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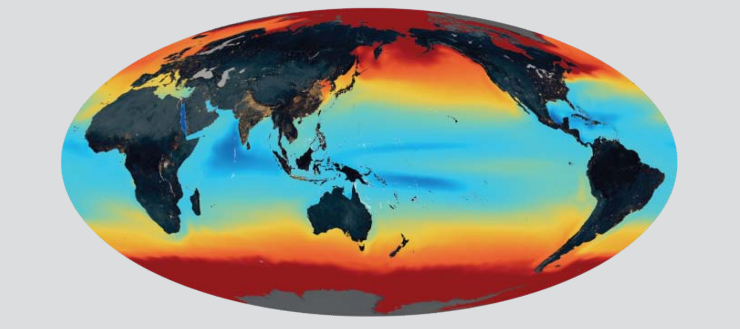
75

An Updated Synthesis of the Impacts of Ocean Acidification on Marine Biodiversity



UNEP

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AN UPDATED SYNTHESIS OF THE IMPACTS OF OCEAN ACIDIFICATION ON MARINE BIODIVERSITY

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Reviewers

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- Countries: Canada, Colombia, France, Honduras, India, Italy, Japan, Mexico, Nigeria, United Kingdom of Great Britain and Northern Ireland, United States of America.
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FOREWORD

Marine and coastal biodiversity – ecosystems, species and genetic material – provide enormous benefits for human well-being. Hundreds of millions of people rely directly on marine biodiversity for their livelihoods. Oceans are critical to many important global geo-chemical processes, such as climate regulation and carbon cycling. Ocean ecosystems provide critical life supporting services to the global population and underpin global productivity and well-being.

However, the oceans are facing major threats due to rising levels of carbon dioxide in the atmosphere. In addition to driving global climate change, increasing concentrations of carbon dioxide affect ocean chemistry, impacting marine ecosystems and compromises the health of the oceans and their ability to provide important services to the global community. The impacts of ocean acidification are beginning to be felt in some areas, but future projections indicate even more broad-reaching deleterious impacts if action is not taken.

At its ninth meeting, the Conference of the Parties to the CBD raised concerns about the potential impacts of ocean acidification on marine and coastal biodiversity and requested the Executive Secretary, in collaboration with Parties, other Governments, and relevant organizations, to compile and synthesize available scientific information on ocean acidification and its impacts on marine biodiversity and habitats. This resulted in the production of CBD Technical Series No. 46 "Scientific Synthesis of the Impacts of Ocean Acidification on Marine Biodiversity" in 2009.

Since then, the amount of research on ocean acidification has grown enormously, as various governments and organizations around the world expanded their research efforts to gain an improved understanding of the ecological and socioeconomic impacts of ocean acidification and means to address this pressing threat.

In recognition of the need for the most up-to-date information in addressing this issue, the COP, in decision XI/18, requested the Executive Secretary to collaborate with the Intergovernmental Oceanographic Commission of the United Nations Educational, Scientific and Cultural Organization, relevant scientific groups, other relevant organizations, and indigenous and local communities in the preparation of an updated systematic review on the impacts of ocean acidification on biodiversity and ecosystem functions, building upon CBD Technical Series No. 46, to provide a targeted synthesis of the biodiversity implications of ocean acidification for marine and coastal systems, including information on the less-reported paleo-oceanographic research.

This report, CBD Technical Series No. 75, "An updated synthesis of the impacts of ocean acidification on marine biodiversity", represents an enormous scientific effort by researchers and experts from around the world to synthesize the best available and most up-to-date information on the impacts of changing ocean pH on the health of the world's oceans.

Among other findings, the report notes that ocean acidification has increased by around 26% since pre-industrial times and that, based on historical evidence, recovery from such changes in ocean pH can take many thousands of years. The report outlines how ocean acidification impacts the physiology, sensory systems and behavior of marine organisms, and undermines ecosystem health. It, furthermore, shows that impacts due to ocean acidification are already underway in some areas and that future projected impacts could have drastic irreversible impacts on marine ecosystems. Despite the growing body of information on ocean acidification, the report points out key knowledge gaps and, in light of the many complex interactions related to ocean chemistry, stresses the difficulty of assessing how future changes to ocean pH will affect marine ecosystems, food webs and ecosystems, and the goods and services they provide.

This report, which presents complex scientific information on ocean acidification in a clear and understandable way, provides an important reference point for scientists, policy-makers and anyone else interested in understanding how ocean acidification affects our oceans and the vital services they provide. As the need for urgent action to address ocean acidification becomes ever more pressing, collaboration among governments and organizations in enhancing and sharing knowledge through efforts such as this report will become increasingly important.

Braulio Ferreira de Souza Dias
Executive Secretary
Convention on Biological Diversity

EXECUTIVE SUMMARY

Ocean acidification and awareness of its consequences

1. **Ocean acidification has increased by around 26% since pre-industrial times**
   In the past 200 years, it is estimated that the ocean has absorbed more than a quarter of the carbon dioxide released by human activity, increasing ocean acidity (hydrogen ion concentration) by a similar proportion. It is now nearly inevitable that within 50 to 100 years, continued anthropogenic carbon dioxide emissions will further increase ocean acidity to levels that will have widespread impacts, mostly deleterious, on marine organisms and ecosystems, and the goods and services they provide. Marine calcifying organisms seem particularly at risk, since additional energy will be required to form shells and skeletons, and in many ocean areas, unprotected shells and skeletons will dissolve.

2. **International awareness of ocean acidification and its potential consequences is increasing**
   Many programmes and projects are now investigating the impacts of ocean acidification on marine biodiversity and its wider implications, with strong international linkages. The United Nations General Assembly has urged States to study ocean acidification, minimize its impacts and tackle its causes. Many United Nations bodies are focusing attention on these issues.

Global status and future trends of ocean acidification

3. **Seawater pH shows substantial natural temporal and spatial variability**
   The acidity of seawater varies naturally on a diurnal and seasonal basis, on a local and regional scale, and as a function of water depth. Coastal ecosystems and habitats experience greater variability than those in the open ocean, due to physical, geochemical and biological processes, and terrestrial influences.

4. **Substantial natural biological variability exists in organisms' responses to pH changes**
   Metadata analyses, combining results from many experimental studies, show that there are different, but consistent, patterns in the response of different taxonomic groups to simulated future ocean acidification. There can also be variability in responses within species, depending on interactions with other factors.

5. **Surface waters in polar seas and upwelling regions are increasingly at risk of becoming undersaturated with respect to calcium carbonate, dissolving shells and skeletons which are not protected by an organic layer**
   In waters where pH is already naturally low (in high latitudes, coastal upwelling regions and on the shelf slope), widespread undersaturation of the commonest forms of biologically-formed calcium carbonate, aragonite and calcite, is expected to develop during this century. Benthic and planktonic molluscs are amongst the groups likely to be affected, as well as cold-water corals and the structural integrity of their habitats.

6. **International collaboration is underway to improve monitoring of ocean acidification, closely linked to other global ocean observing systems**
   A well-integrated global monitoring network for ocean acidification is crucial to improve understanding of current variability and to develop models that provide projections of future conditions. Emerging technologies and sensor development increase the efficiency of this evolving network.

What the past can tell us: paleo-oceanographic research

7. **During natural ocean acidification events that occurred in the geological past, many marine calcifying organisms became extinct**
   High atmospheric carbon dioxide has caused natural ocean acidification in the past, linked to "coral reef crises". During the Paleo-Eocene Thermal Maximum (PETM, ~56 million years ago), the species extinctions were less severe than earlier events; however, the atmospheric changes that occurred then were much slower than those happening today.

8. **Recovery from a major decrease in ocean pH takes many thousands of years**
   The paleo-record shows that recovery from ocean acidification can be extremely slow; following the PETM, for example, this took around 100,000 years.

Impacts of ocean acidification on physiological responses

9. **Ocean acidification has implications for acid-base regulation and metabolism for many marine organisms**
   When external hydrogen ion levels substantially increase, extra energy may be required to maintain the internal acid-base balance. This can lead to reduced protein synthesis and reduction in fitness. Such effects are greatest for sedentary animals, but can be mitigated if food supply is abundant, and increasing metabolism may offset detrimental effects in some species.

10. **Impacts of ocean acidification upon invertebrate fertilization success are highly variable, indicating the potential for genetic adaptation**
    Experimental studies on the impact of ocean acidification on fertilization show that some species are highly sensitive, whilst others are tolerant. Intra-specific variability indicates the scope for a multi-generational, evolutionary response.

11. **Ocean acidification is potentially detrimental for calcifying larvae**
    Early life stages of a number of organisms seem to be particularly at risk from ocean acidification, with impacts including decreased larval size, reduced morphological complexity, and decreased calcification.

12. **Ocean acidification can alter sensory systems and behaviour in fish and some invertebrates**
    Impacts include the loss of ability to discriminate between important chemical cues. Individuals may become more active and liable to exhibit bolder, riskier behaviour.

Impacts of ocean acidification on benthic communities

13. **Around half of benthic species have lower rates of growth and survival under projected future acidification**
    For corals, molluscs and echinoderms, many studies show reduction in growth and survival rates with ocean acidification. However, these responses are variable, and some species can live at low pH conditions.

14. **Many seaweed (macroalgae) and seagrass species can tolerate, or may benefit from, future ocean acidification**
    Non-calcifying photosynthetic species, which are frequently abundant near natural CO_2 seeps, may benefit from future ocean acidification. Calcifying macroalgae are, however, negatively impacted. High densities of seagrass and fleshy macroalgae can significantly alter the local carbonate chemistry, with potential benefit for neighbouring ecosystems.

Impacts of ocean acidification on pelagic communities

15. **Many phytoplankton could potentially benefit from future ocean acidification**
    Non-calcifying phytoplankton (e.g., diatoms) can show increased photosynthesis and growth under high CO_2 conditions. The response of calcifying phytoplankton (e.g., coccolithophores) is more variable, both between and within species. Mesocosm experiments provide insights into the community shifts that might arise through competitive interactions, as well as the balance between increased photosynthesis and decreased calcification. The response of bacterio-plankton to ocean acidification has not been well studied, but altered decomposition rates would have implications for nutrient cycling.

16. **Planktonic foraminifera and pteropods seem likely to experience decreased calcification or dissolution under projected future conditions**
    The shells of both of these groups are liable to experience dissolution if calcium carbonate saturation drops below 1. Decreases in shell thickness and size of planktonic foraminifera may also decrease the efficiency of future carbon transport between the sea surface and the ocean interior.

Impacts of ocean acidification on biogeochemistry

17. **Ocean acidification could alter many other aspects of ocean biogeochemistry, with feedbacks to climatic processes**
    High CO_2 may alter net primary productivity, trace gas emissions, nitrogen-carbon ratios in food webs and exported particulate matter, and iron bioavailability. The scale and importance of these effects are not yet well-understood.

Impacts of ocean acidification on ecosystem services and livelihoods

18. **Impacts of ocean acidification on ecosystem services may already be underway**
    Ocean acidification is apparently already impacting aquaculture in the north-west United States of America, further decreasing the pH of upwelled water, which has a naturally low saturation state for calcium carbonate. High mortalities in oyster hatcheries can, however, be mitigated by monitoring and management measures. Risks to tropical coral reefs are also of great concern, since the livelihoods of around 400 million people depend on such habitats. Research on the socio-economic impacts of ocean acidification has only recently started and is growing rapidly.

Resolving uncertainties

19. **Existing variability in organism response to ocean acidification needs to be investigated further, to assess the potential for evolutionary adaptation**
    Multi-generational studies with calcifying and non-calcifying algal cultures show that adaptation to high CO_2 is possible for some species. Such studies are more difficult to conduct for long-lived organisms, and variability in adaptive capacity is likely. Even with adaptation, community composition and ecosystem function are still likely to change.

20. **Research on ocean acidification increasingly needs to involve other stressors, as will occur under field conditions in the future**
    Acidification may interact with many other changes in the marine environment, local and global; these "multiple stressors" include temperature, nutrients, and oxygen. *In situ* experiments on whole communities (using natural CO_2 vents or CO_2 enrichment mesocosms) provide a good opportunity to investigate impacts of multiple stressors on communities, to increase our understanding of future impacts.

Synthesis

21. **Ocean acidification represents a serious threat to marine biodiversity, yet many gaps remain in our understanding of the complex processes involved and their societal consequences**
    Ocean acidification is currently occurring at a geologically unprecedented rate, subjecting marine organisms to an additional, and worsening, environmental stress. Experimental studies show the variability of organisms' responses to simulated future conditions: some are impacted negatively, some positively, and others are apparently unaffected. Furthermore, responses to ocean acidification can interact with other stressors and vary over time, with some potential for genetic adaptation. This complexity of natural processes makes it extremely challenging to assess how future ocean acidification will affect natural marine communities, food webs and ecosystems, and the goods and services they provide. Nevertheless, substantive environmental perturbations, increased extinction risk for particularly vulnerable species, and significant socio-economic consequences all seem highly likely. Research priorities to reduce the uncertainties relating to future impacts include greater use of natural high-CO_2 analogues, the geological record, and well-integrated observations, together with large-scale, long-term and multi-factorial experimental studies.

1. BACKGROUND AND INTRODUCTION

KEY MESSAGES

1. Ocean acidification is a process caused by increasing levels of carbon dioxide in the atmosphere and seawater, with potentially deleterious consequences for marine species and ecosystems

2. The acidity of the surface ocean has increased by ~26% since pre-industrial levels

3. The increased international attention given to ocean acidification, by the CBD and other bodies, has catalysed research and helped identify knowledge gaps

Ocean acidification, often referred to as the "other CO_2 problem"[1], is a direct result of rising atmospheric carbon dioxide (CO_2) concentrations due to the burning of fossil fuels, deforestation, cement production and other human activities. As atmospheric CO_2 increases, more enters the ocean across the sea surface. This process has significant societal benefits: by absorbing around a quarter of the total human production of CO_2, the ocean has substantively slowed climate change. But it also has less desirable consequences, since the dissolved CO_2 affects seawater chemistry, with a succession of potentially adverse impacts on marine biodiversity, ecosystem services and human society.

The starting point for such changes is an increase in seawater acidity, resulting from the release of hydrogen ions (H^+). Acidity is measured on the logarithmic pH scale, with H^+ concentrations* at pH 7.0 being ten times greater than at pH 8.0. Since pre-industrial times, the mean pH in the surface ocean has dropped by 0.1 units, a linear-scale increase in acidity of ~26%. Unless CO_2 emissions are rapidly curtailed, mean surface pH is projected – with a high degree of certainty – to fall by a further ~0.3 units by 2100[2-4], representing an acidity increase of around 170% compared to pre-industrial levels. The actual change will depend on future CO_2 emissions, with both regional and local variations in the oceanic response (Chapter 3).

Very many scientific studies in the past decade have unequivocally shown that a wide range of marine organisms are sensitive to pH changes of such magnitude, affecting their physiology, fitness and survival, mostly (but not always) in a negative way[4-6]. The consequences of ocean acidification for marine food webs, ecosystems, biogeochemistry and the human use of marine resources are, however, much less certain. In particular, ocean acidification is not the only environmental change that organisms will experience in future, since it will occur in combination with other stressors (e.g., increasing temperature and deoxygenation)[7]. The biological effects of multiple stressors occurring together cannot be assumed to be additive; instead, due to interactions, their combined impacts may be amplified (through synergism) or diminished (antagonism). Furthermore, there is now evidence that some – but not necessarily all – organisms may show genetically mediated, adaptive responses to ocean acidification[8].

This review provides an updated synthesis of the impacts of ocean acidification on marine biodiversity based upon current literature, including emerging research on the geological history of natural ocean acidification events, and the projected societal costs of future acidification. The report takes into consideration comments and feedback submitted by Parties to the Convention on Biological Diversity, other Governments and organizations as well as experts who kindly peer-reviewed the report.

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* pH is defined as the decimal logarithm of the reciprocal of hydrogen ion activity in a solution. Different scales are possible, depending on buffer standards. For seawater, the "total scale" (pH_T) is now preferred, and most data given in this report can be assumed to be on that basis.

1.1 MANDATE OF THIS REVIEW

The Conference of the Parties to the Convention on Biological Diversity initially raised its concern on the potential adverse impacts of ocean acidification at its ninth meeting (COP 9; Bonn, 2008), which instigated the CBD Secretariat's first review on this topic "Scientific Synthesis of the Impacts of Ocean Acidification on Marine Biodiversity" (Technical Series No. 46)[9], carried out jointly with the UNEP World Conservation Monitoring Centre. In response to that review, COP 10 (Nagoya, 2010) recognized ocean acidification as a new and important issue, for consideration as an ongoing activity under the programme of work on marine and coastal biodiversity (decisions X/13 and X/29) and included ocean acidification in the Strategic Plan for Biodiversity 2011-2020 and the Aichi Biodiversity Targets (Target 10; decision X/2).

In decision X/29, the Conference of the Parties to the Convention on Biological Diversity established a series of expert review processes, in collaboration with various relevant organizations, to assess the impacts of ocean acidification on marine biodiversity. To initiate implementation of the request in this decision, an Expert Meeting on Ocean Acidification was convened by the CBD Secretariat, in collaboration with the Intergovernmental Oceanographic Commission of the United Nations Educational, Scientific and Cultural Organization (IOC-UNESCO), in Montreal in October 2011, involving representatives from Parties and relevant organizations. The Expert Meeting identified gaps and barriers in existing monitoring and assessment of ocean acidification in the context of global policy processes; developed options for addressing those gaps and barriers; and considered the need for additional collaborative activities. The workshop report[10] was considered at CBD COP 11 (Hyderabad, 2012), when Parties decided that a new systematic review should be prepared as the basis for further policy action.

COP requested that the updated synthesis – this document – provide "a targeted synthesis of the biodiversity implications of ocean acidification for marine and coastal systems, including information on the less reported paleo-oceanographic research, building upon the synthesis provided in CBD Technical Report Series No 46" (XI/18, paragraphs 22-24). This updated synthesis document (UNEP/CBD/SBSTTA/18/INF/6) was considered by the Subsidiary Body on Scientific, Technical and Technological Advice, at its 18th meeting (Montreal, 23-28 June 2014), which requested the Executive Secretary to transmit it to the Joint Liaison Group of the three Rio Conventions and recommended that the COP request the Executive Secretary to forward it to Parties, other Governments and relevant organizations and to transmit it to the Secretariat of the United Nations Framework Convention on Climate Change.

In response to a request to Parties to assist in implementing COP 11 decisions, the Government of the United Kingdom of Great Britain and Northern Ireland has provided the main financial support for preparing the updated synthesis, through the UK Ocean Acidification research programme, co-funded by the Natural Environment Research Council, the Department for Environment, Food and Rural Affairs, and the Department of Energy and Climate Change. The scientific authorship of this review is, however, fully international, involving contributors from 12 countries, many of whom also participated in the 2011 Expert Meeting. In developing the review, the authors considered "biodiversity implications" to encompass impacts on marine ecosystems and wider environmental considerations (i.e., consistent with the relatively broad definition of biodiversity in Article 2 of the CBD Convention)[11], rather than limiting the term to quantified measures of species richness, heritable variation or habitat diversity.

The increasing international awareness of ocean acidification and its societal implications was demonstrated at the 14th meeting of the UN Open-ended Informal Consultative Process (ICP) on Oceans and Law of the Sea (New York, 17-20 June 2013)[12]. At this meeting, an early draft of this CBD review was presented and discussed at a side event convened by CBD Secretariat, in collaboration with the IOC-UNESCO, and valuable feedback was received.

The United Nations General Assembly recognized the attention given to ocean acidification by the 14th ICP meeting and committed itself to continue to pay attention to this important issue, including taking account of the ongoing work of the recently established Ocean Acidification International Coordination Centre of the International Atomic Energy Agency (A/RES/68/70, para 156; also see Box 2.1 and Table 2.1 below).

1.2 WHAT IS OCEAN ACIDIFICATION?

Ocean acidification can be defined in relatively narrow terms, limiting its meaning to a global-scale, long-term decrease in seawater pH, which currently is primarily due to the human-driven increase in atmospheric CO_2, which will almost certainly intensify. The CO_2-pH relationship has now been observed at many locations, with the longest atmospheric CO_2 time series from the Mauna Loa observatory (Hawaii) and a nearby oceanic time series (Figure 1.1).

The above definition of ocean acidification focuses on the reaction of dissolved anthropogenic CO_2 with water to form carbonic acid (H_2CO_3), which dissociates to form bicarbonate ions (HCO_3^-) and hydrogen ions (H^+, quantified by the pH scale). An additional reaction with carbonate ions (CO_3^{2-}; naturally occurring in seawater) also occurs, reducing their concentration. All these reactions are in dynamic equilibrium (Figure 1.2). As a result, the process of ocean acidification can more generally be considered as changes to the seawater "carbonate system". Whilst pH values are of great interest, it is not straightforward to measure them with high precision. Instead, they are often calculated from other measured parameters, such as dissolved carbon dioxide (pCO_2), total dissolved inorganic carbon (DIC) and total alkalinity (TA; the combined abundance of proton-acceptors, i.e., negatively charged ions that react with strong acid).

One further chemical reaction is noteworthy. A decline in the abundance of carbonate ions in seawater affects the stability of calcium carbonate ($CaCO_3$) in solid form, which may be present as bedrock (such as chalk or limestone), dead shells, or as an exterior covering or structural component of living organisms – such as molluscs (e.g., mussels, oysters and sea-snails), echinoderms (e.g., sea urchins), crustaceans (e.g., crabs and lobsters), warm and cold-water corals, and calcifying algae. Such calcifying organisms require more energy to produce $CaCO_3$

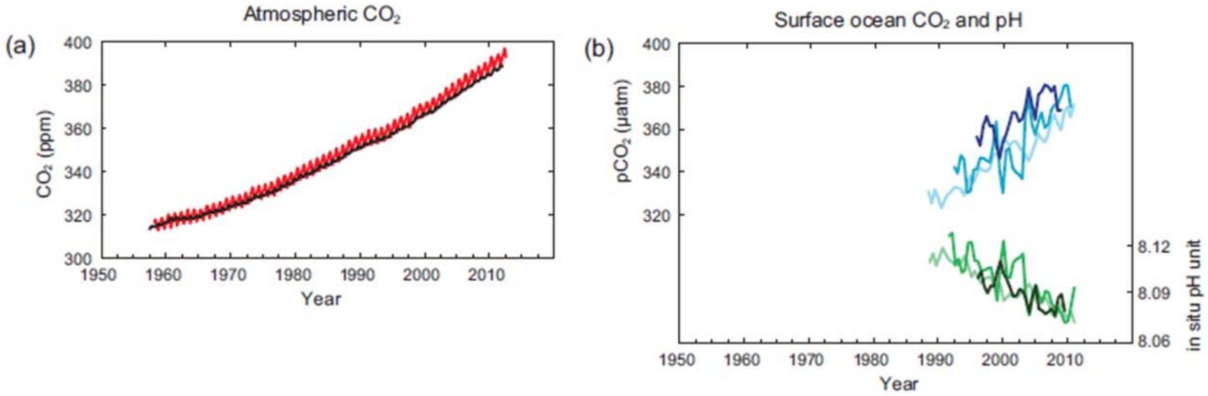

Figure 1.1. **Multiple observed indicators of a changing global carbon cycle: (a) atmospheric concentrations of carbon dioxide (CO_2) from Mauna Loa (19°32'N, 155°34'W – red) and South Pole (89°59'S, 24°48'W – black) since 1958; (b) partial pressure of dissolved CO_2 at the ocean surface (blue curves) and in situ pH (green curves), a measure of the acidity of ocean water. Measurements are from three stations from the Atlantic (29°10'N, 15°30'W – dark blue/dark green; 31°40'N, 64°10'W – blue/green) and the Pacific Oceans (22°45'N, 158°00'W − light blue/light green). Full details of the datasets shown here are provided in the underlying report of the Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change I and the Technical Summary Supplementary Material[13].**

in water with lower pH, but they may also experience shell dissolution, unless their exoskeletons and carapaces are protected by an organic layer.

