Climate change and the oceans – What does the future hold?

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ABSTRACT

The ocean has been shielding the earth from the worst effects of rapid climate change by absorbing excess carbon dioxide from the atmosphere. This absorption of CO_2 is driving the ocean along the pH gradient towards more acidic conditions. At the same time ocean warming is having pronounced impacts on the composition, structure and functions of marine ecosystems. Warming, freshening (in some areas) and associated stratification are driving a trend in ocean deoxygenation, which is being enhanced in parts of the coastal zone by upwelling of hypoxic deep water. The combined impact of warming, acidification and deoxygenation are already having a dramatic effect on the flora and fauna of the oceans with significant changes in distribution of populations, and decline of sensitive species. In many cases, the impacts of warming, acidification and deoxygenation are increased by the effects of other human impacts, such as pollution, eutrophication and overfishing.

The interactive effects of this deadly trio mirrors similar events in the Earth's past, which were often coupled with extinctions of major species' groups. Here we review the observed impacts and, using past episodes in the Earth's history, set out what the future may hold if carbon emissions and climate change are not significantly reduced with more or less immediate effect.

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1. Introduction

The anthropogenic carbon emissions caused by the burning of fossil fuels, cement production and deforestation are having a major impact on the world's largest ecosystem – the oceans. Atmospheric carbon dioxide is the highest it has been for at least the last 15 Ma (Tripati et al., 2009; LaRiviere et al., 2012) and probably longer (300 Ma; Hönisch et al., 2012). The effect is both a warming of the atmosphere and of the oceans (Rayner et al., 2003; IPCC, 2007a; Belkin, 2009; Sherman et al., 2009; Reid and Beaugrand, 2012). Another direct impact of raised atmospheric CO_2 is ocean acidification, through its entry into marine surface waters and its chemical reaction with the water (Caldeira and Wickett, 2003; Caldeira, 2007; Cao and Caldeira, 2008). The physical and chemical impacts of CO_2 emissions are not limited to the direct effects of warming and a lowering of ocean pH. There are processes associated with warming and acidification, many of which are summarised in this review, and these factors can combine to amplify the impact of each other factor on ocean biology. For example, global warming will increase surface ocean stratification, which in turn will affect the surface-water light regime and nutrient input from deeper layers. This will impact primary production (Fig. 1; Rost et al., 2008). Oxygen transport to the deep sea by downwelling

water masses will be weakened by freshening because of increased meltwater input from Greenland and high-Arctic glaciers, altering patterns of ocean mixing, slowing down the conveyor belt and leading to progressive depletion of the ocean's oxygen inventory. The potential effects of these factors are further exacerbated by other anthropogenic stresses, such as pollution, eutrophication and overfishing (see Pitcher and Cheung, this volume), which have destabilised some ecosystems and significantly reduced many species' populations, thus limiting the potential for adaptation. The geological record suggests that the current acidification is potentially unparalleled in at least the last 300 million years of Earth history, and raises the possibility that we are entering an unknown territory of marine ecosystem change (Hönisch et al., 2012). This review summarises the observed impacts of the last century, and the predicted impacts of a continued elevation of CO_2 on the marine environment. The present paper argues that warming and acidification are the major drivers behind oceanographic and biological changes presently documented and projected to develop further throughout all the world's oceans.

Although the human-induced pressures of overexploitation and habitat destruction are the main causes of recently observed extinctions (Dulvy et al., 2009) climate change is increasingly adding to this. Changes in ocean temperatures, chemistry and currents mean that many organisms will find themselves in unsuitable environments, potentially testing their ability to survive. Adaptation is one means of accommodating environmental change,

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migration is another. However, global warming asks for a poleward migration whereas ocean acidification would require an equatorward migration as colder waters acidify faster. Hence, the "green pastures" become scarce and will experience stronger competition. The recent IUCN Red List Assessment on shallow-water reef-forming corals identified a dramatically increased threat to these organisms posed by the climate change effect of mass coral bleaching (Carpenter et al., 2008). Habitat suitability modelling has also identified a threat to deep-water corals from the shoaling of the aragonite saturation horizon, a further symptom of ocean acidification (Tittensor et al., 2010). There are observed trends for some species shifting ranges polewards and into deeper, cooler waters (Reid et al., 2009), but range shifts within short time frames may be unlikely for many species, such as long-lived, slow growing, sessile habitat-forming species, leading to increased extinction risk. In the case of coastal species, a poleward-shift in distribution may be limited by geography as organisms simply "run out" of coastline to migrate along and are faced with a major oceanic barrier to dispersal. Modelling studies have also indicated the likelihood of range shifts, extinctions and invasions in commercial marine species resulting from ocean warming with serious implications in terms of food security, especially for developing states (Cheung et al., 2010). In the present paper we examine the current and potential future impacts of global climate change through temperature rise, ocean acidification and increasing hypoxia, 3 symptoms of carbon pertubations. Carbon pertubations have occurred before in Earth history and have left their fingerprints in the geological archive. We examine these changes in the light of the palaeontological record to see if there are comparisons to be made to historical climate change and mass extinction.

