temperature changes, but little is known about their sensitivity in natural systems.

Perhaps even more substantial changes in ocean biogeochemistry and ecosystems can be expected from the ocean warming-induced increase in stratification. In the NCAR CSM 1.4 model, stratification is stronger at the end of this century nearly everywhere, with the largest increase in stratification occurring in the tropics and in the Arctic (figure 2*b*). In both regions, lower salinity and warmer temperature work together to reduce surface density, thus increasing stratification. While the lower salinity in the tropics is primarily the result of increased precipitation, increased run-off and sea ice melting contribute to the stratification in the Arctic as well [27]. This near-global increase in stratification has major impacts on ocean productivity as it affects two major controls on marine productivity, namely nutrient supply and light availability [8–10]. One expects strongly differing responses in the various biomes, however [10,32]. In the primarily nutrient-limited and permanently stratified regions of the low latitudes, an increase in stratification is bound to reduce primary production. In contrast, in the high latitudes, where surface-mixed layers remain deep for a substantial amount of time, a stratification-induced shoaling of the mixed layer will probably lead to an increase in production, as these systems tend to be light limited. This is indeed what the majority of the models tend to suggest (e.g. [8,9]), and what the few historical observations to date support [33,34]). However, significant uncertainties remain with regard to the potential role of other limiting factors, such as zooplankton grazing and micronutrients (e.g. iron).

Ocean warming and enhanced stratification will also limit the oceanic uptake of a number of greenhouse gases, most importantly that of CO_2 and CFCs, as the transport of these gases from the near-surface ocean into the ocean's interior is the primary rate-limiting step. Model simulations suggest a reduction in the uptake of CO_2 from the atmosphere between 14 and 67 $\mathrm{Pg\,C\,yr^{-1}\,{}^{\circ}C^{-1}}$ of surface warming [35,36]. In certain models that corresponds to a decrease of up to 30 per cent in the uptake up to the year 2100 relative to an unchanging ocean, although most models suggest a more modest reduction.

(*b*) *Ocean acidification*

The magnitude of future ocean acidification, particularly that at the surface, is directly proportional to the amount of CO_2 which will be emitted into the atmosphere in the next decades and centuries. For most of the surface ocean, the magnitude can be rather accurately predicted for a given atmospheric CO_2 concentration pathway. This is because the approximately 20 year time scale associated with the increase in atmospheric CO_2 [37] is much longer than the roughly 1 year time scale associated with the equilibration of CO_2 across the air–sea interface [16]. As a consequence, the near-surface ocean tends to track the atmospheric perturbation, permitting us to estimate the changes in pH and carbonate chemistry relatively well by assuming local equilibrium. For the global mean surface ocean and for an increase in atmospheric CO_2 by 100 ppm, pH falls typically by about 0.07 pH units and the ocean saturation state with regard to aragonite is lowered by 0.3 [13].

Ocean acidification in near-surface waters will exhibit strong spatial variations (e.g. figure 2*c*). The NCAR CSM 1.4 results for the A2 scenario reveal, for 2099, a substantially larger drop of the surface ocean aragonite saturation state in the low- to mid-latitudes when compared with the high latitudes (figure 2*c*). This difference is mostly a result of the low latitudes having a much lower Revelle factor, i.e. the factor that determines how much anthropogenic CO_2 a particular water parcel can take up upon equilibration with an atmospheric perturbation [14,16]. Waters with low Revelle factor are characterized by high concentrations of CO_3^{2-}, which allows them to absorb more CO_2 from the atmosphere as this additional CO_2 is more effectively neutralized by reacting with CO_3^{2-} to form HCO_3^-. This results in large changes in CO_3^{2-} and the saturation state, while moderating the pH changes (not shown). The opposite is the case in the high latitudes. They experience much smaller changes in the saturation state, but larger changes in pH. This can again be explained mostly by differences in the Revelle factor, i.e. the fact that the high latitudes tend to have low concentrations of CO_3^{2-}.

These naturally low concentrations of CO_3^{2-} are also responsible for the observation that the high latitudes have low saturation states with regard to the various mineral forms of $CaCO_3$ to begin with (figure 1*b*). As a result, and despite their lower reduction in saturation state for a given change in atmospheric CO_2, these regions are first to cross the threshold of a saturation state of 1, meaning that they switch from super- to undersaturated conditions. In the Arctic Ocean, this threshold may be passed in the next decade for aragonite [27], and, in the Southern Ocean, waters will become permanently undersaturated with regard to this mineral sometime during the second half of this century [13], with some subregions crossing this threshold seasonally much earlier [38]. By the end of this century, the NCAR CSM 1.4 model suggests for the A2 scenario vast surface regions with undersaturations in the Southern Ocean and in the Arctic, but also extending from the Arctic into the North Atlantic and into the North Pacific (figure 2*c*).