Whether or not such dissolution occurs is determined by the saturation state (Ω) of carbonate, defined as the ratio between dissolved abundances of calcium and carbonate ions and their solubility product constants, the latter being temperature-specific. Thus Ω values need to be greater than 1.0 for unprotected $CaCO_3$ to be stable, and Ω values in the range 3.0 - 5.0 are generally considered optimal for bio-calcification to occur. Currently, the vast majority of the surface ocean is supersaturated with respect to $CaCO_3$, i.e. $\Omega > 1.0$. However, most of the deep ocean (below 1-2 km) is undersaturated, with $\Omega < 1.0$, owing to changes in temperature and pressure (increasing solubility product constants) and the accumulation of biologically produced CO_2 through decomposition (reducing carbonate ion abundance). The depth at which $\Omega = 1.0$ is the saturation horizon, with most of the deep ocean below that horizon and therefore corrosive to unprotected $CaCO_3$. Some calcareous material may be found below that depth if the rate of its supply from the surface or mid-waters exceeds the rate of its dissolution; however, it is very unlikely to be preserved in the fossil record. The few shelled organisms that survive below the saturation horizon have well-protected shells and/or are limited to niche habitats, such as hot vents[17].

An additional complication is that there are two main bio-mineral forms of $CaCO_3$, aragonite and calcite, with the former being slightly more soluble. Thus Ω values for aragonite (and aragonite saturation

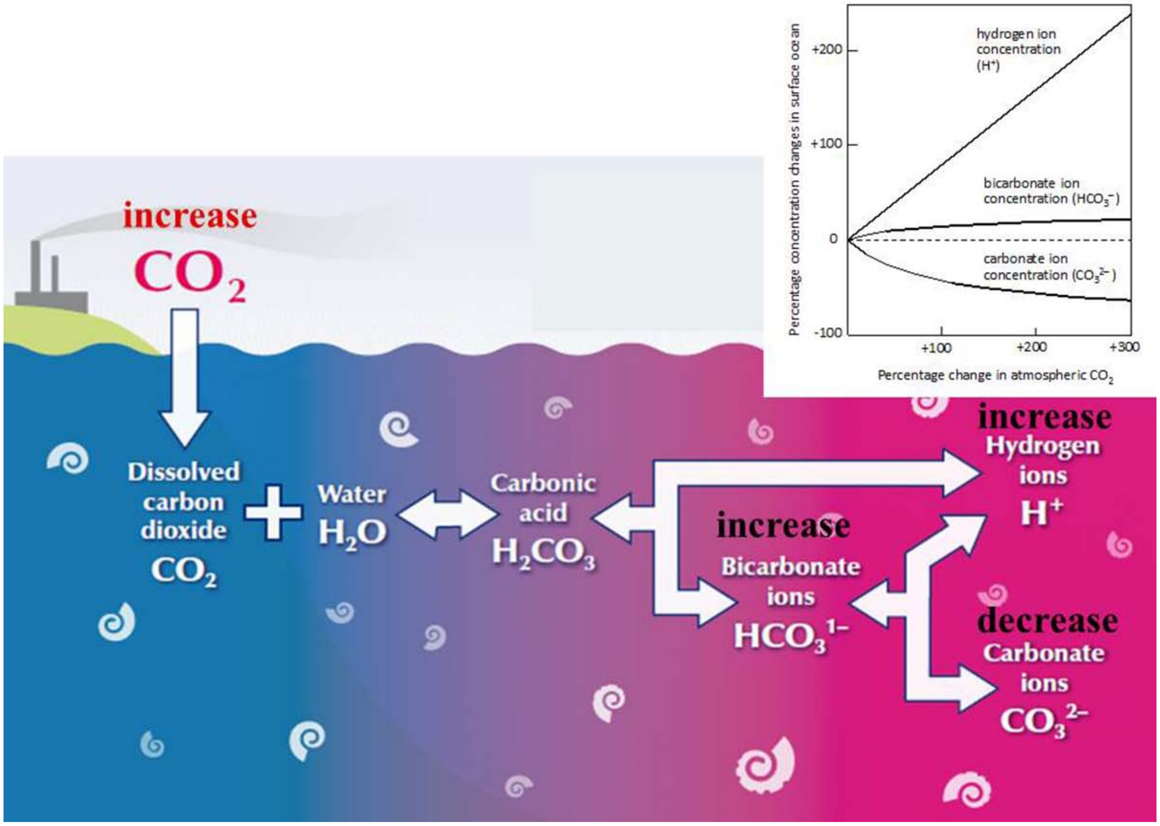

Figure 1.2. The chemical reactions that occur when additional carbon dioxide dissolves in seawater, with net effect of increasing the abundance of hydrogen ions and bicarbonate, whilst reducing carbonate. Inset graph: Model-based global estimates of the percentage changes in hydrogen ions, bicarbonate ions and carbonate ions as mean values in the upper ocean as a result of increases in atmospheric CO_2 of up to 300% on a ~100 year timescale. This model is relatively unsophisticated (e.g., not allowing for temperature and circulation effects), and the results should be considered illustrative of the processes occurring in the main part of this figure. Images, redrawn from[14] and[15]; graph based on data in[16].

horizons) differ slightly from those for calcite, and the form of the mineral in different marine species affects their sensitivity to ocean acidification.

Due to different water mass characteristics, the depth of saturation horizons varies naturally between ocean basins. However, it is currently decreasing everywhere, and will continue to do so, as more anthropogenic CO_2 enters the ocean. By the end of this century, aragonite saturation horizons are projected to shallow from >2000 m to ~100 m in the North Atlantic, from ~150 m to the near-surface in the North Pacific[18], and to reach the surface in the Arctic and Southern Ocean[19]. Due to lower temperatures in polar regions, the shallowing of saturation horizons is more pronounced there, an effect described in more detail in Chapter 3.

Aquatic organisms (particularly microbes) have evolved to survive under a wide range of environmental pH conditions, from alkaline lakes to deep-sea vents. Thus, extremophile algae, fungi and archaea can tolerate pH values as low as 0.5, whilst bacteria, protists and rotifers can survive at pH values as high as 10.5[[20]. Nevertheless, all species have their individual optimal pH ranges and tolerance limits that usually closely match the range of variability naturally encountered in species' habitats.

As discussed in greater detail in Chapter 3, natural seawater pH values can vary greatly over seasonal, daily or annual timescales, and given this variability, it might be thought that the projected pH reduction of ~0.3 units during the current century is unlikely to have substantive biological consequences, at least in coastal waters. However, an analogous situation applies to temperature tolerances and projected global warming. A global surface temperature increase of ~2°C is now generally recognized as having "dangerous" climatic and ecological consequences, increasing extinction risk for many species – despite very many organisms experiencing seasonal (or even daily) temperature ranges that are five to ten times greater. It is key to note that it is not just an absolute value of pH change that is important, but also the change in potential range and variability.

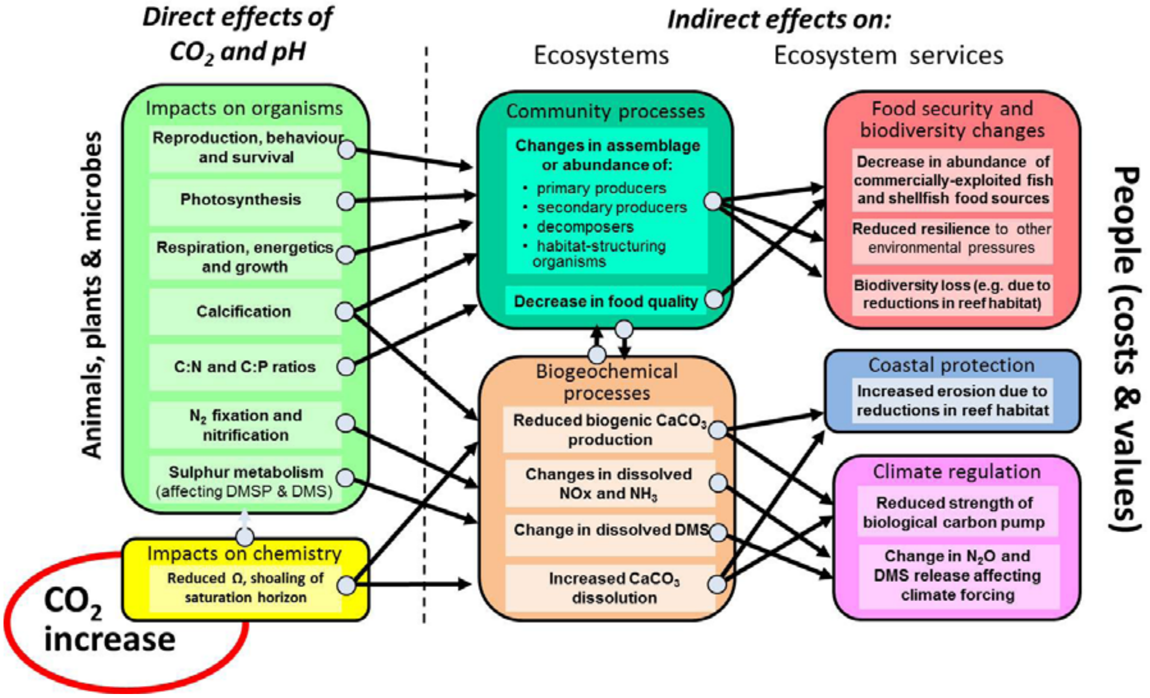

Figure 1.3. Simplified summary of the impacts of ocean acidification on organisms, ecosystems, ecosystem services and hence society. Impacts cascade through marine ecosystems, with societal effects including changes to food security, biodiversity, coastal protection and climate regulation (see Table 5.2 for further detail). DMS, dimethylsulphide; DMSP, dimethylsulphoniopropionate; Ω, $CaCO_3$ saturation state. Based on[15].

Other important framework considerations relating to the effects of ocean acidification on biodiversity include the following:

- In the same way that global warming is not limited to temperature change, ocean acidification is not limited to pH change. Organisms can respond to changes in any one of the components of the carbonate chemistry system (Figure 1.2), and calcification is not the only process that may be affected. In particular, calcifying algae demonstrate the potential for opposite responses to different components: if there is sufficient light and nutrients, their photosynthesis (and growth rates) may benefit from higher CO_2 or bicarbonate; however, their calcification may be negatively impacted by decreased pH, occurring at the same time. Note that decreased calcification under conditions of ocean acidification is unlikely to be directly due to the reduced availability of carbonate, since most calcifiers take up bicarbonate ions from seawater[21].
- Even within closely related taxa, not all organisms respond similarly to ocean acidification under experimental conditions, and different stages in the life cycle may show different sensitivities[5,16]. These mixed responses (together with the complexity of marine ecological interactions) make it difficult to develop a quantitative, model-based understanding of the impacts of projected ocean acidification on communities, food webs, ecosystems and the services they provide to society (Figure 1.3). Nevertheless, recent meta-analyses[6, 22] on individuals and taxa have identified general trends, consistent taxonomic patterns (Figure 1.4) and life-cycle effects, discussed in detail in Chapter 5.
- Ocean acidification has the potential to change the chemical speciation and solubility of metals and other elements in seawater. The pH sensitivity of boron species is noteworthy, affecting the isotopic composition of boron in biominerals, which can be used in paleo-pH reconstructions (see Chapter 4). Boron-borate changes can also affect low-frequency sound transmission, with concerns

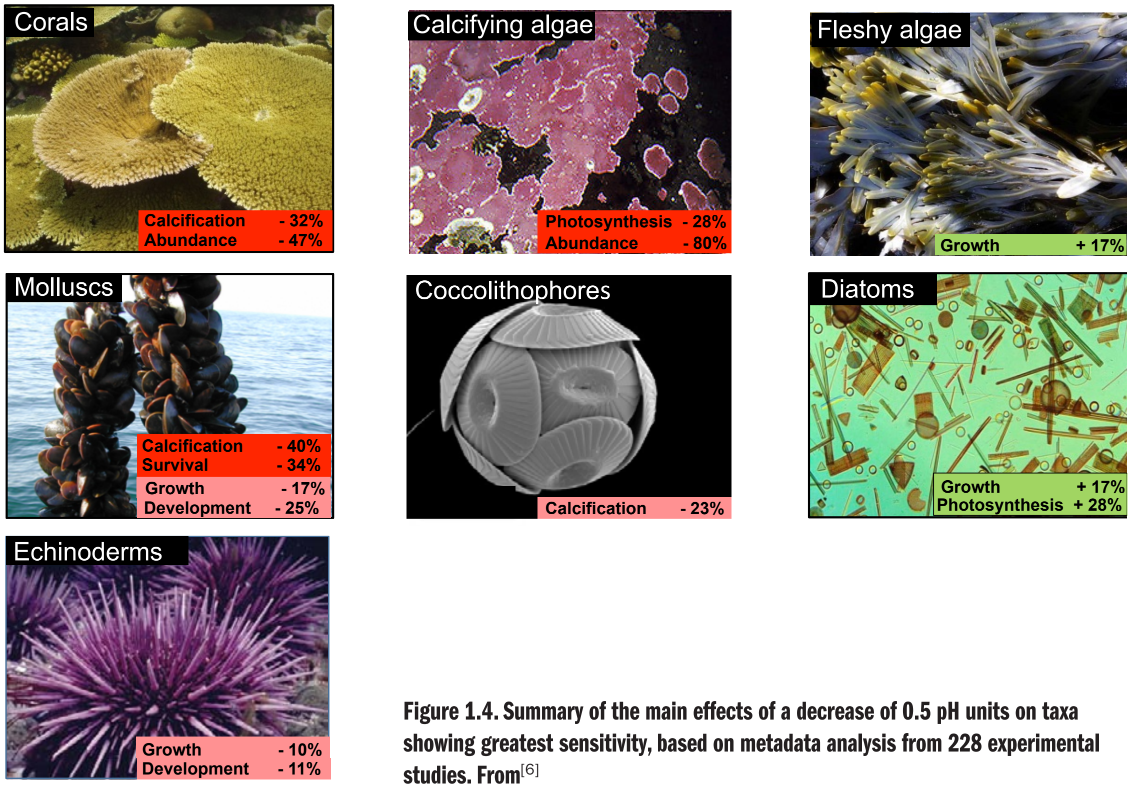

Figure 1.4. Summary of the main effects of a decrease of 0.5 pH units on taxa showing greatest sensitivity, based on metadata analysis from 228 experimental studies. From[6]

that future pH reductions would make the ocean noisier, with biological impacts, for example, on the behaviour of marine mammals[23]. However, additional physically based analyses indicate that the problem seems unlikely to be significant[24,25].

- Marine organisms are currently subject to many other environmental changes, in addition to ocean acidification, with the potential to degrade or disrupt ecosystems. Most of these drivers are directly or indirectly due to human activities. They can be broadly grouped into local/regional stressors, for example, due to over-fishing, habitat loss/destruction, pollution, and enhanced nutrient loading (with associated eutrophication and low oxygen), and global-scale climate-related impacts that are mostly temperature-driven, such as changes in stratification, mixing and other circulation changes, reduced high latitude surface salinity (due to ice melt and river run-off), de-oxygenation and increased ultra-violet (UV) radiation. Key issues relating to the three main global-scale stressors – acidification, warming, and de-oxygenation – are summarized in Table 1.1. Further information on our relatively limited understanding of the interaction between ocean acidification and other factors is provided in subsequent chapters.

Table 1.1. Summary of the causes and impacts of the three main global-scale stressors that will increasingly affect marine biodiversity, with severity of impacts depending on future emissions of greenhouse gases. Note that there may be reinforcing or ameliorating interactions (synergies or antagonisms) for biological responses to these stressors, and that there are likely to be additional interactions with a wide variety of other environmental parameters, at both global and local scales. Based on[26]; also see[7].

Stressor	Causes	Results	Direct effects	Impacts, including climatic feedback
Acidification	• Increasing CO_2 in atmosphere • Some local contributions (eutrophication, industrial emissions)	• Change in ocean pH and carbonate chemistry • Progressive dissolution of calcium carbonate	• Reduced calcification and growth in many species • Reef erosion • Changes in carbon: nitrogen ratio	• Reduced abundance of calcifying species; other food web changes • Effects on aquaculture and human food supply • Risk of coral extinctions, with habitat loss and increased coastal erosion • Reduced ocean uptake of CO_2 • Potential warming feedback via DMS and cloud formation
Warming	• Increasing greenhouse gases in atmosphere	• Temperature increase • Less ocean mixing due to increased stratification • Loss of polar sea ice • More freshwater run-off in polar regions (reducing salinity) • Sea-level rise	• Reduced solubility of CO_2, O_2 and calcium carbonate • Reduced productivity where more stratified; increased productivity in Arctic • Physiological effects on organisms (metabolism, growth and survival)	• Poleward shift of (mobile) species' ranges • Coral bleaching • Changes in community composition and food webs • Global reduction in marine productivity • Reduced ocean uptake of CO_2 • Reduced carbon export to ocean interior
De-oxygenation	• Warming reduces O_2 solubility • Stratification reduces O_2 supply to ocean interior • Local causes: eutrophication	• Reduced O_2 availability for respiration, especially in productive regions and mid/deep water	• Slower metabolism and growth of zooplankton and fish	• Effects on abundances and distributions • Shift to organisms tolerant to low O_2 (mostly microbial) • Reduced fishery yield • Increased marine production of methane and nitrous oxide (greenhouse gases)
All three together	• Increasing CO_2 and other greenhouse gases	• Combined stress of reduced pH, warming and low dissolved O_2	• Damage to organism physiology and energy balance • Disrupted food webs	• Major changes to ocean physics, chemistry and biology • Biodiversity loss, with impacts on ecosystem services • Risk of multiple positive feedbacks, increasing rate of future climate change

1.3 RE-VISITING KEY KNOWLEDGE GAPS IDENTIFIED IN THE PREVIOUS CBD REVIEW

The concluding chapter ("Uncertainties and other considerations") of the 2009 CBD review of ocean acidification[9] identified five questions to assist in focussing research effort on important knowledge gaps. Table 1.2 below briefly revisits these issues, summarizing relevant progress and the current status of our understanding of these topic areas. Additional detail, with supporting scientific citations, is given in subsequent chapters of this review.

Three generic comments can be made on the 2009 research questions. Firstly, all five questions refer to calcification or calcifiers, whereas there is now greater appreciation that a much wider range of physiological and biogeochemical processes, and organisms, may be affected (Figures 1.3, 1.4) – and a recognition that the scale and importance of many of these additional impacts are still very uncertain. Second, these questions only indirectly refer, through adaptation (Q3), to the relevance of genetic and evolutionary processes in determining the scale of future acidification impacts. Such issues are now being given much greater attention[8]. Third, none of the questions explicitly mentions ecosystem services, societal impacts or possible policy responses. Whilst research and understanding in these areas are not yet well-developed, the current review does include some consideration of the 'human dimensions' of ocean acidification and its effects on biodiversity.

Table 1.2. Knowledge gaps identified in 2009[9] and subsequent relevant research developments.

Research question	Summary of recent research progress; other comments
1. How is calcification affected in organisms at different stages of their life cycle?	Significant progress made on life-cycle experimental studies. For many species of echinoderms, acidification slows development of embryos/larvae (hence likely to increase mortality in field); juveniles may also be negatively affected, whilst adults are generally more tolerant. Life-cycle changes in acidification sensitivity not limited to calcifiers. Increased awareness that experimental life-cycle studies should be relevant to natural conditions, with need for 'realistic' (yet well-controlled) pH/carbonate system parameters and controlled food availability. Potential impacts and interactions of multiple stressors (e.g., temperature, nutrients/food, oxygen) require further study.
2. Why do some calcifying organisms seem to be less affected than others?	Increased appreciation that variability of response can be due to: i) different organisms responding to different aspects of carbonate chemistry (CO_2, pH, carbonate, bicarbonate and saturation state); ii) non-standard experimental methods (inter-comparability now much improved through "best practice" protocol development and improved international liaison); iii) confounding effects of other, non-controlled factors (nutrient/food availability; light for phytoplankton studies; seasonal cycles affecting physiology and metabolism); and iv) inherent response variability between strains, species and higher taxonomic groups.
3. How is adaptation and survival influenced by the different mechanisms of calcification or other physiological factors?	This question covers many research topics, not only biological control of the calcification process (that differs between different groups), but also the scope for genetic adaptation on decadal-to-century timescales. Scope for adaptation – difficult to determine, but can be informed by paleo-studies – depends on reproductive strategy, existing genotypic variability (on which selection can operate), and generation time. Such adaptation may be at cost of reduced fitness for other traits, and recent research documents the best approaches for tackling this challenging issue[8,27]. Text on this question in the 2009 report focussed on potential impacts on pteropods (planktonic molluscs, also known as sea butterflies): several new experimental and field studies on this group have confirmed their vulnerability to near-future changes in polar water chemistry.
4. How do other environmental factors, such as carbonate concentration, light levels, temperature and nutrients, affect calcification processes?	There is considerable overlap of this question with the others above, since it addresses the (multi-stressor) context in which acidification occurs, influencing not only calcification but other physiological processes. In the past 5 years, there have been many two-factor studies (mostly with temperature as second variable), providing important insights on potential interactions. However, very few experiments control three or more variables: whilst such studies are needed, their design, implementation and interpretation are not straightforward. Mesocosms and natural gradients provide alternative approaches to resolving issues of environmental complexity.
5. How will communities with a mixture of calcifying and non-calcifying organisms respond to decreasing calcification rates, and what impact will this have on the marine food chain?	Determination of ecosystem-level effects is extremely demanding, and remains an overall goal – taking account of other processes affected by acidification (Figure 1.3), in addition to calcification. Model-based approaches provide scenario-based projections, over a range of spatial and temporal scales, and these can be used for risk-based policy action; however, models cannot be expected to give single answer, definitive predictions. In particular, model outputs will necessarily depend on assumptions regarding future CO_2 emissions, as well as the future scale and influence of other environmental variables. Furthermore, models are unable to take account of factors (e.g., genetic adaptation) that have not yet been well-quantified.

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2. SCIENTIFIC AND POLICY FRAMEWORK

KEY MESSAGES

1. Research interest in and political awareness of ocean acidification have increased exponentially in the past few years

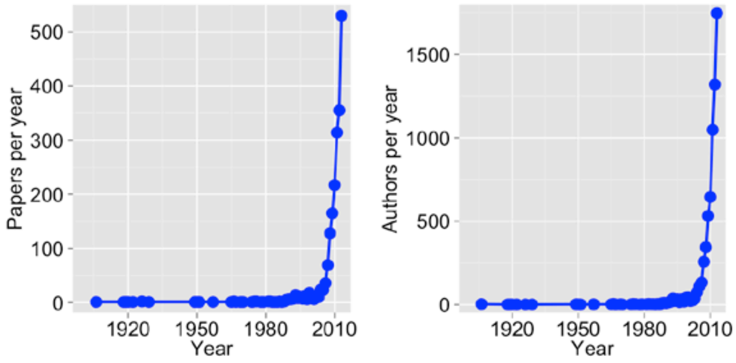
2. International cooperation and interdisciplinary research have helped to advance the science of ocean acidification

3. Many intergovernmental bodies have initiated activities on ocean acidification

2.1 STEPS TOWARD GLOBAL RECOGNITION AND INTERNATIONAL SCIENTIFIC COLLABORATION

Ocean acidification is a relatively young field of research. The first results from laboratory experiments on the effects on marine organisms appeared in the late 1990s. These built upon early landmark studies showing that the uptake of anthropogenic CO_2 decreased ocean buffering capacity[1], and that this could decrease calcification[2,3] by marine organisms. Scientific interest in ocean acidification – not only by chemists and physiologists, but also by ecologists, biogeochemists, paleontologists and economists – has increased exponentially in the past few years, with a more than twenty-fold increase in the number of publications from 2004 to 2013, and a similar increase in numbers of new researchers entering the field (Figure 2.1)[4,5].

The prioritization of ocean acidification as a research topic began around 2003-04, with its inclusion in the Science Plans of two global-change research programmes, the Surface Ocean Lower Atmosphere Study (SOLAS)[6] and the Integrated Marine Biogeochemistry and Ecosystem Research project (IMBER)[7]. In a closely related initiative, the first symposium "The Ocean in a High CO_2 World", was held in Paris in 2004, convened by the Scientific Committee on Oceanic Research (SCOR), the Intergovernmental Oceanographic Commission of the United Nations Educational, Scientific and Cultural Organization (IOC-UNESCO) and the International Geosphere-Biosphere Programme (IGBP).