2. Temperature rise

The average temperature of the upper layers of the ocean has increased by 0.6 °C in the past 100 years (IPCC, 2007b). There are direct physical and biogeochemical consequences of the heat content changes that have been documented by many researchers. These include: thermal expansion, sea level rise, increased meltwater, reduced salinity, increased storm intensity, and greater stratification of the water column (IPCC, 2007a). Stratification has affected nutrient availability and primary productivity (e.g. Hoegh-Guldberg and Bruno, 2010). Whether overall trends of primary production in the oceans are increasing or decreasing has been controversial. Some observations suggest that annual primary productivity has decreased (e.g. Gregg et al., 2003) whilst others suggest that it has increased and is tightly coupled with climate variability occurring interannually or over multidecadal timescales (Behrenfeld et al., 2006; Chavez et al., 2011). Likewise, future projections of changes on global oceanic primary production have also produced mixed results with some predicting a global decrease in primary production (e.g. Moore et al., 2002), and others predicting an increase (e.g. Sarmiento et al., 2004). The latest model projections of future change in global primary production, based on several coupled carbon cycle-climate models that incorporate marine biogeochemical–ecosystem models of different complexity and, critically, explicitly consider the cycling of nutrients and nutrient availability suggest an overall decrease in global primary production and export of particulate organic carbon (Steinacher et al., 2010). A common causative mechanism in models predicting such declines of global primary and export production is the increased stratification of the ocean in low to mid-latitudes and a slowing of the thermohaline circulation, reducing nutrient availability in surface water layers (Steinacher et al., 2010). Regardless of the current controversy in resolving whether ocean primary production has risen or fallen, it is clear that there are many unknown factors
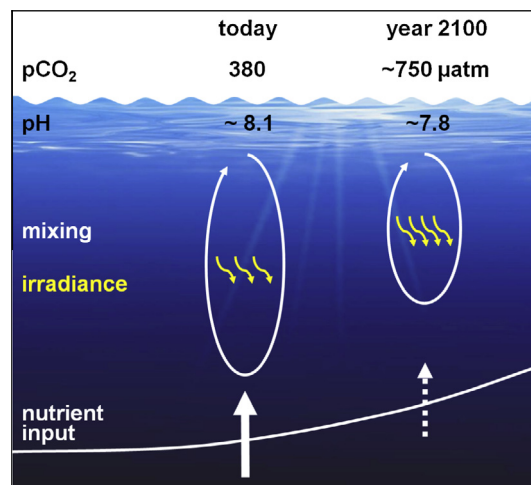

Fig. 1. Main putative physico-chemical changes in the oceanic ecosystem occurring in this century (modified after Rost et al., 2008). Ocean acidification of the surface ocean is expected to intensify. In addition, rising temperatures will impact surface ocean stratification, which in turn will affect the surface water light regime and nutrient input from deeper layers. Phytoplankton will be affected by these environmental changes in many ways, altering the complex balance of biogeochemical cycles and climate feedback mechanisms.

in predicting future trends. These arise from a lack of understanding of what drives interannual and multidecadal climatic variation (Chavez et al., 2011), and the influence of species-specific responses to climate change effects (Chavez et al., 2011) and the overall changes in biological and ecological processes with increasing temperature (e.g. increasing metabolic rate and its influence on pelagic foodwebs via the microbial loop; Taucher and Oschlies, 2011). In the tropics, increased stratification and reduced nutrient supply have been associated with decreased productivity (Doney, 2010). However, regardless of whether primary productivity of a given ocean basin changes, the composition of the phytoplankton may well change, a phenomenon reported from many regions associated with warming sea surface temperatures (e.g. Nehring, 1998; Johnson et al., 2011; Polovina and Woodworth, 2012), and such effects are likely to propagate through ecosystems (Polovina and Woodworth, 2012).

Range shifts and changes in the abundance of algal, plankton and fish populations as well as benthic organisms in low to high latitude oceans are associated with rising water temperatures (e.g. Fischlin et al., 2007; Reid et al., 2009). Such shifts in latitudinal species range are broadly following those expected from climate envelope models predicting the effects of climate change on species distributions (e.g. Cheung et al., 2009). Unifying physiological principles provide access to explaining these effects (Fig. 2). All organisms specialize on a limited range of ambient temperatures, a phenomenon that has traditionally been linked to tradeoffs in structural properties of enzymes or membranes and associated functional adjustments to a range of temperatures. Further work demonstrated that the earliest limits of thermal tolerance are found at the level of whole organisms with thermal ranges narrower here than at molecular or membrane levels (Pörtner, 2002). This reflects the integration of molecular functions into organisms as high-complexity systems. Overall, the specialization on limited temperature ranges implies functional disturbances setting in at temperatures beyond these ranges. For aquatic ectothermic animals, the concept of oxygen- and capacity-dependent thermal tolerance (OCLTT) became available to integrate the various levels of specialization and functioning at molecular, cell and tissue levels into a whole organism picture of temperature-dependent performance (for review see Pörtner, 2010). Following
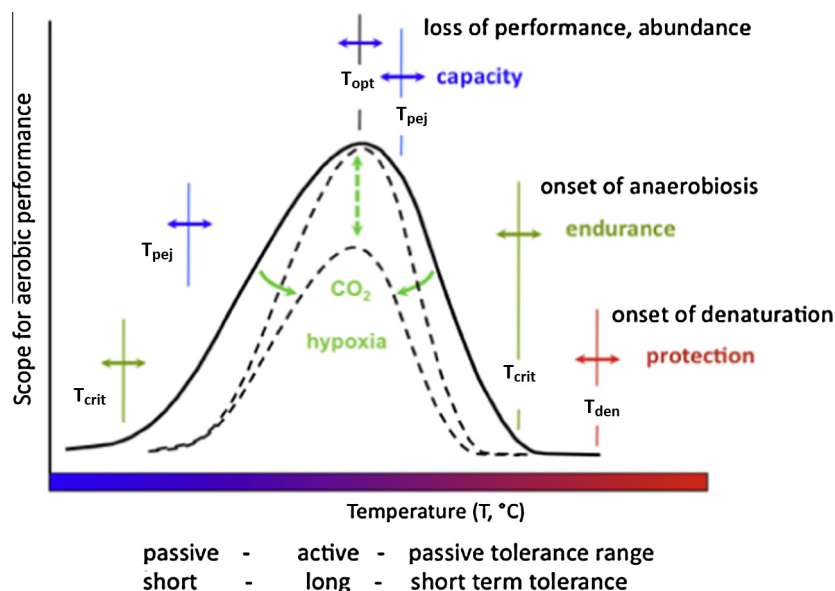
Fig. 2. The window of optimal performance of many organisms is affected by temperature, ocean carbonate chemistry and hypoxia, the three direct symptoms of a massive carbon perturbation. For animals, the concept of oxygen and capacity limited thermal tolerance (OCLTT) provides an explanation for the specialization of animals on specific, limited temperature ranges and their sensitivity to temperature extremes. Furthermore, in allows integration of other stressors on a thermal matrix of performance (Pörtner et al., 2005, 2010). Tcrit = Critical Temperature where there is an onset of anaerobic metabolism; Tpej = Pejus Temperature above and below which oxygen supplies to tissues become sub-optimal; Topt = Optimal Temperature; Tden = Denaturation Temperature where molecules lose integrity.