The anthropogenic CO_2 taken up by the near-surface ocean is propagating downward into the ocean's interior, bringing ocean acidification into the thermocline and into the deep ocean. As this takes years and decades (thermocline) to centuries (deep ocean), ocean acidification will be delayed relative to the surface [12]. Nevertheless, the anthropogenic CO_2 taken up by the ocean since pre-industrial times has already propagated downward detectably to nearly 1000 m, on average [14]. This has already caused the aragonite saturation horizon to shoal notably in a few distinct regions, particularly in parts of the Southern Ocean, the equatorial Atlantic and in the North Pacific [39].

The chemical changes associated with ocean acidification have the potential to affect ocean biogeochemistry and ecosystems in a myriad of ways (see [40]). Most organisms that have been studied so far show either a negative or no response, but there are also several organisms that appear to benefit from ocean acidification. Most emphasis so far has been put on organisms that build carbonate-containing shells, such as coccolithophorids, foraminifera, pteropods, mussels and corals. The vast majority of these species show a reduction in their calcification in response to the lower pH and saturation states. The situation is different for photosynthesis, where the majority of species studied reveal a stimulating effect, probably because of the higher availability of dissolved CO_2, the main substrate for photosynthesis. Nitrogen fixers also appear to benefit [41], while reproductive success in molluscs and echinoderms appears to suffer from ocean acidification. It is too early to draw firm conclusions on the net effect, but it is rather clear that ocean acidification will affect marine organisms and will cause change. And it is also evident that organisms that aim to build and maintain $CaCO_3$ shells in undersaturated waters are challenged.

Ocean acidification also affects biogeochemistry directly. By far the most important effect is the ocean acidification-induced reduction of the ocean's uptake capacity for anthropogenic CO_2. This well-understood effect is responsible for a more than 30 per cent reduction in the ocean's uptake relative to an unacidified ocean [42,43]. Further, more indirect changes in ocean biogeochemistry could arise from ocean acidification-induced changes in the carbon-to-nitrogen stoichiometric ratios of marine phytoplankton [44], which through its effect on oxygen demand during the remineralization of the resulting organic matter could cause major changes in the marine distribution of oxygen [45] (see also [46]). Many additional impacts and feedbacks are currently being discussed (e.g. [47]), but our current understanding and our ability to quantify these effects are poor.

(*c*) *Ocean deoxygenation*

The magnitude of future open ocean deoxygenation tends to scale with the oceanic heat uptake [2]. This is because the two critical governing processes for the ocean's oxygen content, i.e. mean temperature through its effect on solubility and stratification through its effect on oxygen resupply to the ocean's interior, tend to scale with the oceanic rate of warming. Model results and theoretical considerations suggest that the whole ocean loses on average about 6 nmol of O_2 for every joule of heat it takes up [2], which translates into a loss of approximately 32 Pmol of O_2 (approx. $24\,\mu\mathrm{mol\,kg^{-1}}$) per degree Celsius of warming. This scaling varies relatively modestly from one model to another (±20%), but models vary substantially in their mean O_2 concentration and in their projected heat uptake for this century. For the A2 scenario, the NCAR CSM 1.4 model predicts a total loss of about 6 Pmol (4.3 μmol kg^{-1}) by 2100, which corresponds to a decrease of about 2.6 per cent of its inventory [26]. This is in the middle of the large range of declines (1–7%) suggested by the currently published model results, although this range also includes different emission scenarios (e.g. [17,18,45,48,49]).

In the NCAR model, most O_2 is lost from the thermocline in the mid- to high latitudes (figure 2*d*), consistent with the expectations based on the stratification-induced reduced supply of oxygen from the surface into the thermocline. Almost no change is projected to occur in the low-oxygen regions of the tropical and subtropical thermocline (figure 2*d*), owing to these regions experiencing a lesser oxygen demand because of lower biological production and export of organic matter in the overlying near-surface waters [26]. However, the confidence in these projections is low, particularly because current ocean biogeochemistry models have serious limitations in their ability to correctly simulate today's observed oxygen distributions (figure 1*b*). In particular, these models fail to simulate the distribution and extent of the oxygen minimum zones in the tropical and subtropical regions of the world's ocean, probably because of their failure to capture correctly the interplay between physical oxygen supply by ocean circulation and oxygen demand from sinking organic matter (e.g. [50]). The O_2 concentration in these low-oxygen regions responds very sensitively to small changes in either of these two processes, as illustrated by the large increases in the volume of waters with concentrations below 5 μmol kg^{-1} (suboxic conditions) simulated in response to ocean acidification-induced increases in the C : N ratio of organic matter [45] or decreases in carbonate ballast [46].

A reduction in the ocean's oxygen content will mostly affect organisms that have a low tolerance for reduced oxygen concentrations. Many crustacea and fishes cannot tolerate O_2 concentrations below the hypoxic threshold of approximately 60 μmol kg^{-1} for extended periods, and concentrations below approximately 20 μmol kg^{-1} are lethal for virtually all higher organisms [51]. While current model projections suggest that the mean ocean interior concentration of O_2 will stay well above these thresholds, many regions will get perilously close to them and cross them.

