Effects of ocean acidification on marine ecosystems and its chemistry

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Abstract

The climate change is more than a matter of temperature: about 30 percent of the CO_2 released by human activities over the past 200 years has already been absorbed by the ocean, and much more will ultimately end up there. And all that CO_2 is having an unfortunate effect: the ocean is "acidifying," or becoming less basic. The reaction of CO_2 and ocean water produces chemicals such as carbonic acid, which lowers ocean pH, and bicarbonate. On the one hand, increased amounts of carbonic acid should make it more difficult for many organisms, like snails or corals, to build their calcium carbonate shells or skeletons. On the other hand, increased amounts of bicarbonate may stimulate growth in some marine organisms, so the overall effect of rising CO_2 is uncertain and may affect different organisms in varied ways. The ocean's pH has dropped from about 8.2 in preindustrial times to around 8.05. This seemingly small change may already be affecting ocean organisms—and future CO_2 emissions could lower ocean pH even further. Once dissolved in seawater, CO_2 reacts with water, H_2O, to form carbonic acid, H_2CO_3:$CO_2 + H_2O \leftrightarrow H_2CO_3$. Carbonic acid dissolves rapidly to form H+ ions (an acid) and bicarbonate, HCO3-(a base). Seawater is naturally saturated with another base, carbonate ion (CO_3^{-2}) that acts like an antacid to neutralize the H^+, forming more bicarbonate. The net reaction looks like this: $CO_2 + H_2O + CO_3^{-2} \rightarrow 2HCO_3^-$

Introduction:

Rising atmospheric carbon dioxide (CO_2) concentration is causing global warming and ocean acidification, which increasingly are recognized as important drivers of change in biological systems For at least 650 000 years prior to the industrial revolution, atmospheric CO_2 concentrations varied between 180 and 300 ppmv. As a result of human activity, today's atmospheric CO_2 concentration is 380 ppmv and currently is rising at a rate of □ 0.5% per year. Which is □ 100 times faster than any change during the past 650

000 years (Royal Society, 2005; (Siegenthaler et al., 2005). Approximately one-third of the anthropogenic CO_2 produced in the past 200 years has been taken up by the oceans (Sabine et al., 2004). The global ocean inventory of anthropogenic carbon was 118+19 Pg C in 2004 (Sabine et al., 2004), which can be adjusted upwards to 140 Pg C in 2005 based on Denman et al. (2007, Table 7.1). Without this ocean sink, the anthropogenic change in atmospheric CO_2 concentration would be 55% higher than the observed change from 280 to 380 ppmv (Sabine et al., 2004). Although oceanic uptake of anthropogenic CO_2 will lessen the extent of global warming, the direct effect of CO_2 on ocean chemistry may affect marine biota profoundly. Elevated partial pressure of CO_2 (pCO_2) in seawater (also known as hypercapnia) can impact marine organisms both via decreased calcium carbonate ($CaCO_3$) saturation, which affects calcification rates, and via disturbance to acid–base (metabolic) physiology. Recent work indicates that the oceanic uptake of anthropogenic CO_2 and the concomitant changes in seawater chemistry have adverse consequences for many calcifying organisms, and may result in changes to biodiversity, trophic interactions, and other ecosystem processes. Most research has focused on tropical coral reefs and planktonic coccolithophores. Little information is available for other important taxa, for processes other than calcification, or for potential ecosystem-level consequences emerging from the oceanic pCO_2 levels that are predicted to occur over the next 100 years. Here we discuss the present and projected changes in ocean carbonate chemistry, and assess their impacts on pelagic and benthic marine fauna and ecosystem processes. Scientific research on the biological effects of acidification is still in its infancy and there is much uncertainty regarding its ultimate effects on marine ecosystems. But marine organisms will be affected by the chemical changes in their environment brought about by ocean acidification; the question is how and how much. A number of biological processes are already known to be sensitive to the foreseeable changes in seawater chemistry. A prime example is the impairment in the ability of some organisms to construct skeletons or protective structures made of calcium carbonate resulting from even a modest degree of acidification, although the underlying mechanisms responsible for this effect are not well understood. Effects on the physiology of individual organisms can be amplified through food web and other interactions, ultimately affecting entire ecosystems. Organisms forming

oceanic ecosystems have evolved over millennia to an aqueous environment of remarkably constant composition. There is reason to be concerned about how they will acclimate or adapt to the changes resulting from ocean acidification-changes that are occurring very rapidly on geochemical and evolutionary time scales.