this concept, the thermal window of performance in water breathers matches their window of aerobic scope, as set by limitations in tissue, especially cardiocirculatory functional capacity. As a consequence, tradeoffs between oxygen supply and demand capacities exist leading to limitations in oxygen availability to tissues at temperature extremes. The resulting loss of performance thus reflects the earliest level of thermal stress. In warm-adapted and temperate zone animals, it becomes visible at both borders of the thermal envelope as caused by limited functional capacity of oxygen supply systems to match oxygen demand, leading to hypoxemia and then use of anaerobic metabolism. Both capacity and oxygen limitations are intertwined and form a primary link between organismal fitness and its role and function at the ecosystem level. The OCLTT concept is applicable to all water and most air breathers and has successfully explained detrimental effects of rising temperatures on the abundance of fishes in the field (Pörtner and Knust, 2007). In organisms other than animals, thermal windows of performance have occasionally been described but the processes shaping the performance curve have not been identified (Pörtner, 2012). Again, they will have to be identified at the highest level of functional integration (i.e. the organisms performance) (Pörtner, 2002). In general, the need to specialize on a limited temperature range results from temperature dependent trade-offs at several hierarchical levels, from molecular structure to whole-organism functioning. Such specialization also supports maximized energy efficiency. Therefore, thermal acclimatization between seasons or adaptation to a climate regime involves shifting thermal windows and adjusting window widths, in accordance with ambient temperature variability. However, acclimation capacity is limited such that a dynamic thermal niche results which covers the seasonal temperature regime and determines the biogeography of a species.

Various environmental factors like CO_2 (ocean acidification) and hypoxia (reduced dissolved oxygen content constraining aerobic organisms) interact with these principal relationships. Existing knowledge for aquatic animals suggests that elevated CO_2 levels and extreme hypoxia elicit metabolic depression. Depending on the physiological capacity of the organism in question such effects may occur over the whole temperature range but may only set in at thermal extremes. This is adaptive for some organisms, e.g. in the

intertidal zone, as metabolic depression supports passive tolerance to such extremes but such tolerance is time-limited to periods of hours to days. However, these effects also exacerbate hypoxemia (deficiency of oxygen in blood), causing a narrowing of the temperature window of active performance. Such effects are detrimental on long time scales (weeks to months) and may also lead the organism prematurely to the limits of its thermal acclimation capacity (Fig. 2). Overall, the relationships between energy turnover, the capacities of activity and other functions and the width of thermal windows lead to an integrative understanding of specialization on climate and, of sensitivity to climate change including the additional drivers involved in the oceans such as CO_2 and hypoxia (Pörtner, 2010). Such functional relationships might also relate to climate-induced changes in species interactions and, thus, community responses at the ecosystem level (Pörtner and Farrell, 2008).

There are cascading consequences of these impacts, notably for marine biology, including altered food web dynamics, reduced abundance of habitat-forming species, range shifts, and expansion of pathogens (Hoegh-Guldberg and Bruno, 2010). Examples of some of these processes have been identified. At high latitudes analyses of population responses of predators to natural environmental variation (often driven by interannual or multidecadal climatic oscillations; e.g. Trathan et al., 2007; Le Bohec et al., 2008) and modelling studies suggest that aquatic predators are threatened by climate change (Ainley et al., 2010). Observations have supported such contentions (e.g. Trivelpiece et al., 2011; Wassmann et al., 2011) but the exact mechanisms of such declines are not always completely clear. The bottom-up effects of temperature rise coupled with freshening of surface water layers resulting from glacial melt or increased river discharge have been implicated in forcing significant changes in lower/middle trophic levels of food chains (particularly primary producers and grazers), with decreased supply of food to upper trophic levels (e.g. Moline et al., 2008; Li et al., 2009; Wassmann et al., 2011). Changes in the timing of the onset and melting of sea ice also has the potential to cause both direct impacts through reduction of habitat for activities such as breeding and hunting of ice-associated predators and indirect impacts through changing the availability of ice associated algae and zooplankton (e.g. Moline et al., 2008; Quetin and Ross, 2009;

Wassmann et al., 2011). Reduction in sea ice duration may also allow an increase in the range of predators at high latitudes whose distribution was previously restricted with consequent cascades in food webs (e.g. increase in distribution of killer whales in Hudson Bay in the Canadian Arctic; Higdon and Ferguson, 2009). At low latitudes coral bleaching is incontrovertibly linked to warmer sea surface temperatures (Fischlin et al., 2007; Hoegh-Guldberg et al., 2007). This phenomenon commenced in the late 1970s and has increased in intensity and frequency in recent decades (Hoegh-Guldberg et al., 2007). Whilst it is a direct effect of temperature rise, the resilience of coral reefs to bleaching is influenced by other human impacts, such as overfishing of reef grazers. These act through the food web or on other elements of the reef ecosystem to prevent reef recovery and drive a phase shift from a coral-dominated to an algal-dominated system.

Warming is projected to have the following impacts on the oceans to 2050:

- **Accelerated warming of high latitudes** and reduced seasonal sea ice zones (Levitus et al., 2000, 2005; Gille, 2002; Vaughan et al., 2003; Barnett et al., 2005; Meredith and King, 2005; Turner et al., 2005; Trenberth et al., 2007; Arrigo et al., 2008; Stammerjohn et al., 2008; Massom and Stammerjohn, 2010; Wassmann et al., 2011).
- **Increasing stratification** of ocean layers (Behrenfeld et al., 2006; Polovina et al., 2008), reducing biologically important mixing zones and supporting oxygen depletion in mid-water layers (Keeling et al., 2010; Stramma et al., 2011).
- **Changes to winds and currents**, potentially increasing the incidence of hypoxic and anoxic conditions (Chan et al., 2008; Roegner et al., 2011).
- **Decreasing surface oxygen concentrations**, leading to more frequent anoxic and hypoxic events (Diaz and Rosenberg, 2008).
- Large-scale, persistent, and slow **changes to thermohaline circulation** (IPCC, 2007b).
- **Disappearance of Arctic summer sea ice** by 2037 or shortly thereafter (Stroeve et al., 2007; Wang and Overland, 2009) will have a major impact on high latitude ecosystems with direct consequences for all species utilising this habitat (Wassmann et al., 2011).
- **Increased venting of the greenhouse gas methane** from the seabed along the Arctic continental margins (Westbrook et al., 2009; Shakhova et al., 2010).
- **Sea level rise** of 0.5–1.2 m (2100), leading to 10–20% loss of mangroves (Gilman et al., 2008), and a 32% loss of nesting habtitat for Caribbean Sea Turtles (Fish et al., 2005).