Widespread ocean deoxygenation will also have an impact on several of the ocean's major biogeochemical cycles, as O_2 is a key controlling factor for the cycling of carbon, nitrogen, iron and other elements. The production of nitrous oxide (N_2O) is highly sensitive to oxygen concentrations, with an order of magnitude larger production at low O_2 levels when compared with well-oxygenated conditions [50,52,53]. Particularly when the O_2 concentration drops below approximately 5 μmol kg^{-1}, fundamental changes in the cycling of these elements occur. Denitrification, where nitrate replaces O_2 as the terminal electron acceptor, becomes the major pathway for the degradation of organic matter, thereby removing a nutrient that limits ocean productivity from the ocean [54].

While our confidence is high concerning the expectation of the ocean losing dissolved oxygen in the coming century, our ability to project where exactly these changes will occur and what this implies for ocean ecosystems and biogeochemistry is not well developed. The largest changes in O_2 will probably occur close to the outcrops of the thermocline and deep ocean, but the regions with highest vulnerability will probably be the low-oxygen regions of the open ocean.

3. The triple whammy

The three stressors, i.e. ocean warming, ocean acidification and ocean deoxygenation, are acting simultaneously as they are fundamentally driven by the same underlying process, i.e. the increase in atmospheric CO_2 and the resulting changes in the Earth's radiative forcing. Ocean warming and deoxygenation are also driven by the emission of other greenhouse gases, such as methane (CH_4), nitrous oxide (N_2O) and CFCs. But the contribution of CO_2 is by far the most important one, especially when considering the future evolution, where the relative contribution of CO_2 to total radiative forcing most likely will be even larger than it has been in the past.

(*a*) *Synergistic effects*

The three key stressors are known to interact with each other creating synergistic effects, but our ability to quantify these interactions is virtually non-existent as only a handful of studies have explored such interactions (see [55,56]). Perhaps best studied so far is the aforementioned impact of ocean acidification on future marine oxygen levels [45,46]. One mechanism is the possibility that ocean acidification increases the carbon to nitrogen ratio of marine organic matter [44], which then requires more oxygen per unit nitrogen to remineralize this organic matter when it sinks through the water column. This enhanced oxygen demand would occur throughout the water column, but its impact would be greatest at the depths of the oxygen minima. Modelling studies suggest that this effect could lead to a more than 50 per cent increase in the volume of suboxic waters by the end of this century [45]. In addition to creating dead zones, this would increase marine denitrification substantially and hence affect the marine nitrogen inventory. Another mechanism to affect marine oxygen levels is the possible ocean acidification-induced reduction of marine calcification, which would result in the production of a smaller amount of mineral $CaCO_3$ that tends to 'ballast' organic matter on its way down through the water column. As a result, organic matter would tend to sink less rapidly, leading to a shallower remineralization and an upward shift and compression of the oxygen demand profile. This results in a substantial reduction of oxygen in the shallower parts of the thermocline [46], where oxygen is already low, while the deeper parts of the ocean gain oxygen. A third potential mechanism is linked to the possibility that ocean acidification increases marine nitrogen fixation (e.g. [57]). This would tend to cause an increase in organic matter export and ocean interior oxygen demand, with consequences similar to those associated with the ocean acidification-induced high carbon to nitrogen ratio of marine export production [47].

An entirely different set of synergistic effects might occur at the physiological level. Elevated levels of dissolved CO_2 might reduce the amount of energy gained from the oxidation of organic matter [55]. This will increase the respiratory stress of higher order organisms at low oxygen concentrations, effectively resulting in a higher oxygen concentration when the hypoxic threshold is reached. This results in the paradoxical situation in which the volume of hypoxic waters that are lethal to higher order organisms increases, while the actual oxygen concentration remains unchanged. The nonlinearities of the oceanic CO_2 system may aggravate this further. As ocean acidification progresses, and the available CO_3^{2-} ions are