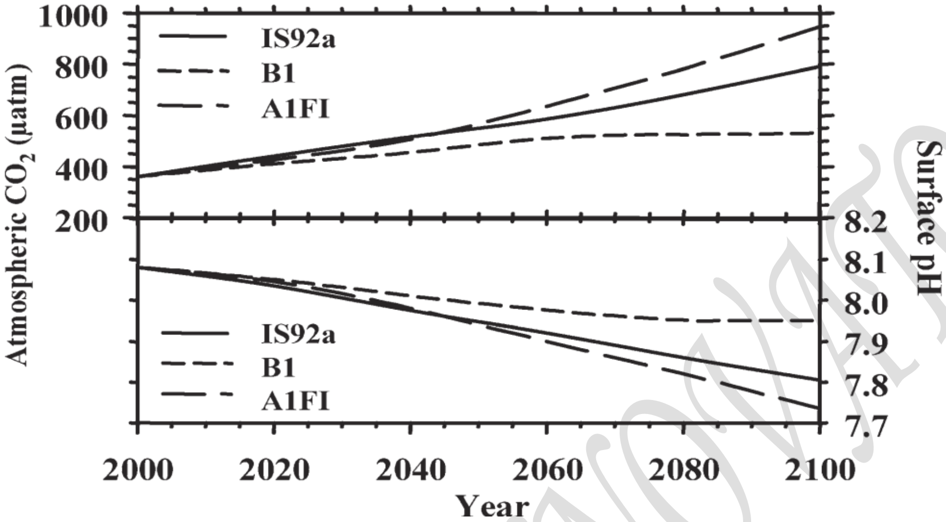

FIGURE 1.

Atmospheric CO_2 concentration projected under the IS92a "business-as-usual" IS92a CO_2 emissions scenario, bounded by the most and least conservative SRES scenario B1 and A1F1, respectively and projected global average surface seawater p^H (modified from Meehl et al 2007)

Seawater Chemistry:

The principal weak acids and bases that can exchange hydrogen ion in seawater and are thus responsible for controlling its pH are inorganic carbon species and, to a lesser extent, borate. Inorganic carbon dissolved in the ocean occurs in three principal forms: dissolved carbon dioxide (CO_2.aq), bicarbonate ion (HCO_3^-), and carbonate ion (CO_3^{2-}). CO_2 dissolved in seawater acts as an acid and provides hydrogen ions (H^+) to any added base to form bicarbonate:

$$CO_2(aq) + H_2O \longrightarrow H^+ + HCO_3^- \qquad (1)$$

CO_3^{2-} acts as a base and takes up H^+ from any added acid to also form bicarbonate:

$$H^+ + CO_3^{2-} \longrightarrow HCO_3^- \qquad (2)$$

Borate [$B(OH)_4^-$] also acts as a base to take up H^+ from any acid to form boric acid [$B(OH)_3$]:

$$H^+ + B(OH)_4^- \longrightarrow B(OH)_3 + H_2O \qquad (3)$$

As seen in reactions 1 and 2, bicarbonate can act as an acid or a base (i.e., donate or accept hydrogen ions) depending on conditions.

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Under present-day conditions, these reactions buffer the pH of surface seawater at a slightly basic value of about 8.1 (above the neutral value around 7.0). At this pH, the total dissolved inorganic carbon (DIC ~ 2 mM) consists of approximately 1% CO_2, 90% HCO_3^-, and 9% CO_3^{2-} (Figure 2).

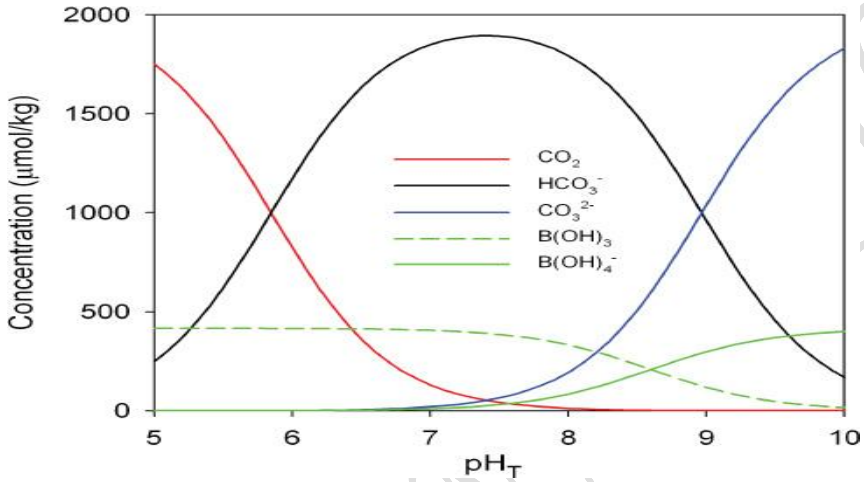

FIGURE 2.

Typical concentrations of the major weak acids and weak bases in seawater as a function of pH. This diagram is calculated for constant dissolved inorganic carbon (DIC) and constant total boric acid using constants from Dickson et al. (2007) and Lueker et al. (2000).