All of these oceanographic impacts will have biological implications:

- **Potential change in primary productivity**, decreasing at low latitudes, the North Pacific, and Southern Ocean; but increasing in the North Atlantic and Arctic; with changes in global average primary productivity currently uncertain.
- **Range shifts and species invasions** driven by changes in temperature, wind patterns and productivity: range limits are projected to shift poleward by 30–130 km and to deeper waters by 3.5 m each decade (Cheung et al., 2010); species invasions are projected to be greatest in the Arctic and Southern Oceans (Cheung et al., 2009). Such model predictions are supported by observed shifts in distribution (e.g. in the North Atlantic, Antarctic and Arctic; Beaugrand et al., 2003, 2010; Wassmann et al., 2011; Weimerskirch et al., 2012).
- **Redistribution of commercial fish and invertebrate species**, with a 30–70% increase in catch potential in high-latitude regions and a 40% decrease in the tropics: catch potential

decreases are projected to occur in the Indo-pacific, Antarctic, tropics, semi-enclosed seas and inshore waters, coastal regions and the continental shelf; catch potential increases are projected for offshore regions of the North Atlantic, North Pacific, Arctic, and parts of the Southern Ocean (Cheung et al., 2010).
- **Species turnover** (loss of 60% of present biodiversity of exploited marine fish and invertebrates), leading to potential ecological disturbances that may disrupt ecosystem services (Cheung et al., 2009). A projection of the distributional ranges of exploited marine fish and invertebrates for 2050, using a dynamic bioclimate envelope model, predicts that climate change may lead to numerous local extinctions in the sub-polar regions, the tropics and semi-enclosed seas. Simultaneously, species invasion is projected to be most intense in the Arctic and the Southern Ocean.
- **Increase in disease prevalence**, driven by pathogen range expansions, changes to host susceptibility, and expansion of potential vectors (Lipp et al., 2002; Hoegh-Guldberg and Bruno, 2010).
- **Increased extinctions**: highest risk in ice-dependent polar species such as seals and penguins (Fischlin et al., 2007), and sub-polar regions, the tropics and semi-enclosed seas (Carpenter et al., 2008; Cheung et al., 2009).
- **Increased coral reef mortality** as a result of mass coral bleaching (Hoegh-Guldberg et al., 2007; Pandolfi et al., 2011), with annual or bi-annual exceeding of bleaching thresholds for the majority of coral reefs worldwide (Donner et al., 2007; Fischlin et al., 2007; Van Hooidonk et al., 2013) and a predicted phase shift to algal dominance on the Great Barrier Reef and Caribbean reefs (Wooldridge et al., 2005).

3. Ocean acidification

Gas exchange between sea and air leads to equilibrium of atmospheric CO_2 and surface waters within a timescale of about a year. The chemistry of CO_2 absorption in the oceans is well understood and results in the lowering of ocean pH (Doney et al., 2009). The world's oceans have absorbed one third of the CO_2 produced by human activities. This has acidified the ocean surface layers, with a steady decrease of 0.02 pH units per decade over the last 30 years and an overall decrease of 0.1 pH units since the pre-industrial period (Hoegh-Guldberg and Bruno, 2010). The rate of change is 30–100 times faster than the recent geological past. The largest relative changes are in the high latitudes where waters are coldest and absorb most of the CO_2 from the atmosphere (Doney et al., 2009; Laffoley and Baxter, 2009). Recent acidification has resulted in a substantial decline in carbonate ion concentrations (Hoegh-Guldberg et al., 2007; Hoegh-Guldberg and Bruno, 2010) and aragonite saturation states (Doney et al., 2009; Veron et al., 2009). A 24 year time series of sea water data from the Iceland Sea have revealed 50% faster surface water rate of acidification in these Arctic waters than in subtropical regions of the Atlantic. The aragonite saturation horizon is currently at 1710 m and shoaling at 4 myr^{-1}. Based on this rate of shoaling and on the local hypsography, each year another 800 km^2 of seafloor becomes exposed to waters that have become undersaturated with respect to aragonite (Olafsson et al., 2009).

The observed biological impacts linked to ocean acidification concern not only calcifying organisms but elevated CO_2 levels affect marine organisms in general (e.g. Pörtner et al., 2005). Ocean acidification is a direct threat to marine organisms that build their skeletons out of calcium carbonate, especially reef-forming corals (Scleractinia) but also protozoans, molluscs, crustaceans, echinoderms and some algae (Orr et al., 2005; Ries et al., 2009; Bednaršek et al., 2012). Experiments and observations show that some calcifying organisms have decreased calcification rates in more

acid waters, but the response is not uniform and the reactions of species differ (Ries et al., 2009; Langer et al., 2009; Doney et al., 2009). Evidence from natural acidified environments clearly indicates biodiversity loss not only among calcifying organisms but also for non-calcifiers (Fig. 3).