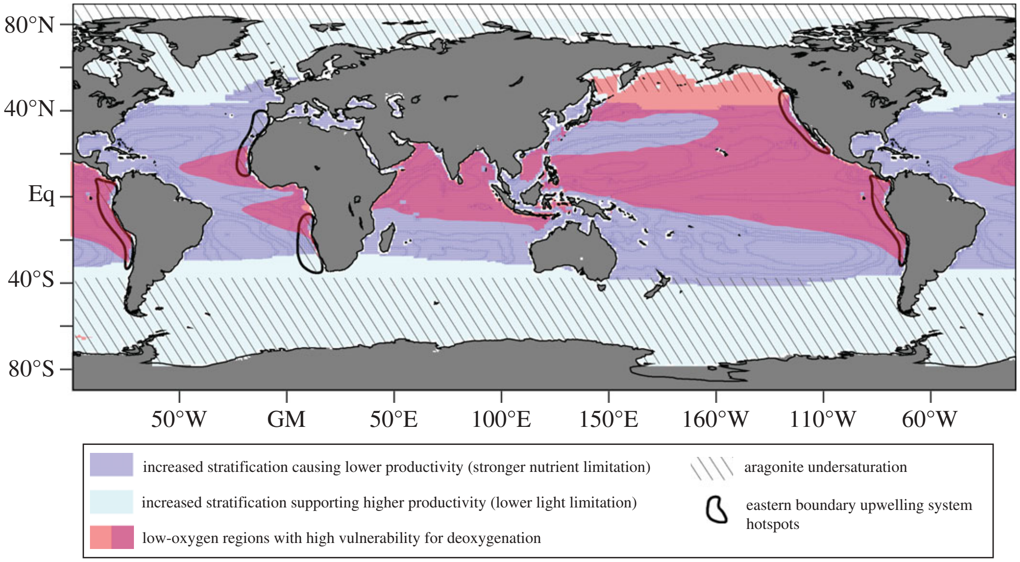

Figure 3. Global map showing regions of particular vulnerability to the three main stressors, i.e. ocean warming, acidification and deoxygenation.

titrated away, the dissolved CO_2 concentration will increase overproportionally, leading to a faster development of respiratory stress. Furthermore, rising temperatures would similarly increase the oxygen demand for higher organisms, yet tend to reduce the supply of oxygen. Finally, elevated CO_2 and lower O_2 levels might reduce the thermal tolerance of certain organisms, increasing the impact of ocean warming [56,58]. Even in the absence of a substantial warming, the reduction in the thermal tolerance by ocean acidification and deoxygenation could cause substantial shifts in species diversity and ecosystem composition through the reduction of the habitat range.

In summary, while there remain many unresolved questions, the tendency is clear. Most potential synergistic effects tend to enhance the effect of the single stressors, so that the fact that these stressors occur synchronously is cause for concern.

(*b*) *Hotspots*

Fundamentally, ocean warming, acidification and deoxygenation are globally acting processes, but with distinct regional patterns of changes and vulnerability (figure 3). Ocean warming will likely reduce biological production in the already stratified low and temperate latitudes, but will tend to enhance production in the high latitudes. Ocean acidification appears to cause most problems in the high latitudes, where waters are naturally low in CO_3^{2-}, and hence have very limited capacity to buffer against the changes induced by the uptake of anthropogenic CO_2 from the atmosphere. Although the largest changes in the ocean's O_2 content will likely occur in the mid- to high latitudes close to the outcrop of the ocean's interior density surfaces, the changes that will cause the highest impact will probably occur in the low-oxygen regions of the low-latitude thermoclines.

One region where all three stressors may conspire is that of the eastern boundary upwelling systems, such as the California, Humboldt, Canary or Benguela upwelling systems [59]. Surface warming and increased stratification may reduce the effective supply of nutrients by upwelling, leading to lower biological productivity. This effect could be modified by global warming-induced changes in the upwelling favourable winds [60], although the exact sign and magnitude of these changes are not well established [61]. Furthermore, these systems are naturally low in pH and in CO_3^{2-}, resulting in their being already close to the threshold of an aragonite saturation state of 1 [62]. Finally, the thermocline waters of these systems tend to be low in O_2 so that relatively small absolute changes could bring them across some of the O_2 thresholds [23]. Few studies have been undertaken to investigate how these particular systems might evolve in the future in response to these stressors, but recent observations clearly point in the direction of these systems being particularly vulnerable, forming critical hotspots. For example, O_2 levels in the California Current System [63,64], but also in the Humboldt Current System off the coast of Peru and in the Canary Current System, have been decreasing [19], leading to a shoaling of the hypoxic boundary. Corrosive waters with saturation states well below unity have been observed to upwell onto the continental shelf of western North America [62], an event that has become more frequent owing to the ocean acidification-induced shoaling of the saturation horizon [65]. A continued shoaling of the hypoxic boundary would actually accelerate the shoaling of the saturation horizon as well, as low-oxygen waters tend to be more corrosive because of the higher addition of CO_2 from the remineralization of organic matter. Therefore, special attention should be given to these eastern boundary upwelling systems, especially when considering their substantial contribution to global fisheries [59].

(*c*) *Commitments and irreversibility*

Ocean warming, acidification and deoxygenation are virtually irreversible on the human time scale. This is because the primary driver for all three stressors, i.e. the emission of CO_2 into the atmosphere, will cause global changes that will be with us for many hundreds, if not thousands, of years (see [66]). Once CO_2 is emitted, a sizeable fraction of it will remain in the atmosphere for more than a thousand years, continuing to contribute to radiative forcing and keeping the Earth's temperatures well above pre-industrial levels. Furthermore, most of the CO_2 that is being removed from the atmosphere actually enters the ocean, leading to ocean acidification there. Thus, the only way these changes can be undone is by removing CO_2 from the atmosphere–ocean–land system. This is largely accomplished by weathering reactions in the ocean and on land that produce CO_3^{2-} ions to replace those that have been titrated away in the ocean by the invading anthropogenic CO_2. But it takes several thousand years for these processes to undo the human CO_2 footprint [67].