	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013
papers	24	23	36	69	128	165	217	314	355	530
authors	75	109	133	257	344	532	645	1048	1320	1748

Figure 2.1. The annual number of peer-reviewed publications on ocean acidification and the number of authors involved 1900-2013. Data from the bibliographic database of the IAEA Ocean Acidification International Coordination Centre (OA-ICC), updated from Gattuso and Hansson[4,5]

However, wider awareness of ocean acidification remained extremely low until the Royal Society's 2005 report "Ocean acidification due to increasing atmospheric carbon dioxide"[8]. Several other policy-related publications have subsequently attracted significant attention, including:

- The 2008 Monaco Declaration[9], signed by 155 scientists from 26 countries and endorsed by HSH Prince Albert II of Monaco. The declaration called upon policymakers to support initiatives in multi-disciplinary research, communication and policy action. It arose from the Second Symposium on the Ocean in a High-CO_2 World, held in Monaco and co-organised by the International Atomic Energy Agency (IAEA).
- The CBD's 2009 report "Scientific Synthesis of the Impacts of Ocean Acidification on Marine Biodiversity"[10], produced jointly with the World Conservation Monitoring Centre of the United Nations Environment Programme (UNEP). Aspects of that report have already been discussed in Chapter 1.
- The 2009 statement on ocean acidification by the InterAcademy Panel on International Issues (IAP)[11], endorsed by over 100 academies of science worldwide. This called on world leaders to respond to the emerging threat of ocean acidification by taking action to reduce CO_2 emissions and mitigate damage to marine ecosystems.
- "Ocean Acidification Summary for Policymakers"[34] arising from the Third Symposium on the Ocean in a High-CO_2 World, held in Monterey, USA in 2012.
- The 2013 assessment of Arctic Ocean acidification and its societal implications, carried out by the Arctic Monitoring and Assessment Programme (AMAP)[12].

The first large-scale, multi-national project on ocean acidification was the European Commission's "European Project on Ocean Acidification" (EPOCA[13], 2008-2012. EPOCA brought together more than 160 scientists from 32 countries to address scientific uncertainties on ocean acidification, including biogeochemical modelling, biological effects and implications for marine biodiversity. A notable output was publication of the book *Ocean Acidification*[5] in 2011 (Figure 2.2). A second EC project on ocean acidification has focused on its links to climate change in the Mediterranean (MedSeA)[14], 2011-2014.

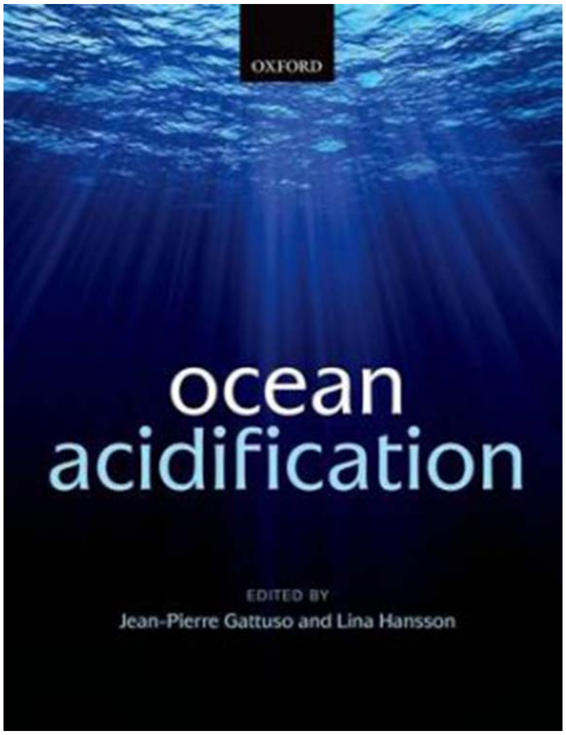

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Figure 2.2. The first book on ocean acidification, with international authorship and arising from the European Commission's EPOCA project.

National research efforts, many with close linkages to international programmes, have included the German programme Biological Impacts of Ocean Acidification (BIOACID)[15], that started in 2009, and is now concluding its second funding phase; US research support (via NSF and NOAA), mandated by the 2009 Federal Ocean Acidification Research and Monitoring (FOARAM) Act[16]; the UK Ocean Acidification Research Programme (UKOA)[17] that began in 2010; and other programmes and, projects in Australia, China, Japan, Republic of Korea, Norway and elsewhere. The current breadth of national involvement in ocean acidification research is indicated in Figure 2.3.

Linkages between these worldwide research efforts on ocean acidification have been encouraged at

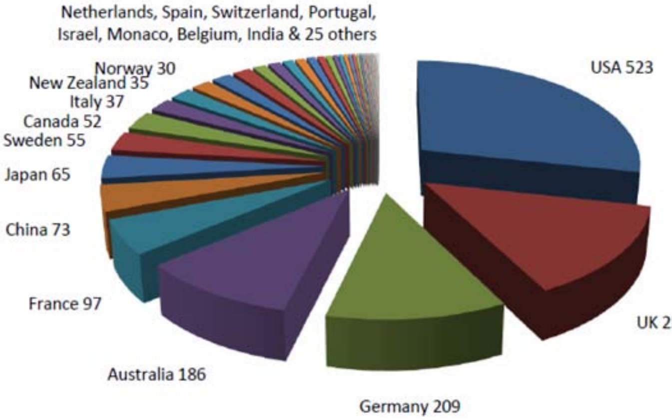

Figure 2.3. National involvement in ocean acidification research, based on first authors' addresses for peer-reviewed papers published in 2005-2013 (OA-ICC data)[4].

the intergovernmental level (see 2.2 below), as well as by national funders and non-governmental science bodies, particularly the SOLAS-IMBER Ocean Acidification Working Group (SIOA-WG)[18], which helped to establish the Ocean Acidification International Coordination Centre (OA-ICC)[19] of the IAEA, based in Monaco.

The OA-ICC became operational in 2012, supported by IAEA member states; its activities include the facilitation of global observation and monitoring; joint-use research platforms and experiments; definition of best practices; data management; capacity building; dissemination and outreach. OA-ICC liaison with policy-makers, the private sector and other stakeholders is assisted by the Ocean Acidification international Reference User Group (OA-iRUG). This body, re-constituted in 2013, was originally established in 2008 through the EPOCA project; it involves scientists and research users from industry, government and non-governmental organizations. OA-iRUG publications[20] aim to provide key policy-relevant messages on ocean acidification to decision makers.

The most recent initiative to enhance international science collaboration has been the development of the Global Ocean Acidification Observing Network (GOA-ON), supported by the OA-ICC, IOC-UNESCO, the Global Ocean Observing System (GOOS), the International Ocean Carbon Coordination Project (IOCCP) and national funding agencies. Further details are given in section 3.3.

2.2 INTERGOVERNMENTAL INTEREST IN OCEAN ACIDIFICATION AND ACTIONS TO DATE

Whilst some local and national policy measures can be taken to address ocean acidification impacts (e.g., formation of a Marine Resources Advisory Council by the State of Washington, USA, charged with safeguarding its shellfish industry against ocean acidification[21]), ocean acidification is essentially a global problem – requiring a global, intergovernmental policy response. At the United Nations Conference on Sustainable Development "Rio+20" (Rio de Janeiro, June 2012) all stakeholders, including UN bodies, intergovernmental organizations and national governments, were invited to make commitments to deliver concrete results for sustainable development on a voluntary basis. There was substantial stakeholder input to the consideration of ocean acidification resulting in a specific ocean acidification statement (number 166) in the Conference's outcome document "The Future We Want"[22].

> *"We call for support to initiatives that address ocean acidification and the impacts of climate change on marine and coastal ecosystems and resources. In this regard, we reiterate the need to work collectively to prevent further ocean acidification, as well as to enhance the resilience of marine ecosystems and of the communities whose livelihoods depend on them, and to support marine scientific research, monitoring and observation of ocean acidification and particularly vulnerable ecosystems, including through enhanced international cooperation in this regard."*

One of the main outcomes of the Rio+20 Conference was the agreement by member States to launch a transparent intergovernmental process to develop a set of Sustainable Development Goals (SDGs) to be

Box 2.1

Extracts from Resolution 68/70, (http://www.un.org/en/ga/search/view_doc.asp?symbol=A/RES/68/70), of the United Nations General Assembly (passed on 9 December 2013) giving specific mention to ocean acidification. The General Assembly is the main deliberative, policy-making and representative organ of the UN.

Paragraph 17

Called upon States and international financial institutions, including through bilateral, regional and global cooperation programmes and technical partnerships, to develop capacity-building activities in and to transfer to developing countries, in particular least developed countries and small island developing States, on mutually agreed terms, and taking into account the Intergovernmental Oceanographic Commission Criteria and Guidelines on the Transfer of Marine Technology, environmentally sound technologies to study and minimize the impacts of ocean acidification

Paragraph 153

Noted the work of the Intergovernmental Panel on Climate Change, including its recent findings on the acidification of oceans, and encouraged States and competent international organizations and other relevant institutions, individually and in cooperation, to urgently pursue further research on ocean acidification, especially programmes of observation and measurement, noting in particular the continued work of the Convention on Biological Diversity and paragraph 23 of decision XI/18 adopted at the eleventh meeting of the Conference of the Parties to the Convention on Biological Diversity, and to increase national, regional and global efforts to address levels of ocean acidity and the negative impact of such acidity on vulnerable marine ecosystems, particularly coral reefs

Paragraph 154

Recalled that, in “The future we want”, States called for support for initiatives that address ocean acidification and the impacts of climate change on marine and coastal ecosystems and resources and, in this regard, reiterated the need to work collectively to prevent further ocean acidification, as well as to enhance the resilience of marine ecosystems and of the communities whose livelihoods depend on them, and to support marine scientific research, monitoring and observation of ocean acidification and particularly vulnerable ecosystems, including through enhanced international cooperation in this regard

Paragraph 155

Noted with concern the approximately 30 per cent increase in the acidity of ocean surface waters since the beginning of the industrial era and the wide range of impacts associated with the continuing and alarming acidification of the world’s oceans, and urged States to make significant efforts to tackle the causes of ocean acidification and to further study and minimize its impacts, to enhance local, national, regional and global cooperation in this regard, including the sharing of relevant information, and to take steps to make marine ecosystems more resilient to the impacts of ocean acidification

Paragraph 156

Committed itself to continue to pay attention to this important issue, including by taking into account the first global integrated assessment and the ongoing work of the recently established Ocean Acidification International Coordination Centre of the International Atomic Energy Agency

Paragraph 217

Recalled that, in “The future we want”, States recognized the significant economic, social and environmental contributions of coral reefs, in particular to islands and other coastal States, as well as the significant vulnerability of coral reefs and mangroves to impacts, including from climate change, ocean acidification, overfishing, destructive fishing practices and pollution, and support international cooperation with a view to conserving coral reef and mangrove ecosystems and realizing their social, economic and environmental benefits, as well as facilitating technical collaboration and voluntary information-sharing

Paragraph 218

Encouraged States and relevant international institutions to improve efforts to address coral bleaching by, inter alia, improving monitoring to project and identify bleaching events, supporting and strengthening action taken during such events and improving strategies

agreed by the General Assembly at its 68th session (2013 – 2014). The progress report[23] of the Open Working Group of the UN General Assembly tasked with the development of the SDGs includes mention of ocean acidification.

Box 2.1 provides relevant text from the 68th session of the UN General Assembly, which recognized ocean acidification as an issue of concern. There have also been actions by several other intergovernmental bodies and organizations, mostly within the UN system, to inform policy makers and support policy development[24] as summarized in Table 2.1. Note that no single UN body currently has a designated lead role for policy development regarding ocean acidification, and there is ongoing debate[25,26] on this issue, particularly with regard to the linkage to the regulatory framework for CO_2 emission reductions. CBD’s major role in raising awareness of ocean acidification and other association actions has already been covered in Chapter 1 and is only briefly re-presented in Table 2.1.

Table 2.1. Summary of activities of United Nations subsidiary bodies, Conventions and other intergovernmental organizations in relation to ocean acidification, based on[24]. This list does not claim to be comprehensive. *Body with government membership but not part of the United Nations.

Body, subsidiary body/agency or Convention; activities			
United Nations Convention on the Law of the Sea (UNCLOS)	Treaty that sets out the legal framework within which all activities in the oceans and seas must be carried out		• Part XII of UNCLOS addresses the protection and preservation of the marine environment • Part XIII of UNCLOS addresses marine scientific research
United Nations Division for Ocean Affairs and the Law of the Sea (DOALOS)	Open-ended Informal Consultative Process (ICP) on Oceans and the Law of the Sea	Forum to facilitate the annual review by the General Assembly of developments in ocean affairs and the law of the sea	• 14th ICP meeting (June 2013) on Impacts of Ocean Acidification on the Marine Environment; report to 2013 UN General Assembly[27]
United Nations Environment Programme (UNEP)	Coordination of UN environmental activities		• 2010 publication: "Environmental Consequences of Ocean Acidification: a Threat to Food Security"[29] • Co-support of 3rd UN Conference on Sustainable Development • Lead for Transboundary Waters Assessment Programme (with IOC-UNESCO and others) that includes assessment of ocean acidification
United Nations Educational, Scientific and Cultural Organization (UNESCO)	*Intergovernmental Oceanographic Commission (IOC)*	The UN body for ocean science, observatories, data, information exchange and services	• Coordination of OA-relevant chemical and biological measurements through the Global Ocean Observing System (GOOS) and the International Ocean Carbon Coordination Project (IOCCP; co-supported by SCOR); support for the Global Ocean Acidification Observing Network (GOA-ON) • Lead for "A Blueprint for Ocean and Coastal Sustainability"[28] (with IMO, FAO and UNDP), including actions to mitigate and adapt to ocean acidification • Major role in developing the Ocean in a High-CO_2 World symposium series and the associated Ocean Acidification Summaries for Policymakers (2009 and 2013)
World Meteorological Organization (WMO)	*Intergovernmental Panel on Climate Change (IPCC; created with UNEP, advises UNFCCC)*	Assessments of climate change and associated impacts	• Ocean acidification included in IPCC 4th Assessment Report, and in greater detail in 5th Assessment Report (AR5, Working Groups I, II and III)[29,30]. High confidence given to pH decrease of 0.1 in ocean surface water since the beginning of the industrial era.
International Maritime Organization (IMO)	*London Convention and Protocol*	Control of marine pollution through regulation of waste disposal	• Control of sub sea-bed CO_2 sequestration • Development of regulatory framework (within the scope of the Convention and Protocol) for research on ocean fertilization and other marine geoengineering relevant to ocean acidification
International Atomic Energy Agency (IAEA)	Encourage peaceful uses and applications of nuclear technology		• Hosting of Ocean Acidification International Coordination Centre (OA-ICC) to assist the worldwide scientific study of ocean acidification • Convening of two workshops (in 2010 and 2012) on socio-economics of ocean acidification • Development, through GOA-ON, of a global network to measure changes in ocean carbon chemistry and its ecological impacts • Improving ocean acidification data management; capacity building, dissemination and outreach.
United Nations Framework Convention on Climate Change (UNFCCC)	Legal framework for global reduction in CO_2 emissions, in order to prevent "dangerous anthropogenic interference with the climate system".		• Limited mention of ocean acidification in UNFCCC decisions and documents, but discussed as an "emerging issue" by Subsidiary Body for Scientific and Technical Advice and by associated research dialogue. • Ocean acidification covered by side-events at UNFCCC Conference of Parties since 2009

Body, subsidiary body/agency or Convention; activities			
Convention on Biological Diversity (CBD)	International treaty to promote conservation and sustainable use of biological diversity		• Concern about ocean acidification raised at the ninth meeting of the Conference of Parties to the CBD (COP 9) in 2008 • 2009 review (with the World Conservation Monitoring Centre of the United Nations Environment Programme, UNEP–WCMC)[10] • At COP 10 (2010), ocean acidification included in CBD Strategic Plan for Biodiversity (2011-2020) and Aichi Biodiversity Targets • Expert review process for ocean acidification initiated by Expert Meeting in 2012 and new review.
Convention for Protection of the Marine Environment of the North-East Atlantic* (OSPAR)	Combines and updates Oslo and Paris Conventions, covering "all human activities that might adversely affect the marine environment of the North East Atlantic"		• Concern on ocean acidification expressed in 2012, resulting in establishment (with ICES) of Study Group on ocean acidification; reports published in 2013 and 2014 • Development of protocols for ocean acidification monitoring and assessment[31]
Commission for the Conservation of Antarctic Marine Living Resources* (CCAMLR)	Conservation of Antarctic marine life		• Expressed concern on potential impacts of ocean acidification on Antarctic marine life, including effects on krill[32]
Joint Group of Experts on the Scientific Aspects of Marine Environmental Protection (GESAMP)	*Sponsored by IMO, FAO, IOC-UNESCO, WMO, IAEA, UNEP, UNIDO and UNDP*	Advises the UN system on scientific aspects of marine environmental protection	• CO_2 considered as pollutant; ocean acidification included in GESAMP contribution to open ocean part of Transboundary Waters Assessment Programme
Arctic Council*	*Arctic Monitoring and Assessment Programme (AMAP)*	Provision of information on status of Arctic environment	• AMAP Arctic Ocean Acidification Assessment (2013)[12]
International Union for Conservation of Nature* (IUCN)	Aim is to conserve biodiversity at global and local level		• Work with IOC-UNESCO, Ocean Acidification international Reference User Group and others to raise awareness of ocean acidification.

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3. GLOBAL STATUS AND FUTURE TRENDS OF OCEAN ACIDIFICATION

KEY MESSAGES

1. Substantial natural temporal and spatial variability occurs in seawater pH, particularly in coastal waters, due to physical, geochemical and biological processes

2. Polar oceans are expected to experience the impacts of ocean acidification sooner than temperate or tropical regions, as their saturation horizons are already shallower than at lower latitudes.

3.1 VARIABILITY

Values for pH and other components of the marine carbon system not only show local and regional natural spatial variability, but can also change temporally, on a diurnal to seasonal basis. Recognition of such variability, and an understanding of its causes, are crucial to the valid interpretation of observational studies and the assessment of anthropogenic ocean acidification trends[1].

The scale of temporal variability can be habitat-specific[2] (Figure 3.1), whilst strong spatial variability can occur both horizontally and vertically in shelf seas (Figure 3.2). It is therefore potentially simpler to detect an ocean acidification signal in the open ocean than in more variable coastal systems[1,3-5]. At many coastal ocean sites, short-term natural variability experienced by benthic organisms has a greater range than the projected pH decline over the next century due to anthropogenic CO_2 emissions[3,6]. For example, the natural daily variability in pH experienced by warm-water corals can range between pH 7.8 and 8.3[7].

The following physical, geochemical and biological factors may contribute to natural pH variability, particularly in shelf and coastal seas:

- A range of mesoscale hydrodynamic features, including wind-driven upwelling, which brings low-pH water to the surface[8]; tidal down-welling[9]; seasonal sea-ice, affecting CO_2 drawdown; and localised temperature gradients (due to frontal features and stratification) that directly affect CO_2 solubility, hence pH and other ocean acidification parameters.
- The biological processes of photosynthesis and respiration/decomposition respectively take up and release CO_2; both processes vary with depth and are generally of greater magnitude and variability in shallow seas than in the open ocean. Changes affecting pH occur over day-night cycles and seasonally[5,10]; as well as locally, due to variable nutrient supply and biological interactions that may promote patchiness of planktonic communities.
- Land and seafloor boundary conditions, and riverine influences, can differ markedly over relatively short distances; all can provide distinct, geologically derived carbon signatures. River nutrient inputs, affected by land use and sewage-derived pollution, can also serve to enhance biological production (eutrophication). At some coastal sites (and also at tectonically active deep-sea locations), vents of CO_2 or methane can cause dramatic localized pH reductions.
- Atmospheric inputs of nitrogen and sulphur compounds produced by the burning of fossil fuels and by agriculture may also influence pH and carbon chemistry close to source regions[11]

Such dynamic "background" conditions could mean that organisms from coastal waters and shelf seas are less susceptible to future ocean acidification than those from the open ocean, as the former may already be adapted to tolerate low pH. But it could also mean that shallow-sea organisms might be exposed to harmful pH thresholds more quickly. In

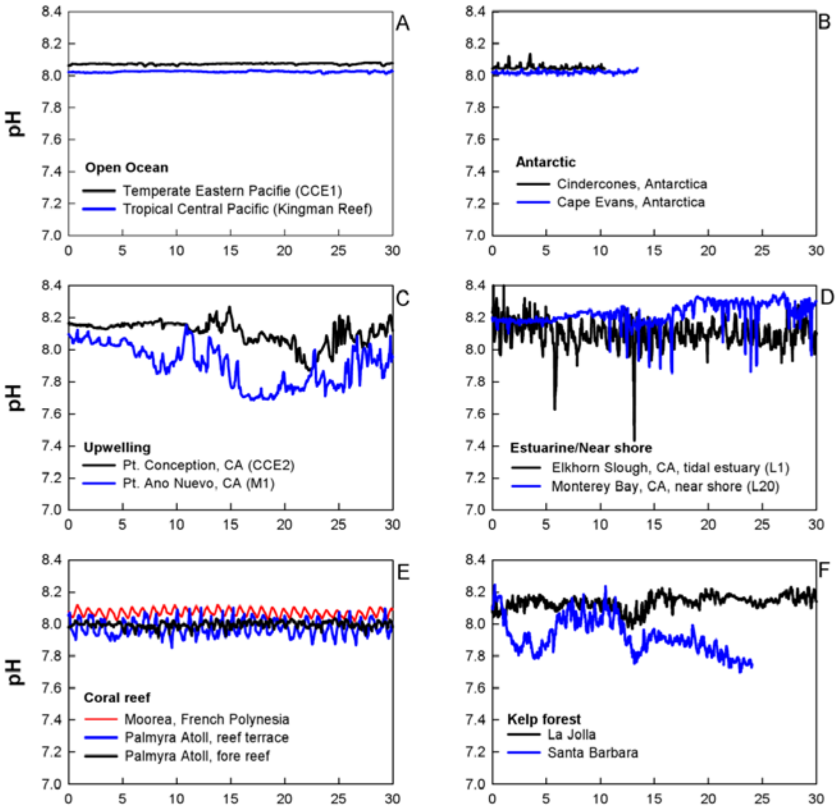

Figure 3.1. Observed temporal variability in pH at 13 locations in the Pacific and Southern Ocean, each over a period of 10-30 days, at 0–15 m water depth[2]. X-axis denotes measurement days. Note: Figure shows selected graphs from Figure 2 in [2]. Not all graphs from original figure are shown.

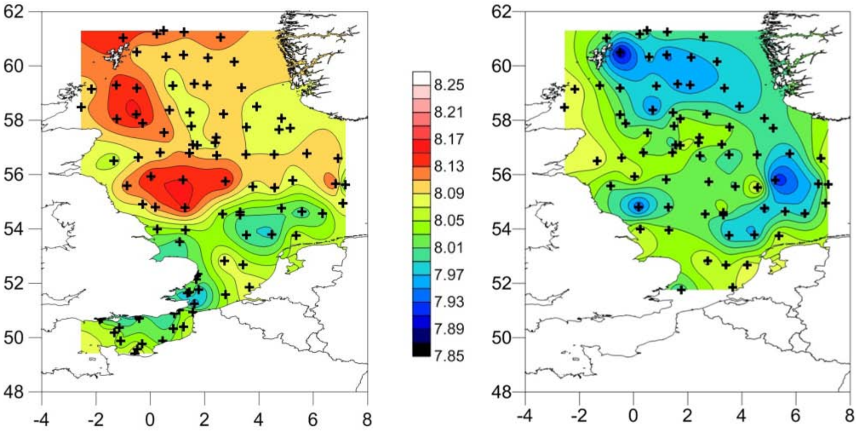

Figure 3.2. Spatial variability in pH in surface (left) and bottom water (right), derived from total alkalinity and dissolved inorganic carbon data for the North Sea in July-August 2011[13]. Many, but not all, of these observed features have been successfully simulated in high-resolution models of the carbon system in the north-west European shelf[14,15]

either case, annual mean values for pH or carbonate saturation are likely to be poor predictors of impacts; instead minimum pH levels and/or potential interactions with other stress conditions, including local pollution,[12] could be more important.