The rate of ocean acidification is projected to accelerate in the near future unless CO_2 emissions are curbed dramatically (Doney et al., 2009). Ocean acidification is projected to have the following impacts on the oceans to 2050:

- **Reduced pH** by 0.2 units from pre-industrial baseline (Doney, 2010).
- **Broad changes in seawater chemistry** besides pH reduction. These include changes in chemical speciation (e.g. Hoffmann et al., 2012) and elemental stoichiometries (e.g. via increased or decreased bioavailability because of pH reduction or increased nitrogen fixation) and carbon storage in the ocean interior via changes in "ballasting" and TEP (Transparent <u>Exopolymer</u> Particles; "glue") production (Doney et al., 2009; Millero et al., 2009). It is still unclear in which direction and to what extent the biological pump will change (Passow and Carlson, 2012).
- **Decline in the aragonite and calcite saturation state**: at atmospheric CO_2 concentrations of 560 ppm (projected to occur in 2050–2080), most ocean surface waters will be undersaturated with respect to aragonite (Orr et al., 2005; Veron et al., 2009).

These chemical changes will directly impact marine biology causing the following:
- **Reduced calcification rates of calcifying organisms** such as reef-building corals (Pandolfi et al., 2011): for atmospheric CO_2 concentrations of 450–500 ppm (projected to occur in 2030–2050), severely diminished reef-building processes (Veron et al., 2009) with erosion exceeding calcification (Hoegh-Guldberg et al., 2007), resulting in extinction of some species (Laffoley and Baxter, 2009), decline in density and diversity of corals and their dependent species (Hoegh-Guldberg et al., 2007) (Fig. 4).
- Large parts of the ocean will cease to support cold-water corals by 2100 (Fischlin et al., 2007; Tittensor et al., 2010).
- **Increased stress on phytoplankton populations** as a result of decreasing uptake of iron in some areas of the ocean (Shi et al., 2010). Alternatively, expected increasing flux of dust from continents might compensate for Fe-limitation.
- **Other biotic impacts** of acidification, including changes to photosynthesis, oxygen exchange, reproduction, nitrogen fixation (decreasing pH will shift the balance from NH_3 to NH_4^+ with important implications for phytoplankton) and navigation (Doney et al., 2009; Laffoley and Baxter, 2009).

The synergistic effects of acidification and warming are likely to lead to rapid and terminal decline of tropical coral reefs by 2050 (Hoegh-Guldberg et al., 2007; Anthony et al., 2008; Veron et al., 2009). It should be noted that changes in the highly complex reef ecosystem itself may accelerate the process when, for instance, (macro)algae begin to dominate the assemblage.

4. Ocean deoxygenation

Evidence is accumulating that the oxygen content of oceans are decreasing (Diaz, 2001; Keeling et al., 2010). This takes two main forms, a general broad trend of declining oxygen levels in tropical oceans and areas of the North Pacific over the last 50 years (Deutsch et al., 2005; Stramma et al., 2008; Keeling et al., 2010) and the dramatic increase in coastal hypoxia associated with eutrophication
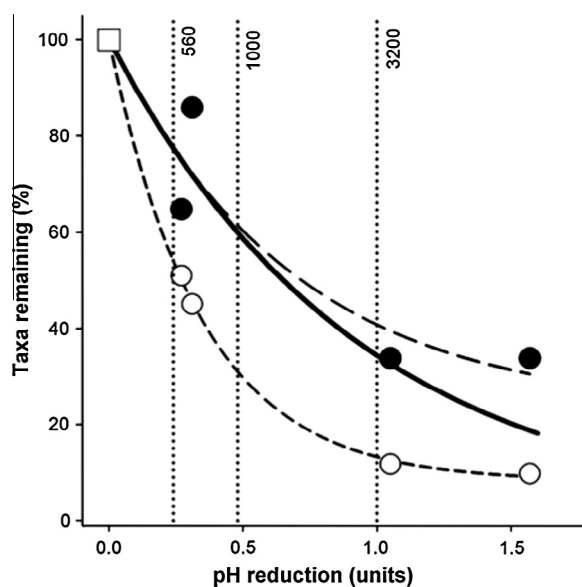

Fig. 3. Change in diversity as a function of pH reduction for organisms living near the Ischia CO_2 vents. The biodiversity remaining (per cent of taxa that occur in areas with no pH reduction, open square) is shown for calcifying taxa (51 taxa total, white circles) and non-calcifying taxa (71 taxa total, black circles). Atmospheric pCO_2 levels (ppmv CO_2) that would be required to cause pH changes in ocean surface waters equivalent to those observed at three locations along the pH gradient at Ischia are indicated by dotted vertical lines. For calcifiers (short dashed curve), non-calcifiers (long dashed curve), and all taxa combined (solid curve, data not shown), exponential regressions explained 99%, 90%, and 88% of the variance, respectively. Fitted regressions indicate a loss of biodiversity of ∼40% for non-calcifiers and all taxa, and ∼70% for calcifiers, for a pH reduction corresponding to the atmospheric pCO_2 level expected by 2100. Data from Hall-Spencer et al. (2008).

(Diaz and Rosenberg, 2008). The first relates to the impact of global warming and regional freshening and the second to increased nutrient runoff.