Even if we limited CO_2 emissions to a level that stabilized atmospheric CO_2 at present levels, some additional changes in the global system inevitably will occur. These are changes that we have already made a commitment for, but have not been realized yet owing to the inertia of the Earth system. With regard to ocean warming, one can expect an additional surface ocean temperature increase of about 0.6°C [68], so that it is highly likely that a substantial additional increase in stratification as well as ocean deoxygenation will occur, even when greenhouse gas concentrations were stabilized at present levels. A large commitment exists for the ocean interior with regard to ocean acidification, as it takes decades to centuries for the atmospheric CO_2 perturbation to be transported to depth, so that ocean acidification will be ongoing at depth for centuries to come.

4. The way ahead

Substantial mitigation measures are required if the ocean is to be spared from this triple whammy. The primary objective must be to reduce the emission of CO_2, but it is important to limit the growth of all greenhouse gases, as all of them contribute to ocean warming and deoxygenation. At the same time, strategies need to developed to cope with the changes that may lie ahead. This includes not only the changes we are already committed to by past emissions, but also those that will occur in the future as it is difficult to foresee a future without a substantial additional increase in the concentration of CO_2 and that of other greenhouse gases.

But given our only weakly developed understanding of the impact of these three stressors on marine biogeochemistry and ecosystems, dedicated research efforts are required to shed more light on these connected issues. While ocean acidification has been recognized as a topic of high research priority leading to a crescendo of studies, deoxygenation has not reached that level of recognition. Also, the study of the direct influences of ocean warming and changes in ocean transport and mixing on ocean ecosystems and biogeochemistry appears to have been unsuccessful in receiving the level of attention it deserves. But what is really missing is the joint perspective, where the full and synergistic effect of all three stressors acting at the same time is investigated. This will require a coordinated approach, requiring methods that span the range from detailed laboratory studies and *in situ* manipulation experiments to large-scale monitoring and modelling approaches.

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References

1 German Advisory Council on Global Change. 2006 *The future oceans: warming up, rising high, turning sour.* Berlin, Germany: WBGU.

2 Keeling, R. F., Kortzinger, A. & Gruber, N. 2010 Ocean deoxygenation in a warming world. *Annu. Rev. Mar. Sci.* **2**, 199–229. (doi:10.1146/annurev.marine.010908.163855)

3 Levitus, S., Antonov, J. & Boyer, T. 2005 Warming of the world ocean. *Geophys. Res. Lett.* **32**, L02604. (doi:10.1029/2004GL021592)

4 Lyman, J. M., Good, S. A., Gouretski, V. V., Ishii, M., Johnson, G. C., Palmer, M. D., Smith, D. M. & Willis, J. K. 2010 Robust warming of the global upper ocean. *Nature* **465**, 334–337. (doi:10.1038/nature09043)

5 Trenberth, K. E. *et al.* 2007 Observations: surface and atmospheric climate change. In *Climate change 2007: the physical science basis. Contribution of Working Group I to the Fourth*

Assessment Report of the Intergovernmental Panel on Climate Change (eds S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. Averyt, M. Tignor & H. Miller). Cambridge, UK: Cambridge University Press.

6 Key, R. M. *et al.* 2004 A global ocean carbon climatology: results from the Global Data Analysis Project (GLODAP). *Global Biogeochem. Cycles* **18**, GB4031. (doi:10.1029/2004GB002247)

7 Garcia, H. E., Locarnini, R. A., Boyer, T. P. & Antonov, J. I. 2006 World ocean atlas 2005. Vol. 4. Nutrients (phosphate, nitrate, silicate). In *NOAA Atlas Nesdis 64* (ed. S. Levitus), p. 396. Washington, DC: US Government Printing Office.

8 Bopp, L., Monfray, P., Aumont, O., Dufresne, J.-L., Treut, H. L., Madec, G., Terray, L. & Orr, J. C. 2001 Potential impact of climate change on marine export production. *Global Biogeochem. Cycles* **15**, 81–99. (doi:10.1029/1999GB001256)

9 Steinacher, M. *et al.* 2010 Projected 21st century decrease in marine productivity: a multi-model analysis. *Biogeosciences* **7**, 979–1005. (doi:10.5194/bg-7-979-2010)

10 Marinov, I., Doney, S. C. & Lima, I. D. 2010 Response of ocean phytoplankton community structure to climate change over the 21st century: partitioning the effect of nutrients, temperature and light. *Biogeosciences* **7**, 3941–3959. (doi:10.5194/bg-7-3941-2010)