Several national and international programmes are now working to provide high-quality, standardized observations that will lead to key knowledge of carbon system changes in the marine environment, hence improving our understanding of present-day variability – and our ability to make reliable projections of future conditions. Global, quality-assured datasets of inorganic carbon, total alkalinity and pCO_2 have now been built through the Global Ocean Data Analysis Project (GLODAP)[16], CARbon in the Atlantic Ocean (CARINA)[17], the Surface Carbon CO_2 Atlas (SOCAT)[18], and the Global Ocean Acidification Observing Network (GOA-ON). Additional details on these initiatives in the context of monitoring ocean acidification are provided in section 3.3 below.

3.2 MODELLED SIMULATIONS OF FUTURE OCEAN ACIDIFICATION

Future changes in ocean carbon chemistry will necessarily be very closely linked to future increases in atmospheric CO_2[19-23], with those increases being emission-dependent (Box 3.1). Thus under the lowest current IPCC emission scenario (RCP 2.6), the projected reduction in global mean surface pH by 2100 would be limited to ~0.1 units; under the highest emission scenario (RCP 8.5, the current trajectory), the mean surface pH reduction this century would be at least 0.3 units (Figure 3.3)[22-25]. Those lower and higher pH changes represent further increases in H^+ concentrations of around 25% and

Box 3.1 IPCC scenarios for future CO_2 emissions

1. Main scenarios used by the Intergovernmental Panel on Climate Change (IPCC) for its 4th Assessment Report (AR4), (IPCC, 2007). These illustrative "families" of pathways were developed in the IPCC Special Report on Emission Scenarios (SRES) (IPCC, 2000), and are referred to in many ocean acidification modelling papers published pre-2012.

A1 – Integrated world, rapid economic growth, limited population growth. Three versions: A1FI (fossil fuel intensive), A1B (balanced) and A1T (non-fossil energy sources).

A2 – Divided world, regional economic growth and continuous population growth (highest emissions in 2100).

B1 – Integrated world, rapid economic growth, limited population growth with global movement towards economic, social and environmental stability (lowest emissions in 2100).

B2 – Divided world, regional economic growth, continuous population growth with regional movement towards economic, social and environmental stability.

2. Main scenarios used by IPCC for its 5th Assessment Report (AR5) (IPCC, 2013), as "Representative Concentration Pathways" (RCPs)[26].

RCP 2.6 – lowest emissions, atmospheric CO_2 peaks at ~443 ppm in 2050 before declining to ~421 ppm by 2100. Assumes unspecified "negative emissions" i.e., active CO_2 removal from the atmosphere.

RCP 4.5 – low emissions; atmospheric CO_2 concentrations reach ~538 ppm by 2100.

RCP 6.0 – moderate emissions; atmospheric CO_2 concentrations reach ~670 ppm by 2100.

RCP 8.5 – high emissions; atmospheric CO_2 concentrations reach ~936 ppm by 2100. Current emissions trend, hence outcome if no substantive mitigation action is taken ("business as usual").

IPCC (2007) Climate Change 2007: Synthesis Report. Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, Pachauri, R.K and Reisinger, A.(eds.)]. IPCC, Geneva, Switzerland, 104 pp.

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IPCC (2013) Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Stocker, T.F., D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and P.M. Midgley (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, 1535 pp.

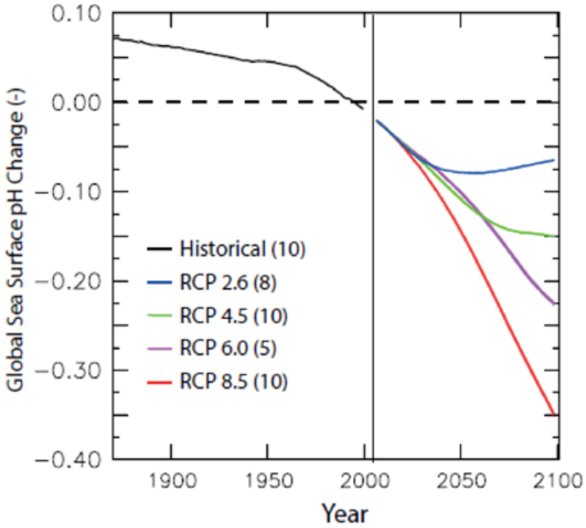

Figure 3.3. Historical and projected changes in global surface ocean pH over 1870-2100 for the four IPCC AR5 scenarios (see Box 3.1). Model means from the Climate Model Intercomparison Project. From[23].

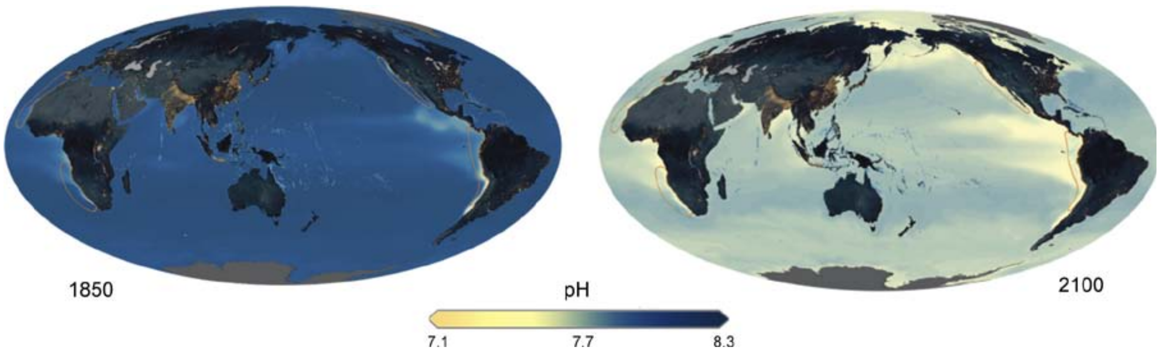

Figure 3.4. Model-derived maps of historical (1850, left) and projected (2100, right) ocean surface pH, with the latter based on the IPCC RCP 8.5 emissions trajectory. Model projections from Max Planck Institute for Meteorology, map by IGBP/Globaia, reproduced with permission from[27]

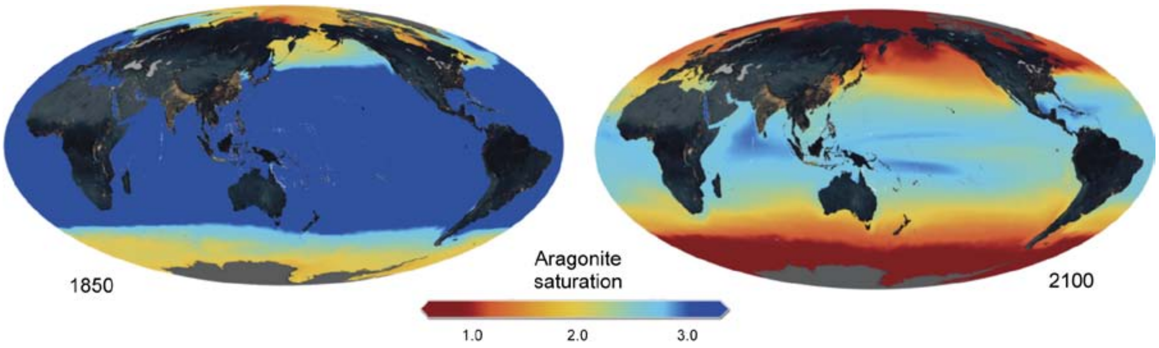

Figure 3.5. Model-derived derived maps of historical (1850, left) and projected (2100, right) aragonite saturation state, with the latter based on the IPCC RCP 8.5 emissions trajectory. Model projections from Max Planck Institute for Meteorology, map by IGBP/ Globaia, reproduced with permission from[27]

170% respectively, in addition to the increase of around 25% that has already occurred since the industrial revolution. The future surface pH change will not be globally uniform but will vary regionally (Figure 3.4), due to latitudinal differences in temperature and future warming, affecting CO_2 solubility, and basin-scale (and more local) circulation patterns and their future changes.

The aragonite saturation horizon, below which aragonite (the more soluble form of calcium carbonate) dissolves, is projected to rise from a few thousand metres to just a few hundred metres in many temperate and tropical oceans by 2100[24]. As a result of temperature effects on carbon chemistry, high latitude (polar) areas will experience larger declines in surface pH for any given addition of CO_2 from the atmosphere. In Southern Ocean surface water, an atmospheric concentration of about 450 ppm is sufficient for large areas of this region to be under-saturated with respect to aragonite[28]. Similarly, much of the surface Arctic Ocean is projected to become undersaturated for aragonite throughout the year within the next 50 years under most scenarios[21,23] (Figure 3.5).

The seasonally variable presence of sea-ice in polar regions, and its near-certain future decrease, is an additional confounding influence that is not currently well-represented in projections of future ocean acidification. Sea-ice can significantly affect pH and other components of the carbon system in many ways, including the following:

- Under conditions of offshore transport of sea-ice, the processes of freezing and melting may be spatially separated, that can result in a net transport of inorganic carbon to the deep ocean[29].
- Projected future reductions in sea-ice cover will increase the area of ocean exposed to the atmosphere, enhancing air-sea CO_2 exchange. When coupled with the likely freshening of the surface water (due to melt of land-derived ice) pH decrease will accelerate in the upper ocean[30].
- Seasonal sea-ice melt can locally enhance stratification and primary production, with indirect effects on pH and other carbon chemistry parameters.

To quantify the importance of such factors, high-resolution ocean carbon models are being developed for high latitude regions, with current emphasis on the Arctic. These models include improved representations of climate-driven changes in ice cover, freshwater inputs, topographically influenced circulation and biogeochemical processes. Two such models have been developed in association with the Arctic Monitoring and Assessment Programme (AMAP): a 1-D simulation of carbon transformations and fluxes at an Arctic shelf sea site subject to seasonal sea-ice cover and strong riverine influence (Figure 3.6)[31,32], and a regional model for the Atlantic-Arctic gateway region, between Greenland, Kingdom of Denmark; Svalbard, Norway; and the Norwegian mainland[30]. An additional uncertainty for the Arctic relates to the potential release of methane, and its subsequent oxidation to CO_2: locally, this could cause a further pH reduction of up to 0.25 units by 2100[33].

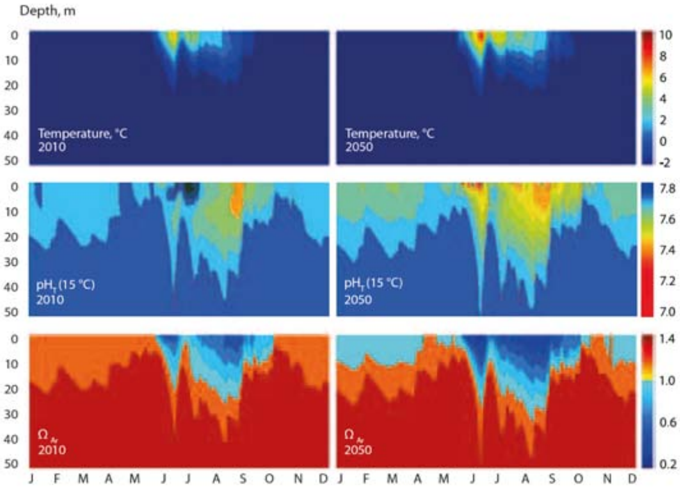

Figure 3.6. Modelled seasonal changes (January to December) in temperature (upper), pH (middle) and aragonite saturation state (lower) for 2010 and projected for 2050 under IPCC SRES B1 for a site at 50m water depth in the Siberian Arctic shelf (Central Laptev Sea). Note that pH mostly increases with water depth (unlike the situation in temperate shelf seas, Fig. 3.2, and the open ocean, Fig. 3.7) and undersaturation is projected to extend from summer-only to year-round within 40 years under a low emissions scenario. From[30]

An important factor to recognize is the longevity of ocean acidification: long after carbon emissions are curtailed, ocean acidification will remain. Anthropogenic increases in atmospheric CO_2 and perturbations to ocean chemistry will take tens to hundreds of thousands of years to return to pre-industrial values[34], as CO_2 will be slowly buffered by the dissolution of calcium carbonate sediments and the weathering of silicates to promote the return of carbon back into geological reservoirs.

3.3 CURRENT STATUS OF GLOBAL OBSERVATIONS

Observations of ocean acidification are not yet on a fully global scale, not only because of the relatively short time of awareness of the importance of such changes, but also due to the high cost of research expeditions; the inaccessibility of many regions; the relative unavailability of highly accurate and reliable pH sensors; and the current limitations of autonomous monitoring techniques. There is also a need to collect data on other environmental variables for valid interpretation. Nevertheless, long time series do exist on the changing marine carbon system in the central Pacific (Hawaii Ocean Time series, HOT) and North Atlantic (Bermuda Atlantic Time-series Study, BATS; European Station for Time-series in the Ocean, ESTOC), quantifying surface pH decline over the last several decades (over the range -0.0016 to -0.0019 yr^{-1})[35-37]. The observed decline in surface pH at these three open-ocean stations is consistent with a surface ocean that is closely tracking the increase in atmospheric CO_2 levels over the past three decades[38].

Synthesis products on observations of ocean pCO_2 and air-sea CO_2 fluxes have been developed by the Global Ocean Data Analysis Project (GLODAP)[16], CARbon in the Atlantic Ocean (CARINA)[17], the Surface Carbon CO_2 Atlas (SOCAT)[18], and PACIFICA[39]. These initiatives include analyses of the penetration of anthropogenic carbon to the ocean interior, due to entrainment, mixing, and deep-water formation. In the North Atlantic and Southern oceans, signals of decreasing pH have already been observed at the ocean floor[40-43]. Such changes involve more than a simple shoaling of aragonite and calcite saturation horizons, since the zone of low pH water may be extending downwards as well as upwards (Figure 3.7). In the Pacific and the South Atlantic, signals of anthropogenic carbon have also been observed in intermediate waters[44,45]. For all ocean basins, model projections indicate that ocean acidification will occur throughout the water column by 2100.

Recent international effort has been directed at extending and complementing these existing programmes to more explicitly address ocean acidification and its impacts, with increased attention to shelf seas and coastal regions. Relevant activities are being initiated and implemented at

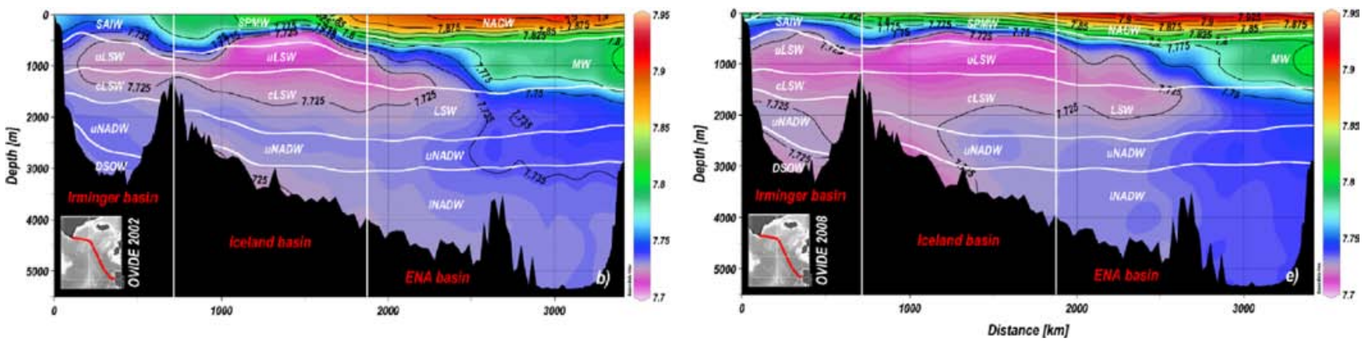

Figure 3.7. Measured pH profiles in the north-east Atlantic along a 3,400 km transect from south-east Greenland to Portugal in 2002 (left) and 2008 (right). Additional transect data were collected in 1991, 1993, 2004 and 2006, and were fully consistent with this rapid expansion in the volume of low-pH intermediate water, and associated changes in seafloor conditions. From[40].

the regional level, for example, through the US Ocean Margin Ecosystems Group for Acidification Studies (OMEGAS)[46], and also on a worldwide basis, through the recently established Global Ocean Acidification Observing Network (GOA-ON)[47] (Figure 3.8). GOA-ON aims to provide an understanding of ocean acidification conditions and the ecosystem response, as well as to deliver the data needed to optimize ocean acidification modelling. Since the potential scope for biological observing is extremely wide, GOA-ON will build on, and work in close liaison with, the Global Ocean Observing System (GOOS) and its Framework for Ocean Observation. Other bodies contributing to the development of the network include the IAEA Ocean Acidification International Coordination Centre (OA-ICC), IOC-UNESCO, the International Ocean Carbon Coordination Project (IOCCP), and a range of national funding agencies. To date, most ocean acidification observations have been ship-based. However, increasing use is expected to be made of pH sensors on profiling floats[48] and using underwater gliders; such issues are also considered in Chapter 9.

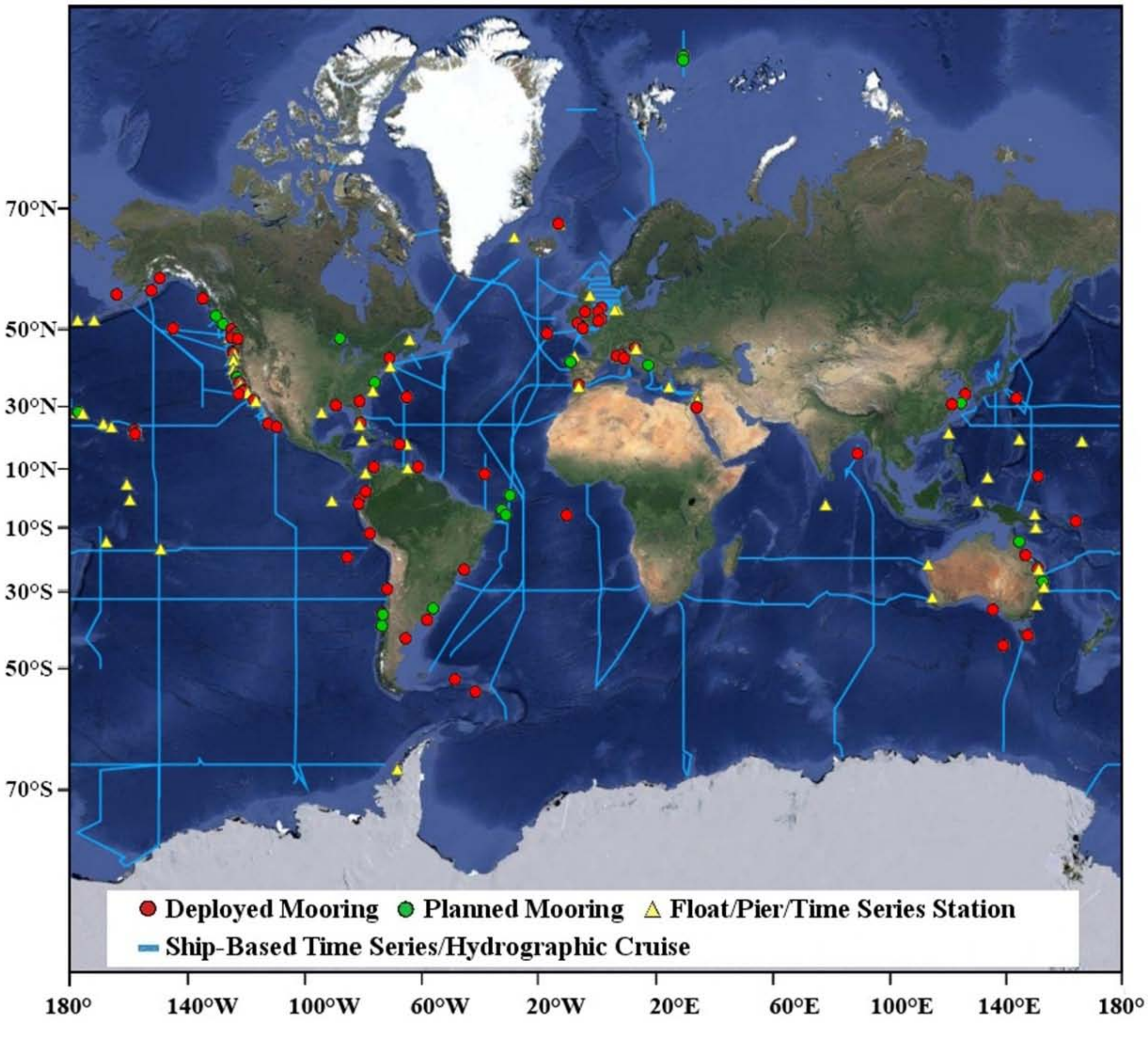

Figure 3.8. Components of the developing Global Ocean Acidification Observing Network (GOA-ON), including moorings, time-series stations, and ship-based surveys, by voluntary observing ships (VOS), ships of opportunity (SOO) and research vessels. Status at May 2014 from GOA-ON Requirements and Governance Plan[47].

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4. WHAT THE PAST CAN TELL US — PALEO-OCEANOGRAPHIC RESEARCH

KEY MESSAGES

1. During a previous period of ocean acidification, which occurred ~56 million years ago and lasted ~6000 years, several deep-sea calcifying organisms became extinct
2. Current ocean acidification is projected to reach similar levels over the next 500 years
3. Ocean acidification may have been a contributing factor in four “coral reef crises” in the last 500 million years
4. The paleo-record confirms that ocean acidification takes many thousands of years to return to original levels following a CO_2 input event

As well as using models to project climate change, we can better understand the future impacts of ocean acidification by studying how biogeochemical cycles operated in the past, and the impact past events had on marine ecosystems.

In addition to variations in seawater acidity from place to place because of circulation patterns, biological activity, and other oceanographic processes (see previous chapter), the average state of the ocean can also change through time in response to natural variations in the global carbon cycle. Past changes in ocean acidity can be studied by chemical analysis of the skeletons of dead organisms such as molluscs, foraminifera, corals and algae, or of ocean sediments, which are accessible by drilling into the seabed. Deep-sea cores commonly contain abundant fossils of calcifying (carbonate producing) plankton, such as foraminifera and coccolithophores (Figure 4.1), which are among the groups considered most at risk in future ocean acidification.

The paleo-record can be used to extend the current record of acidity changes as it stretches back millions of years in time. Over the longer term, it contains evidence of: (1) cyclic changes in ocean chemistry associated with glacial / interglacial cycles with sometimes abrupt transitions; (2) multi-million

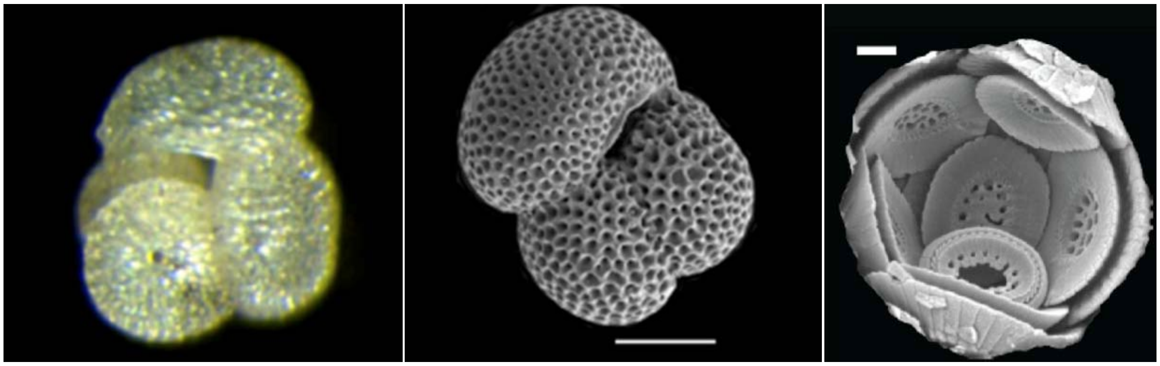

Figure 4.1. Light microscope (left panel) and scanning electron microscope (middle panel) images of planktonic foraminifera from Paleocene-Eocene Thermal Maximum (PETM, ~56 million years ago) sediments from Tanzania. Geochemical analysis of foraminifera shells can provide information about oceanic chemistry millions of years ago. Scale bar 100 µm. The right panel is a well preserved coccosphere. Source: P. Pearson (foraminifera), P. Bown (coccosphere).

year trends related to global tectonics; and, perhaps of most interest, (3) past sudden events of similar scale (if not rate) to the current human-induced change to the carbon cycle. These abrupt events provide us with real-world examples of profound environmental changes that allow us to study the past long-term response of marine organisms to ocean acidification including, for example, their extinction, migration, assemblage changes, and changes in calcification style. This information from the past can be compared with the results of modern field and laboratory research.