In terms of the broad trend in decreasing oxygen content of the oceans a number of important factors related to climate change such as decreased solubility of oxygen as waters warm, enhanced respiratory oxygen demand at elevated temperatures, decreased ventilation at high latitudes associated with increased ocean stratification, may be involved. It is unclear whether the loss throughout the basins in the open ocean is a long-term, non-periodic (secular) trend related to climate change, the result of natural cyclical processes, or a combination of both factors. The impacts of this oxygen loss on marine species and ecosystems are varied. For example, observed shoaling of the depth of the oxygen minimum zone is associated with compression of habitat for large ocean predators such as marlin which have a high metabolic rate and oxygen demand (Stramma et al., 2011). This habitat compression is likely to alter the encounter rates between these predators and their prey but also has the likely impact of increasing vulnerability of billfishes and many tuna species to fishing (Stramma et al., 2011). Another symptom of climate change has been the occurrence of the incursion of anoxic waters onto the inner shelf adjacent to the upwelling zone along the west coast of North America (Chan et al., 2008). This region showed no evidence of severe inner shelf hypoxia prior to 2000 but in 2006 large-scale mortalities of benthic marine animals and an absence of bottom-dwelling fish occurred as a result of an anoxic event (Chan et al., 2008). Events in 2006, 2007 and 2008 also caused the influx of oxygen depleted waters into the Columbia River estuary with levels of hypoxia sufficient to have negative impacts on the fauna (Roegner et al., 2011). These waters are not only oxygen depleted but also undersaturated with respect to aragonite (Roegner et al., 2011). The occurrence of the upwelling of oxygen depleted waters along
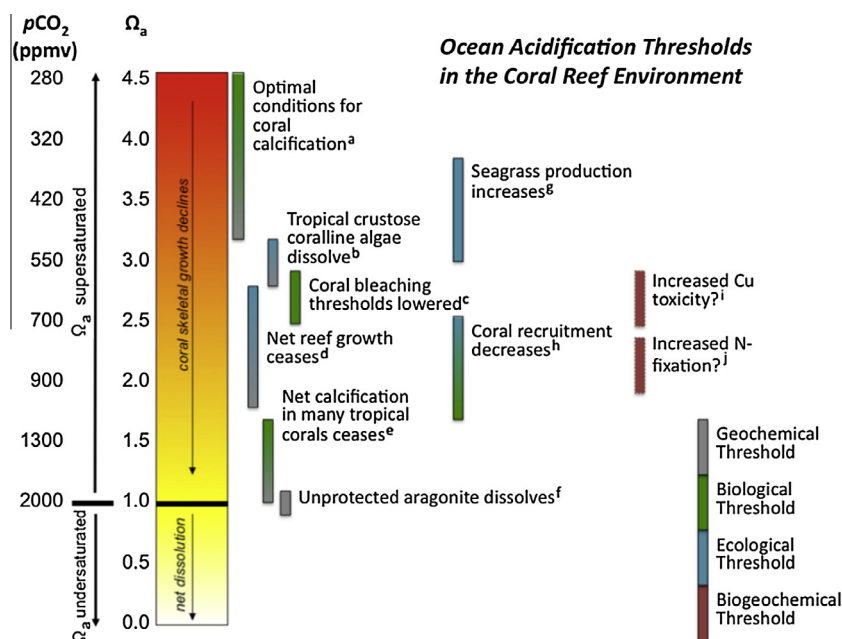
Fig. 4. The impacts of different levels of atmospheric carbon dioxide on coral reef environments.

this coastline have occurred because of an increase in the strength and frequency of upwelling inducing winds and evidence suggests that such events are increasing in frequency and intensity (Chan et al., 2008; Roegner et al., 2011). Major anoxic events in the Benguela upwelling zone off South Africa has also been implicated in large-scale shifts in the distribution of species and their predators generally from the western Cape eastwards towards the eastern cape region (Cury and Shannon, 2004; Cockcroft et al., 2008; Crawford et al., 2008).

The other form of oxygen depletion in coastal regions results from the release of large quantities of nutrients, mainly from runoff of agricultural fertilisers, but also arising from sewage pollution. The impacts of eutrophication include the generation of oxygen depleted or "dead zones", the formation of harmful algal blooms (HABs), increased occurrence of microorganisms pathogenic to marine life and even humans and the promotion, usually in combination with other human stressors, of plagues of gelatinous zooplankton. Dead zones may first manifest in coastal ecosystems as a deposition of organic material which promotes microbial growth and respiration creating a greater biological oxygen demand (Diaz and Rosenberg, 2008). If accompanied by stratification of the water column this can lead to oxygen depletion progressing to extreme hypoxia along with mass mortality of marine organisms if the process of eutrophication continues (Diaz and Rosenberg, 2008). Extreme hypoxia is generally regarded as when the oxygen concentration reaches $< 2\ ml\ l^{-1}$ at which point benthic infauna exhibit stress-related behaviour, such as abandonment of burrows with significant mortality occurring at levels of $<0.5\ ml\ l^{-1}$ (Diaz and Rosenberg, 2008). However, recent meta-analyses of studies of oxygen thresholds indicate that for sensitive taxa, such as fish or crustaceans, lack of oxygen may be lethal at concentrations well above $2\ ml\ l^{-1}$ and there is considerable variability amongst taxa in sensitivity to hypoxia (Vaquer-Sunyer and Duarte, 2008). Progressive accumulation of organic material and nutrients can result in seasonal hypoxia with regular mortality events of marine organisms. In the worst cases, where nutrients continue to accumulate in the system over several years, the hypoxic zone will expand and anoxia may be established accompanied by release of H_2S by microbial communities (Diaz and Rosenberg, 2008). As well as direct mass mortality of marine organisms, as with oceanic species,

hypoxia or anoxia can also cause habitat compression, potentially affecting the life cycle, local movement and even large-scale migration of affected species. Over long periods of time hypoxia or anoxia will eliminate almost all the benthic fauna with the result that the ecosystem become progressively more dominated by microorganisms with consequences for energy fluxes and ecosystem services such as the nitrogen cycle. Oxygen depleted zones have spread since the introduction of industrial fertilisers in the late 1940s with a lag of about 10 years between their widespread use and the occurrence of coastal hypoxia. Since the 1960s the number of dead zones has approximately doubled every 10 years with their occurrence correlated to centres of human population and major watersheds (Diaz and Rosenberg, 2008). Areas where exchange of water is restricted, such as inland seas or estuaries are particularly prone to these effects for obvious reasons. Seriously affected regions include the northern Adriatic Sea, the Black Sea, the Kattegat, the Baltic Sea, the northern Gulf of Mexico and Chesapeake Bay (Diaz and Rosenberg, 2008). Numbers of dead zones are likely to be underestimated as their occurrence is probably unreported in many geographic regions.

Both climate induced- and eutrophication-induced hypoxia may interact. Elevated temperatures enhance stratification and are likely to increase the severity of eutrophication-induced coastal hypoxia. Along natural zones of upwelling, occurring at the eastern boundary of oceans, such as those off California, Peru, Chile and Namibia and also that along the western part of the Indian Ocean, expanding oxygen minimum zones, and the potential interaction with eutrophication may further enhance hypoxic or anoxic events occurring on inner continental shelves (Stramma et al., 2010).