Life in the oceans modifies the amount and forms (or species) of inorganic carbon and hence the acid-base chemistry of seawater. In the sunlit surface layer, phytoplankton convert, or "fix," CO_2 into organic matter during the day a process also known as photosynthesis or primary production. This process simultaneously decreases DIC and increases the pH. The reverse occurs at night, when a portion of this organic matter is decomposed by a variety of organisms that regenerate CO_2, resulting in a daily cycle of pH in surface waters. A fraction of the particulate organic matter sinks below the surface where it is also decomposed, causing vertical variations in the concentrations of inorganic carbon species and pH. The net result is a characteristic maximum in CO_2 concentration and minima in pH and CO_3^{2-} concentration around 500 to 1,000 meters depth.

Changes in ocean pH can be documented beyond the instrumental period of direct measurements using a proxy based on the incorporation into $CaCO_3$ of the borate ion, $B(OH)_4^-$ which has a lighter isotope composition than boric acid, $B(OH)_3$ (Spivack et al., 1993; Sanyal et al., 1995). For time scales shorter than the residence time of boron in the ocean 5-10 million years—measured values in sedimentary carbonates appear to accurately reflect the pH of the growth medium for several calcifying taxa. Results from glacial-interglacial times generally reflect the pH-buffering effect of the $CaCO_3$ cycle (Hönisch, 2005), while records from more recent time intervals reflect acidification of the ocean from rising CO_2 concentrations over the past centuries (Liu, 2009).