11 Sarmiento, J. L., Hughes, T. M. C., Stouffer, R. J. & Manabe, S. 1998 Simulated response of the ocean carbon cycle to anthropogenic climate warming. *Nature* **393**, 245–249. (doi:10.1038/30455)

12 Caldeira, K. & Wickett, M. E. 2003 Anthropogenic carbon and ocean pH. *Nature* **425**, 365. (doi:10.1038/425365a)

13 Orr, J. C. *et al.* 2005 Aragonite undersaturation in the high-latitude surface ocean within the 21st century. *Nature* **437**, 681–686. (doi:10.1038/nature04095)

14 Sabine, C. L. *et al.* 2004 The oceanic sink for anthropogenic CO_2. *Science* **305**, 367–371. (doi:10.1126/science.1097403)

15 Meinshausen, M., Meinshausen, N., Hare, W., Raper, S. C. B., Frieler, K., Knutti, R., Frame, D. J. & Allen, M. R. 2009 Greenhouse-gas emission targets for limiting global warming to 2°C. *Nature* **458**, 1158–1162. (doi:10.1038/nature08017)

16 Sarmiento, J. L. & Gruber, N. 2006 *Ocean biogeochemical dynamics*. Princeton, NJ: Princeton University Press.

17 Plattner, G.-K., Joos, F. & Stocker, T. F. 2002 Revision of the global carbon budget due to changing air-sea oxygen fluxes. *Global Biogeochem. Cycles* **16**, 1096. (doi:10.1029/2001GB001746)

18 Bopp, L., Le Quéré, C., Heimann, M., Manning, A. & Monfray, P. 2002 Climate-induced oceanic oxygen fluxes: implications for the contemporary carbon budget. *Global Biogeochem. Cycles* **16**, 1022. (doi:10.1029/2001GB001445)

19 Stramma, L., Johnson, G. C., Sprintall, J. & Mohrholz, V. 2008 Expanding oxygen-minimum zones in the tropical oceans. *Science* **320**, 655–658. (doi:10.1126/science.1153847)

20 Gruber, N. *et al.* 2009 Oceanic sources, sinks, and transport of atmospheric CO_2. *Global Biogeochem. Cycles* **23**, GB1005. (doi:10.1029/2008GB003349)

21 Manning, A. C. & Keeling, R. F. 2006 Global oceanic and land biotic carbon sinks from the Scripps atmospheric oxygen flask sampling network. *Tellus Ser. B* **58**, 95–116. (doi:10.1111/j.1600-0889.2006.00175.x)

22 Gilbert, D., Rabalais, N. N., Diaz, R. J. & Zhang, J. 2010 Evidence for greater oxygen decline rates in the coastal ocean than in the open ocean. *Biogeosciences* **7**, 2283–2296. (doi:10.5194/bg-7-2283-2010)

23 Rabalais, N. N., Diaz, R. J., Levin, L. A., Turner, R. E., Gilbert, D. & Zhang, J. 2010 Dynamics and distribution of natural and human-caused hypoxia. *Biogeosciences* **7**, 585–619. (doi:10.5194/bg-7-585-2010)

24 Doney, S. C. 2010 The growing human footprint on coastal and open-ocean biogeochemistry. *Science* **328**, 1210–1216. (doi:10.1126/science.1185198)

25 Meehl, G. A. *et al.* 2007 Global climate projections. In *Climate change 2007: the physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (eds S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. Averyt, M. Tignor & H. Miller). Cambridge, UK: Cambridge University Press.

26 Frölicher, T. L., Joos, F., Plattner, G.-K., Steinacher, M. & Doney, S. C. 2009 Natural variability and anthropogenic trends in oceanic oxygen in a coupled carbon cycle-climate model ensemble. *Global Biogeochem. Cycles* **23**, GB1003. (doi:10.1029/2008GB003316)

27 Steinacher, M., Joos, F., Frölicher, T. L., Plattner, G.-K. & Doney, S. C. 2009 Imminent ocean acidification projected with the NCAR global coupled carbon cycle-climate model. *Biogeosciences* **6**, 515–533. (doi:10.5194/bg-6-515-2009)

28 Eppley, R. W. 1972 Temperature and phytoplankton growth in the sea. *Fish. Bull.* **70**, 1063–1085.

29 Laws, E. A., Falkowski, P., Carpenter, E. & Ducklow, H. 2000 Temperature effects on export production in the open ocean. *Global Biogeochem. Cycles* **14**, 1231–1246. (doi:10.1029/1999GB001229)

30 White, P. A., Kalff, J., Rasmussen, J. B. & Gasol, J. M. 1991 The effect of temperature and algal biomass on bacterial production and specific growth rate in freshwater and marine habitats. *Microb. Ecol.* **21**, 99–118. (doi:10.1007/BF02539147)

31 Kwon, E. Y., Primeau, F. & Sarmiento, J. L. 2009 The impact of remineralization depth on the air–sea carbon balance. *Nat. Geosci.* **2**, 630–635. (doi:10.1038/NGEO612)