Predictions for ocean oxygen content suggest a decline of between 1% and 7% by 2100 with the range of uncertainty linked with both the biological and physical elements of the models including varying assumptions of climate sensitivity (Keeling et al., 2010). There are historical precedents for a link between oceanic warming and decrease in oxygen. Records from the Pleistocene indicate that ocean warming reduced the ventilation of thermocline waters and an increase in oxygen minimum zones (Keeling et al., 2010). Indeed, most of the ocean anoxic events in subsurface oceans in Earth History occurred during times when both atmospheric carbon dioxide and inferred temperature were high, and seem to

Table 1

While demonstrating ocean acidification in the modern is relatively straightforward, identifying palaeo-ocean acidification is problematic because the rock record is a constructive archive while ocean acidification is essentially a destructive (and/or inhibitory) phenomenon. This is exacerbated in deep time without the benefit of a deep ocean record (Greene et al., 2012a; Kershaw et al., 2012).

References	Period	Major cause	Comment
Alegret et al. (2012)	K/T	Asteriod impact followed by OA	Not a productivity collapse
Greene et al. (2012b)	T/J	OA very probable	Short-term OA may have long term effects on ecosystems; T/J analogue for modern OA
Greene et al. (2012a)	T/J	OA very probable	Early diagenetic carbonate formation as a first step of carbonate chemistry restoration after OA
Hautmann (2012)	T/J	CAMP volcanism resulting in anoxia, global warming, OA and release of toxic compounds	Extensive comparison of scenarios
Trecalli et al. (2012)	T/J	OA	Based on $\delta^{13}C$
Suan et al. (2011)	T/J	Warming, poor oxigenation	Carbon injection
McRoberts et al. (2012)	T/J	OA	Based on macrofauna response
Shen et al. (2013)	P/T	Volcanically generated stresses (suboxia)	Weakening marine ecosystem resilience
Winguth and Winguth (2013)	P/T	Periodic anoxia in near sfc-to-intermediate depth	No widespread deep-sea anoxia
Beauchamp and Grasby (2012)	P/T	OA	Global warming accelerated silicate weathering
Sano et al. (2012)	P/T	Anoxia	Increase in primary productivity/weakened circulation induced by global warming.
Zhao et al. (in press)	P/T	Suboxic to anoxic seawater conditions after Siberian Traps	Based on Ce-anomaly and REE profiles from conodonts
Brand et al. (2012)	P/T	Extreme greenhouse, global warming	Anoxia only briefly relevant
Kaiho et al. (2012)	P/T	Anoxia and OA	Euxinic conditions
Song et al. (2012)	P/T	Anoxia	Based on Ce-anomaly and Th/U ratios from conodonts
Hinojosa et al. (2012)	P/T	OA	Based on Ca isotopes from conodonts
Zhou et al. (2012)	P/T	Anoxia	Based on U/Mo and Mo isotopes
Payne and Clapham (2012)	P/T	Warming, OA, anoxia	Ancient analogue for present
Georgiev et al. (2011)	P/T	Warming, OA, anoxia	Based on $^{187}Re/^{188}Os$ and $^{187}Os/^{188}Os$
Williams et al. (2012)	P/T	Reduction in O_2 availability	
Sun et al. (2012)	P/T	Extreme warming	
Kershaw et al. (2012)	P/T	OA very likely	Limited confindence in comparisons between ancient and modern OA
Speijer et al. (2012)	PETM	Carbon pertubation	Not a mass extinction event; response of most marine invertebrates to OA, deoxygenation virtually unknown
Zamagni et al. (2012b)	PETM	OA combined with moderately high nutrient levels; significant shallow water OA questionable	Progressive reduction of reef building potential
Zamagni et al. (2012a)	PETM	No shallow water OA	Based on $\delta^{13}C$
Winguth et al. (2012)	PETM	OA, oxygen depletion in the deep sea, reduced food supply	Model based
Harnik et al. (2013)	General	Most mass extinctions related to symptoms of carbon pertubations	See Table 1
Rees (2012)	Modern	Carbon pertubations + other anthropogenic stressors	Scope and extent of adaptation unresolved
Honisch et al. (2012)	General	Carbon pertubation	
Kravchinsky (2012)	Paleozoic	Volcanism and anoxia	Increasing agreement between volcanic eruptions, anoxia and mass extinctions

Oceans are Acidifying Fast ………

Changes in pH over the last 25 million years
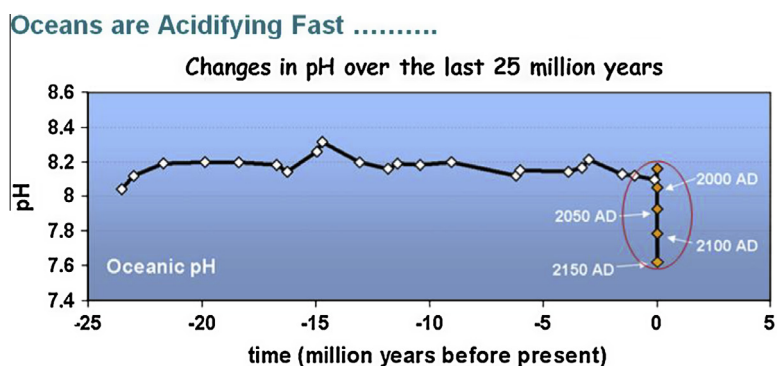
It is happening now, at a **rate and to a level not experienced by marine organisms for ~ 20MY**

Fig. 5. The palaeohistorical record of ocean pH demonstrates that present levels are unseen in the last 20 million years (Turley et al., 2006). Note that depending on the rate (and magnitude) of a carbon perturbation, pH and the saturation state may be decoupled (slow rate) or change simultaneously (fast rate as today).

be associated with massive tectonic and volcanic events (Falkowski et al., 2011).