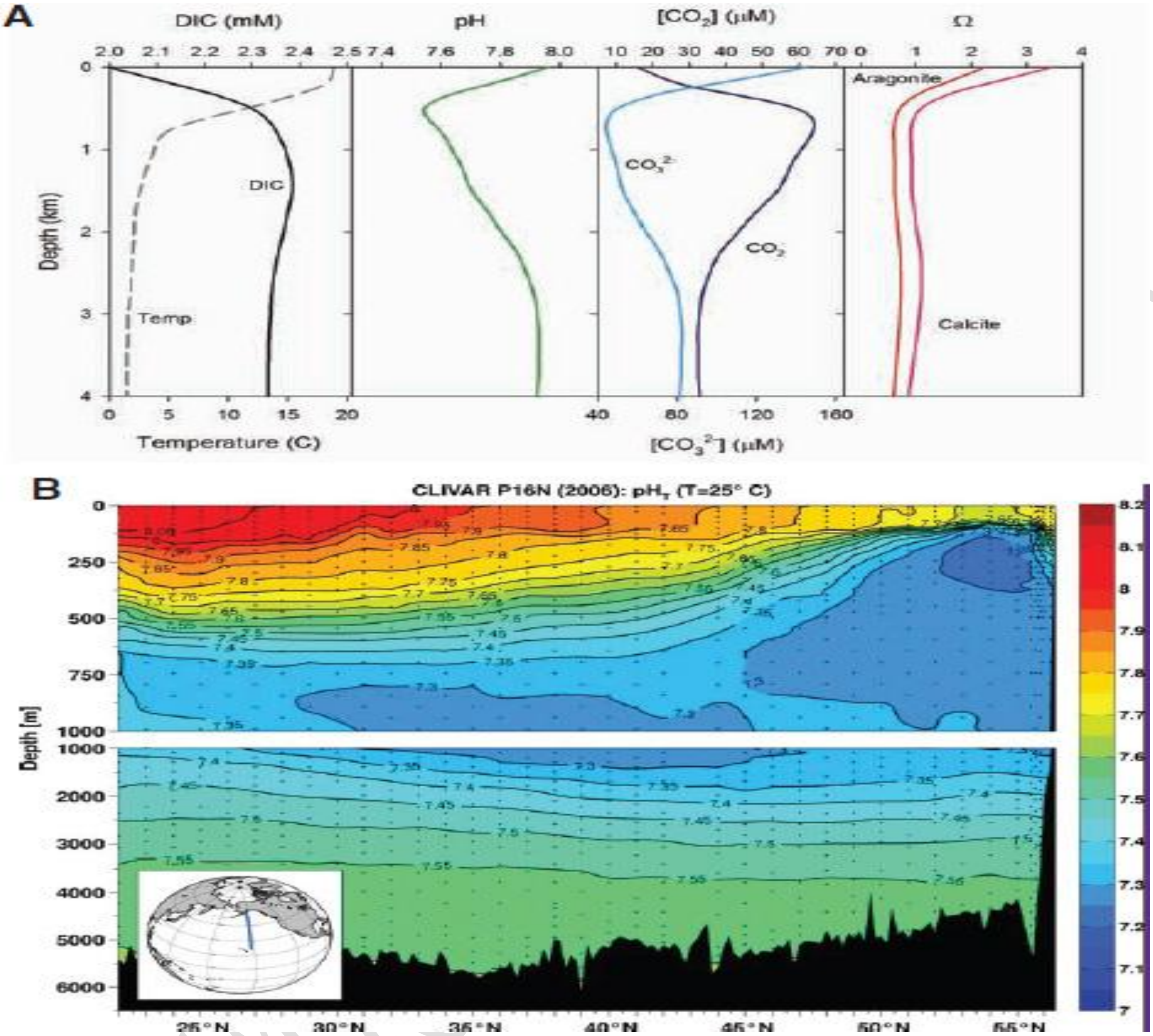

FIGURE3. Inorganic carbon and pH vary as a function of depth and latitude. (a) Vertical profiles typical of the mid-North Pacific showing variations of several seawater chemical parameters with depth. Adapted from Morel and Hering (1993) with calculations us Orr et al. (2005) developed model scenarios of future changes.

Orr et al. (2005) developed model scenarios of future changes in surface ocean carbonate chemistry as a function of changes in atmospheric CO_2, using the IPCC IS92a “business-as-usual” CO_2 emission scenario, with the median projection of DIC changes from 13 ocean models that participated in the OCMIP-2 project. Based on their model outputs and global gridded data (Key et al., 2004), we plotted the projected aragonite saturation state of the surface oceans for the years 1765, 1994, 2050, and 2100 (Figure 4). The model results indicate that, by the time atmospheric CO_2 reaches 780 ppmv near the end of this century under the IPCC IS92a “business-as-usual” CO_2 emission scenario, portions of the Subarctic North Pacific and all of the Southern Ocean south of 608s will become under saturated with respect to aragonite (Orr et al., 2005). At that point, the global average surface water CO_3 22 concentration and aragonite and calcite saturation state will be nearly half of what they are today.

The aragonite saturation horizons would also shoal from its present average depth of 730 m to the surface in the Southern Ocean, from 2600 to 115 m in the North Atlantic, and from 140 m to the surface in parts of the North Pacific (Orr et al., 2005). In the cold, high-latitude surface waters typical of polar and subpolar regions of the Southern Ocean, aragonite and calcite undersaturation will occur when seawater pCO_2 values reach 560 and 900 ppmv, respectively. In the slightly warmer surface waters of the subpolar North Pacific, aragonite and calcite undersaturation will occur later, when pCO_2 reaches 740 and 1040 ppmv, respectively. The cold waters of the Arctic Ocean are also naturally low in CO3 22 concentration. Continuing research is evaluating how the Arctic Ocean's changes in carbonate chemistry during the 21st century will differ from those in the Southern Ocean (Orr et al., 2006).