32 Sarmiento, J. L. *et al.* 2004 Response of ocean ecosystems to climate warming. *Global Biogeochem. Cycles* **18**, GB3003. (doi:10.1029/2003GB002134)

33 Boyce, D. G., Lewis, M. R. & Worm, B. 2010 Global phytoplankton decline over the past century. *Nature* **466**, 591–596. (doi:10.1038/nature09268)

34 Behrenfeld, M. J. *et al.* 2006 Climate-driven trends in contemporary ocean productivity. *Nature* **444**, 752–755. (doi:10.1038/nature05317)

35 Friedlingstein, P. *et al.* 2006 Climate-carbon cycle feedback analysis: results from the C4MIP model intercomparison. *J. Clim.* **19**, 3337–3353. (doi:10.1175/JCLI3800.1)

36 Plattner, G.-K. *et al.* 2008 Long-term climate commitments projected with climate-carbon cycle models. *J. Clim.* **21**, 2721–2751. (doi:10.1175/2007JCLI1905.1)

37 Gloor, M., Gruber, N. & Sarmiento, J. 2010 What can be learned about carbon cycle climate feedbacks from the CO_2 airborne fraction? *Atmos. Chem. Phys.* **10**, 7739–7751. (doi:10.5194/acp-10-7739-2010)

38 McNeil, B. I. & Matear, R. J. 2008 Southern Ocean acidification: a tipping point at 450 ppm atmospheric CO_2. *Proc. Natl Acad. Sci. USA* **105**, 18 860–18 864. (doi:10.1073/pnas.0806318105)

39 Feely, R. A., Sabine, C. L., Lee, K., Berelson, W., Kleypas, J., Fabry, V. J. & Millero, F. J. 2004 Impact of anthropogenic CO_2 on the $CaCO_3$ system in the oceans. *Science* **305**, 362–366. (doi:10.1126/science.1097329)

40 Doney, S. C., Fabry, V. J., Feely, R. A. & Kleypas, J. A. 2009 Ocean acidification: the other CO_2 problem. *Annu. Rev. Mar. Sci.* **1**, 169–192. (doi:10.1146/annurev.marine.010908.163834)

41 Hutchins, D. A., Mulholland, M. R. & Fu, F. 2009 Nutrient cycles and marine microbes in a CO_2 enriched ocean. *Oceanography* **22**, 128–145.

42 Sarmiento, J. L., Le Quéré, C. & Pacala, S. W. 1995 Limiting future atmospheric carbon dioxide. *Global Biogeochem. Cycles* **9**, 121–137. (doi:10.1029/94GB01779)

43 Gruber, N., Friedlingstein, P., Field, C. B., Valentini, R., Heimann, M., Richey, J. E. Romero-Lankau, P., Schulze, E.-D. & Chen, C.-T. A. 2004 The vulnerability of the carbon cycle in the 21st century: an assessment of carbon–climate–human interactions. *The global carbon cycle: integrating humans, climate, and the natural world* (eds C. B. Field & M. R. Raupach), pp. 45–76. Washington, DC: Island Press.

44 Riebesell, U. *et al.* 2007 Enhanced biological carbon consumption in a high CO_2 ocean. *Nature* **450**, 545–548. (doi:10.1038/nature06267)

45 Oschlies, A., Schulz, K. G., Riebesell, U. & Schmittner, A. 2008 Simulated 21st century's increase in oceanic suboxia by CO_2-enhanced biotic carbon export. *Global Biogeochem. Cycles* **22**, GB4008. (doi:10.1029/2007GB003147)

46 Hofmann, M. & Schellnhuber, H.-J. 2009 Oceanic acidification affects marine carbon pump and triggers extended marine oxygen holes. *Proc. Natl Acad. Sci. USA* **106**, 3017–3022. (doi:10.1073/pnas.0813384106)

47 Gehlen, M., Gruber, N., Gangsto, R., Bopp, L. & Oschlies, A. 2011 Biogeochemical consequences of ocean acidification and feedbacks to the earth sysatem. In *Ocean acidification* (eds J.-P. Gattuso & L. Hansson), ch. 12. Cambridge, UK: Cambridge University Press.

48 Matear, R. J., Hirst, A. C. & McNeil, B. I. 2000 Changes in dissolved oxygen in the Southern Ocean with climate change. *Geochem. Geophys. Geosyst.* **1**, 1050. (doi:10.1029/2000GC000086)

49 Schmittner, A., Oschlies, A., Matthews, H. D. & Galbaith, E. D. 2008 Future changes in climate, ocean circulation, ecosystems, and biogeochemical cycling simulated for a business-as-usual CO_2 emission scenario until year 4000 AD. *Global Biogeochem. Cycles* **22**, GB1013. (doi:10.1029/2007GB002953)

50 Jin, X. & Gruber, N. 2003 Offsetting the radiative benefit of ocean iron fertilization by enhancing N_2O emissions. *Geophys. Res. Lett.* **30**, 2249. (doi:10.1029/2003GL018458)