4.1 RECONSTRUCTING PAST OCEAN ACIDIFICATION EVENTS

To understand the rate and magnitude of past carbon cycle perturbations and their effect on seawater pH it is necessary to generate data of various sorts to help constrain geochemical models. One approach is the study of the calcium carbonate content of deep-sea sediments deposited at different water depths. Another valuable tool is to measure the boron isotopic composition ($\delta^{11}B$) of marine carbonates which is influenced by the pH of the water from which it was precipitated. Ratios of trace elements to calcium carbonates and the carbon isotope ratio ($\delta^{13}C$) can also help identify changes in the global carbon cycle.

4.2 THE PALEOCENE-EOCENE THERMAL MAXIMUM – A NATURAL PAST “EXPERIMENT” IN OCEAN ACIDIFICATION

The Paleogene (23-65 million years ago, comprising the Paleocene, Eocene and Oligocene epochs) was a period of elevated global temperatures with high levels of atmospheric CO_2 that at times exceeded 1000 ppm[1]. It was punctuated by a series of “hyperthermals”, which are geologically short-lived warming events characterized by evidence of acidification of the oceans[1]. The largest of these was the Paleocene-Eocene Thermal Maximum (PETM) ~56 million years ago,[2] which has been proposed as the closest geological analogue to modern day ocean acidification due to the volume of carbon released[3]. During this period ~2000-3000 petagrams (also known as gigatonnes) of carbon were released into the Earth’s atmosphere over thousands of years[4,5] and global temperatures increased by about 5°C[6]. Coincident with this climatic shift was a lowering of oceanic pH, as evidenced by dissolution of carbonate at the seafloor[7] (Figure 4.2).

Figure 4.2. Atlantic Ocean deep-sea core from the Integrated Ocean Drilling Program. Note the brown section of the core, which represents the dissolution of deep-sea carbonate at the Paleocene-Eocene boundary. This could represent a lack of calcifiers during that time period or the dissolution of dead shells. Source: James Zachos.

4.3 THE IMPACT OF PAST OCEAN ACIDIFICATION UPON CALCIFIERS

Good geological records of corals and calcifying plankton can be collected due to their structure and their settlement, respectively. Understanding the geological history of coral reefs, and whether past coral reef "crises" were initiated by ocean acidification is of great importance as we consider the future fate of coral reefs. Kiessling and Simpson (Table 4.1)[8] investigated whether reef crises (declines in carbonate production) and reef mass extinctions were associated with ocean acidification, and concluded that it was likely that at least four of the reef crises in the last 500 million years were partly caused by ocean acidification whilst also linked to rapid global warming (Table 4.1).

However, a full understanding of the geological history of coral reefs may require a combined environmental and evolutionary approach. The modern Scleractinia (the framework-forming corals that we know today) appeared in the middle Triassic period, and two main orders of coral, the Rugosa and the Tabulata, became extinct before this at the end of the Permian period. These corals were believed to be calcitic, rather than aragonitic like the vast majority of today's corals. This period was clearly characterized as a time of environmental perturbations with unusual seawater chemistry[9,10], and thus the "Sandberg curve"[11] which details the dominance of calcitic and aragonitic biomineralization strategies by marine organisms through time, may be an important component of future historical coral research with respect to changing climates.

It appears that not all groups of organisms with exposed skeletal structures were affected by ocean acidification in the same way over the last 300 million years. Some climate and ocean acidification events are associated with widespread extinction, whereas others are characterized by evolutionary turnover[3]. For example, during the PETM both planktonic foraminifera and coccolithophore communities demonstrated significant range shifts but they were not subject to mass extinction. Tropical communities migrated to higher latitudes, coincident with the appearance of short-lived "excursion taxa" that appear in the fossil record in lower latitude

Table 4.1. Assessment of ocean acidification as a probable cause of mass extinctions of corals/other reef-builders and associated "reef crises" (reduced $CaCO_3$ production) during the past 500 million years, based on[8].

Geological period/epoch	Time (million years ago)	Effect on corals and other reef-forming organisms	Evidence for ocean acidification
Paleocene – Eocene	55.8	Background extinction, except for benthic foraminifers; coral reef crisis	Strong
Cretaceous – Paleogene	65.5	Mass depletion of biodiversity and mass extinction, selective against buffered organisms	Weak
Early Jurassic	183	Modest but selective extinction of corals and other unbuffered organisms; coral reef crisis	Strong
Triassic – Jurassic	199.6	Mass depletion of biodiversity and mass extinction selective against corals, sponges and unbuffered organisms; coral reef crisis for all reef types	Strong
Permian - Triassic	251	Mass depletion of biodiversity and mass extinction, especially for unbuffered organisms; coral reef crisis for all reef types	Strong
Middle - Late Permian	260.4	Substantial extinction, weakly selective with respect to buffering; coral-sponge reef crisis only	None
Late Devonian	374.5	Mass depletion of biodiversity. Selective extinction of corals and sponges over prolonged period of time; reef crisis for corals and sponges	Weak
Late Ordovician	445.6 – 443.7	Mass depletion of biodiversity during double mass extinction. Unselective with respect to buffering	None

assemblages[6]. In contrast, there was a severe extinction of deep-sea benthic foraminifera with up to 50% of species lost from the fossil record[12]. The extinction saw the disappearance of long-lived Paleocene species, and the post-extinction taxa were commonly smaller and had thinner shells[12].

Recent research has provided detailed information on biomineralization of the skeletons of pelagic organisms that are likely sensitive to changes in surface water chemistry. Analysis of the architecture of coccolithophores has distinguished impacts on the skeleton that are associated with cellular function versus those associated with external carbonate chemistry of the water they experienced during the PETM[13]. Currently, observed changes suggest that the impact of ocean acidification across the PETM was relatively low compared to biogeographic range changes driven by warming and changes in circulation and the hydrologic cycle.

This does not mean we should not be concerned for calcifiers under our current climate regime. Clearly, communities responded significantly to the combined environmental impacts of the PETM, which like today, consisted of ocean acidification with additional environmental changes associated with increased CO_2, such as changes in temperature and oxygenation[14]. This is particularly the case for organisms that are unable to migrate in order to avoid environmental change, such as longer lived, sessile organisms like oysters and corals. It is especially important to remember that the changes seen during the PETM took place over many thousands of years, at least 10 times slower than anticipated rates of warming and OA in the century ahead[14]. When the rate of carbon uptake into the ocean outstrips its capacity to absorb it, a reduction in pH goes hand-in-hand with a lowering of its saturation state[15]. It is this saturation state (buffering capacity) of the ocean that could impact the functioning of many calcifying organisms, such as tropical reef-forming corals and planktonic organisms that form the base of pelagic food webs, especially in the vulnerable Arctic and Antarctic regions[14].

4.4 USING THE GEOLOGICAL RECORD TO INFORM OUR UNDERSTANDING OF OCEAN ACIDIFICATION

The geological record provides tangible evidence of the impacts of ocean acidification on environments and ecosystems, and provides a unique long-term perspective. Distinguishing the effects of acidification from associated environmental variables in the past is difficult, however, and there is no perfect geological analogue for modern day ocean acidification. The PETM, in particular, is widely studied because it is comparable in magnitude to predicted anthropogenic CO_2 release, but it differs markedly in terms of rate of change as it occurred over thousands rather than tens or hundreds of years, as is the case today. Even so it provides an invaluable testbed for studying the overall impact and subsequent recovery of the Earth system and biotic communities, as well as potential biotic sensitivity to abrupt climate change.

4.5 TIMESCALES OF OCEAN ACIDIFICATION

In Earth history, ocean carbonate saturation is generally well regulated by the simple requirement that on “long” (>10,000 year) timescales, sources (weathering) and sinks (shallow- and deep-water $CaCO_3$ burial) are kept in balance and regulated by the position of the calcium carbonate saturation depths. Only events involving geologically “rapid” (<10,000 year) CO_2 release will overwhelm the ability of the ocean and sediments to regulate, producing a coupled decline in both pH and saturation state[15]. The onset of the PETM occurred over a timescale of <10,000 years[16] and released ~2000-3000 petagrams of carbon into the Earth’s atmosphere[17](1 petagram = 1 gigatonne = thousand million tonnes).

Today's climate change projections calculate that ~ 5000 petagrams of carbon will be released into the atmosphere over the next 500 years if we follow a 'business as usual' scenario[18,19]. In Figure 4.3A, carbon released into the atmosphere during the PETM, and projected anthropogenic carbon emissions have been overlaid to provide perspective on the timescales involved. As a result of the carbon released in 4.3A, the saturation state of calcite (one of the mineral forms of calcium carbonate) decreases (Figure 4.3B). An important point to note is the timescale for the saturation state for calcite to "recover" to previous levels. Following the PETM, this took ~100,000 years[7], and it is projected to take a similar length of time following projected anthropogenic carbon emissions. Thus we can see that ocean acidification is not a short-lived problem and could take many thousands of years to return to pre-industrial levels even if carbon emissions are curbed.

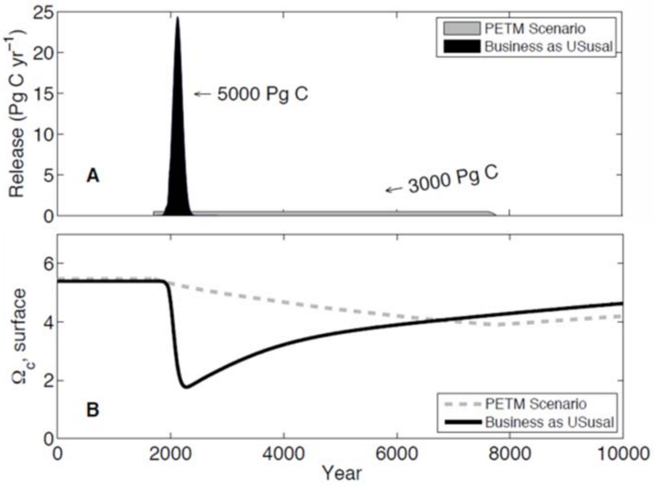

Figure 4.3. Paleocene-Eocene Thermal Maximum (PETM) versus present-day time scales.(A) Carbon emission scenarios as projected for the future (5000 petagrams of carbon over ~500 years)[17,18] and the PETM (3000 petagrams of carbon over ~6000 years). The onset of the PETM has been aligned with the onset of industrialization. (B) Changes in surface-ocean saturation state of calcite simulated with the Long-term Ocean-atmosphere-Sediment Carbon Cycle Reservoir (LOSCAR) model in response to the carbon input shown in (A). Source: Gattuso and Hansson 2011[20] © By permission of Oxford University Press.

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5. PHYSIOLOGICAL RESPONSES TO OCEAN ACIDIFICATION

Ocean acidification will have direct impacts upon a variety of different taxa through different mechanisms such as metabolism, pH regulation, calcification and photosynthesis. These impacts will influence ecosystem dynamics with an end result of potentially altered ecosystem services. Figure 1.3 summarizes the interaction between direct effects of CO_2 and pH (non-comprehensive) and ecosystem services; in this chapter, physiological responses are considered in greater detail.

5.1 OCEAN ACIDIFICATION AND CELLULAR PROCESSES

KEY MESSAGES: 5.1

1. Ocean acidification can lead to acid-base imbalance in many marine organisms, such as fish, invertebrates and sediment fauna
2. Acid-base imbalance can lead to metabolic suppression, reduced protein synthesis and reduction in long-term fitness
3. Some species can modify energetic allocation to compensate for increased energetic costs of ocean acidification

Most organisms regulate some aspects of their internal (extra- or intra-cellular) pH, either for calcification purposes, or because their metabolic activity requires some level of regulation. This "acid-base balance" or regulation is an energetic process, so a disruption caused by changing external CO_2 levels will require energy to maintain aspects of extra- or intra-cellular balance. Several studies, for example on deep-sea invertebrates[1] and fish,[2,3] indicate that animals at high pCO_2 require more energy as compared to those at low pCO_2, leading to the hypothesis that additional energy is needed to maintain the acid-base balance. This implies that, if a constant total energy budget is assumed, then increasing energetic investment into acid-base regulation will decrease allocation to other functions, such as reproduction or growth (Figure 5.1). Some studies are now demonstrating energetic compensation behaviours[4], but if acid-base balance is not achieved, metabolism can become depressed as a short-term response to extend potential tolerance[5]. However, this is not advantageous as it is typically at the expense of processes such as protein synthesis[5-7].

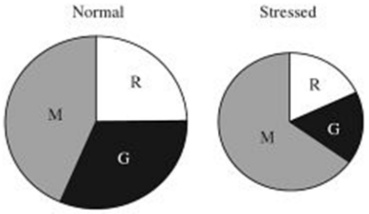

Figure 5.1. Hypothetical energy budget for normal and stressed organisms. M, maintenance costs; R, reproduction; G, growth. In this hypothetical energy budget, if metabolic depression is also induced by ocean acidification, the total energy budget may also decrease (hence the smaller pie on the right). From[8] in[9]. © By permission of Oxford University Press

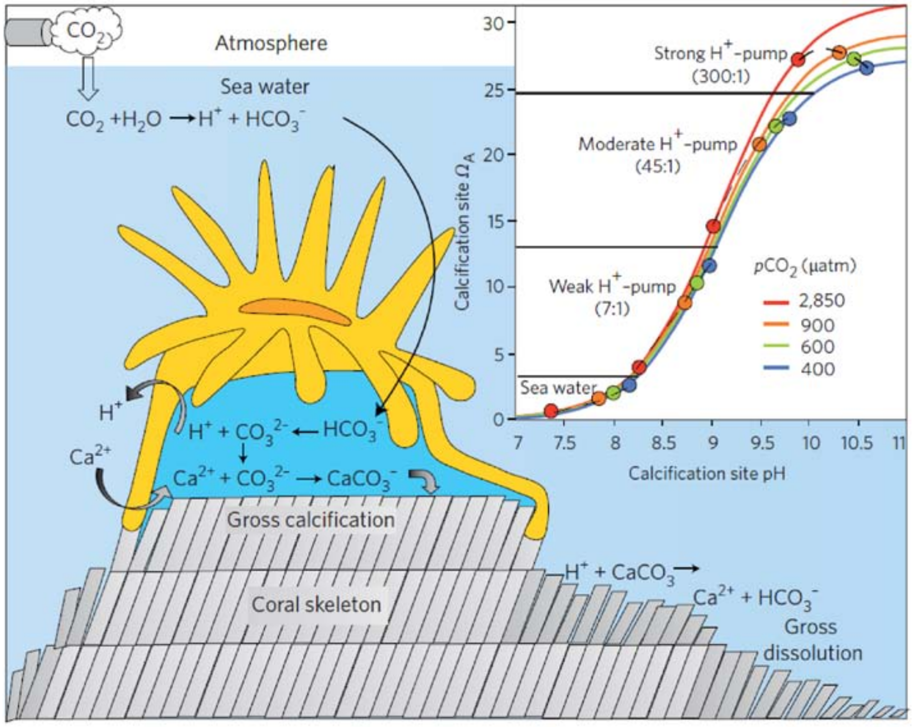

Figure 5.2. Schematic representation of coral calcification and dissolution, showing how the saturation state of the calcifying fluid (shaded dark blue; vertically exaggerated) is affected by external pH and the strength of the H^+ pump. The latter might be weak, moderate or strong; for strong H^+-pumping corals, the rate of gross calcification may initially increase under increased CO_2 levels, as shown in the inset graph, while net calcification rates may decline owing to dissolution of exposed skeleton. From[16]. Reprinted by permission from Macmillan Publishers Ltd: *Nature Climate Change* 1: 294-295, © 2011

Many marine organisms produce shells and other structures composed of calcium carbonate ($CaCO_3$). Future ocean acidification will lower the saturation state of calcium carbonate (aragonite and calcite) and if the water is undersaturated, dissolution of unprotected calcium carbonate will occur. The chemistry of that dissolution process is well-established[10,11]. However, the effects on calcium carbonate formation – biocalcification – are very much harder to predict. This is because in most organisms biocalcification does not occur directly from seawater but rather in a compartment or space with regulated chemistry and biochemistry, which allows controlled crystal formation. Relevant ions have to be transported into these compartments, and under future ocean acidification scenarios, these transport mechanisms may become slower and less efficient; alternatively, compensation responses may occur. The degree to which different groups of organisms are sensitive to changes in carbonate chemistry has become a major focus of ocean acidification research. Here we give a more in-depth explanation in corals, as they are one of the key marine calcifiers that engineer important marine habitats.

In corals, skeletons are laid down in a process controlled by specialized calcifying cells in an extracellular calcifying medium semi-isolated from the surrounding seawater environment[12]. Since the growing skeleton is not in direct contact with seawater, it is not immediately clear why coral calcification should be affected by ocean acidification occurring in the exterior seawater[13]. Recent research on cellular processes associated with calcification has started to identify the pathways that underlie the sensitivity of corals to ocean acidification. Firstly, it has been shown that there is a passage of ions and molecules from exterior seawater to the calcifying fluid[14]. However, the passage of seawater is restrictive, and coral tissues protect the skeleton from potential dissolution[15,16]. One way for corals to exert biological control to buffer against the effects of ocean acidification is to increase pH in the calcifying fluid[17], effectively increasing Ωaragonite at the site of calcification[18,19]. This process (the "H^+ pump") involves expelling hydrogen ions into the surrounding seawater across a concentration gradient. Under ocean acidification, the gradient is increased; the expulsion of H^+ therefore involves greater energetic cost to the coral[18-21]. Gene expression data in corals show signs that ocean acidification may start to impair the calcification process when coral acid-base and ion regulatory systems struggle to maintain homeostasis in the calcifying cells[21,22].

5.2 FERTILIZATION, EARLY LIFE AND SETTLEMENT

KEY MESSAGES: 5.2

1. Impacts of ocean acidification on fertilization success are highly variable and highlight the potential for genetic adaptation

2. Ocean acidification is generally detrimental for calcifying larvae

Many marine invertebrates have "mixed" life-cycles, inhabiting benthic and pelagic environments during different developmental stages. The persistence and success of these species therefore require that they can overcome stresses in multiple habitats. Exposure to stress, even at seemingly mild levels, can result in negative effects on subsequent stages of the life-cycle[23]. Consequently, a comprehensive understanding of the sensitivities of all life-stages, from planktonic (fertilization, embryos, larvae) to benthic/pelagic (juveniles, adults) in a changing ocean is vital if we are to identify vulnerabilities that can threaten species persistence in the future.

Reported impacts of ocean acidification on fertilization success are highly variable, ranging from none to very negative effects. This variation reflects biological reality – some species are much more tolerant than others – however, it almost certainly also results from different experimental approaches[24,25]; for example, relating to different source populations[25,26], the concentration of gametes[27], the number of parents[28], and the dominance of different parental genotypes in mass spawnings[29]. Such variability has been noted in recent meta-analyses[30-32]; in particular, variability can be enhanced when organisms are exposed to experimental conditions as part of a multi-species assemblage, where species-species interactions and indirect effects also become important[32]. Importantly, fertilizations using gametes pooled from multiple parents, mimicking the multiple spawner scenario in the field, show some resilience to near-future (~pH 7.8) ocean acidification conditions[33-35], as opposed to single crosses[36-40]. High variability in responses of single crosses to ocean acidification also highlights the potential for selection and genetic adaptation, supporting the concept of winners and losers in the face of changing ocean conditions[37-39].

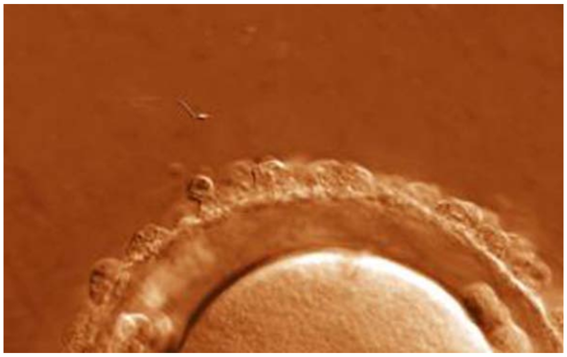

Figure 5.3. Sperm and egg of *Ascidia mentula*. Image courtesy of Jon Havenhand.

The response of isolated sperm to ocean acidification within the range of near future projections is also variable. Acidification reduces the percentage of motile (i.e., moving) sperm (but not swimming speed) in one species of sea urchin[38], increases sperm swimming speed in a different echinoid species[41], has variable and non-linear effects on both sperm motility and swimming speed in a polychaete worm[26], and no effect on sperm swimming speed in an oyster[37]. Established theory shows that reductions in sperm speed and motility would reduce fertilization success. On the other hand, increases in temperature have been seen to have a stimulatory effect on sperm swimming and enhance fertilization success[35,42,43]. Overall, ocean acidification can cause a reduction in fertilization at low sperm concentrations in some species but not others, and responses vary markedly among populations.

Prelarval stages - The few studies that have investigated the effects of ocean acidification on the very earliest embryos (pregastrula) have not detected any negative effects at projected near-future levels[44-46]. Additional work is required to illuminate the possibility that acidification-related changes are selecting a robust subset of progeny that possess phenotypic/genetic variation appropriate to future ocean conditions.

Development of larvae and juveniles - Larval shells are among the smallest and most fragile shells in the ocean and are potentially extremely vulnerable to decreased mineral saturation caused by ocean acidification. Consequently, most studies have focused on calcifying larvae[32,46-51]. Increased pCO_2 within the range of near-future projections is in general negative to calcifying larvae, including mollusc veligers and sea urchin echinoplutei[46,52-55] (Figure 5.4). In studies where several pH levels were tested, deleterious effects (smaller or abnormal larvae, lower weight juveniles) are evident at pH 7.8 (0.3 to 0.4 pH units below ambient). One study reported reduced growth in bivalve larvae with just a slight decrease to pH 8.0[53]. Oyster larvae may be particularly vulnerable, with emerging evidence that pH declines of 0.4 to 0.7 units can induce mortality rates of 80 to >90%[56]. Mollusc larvae with unprotected external skeletons directly exposed to changing ocean chemistry may be more sensitive to increasing ocean CO_2 compared with echinoderm larvae that have internal skeletons protected by overlying tissue. In the latter, hypercapnic (increased organism pCO_2) alteration of metabolism can also have a negative effect on larval growth and calcification[57-59]. Warming (up to the thermal limit) may ameliorate the negative effects of acidification on growth in marine calcifiers by stimulating growth in addition to changing CO_2 solubility[55,60-62], but such an effect may depend on food availability and other conditions; for some species, increased temperatures may exacerbate detrimental impacts of ocean acidification[63].

Non-calcifying larvae, including coral and some sea star larvae, are generally more resilient than calcifying larvae to near-future acidification[64-68]. However, some non-calcifying species (e.g., polychaetes) also show negative responses to acidification[26], and long-term experiments show that acidification of the parental environment can lead to impaired larval growth in species that are “robust” in shorter term experiments[65,67]. Crustacean larvae with poorly calcified exoskeletons (e.g., amphipods, barnacles, crabs) appear tolerant to acidification[61,69-72].

There is limited information on the impact of increased ocean pCO_2 and temperature on the metamorphic transition to a benthic life in marine invertebrates and subsequent early juvenile stages. The transition to the benthos may be affected by the negative effect of high CO_2, as shown by reduced coral larvae settlement[73]. Deleterious effects of ocean acidification (through smaller or lower weight juveniles) have been reported for corals, bivalves, polychaetes and echinoderms[26,74-79], with emerging evidence that current CO_2 values compared to pre-industrial levels could already have caused a reduction in some larval sizes[79]. Reduced larval size in a high pCO_2 ocean would have a negative impact on feeding and swimming ability and make larvae more vulnerable to predation.

By contrast, no effects of near-future acidification were evident for juvenile bivalves *Mercenaria mercenaria*, well-fed juvenile *Mytilus galloprovincialis*[77], or *Mytilus edulis*[80]. Tolerance of these species to acidification may reflect the adaptation to life in low pH and highly variable environments[80]. Juvenile crustaceans are comparatively tolerant of acidification[70,72], although again there is variability[81-83].