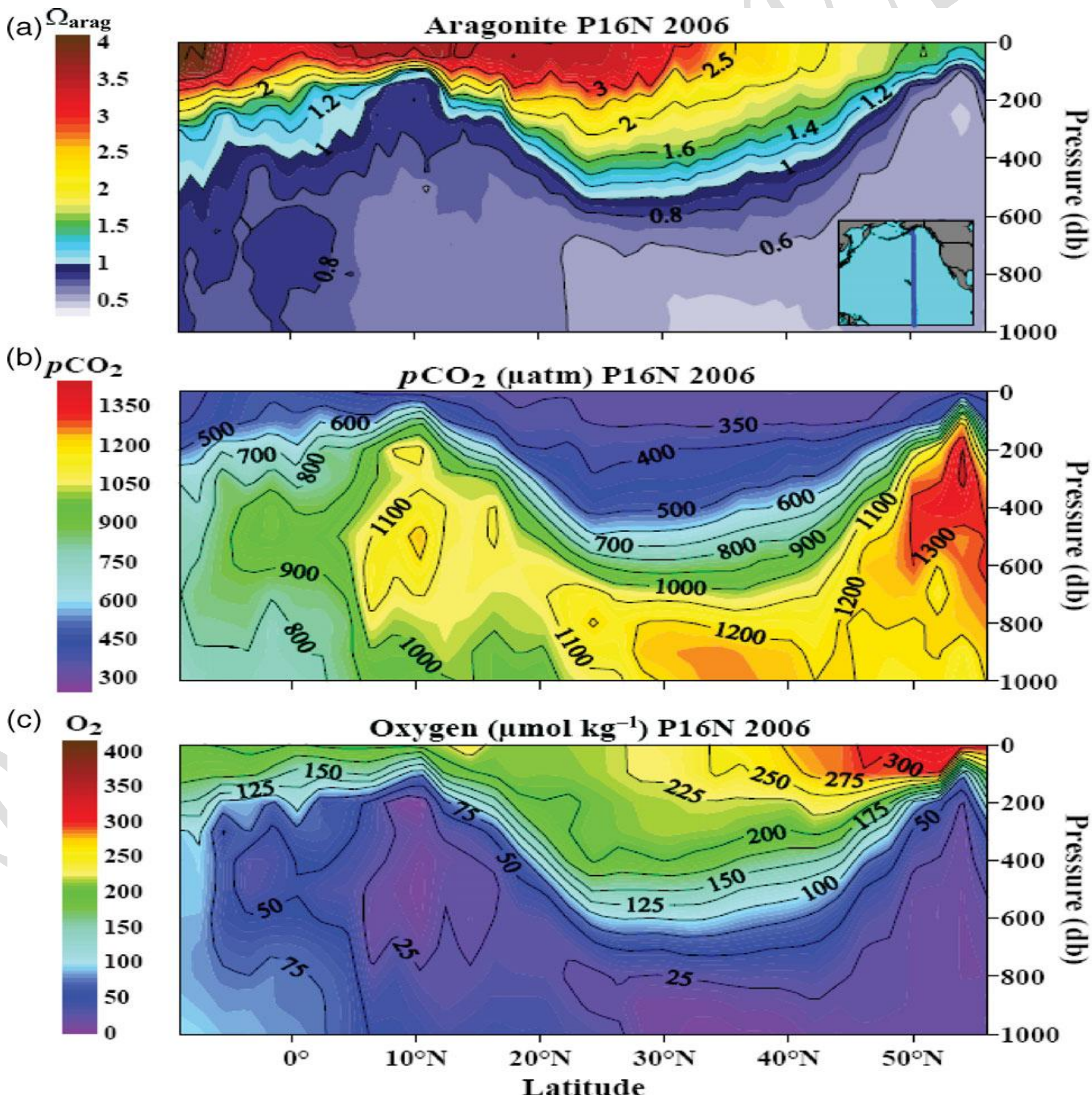

Figure 4. Distribution of (a) aragonite saturation; (b) partial pressure of CO_2 seawater (pCO_2); and (c) dissolved oxygen along the March 2006 P16 N transect along 1528W in the North Pacific.

Impact of Ocean Acidification on Plankton, Bacteria, Corals and Swimming Oranism (Like Fish):

Benthic ecosystems comprise some of the key ocean communities that we rely upon for food and ecosystem services, and occur throughout the world's oceans from the splash zones of all shores to the deepest waters. While none will be able to avoid future ocean acidification, it remains unclear how changes in ocean conditions will affect the composition and function of benthic communities in different environments. Although environmental conditions are less variable through time in the deep ocean than at the surface, there is considerable spatial variability, since carbonate chemistry of deep-sea waters is strongly related to large-scale thermohaline circulation patterns. Consequently, abyssal pH is ~0.2 pH units lower in the Pacific than in the Atlantic. Basin-scale differences in carbonate saturation are even larger. Whereas the aragonite saturation boundary (the depth at which seawater is corrosive to aragonite) is deeper than 2000 m for much of the North Atlantic, in the North East Pacific it shoals to ~ 200 m depth. The most widespread and abundant benthic communities in the global ocean are those in the deep sea, and some of these are expected to be particularly vulnerable to ocean acidification.

Benthic communities will be affected by the direct and indirect responses of its inhabitants to low pH, reduced carbonate saturation, or related parameters. Meta-analyses of laboratory and field experiments, and observations in naturally high-CO_2 marine environments have shown lower rates of growth, survival, or other performance measures for many benthic organisms in acidified waters, although with considerable variability between species and higher taxonomic groups. Many other factors and indirect effects contribute to sensitivity to ocean acidification, including biological processes that may offset potentially detrimental impacts.

A recent meta-analysis compared responses of benthic organisms at different CO_2 concentrations: the commonest response up to around 1000 ppm was a negative impact; at higher concentrations the proportion of negative impacts increased greatly (Figure 5). Crustaceans appear less sensitive to smaller increases in CO2 than other groups (Figure 5), and may be affected through indirect influences, such as effects on food palatability. Their tolerance appears to include juvenile as well as adult growth stages, although there is variability. Further discussion below focuses on the more sensitive taxa, corals, echinoderms and molluscs (Figure 5), although recognizing that the responses of benthic plants and microbes can also be of high ecological importance.