5. The deadly trio – warming, ocean acidification and deoxygenation – in Earth history

As documented by a flood of recent literature, most, if not all, of the Earth's five global mass extinction events have left footprints (Table 1), of at least one or more, of the main symptoms of global carbon perturbations: global warming, ocean acidification and hypoxia (e.g. Pörtner et al., 2005; Knoll et al., 2007; Veron, 2008; Metcalfe and Isozaki, 2009; Ridgwell and Schmidt, 2010; Barnosky et al., 2011; Georgiev et al., 2011; Suan et al., 2011; Payne et al., 2010; Zamagni et al., 2012a,b; Kravchinsky, 2012; Winguth et al., 2012; Alegret et al., 2012; Harnik et al., 2013; Hönisch et al., 2012). Although, it can be argued whether or not the end-Ordovician or the end-Cretaceous event were driven by "big threeism", it can be said that the end-Permian and end-Triassic almost certainly, and the end-Devonian very likely (e.g. Bambach et al., 2004), as well as a handful of smaller extinction events, are related to a carbon perturbation. Hence, we can call these three factors a 'deadly trio', and worryingly these are all present in the ocean today. In fact, the present day carbon perturbation and the concurrent ocean acidification is unprecedented in the Earth's history and occurring much faster than at any time in the past 55 million years (Kump et al., 2009) or even 300 million years (Hönisch et al., 2012; Fig. 5).

It is this combination of factors that seriously affects how productive and efficient the ocean is (Fig. 1), as ocean temperature, surface stratification, nutrient supply, ocean overturning and deep-ocean oxygen supply are all affected. Even though some species are shown to proliferate in a warmer and more acidic ocean, the process of extinction may have already begun. Projecting geological time scales onto human lifespan, mass extinctions happen overnight, but on human time scales we may not even realize whether we have entered such an event, even when keeping close track of the "red list index" of species extinctions (Barnosky et al., 2011).

It is known, with a high level of confidence from geological evidence, that ocean acidification occurred in the past. The most critical factor is the **rate** of the carbon perturbation. During the End Permian mass extinction (ca. 251 million years ago), the carbon perturbation is estimated to be on the order of 1–2 Gt CO_2 per year (Kump et al., 2009). For comparison, 1 gigaton is one billion tons, or the equivalent of around one billion middle-sized cars. For the most recent major extinction event – the Paleocene Eocene Thermal Maximum extinction (PETM; ca. 55 million years ago is considered the closest analogue to currently ongoing ocean acidification), estimates of the rate of the carbon perturbation vary, but values of 0.3–2.2 Gt CO_2 per year during an estimated span of up to 20,000 years have been proposed (Zeebe et al., 2009; Cui et al., 2011). Both these estimates are dwarfed in comparison to today's emissions of roughly 30 Gt of CO_2 per year (IPCC, 2007c). The current rate of carbon release is at least 10 times that which preceded the last major species extinction. When comparing the rate of CO_2 increase between today and the past, it is also important to realise that carbon pertubations in Earth history, albeit slower than today, were sustained over tens of thousands of years. Releasing similar amounts of carbon on a much shorter timescale and causing a fast perturbation adds two other important aspects: 1. This rate is exceeding the Earth system's capacity to buffer such changes; 2. It exposes organisms to unprecedented evolutionary pressure.

At present, it can be said with certainty that the uptake of CO_2 into the ocean is outstripping its capacity to absorb it, known as buffering capacity, thereby coupling a reduction in pH tightly to a lowering of its "saturation state" (Cao and Caldeira, 2008; Ridgwell and Schmidt, 2010). It is this saturation state ("buffering capacity") of the ocean that mirrors the critical impact of unbuffered acidification and hypercapnia on the functioning of most calcifying organisms, such as tropical reef-forming corals but also planktonic organisms that are at the base of pelagic food webs, especially in the vulnerable Arctic and Antarctic regions. If the current trajectory of carbon perturbation continues, we should expect more serious consequences for the marine ecosystem than during the PETM because of more severe acidification and carbonate dissolution in the present and near future. Evidence of impacts of this event on marine ecosystems is restricted to analysis of microfossils where 30–50% of benthic foraminiferans were found to have gone extinct (McInerney and Wing, 2011). Although, this marks the largest loss of species in this group over the last 90 million years, the interesting question of the PETM is why its long-term consequences seem to have been so small for marine organisms, as deep-sea benthic foraminiferans are "small potatoes" in the overall diversity of life. Although, pelagic ecosystems also underwent significant changes with tropical groups of pelagic foraminifera occurring at high latitudes and an increase in warm-water groups occurring in mid- and low-latitudes (McInerney and Wing, 2011), this level of extinction was not reflected in any other group for which data exist, such as the ostracods. Today, there are also accounts of "winners and losers" but this may not reflect the overall ecosystem change in action. Is it possible that the role of temperature and especially hypoxia may have been less during the PETM?

Last but not least, it is worth noting that the ocean's chemical restoration after the PETM took ca. 170,000 years (Cui et al., 2011), which is equivalent to >5000 human generations (generation time of 30 years). For comparison, this is longer than many estimates of the existence of species *Homo sapiens*, and the earliest known hominid dates back only 4.4 million years. In addition, the marine ecosystem as we know it today mainly evolved during a time of low atmospheric CO_2 and well-buffered seawater which is no longer the case.

Regardless of whether or not an extinction event has started, the current carbon perturbation will have huge implications for humans. It is difficult to predict how a possible mass extinction will affect society, but the current carbon perturbation might be the most dramatic challenge faced by our exponentially growing world population ever since the first hominids evolved. The developed society lives above the carrying capacity of the Earth and its ocean and, more than ever, we need to reduce the pressure of all stressors, especially CO_2 emissions.

6. Conclusion

The appearance of the "deadly trio" of risk factors, ocean warming, acidification and deoxygenation are all consequences of a perturbation of the carbon cycle (fast release of carbon dioxide and/or methane) and are a major cause of concern. Historically these factors have combined to contribute to mass extinction events. The present rate of change is unprecedented. Perhaps most worrying is that this is happening to ecosystems that are already undermined by many man-made stressors such as overfishing, eutrophication and pollution (Harnik et al., 2013). To re-emphasize one example, the combination of temperature rise, increased frequency and intensity of extreme events and acidification may irreversibly destroy coral reefs, the most species-rich ecosystems in the ocean, within 50–100 years (Veron et al., 2009).

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