Understanding how effects at early life-stages can “carry-over”[23] to influence growth and reproduction of the adult remains a significant challenge and knowledge gap.

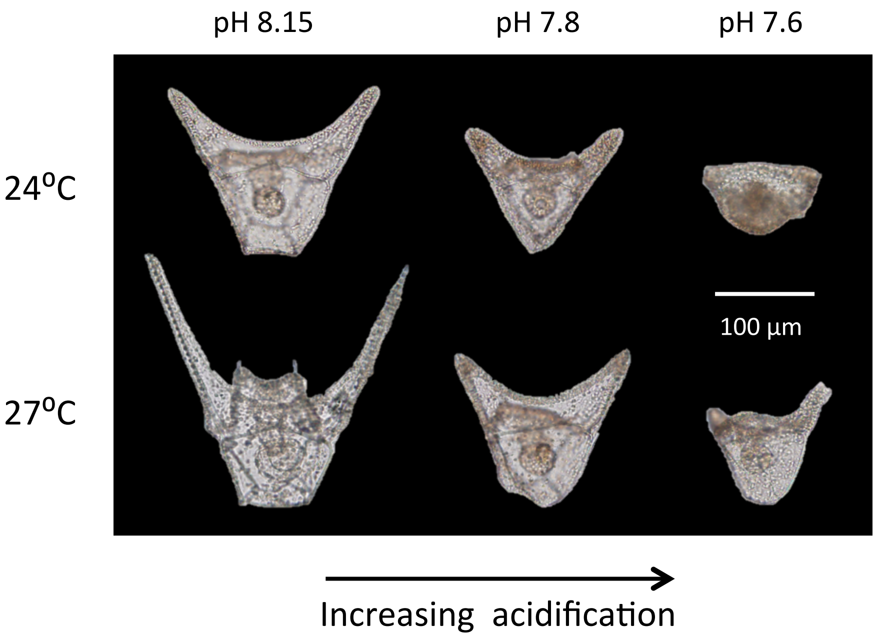

Figure 5.4. Effect of acidification on larval development (after 5 days) of the sea urchin *Tripneustes gratilla*; pH 8.15 at 24°C represents the control. For this species, a 3°C increase in temperature reduced the negative effect of pH on larval growth and calcification. Feeding effects were not involved, since early larval growth depends on food reserves from the fertilized egg. From [60].

5.3 SENSORY CAPACITY AND BEHAVIOUR

KEY MESSAGES: 5.3

1. Ocean acidification can alter sensory systems and behaviour in fish and some invertebrates
2. Impacts include the loss of ability to discriminate between important chemical cues

Ocean acidification can have significant direct and indirect effects on the behaviour of marine organisms. A potentially serious consequence of rising pCO_2 is that it can affect sensory systems and behaviour of marine fish and some invertebrates[84,85]. Reef fish larvae exposed to elevated CO_2 lose their ability to discriminate between ecologically important chemical cues, such as odours from different habitat types, kin and non-kin, the smell of predators[86,87,88] and visual function[89,90]. Response to auditory cues is altered[91], behavioural lateralization is lost,[92] and fish are no longer able to learn[93]. Impaired ability to discriminate between olfactory and auditory cues, or attraction to inappropriate cues, could have serious consequences for ability of larvae to successfully transition from the pelagic to benthic environments. Furthermore, larvae exposed to elevated CO_2 exhibit bolder and more risky behaviour once they settle to the reef, potentially leading to higher mortality from predators[94,95]. Behavioural effects are not restricted to larvae and juveniles. Recent experiments have shown that adult reef fish also suffer impaired olfactory ability and altered behaviour when exposed to elevated

pCO_2, with potential effects on predator-prey interactions[96,97], habitat selection[98] and homing to resting sites[99]. A wide range of reef fish species appear to be affected[95], including important fisheries species such as the coral trout *Plectropomus leopardus*[100]. Impaired behaviour at all life stages occurs as a result of permanent exposure to CO_2 levels ≥ 600-700 µatm CO_2, well within the range that could occur in the ocean this century. The ecosystem effects of impaired sensory behaviour, altered predator-prey interactions, and changes in behavioural attributes is unknown, but has the potential to be significant, including for functionally and economically important species.

Elevated pCO_2 alters behaviour of fish, and possibly of invertebrates, by interfering with brain neurotransmitter function[101]. Sustained exposure to elevated CO_2 induces acid-base regulatory changes in fish that could affect the function of GABA-A receptors, a major inhibitory neurotransmitter. The GABA-A receptor is an ion-channel with conductance for chloride (Cl^-) and bicarbonate (HCO_3^-), and these two ions are also important to acid-base regulation in fish. Given the ubiquity of GABA-A receptors in marine organisms, there is good reason to suspect that elevated CO_2 levels could cause behavioural abnormalities in a wide range of marine organisms. One example of GABA-A alteration causing behavioural problems is in the rockfish *Sebastes diploproa*[102], which became more anxious under future ocean acidification conditions. Interestingly, sensory behavioural "compensation" may partially reduce detrimental impacts of ocean acidification with regard to anti-predator responses[103]. With regard to GABA-A receptors, other organisms that use Cl^- and/or HCO_3^- to maintain their acid-base balance when exposed to elevated CO_2 may be at particular risk, and some invertebrates that are weak acid-base regulators suffer metabolic depression when exposed to high CO_2[104,105]. Reduced metabolic rate could also influence a wide range of behaviours in these species.

A critical question in assessing the impact of behavioural changes in marine organisms is whether individuals and populations will be able to acclimate or adapt to rising concentrations of CO_2. There is some hope that adaptation by selection of tolerant genotypes may occur, because larval damselfish reared at 700 µatm CO_2 exhibit considerable variation in responses to olfactory cues, with approximately half of the larvae responding like unaffected controls[93]. These individuals have much higher survivorship when exposed to predators compared with the individuals that are significantly affected by 700 µatm CO_2[106]. If this variation has a genetic basis, we might expect rapid selection of tolerant individuals throughout the population. Understanding the basis of variation in responses to elevated CO_2 among individuals will be key to making predictions about the potential for adaptation to rising CO_2 levels.

5.4 IMMUNE RESPONSES AND DISEASE

KEY MESSAGES: 5.4

1. Impacts of ocean acidification on immune responses and disease is an emerging field: few studies have been performed to date

2. Future ocean acidification has the potential to impact immune functions in marine organisms. It could also affect the virulence and persistence of pathogens

The majority of early research on the effects of ocean acidification on marine organisms has focussed on whole organism, or end point measures of impact – from assessments of increased mortality to changes in growth rate or calcification. More recently however, there has been the realization that whilst many organisms can acclimate to increases in environmental pCO_2 at relevant timescales, this acclimation might take place at a cost to other physiological processes, such as reproductive investment, immune function, or activity/ecological function.

As a consequence, recent work has considered impacts of ocean acidification on other physiological responses, such as the maintenance of immune function. To date, this work has focussed on commercially important species (crustaceans and molluscs), which are being increasingly seen as important for the maintenance of global food security[107].

Elevated pCO_2 can impact the immune system of marine organisms indirectly, especially if the changes have a negative impact on protein synthesis rates, thus reducing the synthesis of key immune enzymes and peptides. Immune system maintenance has conventionally been regarded as an energetically expensive constraint on an organism's energy budget[108], and it has been speculated that even chronic moderate reductions in pH[109] could be significant, especially in resource-limited environments. However, early published work in this area has tended to only consider short-term or acute impacts, which are of limited value in making predictions of the impact of climate relevant increases in sea water pCO_2.

Few studies have gone beyond initial acute shock responses to consider immune impacts once acclimation to the modified environment has taken place, but the limited few have found a significant impact upon bivalve haemocyte functionality[110], acidosis and phagocyte numbers in echinoderms (variable between species)[111] and that over 6 months, immunity was impaired in sea stars as evidenced by reduced phagocytic capacity[112]. As environmental factors play a significant role in determining the course of infection[7], climate change has the potential to increase susceptibility to disease[113]. From the limited number of examples that are available, it can be concluded that there is the *potential* for future ocean acidification to have an impact on the immune function of marine organisms, particularly with reference to commercially important shellfish. It could be speculated that this will result in an increased incidence of disease, particularly when combined with other stresses typically associated with aquaculture.

In conclusion, early research using short-term exposure experiments has suggested that there may be direct and indirect impacts on the immune function of marine organisms in a future climate. As this field matures, it is imperative that more effort should focus on identifying the long-term (months to years) impacts of climate-relevant increases in pCO_2 to immune function in marine invertebrates, especially in resource or energy-limited environments. Future efforts should also establish the impacts to disease resistance using live pathogen infections, to establish the real endpoint of immune system perturbation (mortality), whilst acknowledging that environmental change can simultaneously affect the virulence and persistence of pathogens[114].

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6. IMPACTS OF OCEAN ACIDIFICATION ON BENTHIC COMMUNITIES

KEY MESSAGES

1. Responses are highly variable, but many benthic species generally have lower growth rates and survival under projected future acidification

2. For corals, many studies show reduction in growth and increased sensitivity with ocean acidification, but this response is variable

3. Most adult molluscs are negatively impacted by ocean acidification, but some species can live in low pH

4. Many macroalgae species are tolerant or may benefit from future ocean acidification

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[1,2], and observations in naturally high-CO_2 marine environments[3,4] 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[2], including biological processes that may offset potentially detrimental impacts[5].

A recent meta-analysis[1] 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 6.1). Crustaceans appear less sensitive to smaller increases in CO_2 than other groups (Figure 6.1)[2,6], and may be affected through indirect influences, such as effects on food palatability[7]. Their tolerance appears to include juvenile as well as adult growth stages, although there is variability (see Chapter 5). Further discussion below focuses on the more sensitive taxa, corals, echinoderms and molluscs (Figure 6.1), although recognizing that the responses of benthic plants and microbes can also be of high ecological importance.

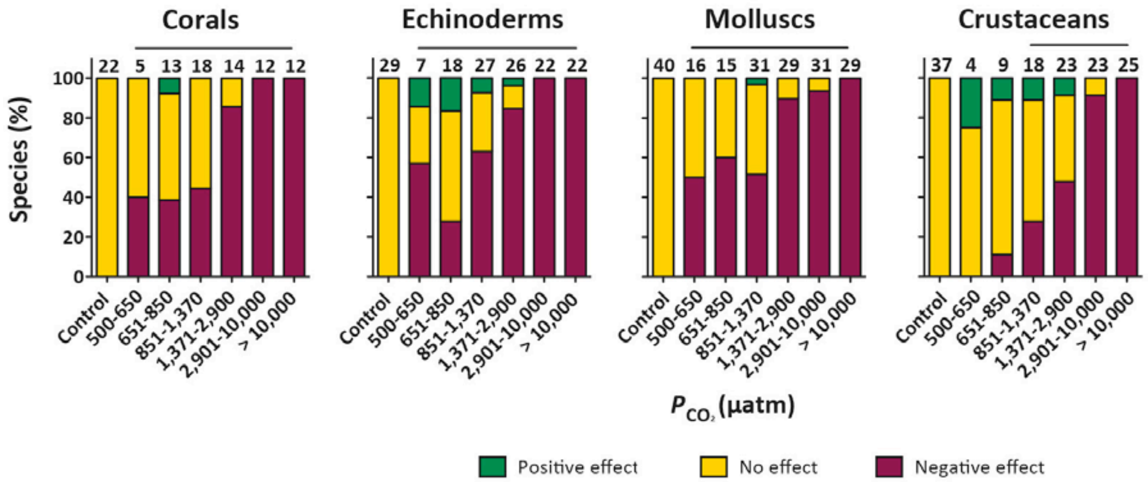

Figure 6.1. Sensitivity of animal taxa to ocean acidification. Fractions (%) of corals, echinoderms, molluscs and crustaceans exhibiting negative, no or positive effects on performance indicators reflect individual fitness in response to increased CO_2. Bars above columns denote count ratios significantly associated with pCO_2. Modified from[1]. Reprinted by permission from Macmillan Publishers Ltd: *Nature Climate Change* 3: 995-1001, © 2013

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.

Organisms that can create substantial calcifying structures, such as coral reefs, calcifying algae and polychaete structures, are considered key habitats to study, as they support substantial associated biodiversity and provide other functions such as coastal protection. Coral reefs are the best studied and one of the best known examples of calcareous structures, and as such have received most research attention to date. However, other structures, such as vermetid reefs (built by gastropods and coralline algae) could have impaired recruitment and increased dissolution under future CO_2 scenarios[9]. Considering the socioeconomic and ecological importance of calcareous structures other than coral reefs, it is also critical that they undergo further research.

6.1 CORALS

Tropical coral reef ecosystems represent one of the most biodiverse habitats in the oceans, directly or indirectly supporting about a third of all marine species[10,11]. Occurring in both cold- and warm-water environments, stony corals are key engineers of the coral reef ecosystem, contributing to the reef's structural framework and the exchange of nutrients between several trophic levels[12]. In light of their ecological and economic importance at regional and global scales, corals are one of the most intensively studied groups of calcifiers in terms of their calcification response to ocean acidification.

Cold-water corals, also often referred to as deep-water corals, are found in all of the world oceans,[13-15] with new information on their distribution being updated through national mapping programmes such as MAREANO in Norway (www.mareano.no), The

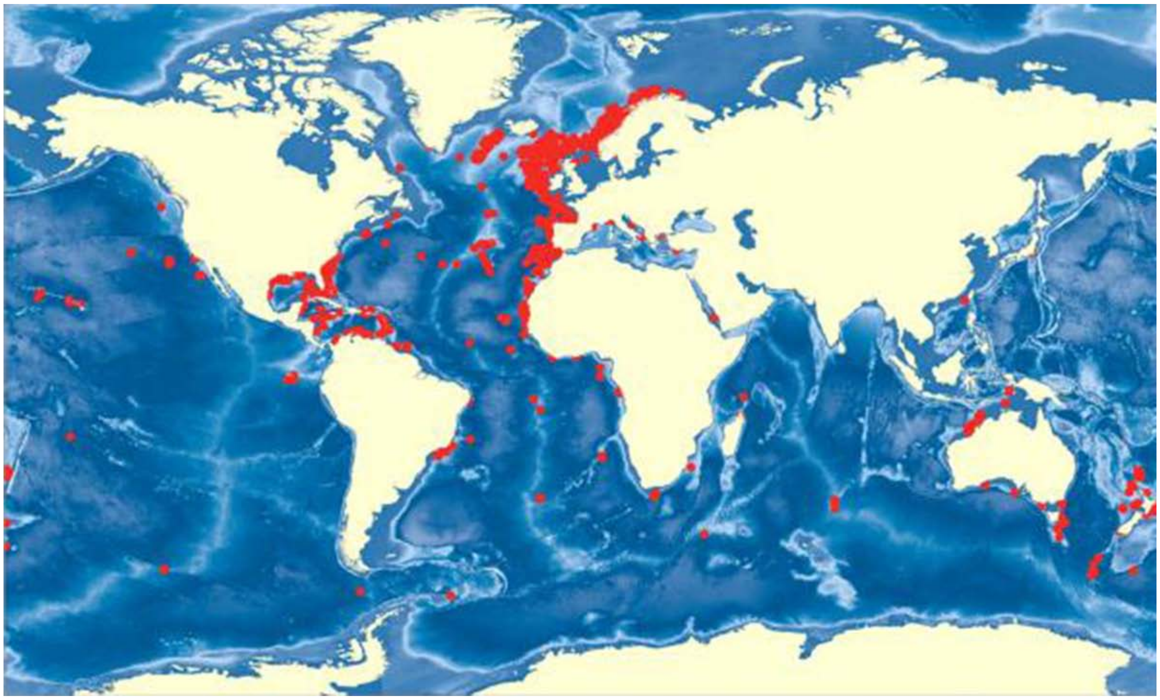

Figure 6.2. Global distribution of reef framework–forming cold-water corals. From[18]. Reprinted with permission from AAAS.

Deep Sea Coral Research and Technology Program (USA), and through European Community projects including HERMES, HERMIONE and CoralFISH. Figure 6.2 demonstrates the distribution of framework-forming cold-water corals such as *Lophelia pertusa*, but does not represent the occurrence of the myriad of other cold-water coral species. Many cold-water coral species require hard substrate for attachment and growth, and in general they thrive where there are strong currents that supply them with food, disperse eggs, sperm and larvae, remove waste products and keep the surfaces of the coral free of sediments. This means that they are often found on parts of the continental slope or on the summits of seamounts where currents are strongest. It has often been assumed that these deep-water habitats are relatively stable in terms of their carbonate chemistry, but recent evidence suggests that within and between habitats, a significant amount of variability can exist, even on a daily basis[16,17].

Cold-water coral reef systems are often structurally complex environments including gorgonians, stylasterid corals (lace corals), sponges and a variety of fish and invertebrates in the Arctic and sub-Arctic[19,20], and are defined as vulnerable marine ecosystems. Impact or damage to these ecosystems may lower the local biodiversity and diminish the possibility for many species to find shelter and feeding grounds.

Due to the uptake of anthropogenic CO_2 in the ocean both the aragonite saturation horizon (ASH) and calcite saturation horizon (CSH) are becoming shallower. In places, *Lophelia pertusa* already lives very close to the ASH, for example in the Gulf of Mexico[21]. By the end of the century, many deep-sea corals are predicted to be in water undersaturated with calcium carbonate [22,23]. It has been estimated that >95 % of corals were above the depth of the ASH in pre-industrial times (year 1765), but by the end of the century, only ~30 % of coral locations will be found above this saturation depth[22] (Figure 6.3). While gorgonians and stylasterids have not been well studied with regard to ocean acidification compared to *Lophelia pertusa*, their calcium carbonate and proteinaceous structures also merit further attention with regard to ocean acidification.

The limited evidence available for how ocean acidification will impact cold-water corals such as *Lophelia pertusa* indicates that in the short term, projected decreases in pH can decrease metabolism and growth[24-26], but over 6-12 months, *L. pertusa* does

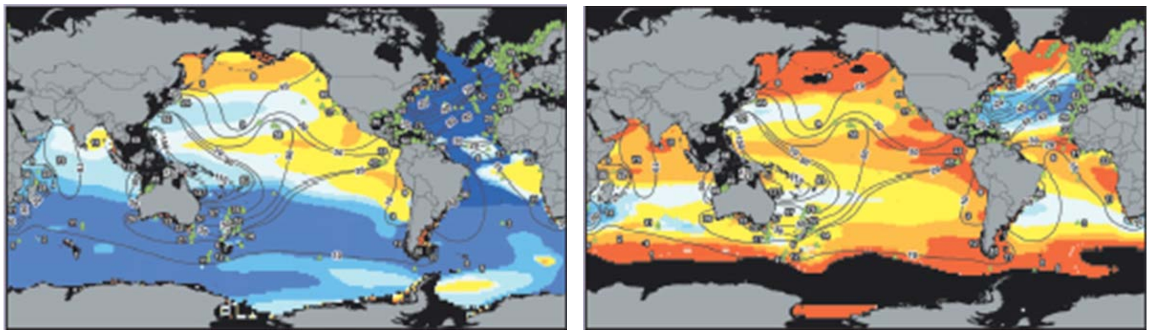

Figure 6.3. Modelled depth of aragonite saturation horizon (ASH) in relation to locations of cold-water corals (green triangles). Left: ASH depth for the year 1995; pCO_2 = 365 ppmv. Right: Projected ASH for the year 2099; pCO_2 = 788 ppmv. Black areas appearing in Southern Ocean and North Pacific in bottom panel indicate where ASH depth has reached the surface. Contours indicate diversity for 706 species of azooxanthellate (without microalgal symbiont) corals. From[22].

not display reductions in growth when subjected to predicted end of the century CO_2 conditions[25-27]. However, these long-term experiments still do not account for any impact on future reproduction of cold-water corals, so the question remains whether key species such as *L. pertusa* can merely temporarily tolerate future conditions, or whether they can thrive under projected future climates. The current low abundance of cold-water corals below the ASH suggests not, since the increased energetic demands for living below the ASH cannot usually be met. Thus the long-term survival of cold-water corals below future calcium carbonate saturation depths seems unlikely[28].

Although scleractinian corals can up-regulate their extracellular pH within the calicoblastic layer at the sites of calcification through energy intensive processes[29-32], the regulation only applies for coral skeleton that is covered by living coral tissue. Cold-water coral reefs are typically composed of a significant amount of bare, dead skeleton beneath the living material (Figure 6.4), which would start to dissolve in undersaturated conditions, and be eroded with increased efficiency by bio-eroding sponges[33]. Thus future changing conditions could potentially have large impacts upon current cold-water coral habitats and associated biodiversity[34].

For warm-water corals, many studies demonstrate a reduction in growth (net calcification rates) in response to ocean acidification[29, 35-39]. However, this is not a ubiquitous response, with different species exhibiting negative responses[40], no measureable response[41], or variable responses[35] to reduced pH[42]. Examining coral growth rates through time by analysing coral cores remains difficult, due to ontogenetic effects and growth variability from coral age and size[43]. Furthermore, responses may be non-linear, such that there may be no response until a "tipping point" is reached[44].

Meta-analysis has proved very useful in synthesizing the data obtained from these multiple studies, and in identifying the factors that may explain variation between them[2,45-47]. The general conclusion of these analyses and other reviews[48-51] is that warm-water corals are sensitive to ocean acidification,

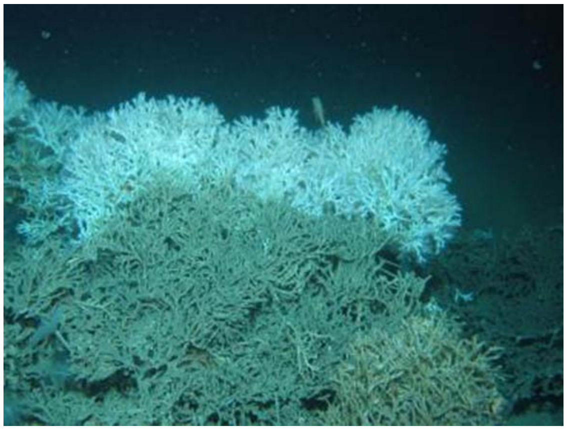

Figure 6.4. Image of live *Lophelia pertusa* with underlying dead framework (Rockall Bank, NE Atlantic). Source: Heriot-Watt University/UK Ocean Acidification research programme.

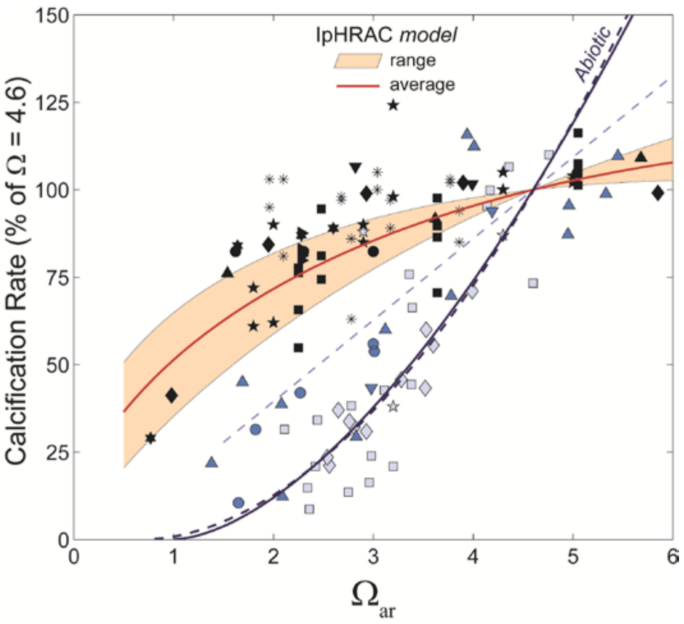

Figure 6.5. Percentage change in scleractinian coral calcification rates (relative to seawater Ω = 4.6) plotted against aragonite saturation state, Ω_{ar}. Coral species showing low sensitivity (black symbols) are able to regulate their internal pH much more effectively than those showing high sensitivity (dark blue symbols). Data for calcareous algae (light blue symbols) also included for comparison. From[29]; the IpHRAC model developed by those authors combines information on internal pH regulation of calcifying fluid with abiotic calcification, enabling carbonate precipitation rates to be quantified as a function of seawater saturation state and temperature; the range of values relates to the variability in species' ability to regulate their internal pH. Adapted by permission from Macmillan Publishers Ltd: *Nature Climate Change* 2: 623-627, © 2012

with declines in coral calcification associated with declining aragonite saturation state and seawater pH[29, 51,52]. However major questions remain, notably *how* and *why* coral calcification is sensitive to ocean acidification. This is the subject of recent research initiatives that investigate the mechanism of calcification, with attention focussing on internal pH regulation[29] (Figure 6.5).