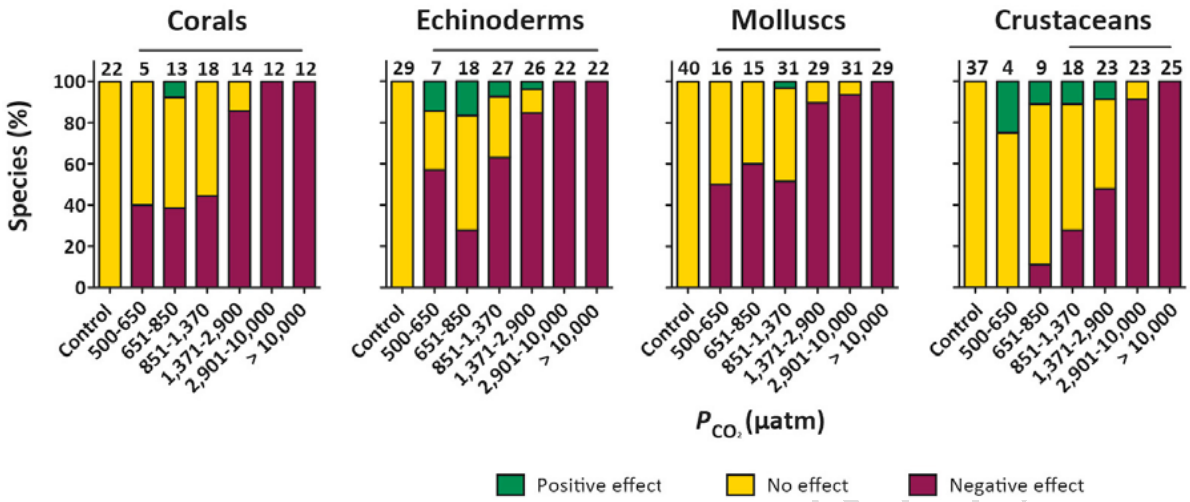

FIGURE 5. Sensitivity of animal taxa to ocean acidification. Fractions (%) of corals, echinoderms, molluscs and crustaceans exhibiting negative, no or positive effects on performance indicators reflect individual fitness in response to increased CO_2. Bars above columns denote count ratios significantly associated with pCO_2.

The sensitivity of entire benthic communities to ocean acidification is also expected to be linked to the scale of natural variation in the environment. Populations inhabiting highly variable habitats, such as coastal systems, may possess the phenotypic and genetic diversity to tolerate and perhaps thrive across the range of variation in carbonate parameters. Observations of pH variability from coastal and open-ocean sites show large differences in the magnitude of variation[8], with only small variation (< 0.1 pH units) in the open ocean over 30 days, but large daily variation (up to 0.8 pH units) at coastal sites over a single day, driven principally by the photosynthesis / respiration balance. It is therefore crucial that future studies expand upon current research to represent and compare different habitats globally.

Plankton and bacteria

Plankton drifting organisms are taxonomically diverse, comprising phytoplankton (photosynthetic algae and bacteria), zooplankton (invertebrates and unicellular animals that spend their whole life in the water column, as well as larval fish, and the juveniles and gametes of many benthic organisms), and heterotrophic bacteria. These plankton, calcifiers and non-calcifiers, form a key component of the marine food chain and also play an important role in biogeochemical cycling.

Biocalcification (by both phyto- and zooplankton) affects the ocean carbon cycle by assisting the export of organic matter from the upper ocean and its burial in deep-sea sediments. Sedimentologists studying the flux of particles collected in deep-sea sediment traps have found that “ballasting” of organic matter aggregates by biominerals may facilitate the flux of organic carbon from the upper ocean to the seafloor. If there is a significant decrease of biocalcification by planktonic organisms as a result of ocean acidification, then a likely secondary effect is reduced export of organic carbon from the Surface Ocean and reduction of the capacity of the ocean to buffer the rise in anthropogenic carbon dioxide.

Non-calcifying phytoplankton forms a significant proportion of the phytoplankton and includes diatoms, cyanobacteria and dinoflagellates, including many harmful algal bloom (HAB) species. The stimulating effects of increased CO_2 on photosynthesis and carbon fixation have been noted in all of these groups. Increased CO_2 could also affect mitochondrial and photorespiration (which produce CO_2); therefore the net effect on primary production needs to account for both CO_2 fixation and loss. It is hypothesised that an increase in CO_2 will be of overall benefit to phytoplankton, as the increased CO_2 in external seawater will reduce CO_2 diffusion leakage from biological cells (where the CO_2 is concentrated) to the surrounding seawater. However, photosynthetic mechanisms vary widely between photosynthetic organisms, and this may lead to a shift in community composition in the future. Assessing whether HAB species will be among those that will benefit from future environmental change remains a key focus for future research, as there is some evidence suggesting that the release of toxic compounds could increase, or that the lack of carbon concentrating mechanisms in many HAB species will be of benefit to them in future climates.