51 Vaquer-Sunyer, R. & Duarte, C. M. 2008 Thresholds of hypoxia for marine biodiversity. *Proc. Natl Acad. Sci. USA* **105**, 15 452–15 457. (doi:10.1073/pnas.0803833105)

52 Suntharalingam, P., Sarmiento, J. L. & Toggweiler, J. R. 2000 Global significance of nitrous-oxide production and transport from oceanic low-oxygen zones: a modeling study. *Global Biogeochem. Cycles* **14**, 1353–1370. (doi:10.1029/1999GB900100)

53 Nevison, C. D., Butler, J. & Elkins, J. 2003 Global distribution of N_2O and the δN_2O/AOU yield in the subsurface ocean. *Global Biogeochem. Cycles* **17**, 1119. (doi:10.1029/2003GB002068)

54 Gruber, N. 2008 The marine nitrogen cycle: overview and challenges. In *Nitrogen in the marine environment* (eds D. G. Capone, D. A. Bronk, M. R. Mulholland & E. Carpenter), ch. 1, 2nd edn. San Diego, CA: Academic Press.

55 Brewer, P. G. & Peltzer, E. T. 2009 Limits to marine life. *Science* **324**, 347–348. (doi:10.1126/science.1170756)

56 Portner, H.-O. 2010 Oxygen- and capacity-limitation of thermal tolerance: a matrix for integrating climate-related stressor effects in marine ecosystems. *J. Exp. Biol.* **213**, 881–893. (doi:10.1242/jeb.0375523)

57 Hutchins, D. A., Fu, F. X., Zhang, Y., Warner, M. E., Feng, Y., Portune, K., Bernhardt, P. W. & Mulholland, M. R. 2007 CO_2 control of *Trichodesmium* N_2 fixation, photosynthesis, growth rates and elemental ratios: implications for past, present and future ocean. *Limnol. Oceanogr.* **52**, 1293–1304. (doi:10.4319/lo.2007.52.4.1293)

58 Metzger, R., Sartoris, F., Langebuch, M. & Pörtner, H. O. 2007 Influence of elevated CO_2 concentrations on thermal tolerance of the edible crab, *Cancer Pagurus. J. Thermal Biol.* **32**, 144–151. (doi:10.1016/j.jtherbio.2007.01.010)

59 Fréon, P., Barrange, M. & Aristegui, J. 2009 Eastern boundary upwelling ecosystems: integrative and comparative approaches. *Prog. Oceanogr.* **83**, 1–14. (doi:10.1016/j.pocean.2009.08.001)

60 Bakun, A. 1990 Coastal ocean upwelling. *Science* **247**, 198–201. (doi:10.1126/science.247.4939.198)

61 Diffenbaugh, N. S. 2005 Response of large-scale eastern boundary current forcing in the 21st century. *Geophys. Res. Lett.* **32**, L19718. (doi:10.1029/2005GL023905)

62 Feely, R. A., Sabine, C. L., Hernandez-Ayon, M., Ianson, D. & Hales, B. 2008 Evidence for upwelling of corrosive ‘acidified’ water onto the continental shelf. *Science* **320**, 1490–1492. (doi:10.1126/science.1155676)

63 Bograd, S. J., Castro, C. G., Lorenzo, E. D., Palacios, D. M., Bailey, H., Gilly, W. & Chavez, F. P. 2008 Oxygen declines and the shoaling of the hypoxic boundary in the California Current. *Geophys. Res. Lett.* **35**, L12607. (doi:10.1029/2008GL034185)

64 Chan, F., Barth, J. A., Lubchenco, J., Kirincich, A., Weeks, H., Peterson, W. T. & Menge, B. A. 2008 Emergence of anoxia in the California Current large marine ecosystem. *Science* **319**, 920. (doi:10.1126/science.1149016)

65 Hauri, C., Gruber, N., Plattner, G.-K., Alin, S., Feely, R. A., Hales, B. & Wheeler, P. 2009 Ocean acidification in the California Current System. *Oceanography* **22**, 60–71.

66 Solomon, S., Plattner, G.-K., Knutti, R. & Friedlingstein, P. 2009 Irreversible climate change due to carbon dioxide emissions. *Proc. Natl Acad. Sci. USA* **106**, 1704–1709. (doi:10.1073/pnas.0812721106)

67 Archer, D. *et al.* 2009 Atmospheric lifetime of fossil fuel carbon dioxide. *Annu. Rev. Earth Planet. Sci.* **37**, 117–134. (doi:10.1146/annurev.earth.031208.100206)

68 Meehl, G. A., Washington, W. M., Collins, W. D., Arblaster, J. M., Hu, A., Buja, L. E., Strand, W. G. & Teng, H. 2005 How much more global warming and sea level rise? *Science* **307**, 1769–1772. (doi:10.1126/science.1106663)