Insight into the physiological mechanisms that corals use to cope with ocean acidification may explain inter-species differences in sensitivity, and may help to predict winners and losers in a higher CO_2 ocean. The capacity to regulate ions / pH under ocean acidification may be a defining physiological trait that facilitates future survival, with emerging evidence from coral skeletons that there is strong inter-specific variability in their ability to up-regulate pH control[53]. For some species, temperature and ocean acidification can act synergistically in reducing calcification rates, i.e., more than the additive effects of these factors acting alone[54]. Thus future studies have to consider multiple stressors to determine the future fate of these key ecosystems.

Further discussion of the physiological responses of corals is given in section 5.1, and of the socio-economic consequences of the loss of warm-water coral reefs in section 8.2.

6.2 MOLLUSCS

Bivalve molluscs were identified in early ocean acidification research to be strongly affected by ocean acidification[55], with many species negatively impacted by relatively low pH decreases (Figure 6.1). Reduced growth rates can lead to knock-on effects such as increased predation for smaller oysters[56]. Nevertheless, while acute experiments without an acclimation period can result in strong reductions in calcification[57], adult mytilid mussels can maintain significant calcification in longer-term incubations with realistic food regimes even when the seawater is undersaturated with respect to calcium carbonate[58-60]. Some mussel species (e.g., *Bathymodiolus brevior*) are able to grow close to deep-sea hydrothermal vents, at pH values as low as 5.4. This feature indicates great biological control over the calcification process[61], together with a fundamental role of the external organic cover, the periostracum, to enable persistence at such extreme locations. A similar role of the periostracum has been suggested for coastal *Mytilus edulis*, which can also calcify at high rates even when calcium carbonate is undersaturated[59]. Results from the western Baltic Sea indicate that successful settlement and dominance of mytilid mussels and other calcifying invertebrates is possible at seawater $p\mathrm{CO}_2$ values similar to those projected for the end of the century[59,62]. Where reductions in growth and calcification are observed, energy budget reallocation may be the cause[63], or potentially increased oxidative stress[64]. Future research should thus focus on determining cellular energy budgets to analyse energetic trade-offs.

The impact of ocean acidification to larval stages of bivalves is potentially of great importance to their continued survival[65-67]. This topic is covered in more depth in section 5.2.

6.3 ECHINODERMS

Echinoderms have been extensively studied with respect to sensitivity to simulated ocean acidification, and in particular with respect to their larval stages (see section 5.2). While early life stages of some species react with severely increased mortality to experimental ocean acidification[68], most species respond with slight reductions in larval growth[69,70].

When exposed to simulated ocean acidification, echinoderms experience energy budget reallocation, with only few examples of increased mortality[71]. Moderately elevated $p\mathrm{CO}_2$ (<1,000 µatm) can increase feeding and growth rates in intertidal sea stars[72]; however, other studies have shown reduced investment in growth, calcification, reproduction or immunity[73-77]. Despite studies highlighting the potential for long-term, trans-generational and adaptive responses of echinoderms to ocean acidification[69,70,78,79], little research attention has been devoted to these factors; future studies should reflect this.

6.4 MACROALGAE, SEAGRASS AND BENTHIC MICROBIOTA

Macroalgae and seagrass are important components of many coastal ecosystems, as primary producers and habitat engineers. They generally grow in relatively shallow coastal waters, where they are likely to experience wide daily and seasonal variability in seawater pH[80]. The complex interaction between a wide range of environmental changes in coastal waters, including eutrophication and hypoxia, may lead to faster declines in pH with increasing atmospheric CO_2[81]. The responses of benthic flora to ocean acidification can be positive or negative, depending on their distribution and species.

Macroalgae – seaweeds – can be calcareous or non-calcareous (fleshy). Ocean acidification is generally detrimental to calcareous algae[82-84], with loss of structural integrity[85,86] and associated changes in growth forms that can affect competitive interactions[87]. Nevertheless, some calcareous algae may thrive under naturally low pH conditions (e.g., around CO_2 vents), even after decalcification[88]. Increased productivity has also been observed under experimental ocean acidification and is likely to be due to higher CO_2 favouring photosynthesis – with a similar stimulatory effect also occurring for non-calcareous species[4,80,82,89-91].

Future impacts do, however, need to be considered in the context of temperature changes, which may be highly detrimental to larger non-calcareous macroalgae (kelp) in temperate regions[92]. Effects of ocean acidification on the consumption of seaweeds by

Figure 6.6. Seagrass and a natural CO_2 seep. Source: Giorgio Caramanna.

grazers could also be important. Around CO_2 vents, invertebrate grazing pressure is reduced; however, there is also evidence that high CO_2 can decrease the production of protective phenolic substances used to deter grazers[93]. This apparent contradiction could be due to grazing itself stimulating the production of the deterrents, an issue that warrants further attention.

Seagrasses seem likely to benefit from ocean acidification[92,94] and can be abundant around CO_2 seeps (Figure 6.6). Elsewhere, they are able to substantially modify the carbonate chemistry of their environment through photosynthesis (involving CO_2 uptake) [95], resulting in substantial diel variability in seawater pH[96,97]. In the case of tropical seagrasses, they could potentially mitigate ocean acidification for adjacent coral reef systems by elevating pH (by up to 0.38 pH units) at tidal intervals[96].

The effects of ocean acidification on benthic microbiota (including benthic diatoms and dinoflagellates, as well as single-celled animals and bacteria) are not well understood. Large gradients in pH naturally occur at the seawater-seafloor interface and in the upper layers of sediment[98]; it may therefore be thought that future carbonate chemistry changes would be unlikely to have significant impact. Nevertheless, experimental studies on benthic foraminifera show functionally important morphological changes at 750ppm and 1000ppm CO_2[99], and major changes have been found in the abundance and diversity of benthic microphytobenthos[100], epilithic bacteria[101] and foraminifera[102,103] around natural CO_2 seeps. Near-future extinctions of benthic microbiota, similar to those occurring at the PETM (Chapter 4), are therefore considered likely[103].

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7. IMPACTS OF OCEAN ACIDIFICATION ON PELAGIC COMMUNITIES

7.1. PLANKTON

KEY MESSAGES

1. Non-calcifying phytoplankton may benefit from future ocean acidification
2. Calcifying phytoplankton such as coccolithophores exhibit variable responses to future ocean acidification
3. Mesocosms combining both calcifying and non-calcifying phytoplankton show enhanced net primary production under elevated CO_2
4. Bacterial responses to ocean acidification are uncertain, but any changes could affect nutrient cycling
5. Planktonic foraminifera and pteropods are expected to experience decreased calcification rates, or dissolution under projected future conditions
6. Impacts on foraminifera may decrease efficiency of future carbon transport between the sea surface and seafloor

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[1,2]. 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 (see also section 8.3).

Phytoplankton and bacteria

Non-calcifying phytoplankton. These organisms form a significant proportion of the phytoplankton and include 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[3-6]. 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[7,8]. 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

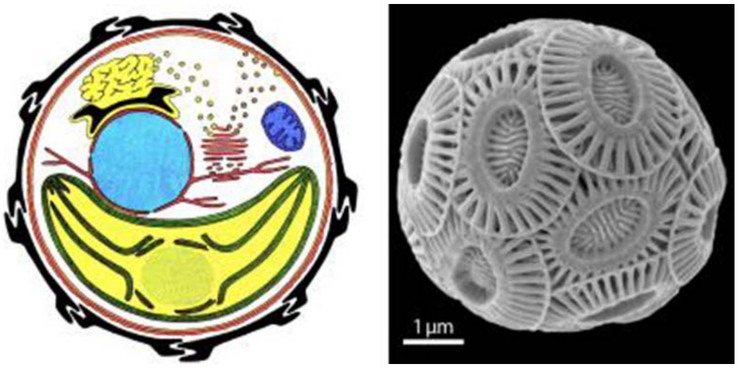

Figure 7.1. Left: Drawing of a single cell of *Emiliania huxleyi* showing coccoliths (black) forming within an intracellular vesicle before being extruded to form the extracellular coccosphere (image: Peter Westbroek). Right: Scanning electron micrograph of an *E. huxleyi* coccosphere.

CO_2 diffusion leakage from biological cells (where the CO_2 is concentrated) to the surrounding seawater[3]. However, photosynthetic mechanisms vary widely between photosynthetic organisms[9], and this may lead to a shift in community composition in the future[10,11]. 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[12,13], or that the lack of carbon concentrating mechanisms in many HAB species will be of benefit to them in future climates[14].

Calcifying phytoplankton. Of the calcifying algae, coccolithophores have received most interest. Coccolithophores are a group of unicellular phytoplankton, which produce calcite plates called coccoliths (Figure 7.1). Their cells are typically 5 to 20 μm across, and can be present in abundances of tens of thousands to millions per litre in the photic zone. They form a major component of the phytoplankton in relatively oligotrophic waters and are biogeochemically important as carbonate producers; they are also extensively studied by geologists, since chalk is predominantly composed of fossil coccoliths.

Some species of coccolithophores (such as *Emiliania huxleyi*) can readily be grown in laboratory cultures, and more than 40 research papers on the impact of ocean acidification on coccolithophores have been published. Early experimental work with laboratory cultures and large-scale semi-enclosed field cultures (mesocosms), suggested there was a reduction in calcification with increasing $p\mathrm{CO}_2$[15-18], with potential synergistic impacts of increased solar UV radiation due to thinner coccoliths[19]. Several ecological studies have indicated that variations in carbonate saturation state might influence the population dynamics and distribution of modern coccolithophores, such as the timing of blooms[20], and absence of coccolithophores from the Baltic Sea[21] and parts of the Antarctic[22]. It has been suggested that coccolith mass in *E. huxleyi* and closely related species is controlled by saturation state in the ocean both currently and historically[23].

However, the changes in calcification, growth rate and cell size by different strains of *E. huxleyi* to elevated $p\mathrm{CO}_2$ conditions can be highly variable, due to shifting balances in potential positives and negatives for photosynthesis and calcification[24]. Culture work on coccolithophore species other than *E. huxleyi* has also shown variable responses, with some species apparently unaffected by experimental ocean acidification[25]. Importantly, recent studies indicate that coccolithophores may be able to adapt to changing conditions, even on the relatively rapid timescales at which they are occurring[26,27]

Conflicting results have also been found from field and geological evidence. Two studies of sediments from the past 200 years have provided evidence for *increased* calcification of coccolithophores over this time period despite the rise in atmospheric CO_2, or even as a (counter-intuitive) response to it[24,28].

Box 7.1 Svalbard mesocosms case study

Large-scale mesocosms provide invaluable data on how communities of both calcifying and non-calcifying organisms will fare under future conditions. Mesocosms have been successfully deployed for ocean acidification studies at a range of locations, including Svalbard, Norway, to assess impacts of high CO_2 over ecologically relevant timescales under close-to-natural conditions. The Svalbard results indicated that under high CO_2 / low pH, phytoplankton community composition changed but the microzooplankton community exhibited high tolerance[29]. Importantly, net carbon uptake by phytoplankton was enhanced, but the systems were pushed towards overall negative effects on export potential[30].

Experimental mesocosms at Svalbard. Source: Maike Nicolai, GEOMAR.

Bacteria. While some planktonic bacteria are photosynthetic (e.g., *Synechococcus, Prochlorococcus*), and can therefore be considered as phytoplankton, most are heterotrophic, obtaining nutrition from organic material. They therefore play a key role in nutrient cycling. They can either be “free-living”, or associated with particles, including other components of the plankton. A significant proportion of the phytoplankton-derived organic carbon ends up as dissolved organic carbon (DOC), and this can be taken up by heterotrophic bacteria. The amount and growth of such bacteria determines the fraction of DOC that can be re-introduced into the food web through subsequent grazing[3].

The response of bacteria to projected future changes is relatively unstudied compared to the calcifying plankton, but recent studies on surface-living bacteria which form biofilms suggests that future changes will alter bacterial community composition[31]. Future nutrient cycling may also change depending on whether bacterial communities change significantly as pH decreases, which could have direct impacts upon nutrient cycling between benthic and pelagic ecosystems[32].

Zooplankton

There are two main groups of biocalcifying zooplankton, pteropods and foraminifera, both of which have been the subject of research on the potential effects of ocean acidification.

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[33] (Figure 7.2). Pteropods occur throughout the global ocean but they are most abundant in sub-Arctic and sub-Antarctic to Antarctic

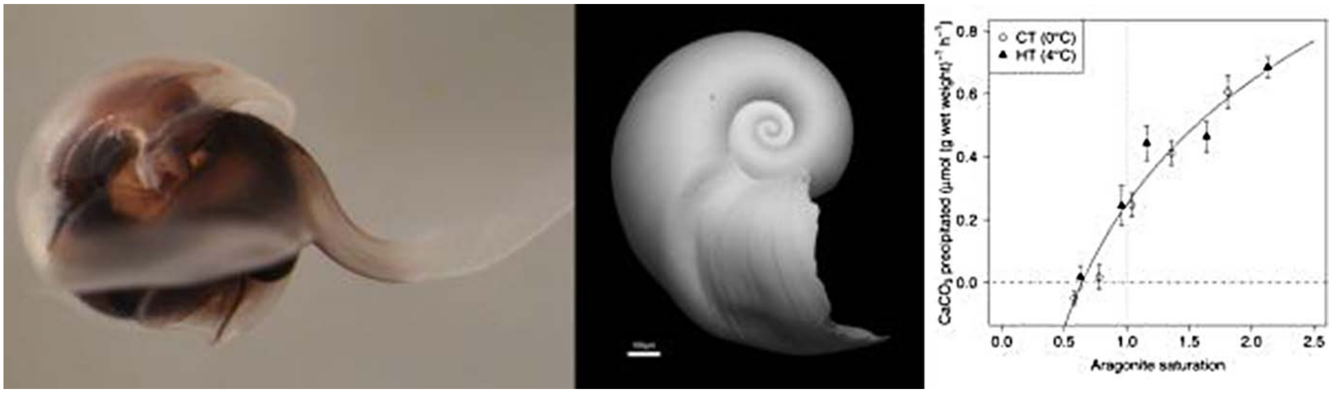

Figure 7.2. Left: A living pteropod from the Arctic (image Vicky Peck, BAS). Centre: The shell of a juvenile pteropod from the South Atlantic. Right: Data from laboratory culture experiments on shell growth rate of *Limacina helicina* incubated under aragonite saturation states equivalent to those seen in the Arctic at present day (ca 2.0) to the year 2100 (<1.0), from[41].

waters, where they can form a significant part of the zooplankton and are important food stocks for fish and other predators[34]. Pteropods have shells formed of aragonite rather than calcite. The combination of thin aragonitic shells[35] 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, as discussed in section 3.2, undersaturation 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[36].

Shipboard incubations have demonstrated that pteropod shell dissolution (erosion) could occur, which has now been confirmed under field conditions in the Antarctic[36,37] and northeast Pacific[38] at $\Omega_{\text{aragonite}} < 1.0$. In addition to no calcification occurring when seawater is undersaturated, it has now also been demonstrated that calcification may be inhibited when $\Omega_{\text{aragonite}}$ values are > 1.0[39-41]. The vulnerability of pteropods to ocean acidification and warming has been demonstrated for the Arctic pteropod *Limacina helicina*, in which shell growth was reduced and degradation increased at moderately elevated temperature and pCO_2 (1100 µatm)[42] despite some regulatory capacity to ameliorate these effects[43], and in the sub-Arctic, where biomass of the dominant pteropod has decreased notably[44]. A modeling study combined predicted aragonite saturation states for the end of the century with data on the likely impact on pteropod calcification, and concluded that "there appears little future for high-latitude shelled pteropods"[45], which will impact organisms which utilize these as a food source[46].

Foraminifera are a group of unicellular pelagic (and benthic) animals forming chambered calcite shells. The shells are elegant structures typically 0.1 - 0.5 mm across; many species have a halo of delicate radial spines supporting a mass of protoplasm, gas bubbles and symbiotic algae (Figure 7.3). Although they usually only form a minor component of the total zooplankton, they leave a prolific record of their existence since their shells sink readily after death and form one of the main components of deep-sea sediments[47]. This makes them important contributors to the ballasting effect, and a group of major interest to geologists, both as rock-forming organisms and as recorders of ocean chemistry.

Laboratory experiments have shown that carbonate concentration has significant impact upon planktonic foraminiferal calcification, with decreases in shell thickness and weight occurring at levels well above $\Omega_{\text{calcite}} = 1$[48-52]. Such an effect is also indicated by most, but not all, geological studies[53-55]. Furthermore, field studies comparing modern plankton from the water column with pre-industrial populations in the surface sediment have indicated that marked reductions in shell weight have already occurred[54,56]. Research on tropical benthic foraminifera has shown greatest vulnerability to ocean acidification amongst non-symbiont bearing species with hyaline or porcelaneous shells[57].

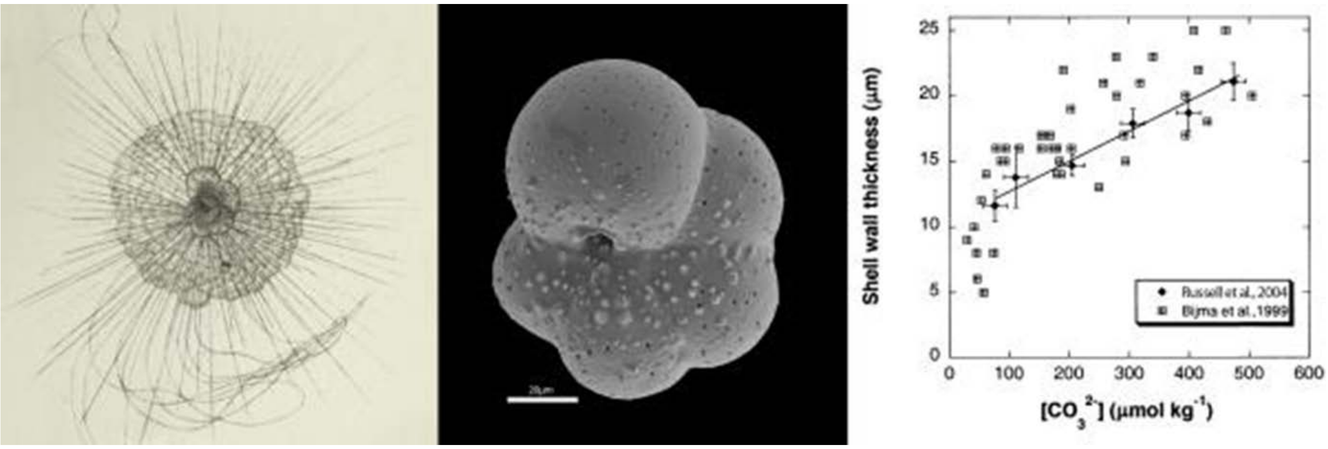

Figure 7.3. Left: Drawing of a modern planktonic foraminifera surrounded by a halo of bubbles and symbiotic algae supported by spines[58]. Centre: Scanning electron micrograph of the shell of juvenile planktonic foraminifera. Right: Laboratory culture data variation in shell wall thickness in *Orbulina universa* cultured under bicarbonate conditions equivalent to those from the modern ocean (~ 250μmol kg^{-1}) to those anticipated in 2100 (~ 100 μmolkg^{-1}), and under rather more extreme conditions. From[50].

The shell mass and thickness of foraminifera are also controlled by other factors such as temperature, depth and gametogenic calcite formation, and to date only a few studies exist on the interaction of such factors with ocean acidification. Nevertheless, the overall evidence strongly suggests that ocean acidification will have a significant effect on planktonic foraminifera and hence on their role in ballasting organic carbon fluxes.

Copepods. Direct effects of elevated pCO_2 on copepods have only recently gained attention, and our knowledge of their response to ocean acidification remains limited. Copepods are holoplanktonic crustaceans that have a maximum size of ~1 cm and are the most abundant group in marine zooplankton communities worldwide, where they are the predominant link in pelagic food webs between primary production and higher trophic levels[59,60]. In controlled experiments, reproductive success (i.e., egg production and hatching) decreased at high CO_2 concentrations (>1000 µatm) compared to low CO_2 levels[61-66]. However, in Arctic mescosm experiments over 30 days, abundance and stage composition of *Calanus* spp., *Oithona similis*, *Acartia longiremis* and *Microsetella norvegica* did not change with CO_2 concentrations, indicating that possible effects of predicted changes in CO_2 were not strong enough to be reflected in the population dynamics[67], although the grazing rates of *Calanus* spp. decreased with increasing CO_2[68]. Other, more sensitive species, such as *Centropages tenuiremis,* increased respiration and grazing rates at 1000 µatm, likely to meet increased energetic demands[69].

On the basis of such results it has been concluded that direct effects of CO_2 on copepods (and other non-calcifiying heterotrophic plankton) may not be as potentially severe as for calcifying organisms. However, differential sensitivity across developmental stages has recently been reported for *Acartia tonsa*[70], which needs to be investigated for other species. Furthermore, if algal biochemical or species composition and thus food quality changes due to increasing pCO_2, limitations in food quality may reduce the reproductive success of copepods[71]. Thus, non-calcifying organisms may also be impacted by ocean acidification via trophic interactions.

7.2 FISH, SQUID AND CUTTLEFISH

KEY MESSAGES

1. Most fish are likely able to maintain sufficient O_2 delivery under future conditions, but cephalopod metabolism may be reduced
2. Ocean acidification causes sensory and behavioural impairment in many fish species
3. Juvenile life stages appear more susceptible to future ocean acidification

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[72]. 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[73,74]. In most species studied to date, almost complete compensation of acidosis occurs within a few hours or days of exposure to elevated CO_2[74-77]. 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[78].