Pteropods are a group of planktonic gastropods (snails) living in the upper layers of the ocean. The normal gastropod foot is modified into a pair of swimming wing-like fins, giving them the common name sea-butterflies, and the shell may be elaborately modified. Pteropods occur throughout the global ocean but they are most abundant in sub-Arctic and sub-Antarctic to Antarctic waters, where they can form a significant part of the zooplankton and are important food stocks for fish and other predators. Pteropods have shells formed of aragonite rather than calcite. The combination of thin aragonitic shells and their abundant occurrence in the Arctic and Southern Oceans makes them likely to be one of the first groups of organisms to be severely affected by ocean acidification. That is because, under saturation will first occur at high latitudes, a combination of the direct effect of low temperatures on CO_2 solubility as well as the initially low carbonate ion concentrations.

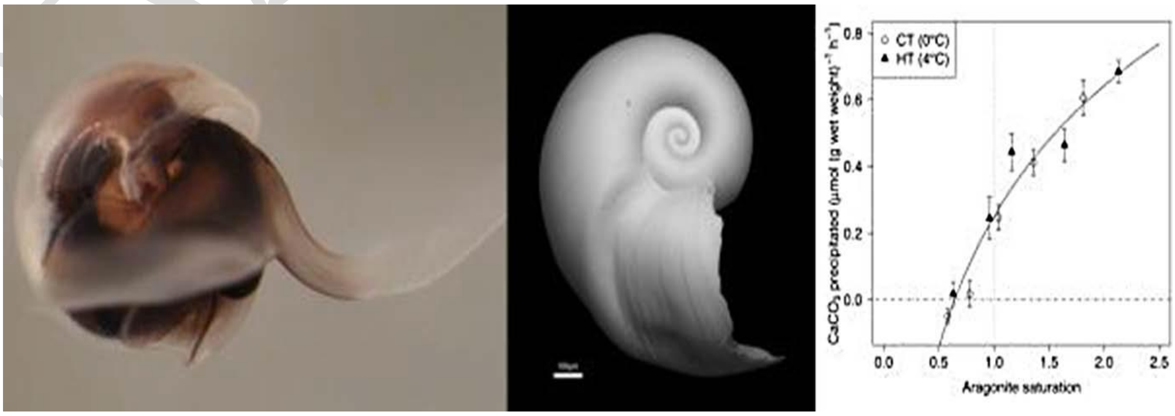

Figure 6. Left: A living pteropod from the Arctic (image Vicky Peck, BAS). Centre: The shell of a juvenile pteropod from the South Atlantic. Right: Data from laboratory culture experiments on shell growth rate of *Limacina helicina* incubated under aragonite saturation states equivalent to those seen in the Arctic at present day (ca 2.0) to the year 2100 (<1.0).

Nektonic (swimming) organisms are those that can move independently of water currents, as opposed to plankton, which are more passive. Although fish represent the majority of nektonic organisms that have been studied with regard to ocean acidification, cephalopods are also important in terms of abundance and economic value. Fish are generally considered to be more resilient to direct effects of ocean acidification than many other marine organisms because they do not have an extensive skeleton of calcium carbonate, and they possess well-developed mechanisms for acid-base regulation. Indirect effects of ocean acidification, such as through "bottom up" changes in the food web, thus need to be considered in future studies as well. Fish compensate for acidosis (increased acidity in blood or tissues) by transport of acid-base relevant ions, mostly across the gills. In most species studied to date, almost complete compensation of acidosis occurs within a few hours or days of exposure to elevated CO_2. This tight regulation of acid-base balance maintains the pH required for efficient cellular function in a high CO_2 environment, but may necessitate additional energy expenditure.

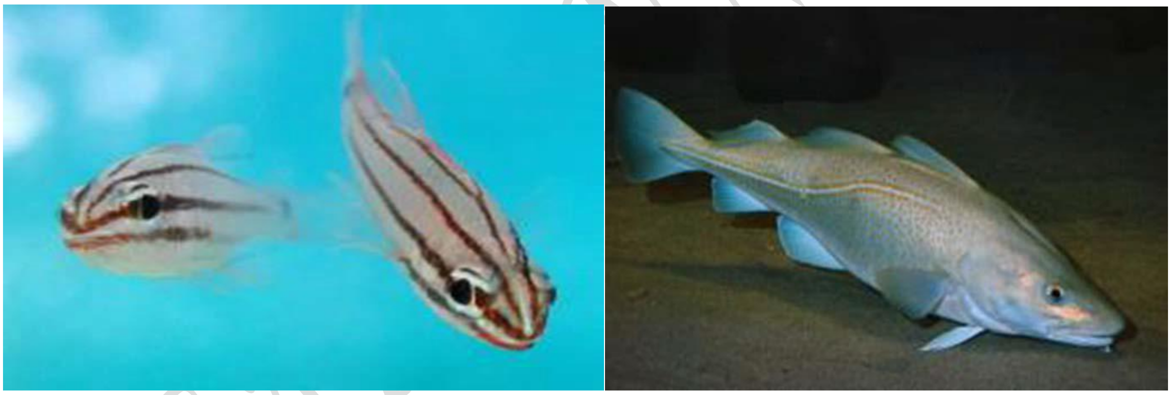

Figure 7. Left: the cardinalfish *Ostorhinchus doederleini*. **Right:** Atlantic cod *Gadus morhua*. **Image:** Goran Nilsson and animalspot.net

The effects of ocean acidification on development, growth and survival of marine fish have largely focused on larval and juvenile stages, because they are expected to be more sensitive to environmental stressors, such as elevated pCO_2, than adults. Despite this expectation, recent studies have found that the early life-history stages of some fish are resilient to projected future levels of ocean acidification. Development, growth and survival of larvae and juveniles of several reef fish species, the pelagic cobia *Rachycentron canadum* and walleye pollock *Theragra chalcogramma* appear relatively robust to near-future CO_2 levels (≤1000 μatm CO_2). In contrast, larval growth declined and mortality increased in the inland silverside *Menidia beryllina*, an estuarine species, at similar CO_2 levels (Figure 7). Tissue development was disrupted in the Atlantic cod *Gadus morhua* reared at relatively high CO_2 levels (1,800 and 4,200 μatm), although the eggs and larval stages did not seem to be affected.

Preliminary studies on the effects of chronic exposure to high CO_2 on fish reproduction have not detected substantial impacts, although long-term consequences in many species remain to be determined. In the short term, reproductive output can be stimulated by high CO_2, for example, in the cinnamon anemonefish *Amphiprion melanopus*. Sperm motility is arrested by mild increases in pCO_2 in some flatfish, but not in the cod, *Gadus morhua*, or 11 other species from a range of families. Furthermore, rearing eggs of Atlantic herring *Clupea harengus* in acidified water had no detectable effect on fertilization success, embryonic development, hatch rate, length and weight at hatching and yolk size. Sensitivity of fish eggs to elevated CO_2 varies markedly between species, but species tested to date typically have 24h LC50 (lethal concentration resulting in 50% mortality over 24 hours) values well above 10,000 µatm CO_2, far in excess of projected end of the century CO_2 levels.

CONCLUSIONS

The rate of ocean acidification that we have experienced since pre-industrial times and its projected continuation are "potentially unparalleled in at least the last ~300 million years of Earth history". As such, current ocean acidification represents a new and unprecedented chapter of marine ecosystem change that seems very likely to have a significant impact on marine species and ecosystems (including economically important species), on various industries and communities, and on global food security. Impacts of ocean acidification will be most keenly and rapidly experienced in the Arctic and Antarctic environments due to their low temperatures, affecting saturation state. The Arctic Monitoring and Assessment Programme (AMAP) has shown that acidification will not be uniform across the Arctic Ocean. While impacts in that region may be positive for some species, other species may face extinction; furthermore, acidification may contribute to an alteration in the abundance of different fish species, with potential impact upon the livelihoods of local communities. The economic costs of ocean acidification are only partially known, with many studies focussing on local rather than global costs. Nevertheless, the global cost of ocean acidification impacts on molluscs and tropical coral reefs is estimated to be over US $1000 billion annually by the end of the century. These calculations are inherently difficult, being based on what we can currently predict, which largely centre on loss of earnings and a limited selection of ecosystem services. The actual costs are likely to be in excess of this figure, particularly when taking account of potentially compounding factors such as overfishing, sedimentation and temperature rise. There is a critical need for information on the sub-lethal calcification and energetic responses of a diverse suite of zooplankton and micro nekton. We need to move forward on several fronts in parallel.

- ✓ Target species for investigation in the above regions include euthecosomatous pteropods, foraminifera, epipelagic squid, and larval stages and adults of commercially and ecologically important benthic invertebrates such as bivalves, sea urchins, Mesocosm and field experiments are necessary to quantify ecosystem impacts from ocean acidification that may include forcing from bottom-up controls, changes in foodweb structure, biogeochemical cycling, and feedback mechanisms.

- ✓ New approaches (e.g. functional genomics and DNA barcoding) and advances in existing technologies (e.g. autonomous chemical sensors and optical plankton samplers) are necessary to investigate the in situ response of organisms that are difficult to maintain in the laboratory, identify sub-lethal effects of chronic exposure to elevated pCO_2 on marine fauna, and address questions of long-term impacts and potential for adaptation over decadal to centennial time-scales.
- ✓ In sensitive regions and for critical species, we need to track the abundances and depth distributions of calcareous and non-calcifying fauna, measure calcification and metabolic rates of these groups, and relate these data to changes in the CO_2 chemistry of the water column. This requires commitment to long-term monitoring programmes at appropriate temporal and spatial scales to detect possible shifts, and distinguish between natural variability and anthropogenically induced changes.

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