One concern is that additional energy expenditure associated with acid-base regulation, or a decline in oxygen carrying capacity associated with incomplete acid-base regulation, may reduce the scope for aerobic performance in fish[79]. While aerobic scope in two tropical cardinal fish *Ostorhinchus doederleini* declined significantly at projected future CO_2 levels[80], Atlantic cod *Gadus morhua* maintained their standard and active metabolic rates, critical swimming speeds and aerobic scope after prolonged exposure (4 and 12 months) to even higher CO_2 levels[81]. Furthermore, studies on freshwater and estuarine fish exposed to CO_2 levels many times greater than end-of-century predictions for

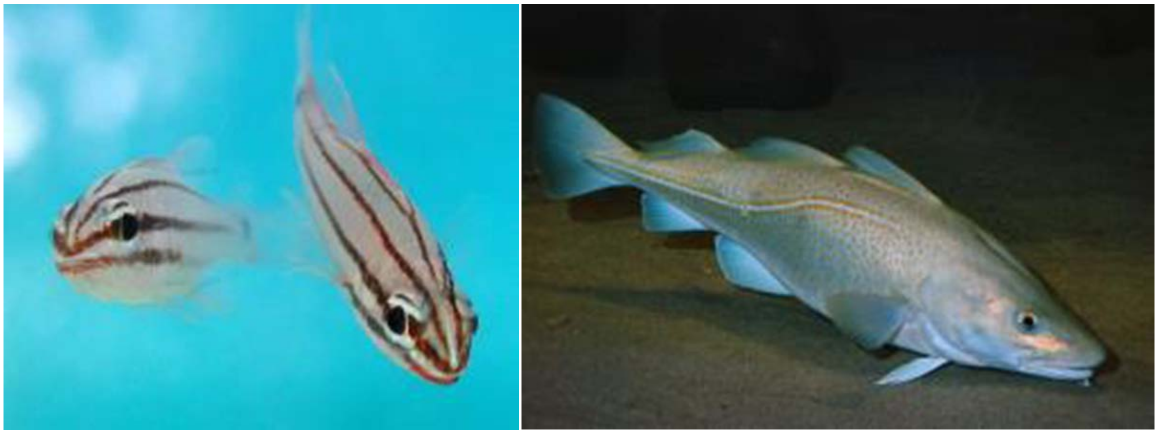

Figure 7.4. Left: the cardinalfish *Ostorhinchus doederleini*. Right: Atlantic cod *Gadus morhua*. Image: Goran Nilsson and animalspot.net

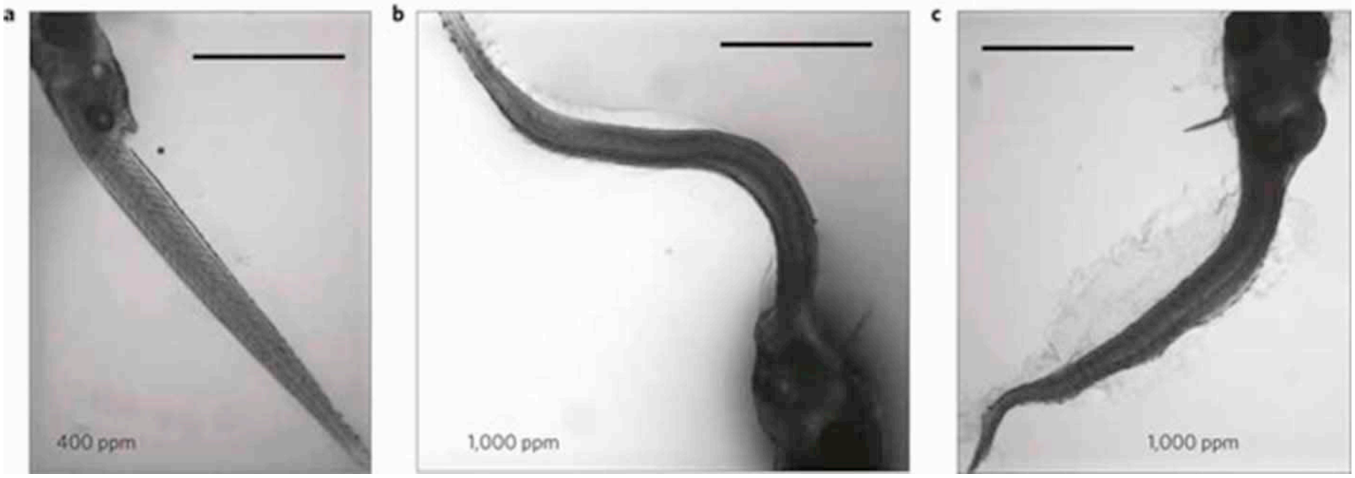

Figure 7.5 Larvae of *Menidia beryllina* with curved or curled bodies were significantly more common at increased CO_2 levels (b,c) when compared with control (a) CO_2 levels. Scale bar=1 mm. From[89], adapted by permission from Macmillan Publishers Ltd: Nature Climate Change.

ocean pCO_2 have generally found no effect on oxygen uptake or swimming performance[74,78,82]. These results indicate that while sensitivity to elevated CO_2 varies among species, most fish are probably able to maintain sufficient oxygen delivery at CO_2 levels predicted to occur in the near-future.

CO_2 effects on cellular energy budgets have scarcely been studied to date, yet it has been shown for the Antarctic marbled rockcod *Notothenia rossii* that several weeks of exposure to elevated pCO_2 (2000 µatm) can lead to reduced mitochondrial capacities and putative shifts in metabolic pathways involved in mitochondrial energy metabolism[76]. Increased intracellular levels of bicarbonate, due to both increased pCO_2 and active pH buffering by bicarbonate uptake[74] can lead to competitive inhibition of enzymes of the Krebs cycle (citrate synthase, succinate dehydrogenase) and may elicit transcriptional changes and functional modifications of mitochondrial proteins by activation of a soluble adenylyl cyclase and subsequent action of protein kinase A (PKA)[83].

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[78,84]. 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[85,86], the pelagic cobia *Rachycentron canadum*[87] and walleye pollock *Theragra chalcogramma*[88] 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[89] (Figure 7.5). Tissue development was disrupted in the Atlantic cod *Gadus morhua* reared at relatively high CO_2 levels (1,800 and 4,200 µatm)[90], although the eggs and larval stages did not seem to be affected[91].

These studies suggest that the sensitivity of larval and juvenile fish to rising CO_2 levels is highly variable. Furthermore, there may be trans-generational effects. Thus reduced growth and survival of juvenile anemone fish *Amphiprion melanopus* reared at high CO_2 levels was reversed when the parents experienced the same CO_2 conditions as the juveniles[92]. It may therefore be premature to conclude that near-future CO_2 levels will have significant negative effects on the growth, development or survival of marine fish until additional studies have included exposure to high CO_2 during both the parental and offspring generations.

Preliminary studies on the effects of chronic exposure to high CO_2 on fish reproduction have not

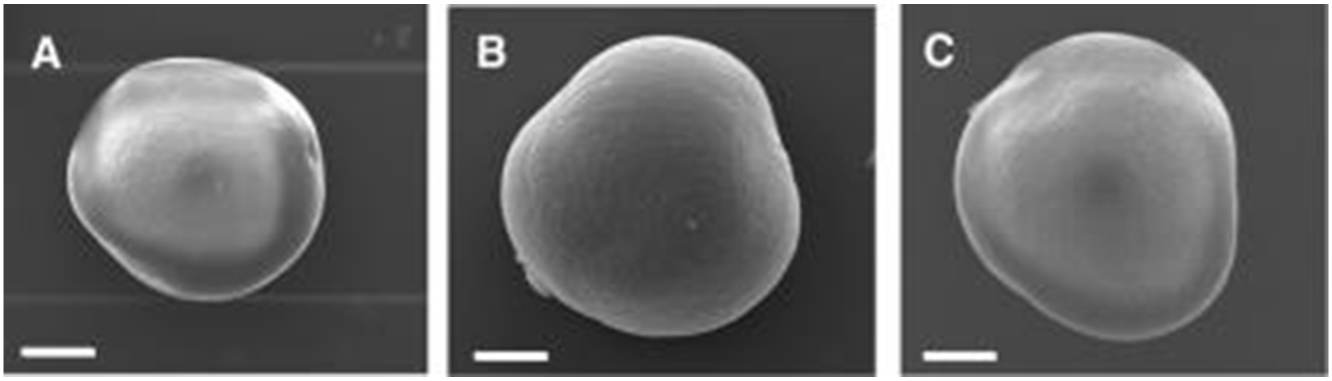

Figure 7.6 Dorsal view of sagittal otoliths of 7-day-old white sea bass *Atractoscion nobilis* grown in seawater at (A) 430, (B) 1000, and (C) 2500 µatm pCO_2. Scale bars indicate 10 µm. From[97]. Reprinted with permission from AAAS.

detected substantial impacts, although long-term consequences in many species remain to be determined[93]. In the short term, reproductive output can be stimulated by high CO_2, for example, in the cinnamon anemonefish *Amphiprion melanopus*[93]. Sperm motility is arrested by mild increases in pCO_2 in some flatfish[94], but not in the cod, *Gadus morhua*[95], or 11 other species from a range of families[94]. 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[96]. 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[78], far in excess of projected end of the century CO_2 levels.

There are two areas in which consistent effects of elevated CO_2 have been detected for marine fish. First, otolith (earbone) size is consistently larger in larval and juvenile fish reared under elevated CO_2. Larger ear bones have been observed in larval seabass *Atractoscion nobilis*[97] (Figure 7.6), clownfish *Amphiprion percula*[98], cobia *Rachycentron canadum*[87] and Atlantic cod *Gadus morhua*[99] reared between 800-1800 µatm CO_2. While the ecological significance of larger otolith size is uncertain, auditory models suggest that larger otoliths could potentially enhance auditory acuity[100]. Second, exposure to elevated CO_2 can cause sensory and behavioural impairment in a range of marine fish[101,102], including effects on vision and retinal function[103, 104, 105] (see section 5.3).

While results indicate that most fish are probably able to maintain sufficient oxygen delivery at CO_2 levels predicted to occur in the near-future, the effect on squid may be more pronounced. Epipelagic squid (e.g., *Ommastrephidae, Gonatidae, Loliginidae*) are considered to be most severely impacted by the interference of CO_2 with oxygen binding at the gills, as they have a very finely tuned blood oxygen transport system to maintain high metabolic rates using the respiratory pigment haemocyanin[106]. Haemocyanin is very sensitive to CO_2 and as such, blood oxygen transport can be easily disturbed to reduce activity[107,108] as demonstrated in the Pacific jumbo squid *Dosidicus giga,* which had significant reduction of metabolic rates and activity levels under 1000 µatm of CO_2[109]. Elevated CO_2 could also affect squid paralarvae, as demonstrated by abnormal shapes of aragonite statoliths in the Atlantic Longfin squid *Doryteuthis pealeii*, which are critical for balance and detecting movement[110].

The cuttlefish *Sepia officinalis*, one of the most common and commercially important cephalopods in Europe, does not appear detrimentally impacted by ocean acidification during development and may even show increased calcium uptake into its cuttlebone[111]. However, when reduced pH is combined with increased temperature, *S. officinalis* does display shorter embryonic periods, lower survival rates and enhanced premature hatching[112].

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8. IMPACTS OF OCEAN ACIDIFICATION ON BIOGEOCHEMICAL CYCLES, ECOSYSTEM SERVICES AND LIVELIHOODS

KEY MESSAGES

1. Rising CO_2 is expected to affect net primary production and other carbon-cycling processes in the ocean
2. The net effect of ocean acidification on carbon storage is uncertain
3. Decreased dimethyl sulphide (DMS) production could lead to exacerbated global warming
4. Ocean acidification has already affected provisioning ecosystem services through impacts on aquaculture
5. Future ocean acidification could also impact regulating, cultural, and supporting services
6. Impacts of unmitigated ocean acidification are estimated to represent a loss to the world economy of more than US $1 trillion annually by 2100

The previous chapters show how a high CO_2 world is likely to affect marine biodiversity at the level of organisms and ecosystems. Here we consider the wider implications of such changes. In particular, how ocean acidification might affect other Earth system process, through ocean biogeochemistry and climatic feedbacks, and human society. Societal implications will occur if ocean acidification causes changes in ecosystem services that depend on the health, abundance or distribution of marine species of direct or indirect economic importance[1]. To date, however, scaling-up the effects of pH change from individual organisms to populations, communities and ecosystems has received less attention[2], although this is changing[3,4].

8.1 OCEAN BIOGEOCHEMISTRY AND CLIMATE

Ocean acidification has the potential to affect major biogeochemical cycles in several ways[5] with feedbacks to the global climate. Such impacts will not occur in isolation, but in conjunction with other global changes (including ocean warming, deoxygenation and potentially increased ultra-violet (UV) radiation), that might significantly modulate future consequences[6].

Positive climatic feedback would enhance future global warming due to increasing greenhouse gases; negative feedback would reduce future warming. Biogeochemical processes that can alter ocean uptake and storage of carbon are of particular interest, although others may also be important. A summary is provided in Table 8.1, with discussion below covering ocean acidification impacts that may alter either biological production in the photic zone (where light penetrates), or the remineralization (breakdown) of sinking particulate organic and inorganic carbon.

Biological production

Rising CO_2 concentrations in the upper ocean and associated ocean acidification have the potential to affect biological production through the following processes:

- Increase net primary productivity and particulate organic carbon (POC) production by making photosynthesis more efficient[7,8]. However, increased vertical stratification of the upper ocean is likely to reduce nutrient supplies to the euphotic zone, which may counteract potential effects of rising pCO_2 on phytoplankton production in the open ocean[9].
- Alter the stoichiometric nitrogen-to-carbon ratio in exported particulate organic matter (POM), as observed in mesocosm experiments[10,11] by around a third (C:N ratio increase from 6.0 at 350 µatm to 8.0 at ~1050 µatm). Assuming sufficient supplies of N and other essential nutrients, this would increase the storage of carbon in the ocean[12].
- Affect dinitrogen (N_2) fixation by cyanobacteria, which could also alter primary production in nitrogen-limited areas. Initial experiments showed that *Trichodesmium* may increase its nitrogen fixation under elevated CO_2[13], however, there were strain-specific differences[14] and other cyanobacteria did not respond similarly[15,16]. Under realistic (low Fe) nutrient levels, low pH may reduce nitrogen fixation by Trichodesmium through effects on iron uptake[17].
- Impede the ability of organisms to calcify[18]. This is anticipated to reduce the production of calcium carbonate.
- Decrease the bioavailability of dissolved iron (Fe) to some phytoplankton species. Acidification of seawater decreases the Fe uptake rate of diatoms and coccolithophores[19].

Table 8.1. Summary of likely main effects of future ocean acidification on global-scale biogeochemical processes and feedbacks to the climate system (primarily by increasing or decreasing atmospheric CO_2) based on Table 12.1 of[5] and the ~70 references cited in that paper. Note that: i) this table focuses on water column effects in the open ocean; ii) all processes except (1) and (5) involve indirect effects, mediated by marine biota (mostly phytoplankton and bacteria); iii) information for processes (7) and (8) is based on[20] and[21]; and iv) information for (9) based on references discussed in text. Level of understanding: H, high; M, medium; L, low.

Process	Effect of future OA	Feedback	Magnitude	Level of under-standing
1. Ocean's ability to buffer atmospheric CO_2 levels	Decreased ocean uptake capacity	+ ve	Large	H
2. Photosynthesis	Enhanced biological production and organic export from upper ocean	– ve	Medium	M
3. C:N ratio of biomass	Increased C:N ratio, affecting food quality and carbon export	– ve	Small to medium	L
4. Calcification	Overall decrease in biocalcification (but not all species/strains?)	– ve	Small to medium	L/M
5. Carbonate dissolution	Increased $CaCO_3$ dissolution in particles and sediments, increasing ocean alkalinity	– ve	Small in short-term; large in long-term	M
6. Ballast effect (sinking particles)	Decreased $CaCO_3$ production will reduce organic matter export	+ ve	Small to medium	L
7. Dimethyl suphide (DMS)	Reduced production	+ ve*	Uncertain	L
8. Organo-halogens	Contradictory evidence: both enhancement and reduction may occur	?	Uncertain	L
9. Nitrogen fixation	Contradictory evidence: both enhancement and reduction may occur	?	Uncertain	L
10. Oxygenation	Shallower remineralization increases O_2 demand; expansion of low O_2 regions	+ ve	Medium	L
11. Nitrification	Reduced	?	Small	L
12. Nitrous oxide production	Decreased O_2 levels will increase N_2O production	+ ve	Medium	L

*feedback via cloud formation

Remineralization (breakdown) of particulate material

Dissolution of $CaCO_3$ is expected, with high certainty, to increase in response to projected declines in saturation state[22]. Currently, most of the exported organic carbon is broken down in the upper 1000 m, but around 10% continues to the deep ocean, where it is broken down in the water column or buried in sediments and sequestered from the atmosphere on millennial timescales[23]. The analysis of particulate inorganic and organic carbon (PIC and POC) fluxes to water depths greater than 1000 m suggests a close association between these fluxes[24]. Particles rich in $CaCO_3$ are likely to act as "ballast" for transporting POC from the near-surface to deeper waters, thereby increasing its sinking speed[25]. It is hypothesized that the association between $CaCO_3$ and POC might protect the latter from bacterial degradation. If deep-water POC fluxes are controlled by $CaCO_3$, then a decrease in $CaCO_3$ production would reduce POC transport to the deep ocean. POC would break down at shallower depths, and the overall efficiency of the biological pump would decrease, resulting in reduced carbon storage in the ocean and seabed, thereby increasing atmospheric CO_2. There is also evidence from different regions that bacterial exo-enzyme activity may increase under elevated CO_2[26,27]. One potential outcome is an increase in the breakdown of organic carbon in surface waters, potentially decreasing the biological pump and carbon storage in the ocean.

Earth system models (ESMs) have been used to explore the potential consequences of ocean acidification (and other projected changes) on the marine biogeochemical processes listed in Table 8.1, and assess which might be significantly altered[28]. These include aragonite and calcite saturation state, export production, and interior dissolved oxygen concentrations. The general consensus of multi-model climate projections is a reduction in primary production and export production with global warming[29,30] although there are important regional differences between model projections. Where ocean acidification impacts could be significant is on the POC and PIC export from the upper ocean[28,31]. This would affect the flow of energy through ecosystems and could have significant impacts on marine ecosystem productivity and biodiversity.

Large changes in PIC and POC export could also significantly alter oxygen levels of the ocean interior. Oceanic oxygen levels are expected to decline under global warming[32,33], and recent ESMs project a small decrease in the total ocean inventory of dissolved oxygen (2% - 4%) by the end of 2100[29]. However, the projections vary regionally, and the total volume of hypoxic and suboxic waters remains relatively unchanged by the end of 2100. The decline in oxygen with rising CO_2 could also have important consequences for marine organisms with high metabolic rates. Global warming, lower oxygen and higher CO_2 levels thus represent physiological stresses for marine aerobic organisms that may act synergistically with ocean acidification[34].

Effects of ocean acidification on climatic feedbacks

While CO_2 is the most important greenhouse gas modulated by the ocean, the air-sea exchanges of other greenhouses gases may also be altered by ocean acidification. These include methane (CH_4) and nitrous oxide (N_2O), as their production in the ocean is linked to the breakdown of organic matter in low oxygen water[35,36]. Declining oxygen levels should be associated with increased production of both these gases[37,38], but it is expected that the impact of increased production of CH_4 and N_2O would be less than the projected impacts of increased CO_2[28]. However, increased warming could also potentially destabilise methane hydrates stored in sediments along continental margins, leading to additional release of CH_4[39].

The potential effects of increasing anthropogenic CO_2 on trace gas production in the oceans are poorly understood. These trace gases include climatically important gases, such as dimethyl sulphide (DMS), which can alter cloud properties. DMS is a gaseous sulphur compound produced by marine biota in surface seawater[40] and provides 90% of the biogenic sulphur in the marine atmosphere[41]. Modelling studies vary substantially in their predictions of the change in DMS emissions with climate change; studies for polar waters suggest increases in DMS emission ranging from 30% to more than 150% by

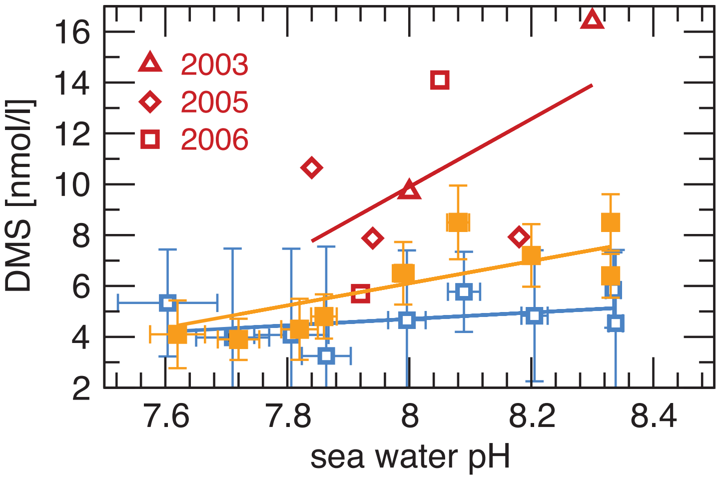


Figure 8.1. Relationship between dimethyl sulphide (DMS) concentration and pH based on data from mesocosm experiments. Measurements of DMS and seawater pH are averaged from the mid-phase of Svalbard experiments (orange) and over the entire experiment (blue). Red denotes measurements from Norwegian mesocosm experiments from three different years. From[21]. Reprinted by permission from Macmillan Publishers Ltd: *Nature Climate Change* 3: 975-978, © 2013

2100[42-44], whilst elevated CO_2 predictions in isolation of other environmental change suggest a significant decrease in future concentration of DMS[20, 21] (Figure 8.1). When combined in Earth system models to simulate future climate change, decreased DMS production of this magnitude could exacerbate global warming[21]. However, DMS production responses measured to date are variable, and the sensitivity of the climate system to such changes is uncertain, and may be low[45]. Thus full understanding of the combined global warming and ocean acidification impact on marine DMS and other trace gas production needs further study to determine its importance.

8.2 ECOSYSTEM SERVICES

To examine the societal implications of ocean acidification, an ecosystem services framework can be used. Ecosystem services are the components of nature that (actively or passively) help create human well-being and economic wealth[46]. They result from ecological processes, functions and biodiversity[47], and society is dependent upon them as a life support system as well as for enhancing its well-being[48]. At a general level, ecosystem services can be categorised into four distinct groups[49]: **provisioning services** (e.g., food and fibres); **regulating services** (e.g., gas and climate regulation, bioremediation of waste); **cultural services** (e.g., education, recreation and inspiration); and **supporting services** (e.g., nutrient cycling, primary production and ecosystem resilience) (Figure 8.2).

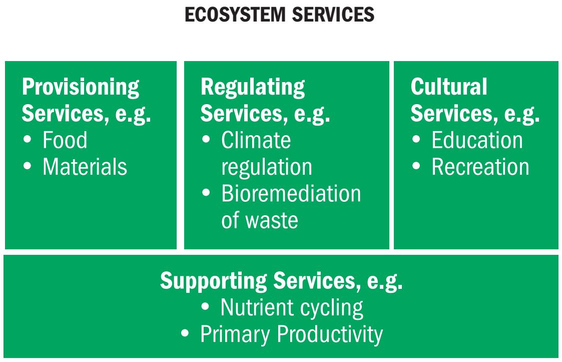


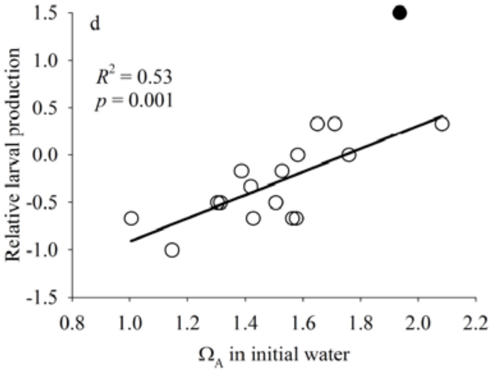
Figure 8.2 Simplified summary of ecosystem services with selected examples given

Supporting services. These comprise the processes and functions that contribute to all other ecosystem services. Any changes in these will have consequences through provisioning, regulating and cultural services. For example, many species that are likely to be negatively impacted by pH changes (e.g., calcifiers) are habitat-forming organisms providing shelter, food and nursery functions to other marine species, including commercially important fish. They also contribute to coastal protection, leisure, recreation and other cultural benefits. Nutrient cycling e.g., changes in N-fixation[50,51], or changes in bioturbator and bio-irrigator communities, will also change fundamental processes within ecosystems[2].

Provisioning services. Ocean acidification can be expected to affect provisioning services; however, direct evidence is limited. Molluscs and crustaceans harvested for food are likely to be affected as they have calcareous shells and exoskeletons, with their sensitivity demonstrated in experimental studies. Field-based evidence of the impact of ocean acidification on molluscs has been reported at sites along the Pacific coast of the United States of America, where the failure of oyster reproduction in hatcheries has been attributed to high levels of CO_2 in the water that upwells in that region[52,53] (Box 8.1). Impacts such as these may have different implications depending upon their location. For example, small island developing states that are reliant upon shellfish aquaculture for export and for protein intake could be particularly vulnerable[54], and for both shellfish and finfish, less developed nations that rely heavily on artisanal fleets will be more exposed to the direct socio-economic consequences of ocean acidification[55].

Box 8.1 Impact of ocean acidification on oyster hatcheries

Due to the naturally low and variable pH of upwelled water off the north-west coast of the United States of America, there is strong evidence that additional acidification due to anthropogenic CO_2 is already having biological impacts in that region – where carbonate saturation values are now at levels projected for elsewhere 50-100 years in the future. Thus established oyster hatcheries in Oregon and Washington have increasingly suffered high larval mortalities (up to 80%) since 2006, threatening the viability of an industry with total economic value of around $280 million per year[56]. The variable carbonate chemistry and pH of the hatchery water (due to periodic upwelling events) have been shown to be major factors affecting the success of larval production and mid-stage growth cohorts of the Pacific oyster *Crassostrea gigas*[53]. The oyster hatcheries have now adapted their working practices so that they avoid using very low pH seawater, either by re-circulating their seawater or treating their water during upwelling events. With these new practices, the north-west coast oyster hatcheries are producing near to full capacity again.



Relationship between aragonite saturation state (Ωaragonite) in incoming seawater and relative larval production at the Whiskey Creek oyster hatchery, Oregon, United States of America. Negative production values indicate reduction in total biomass, due to mortality exceeding growth. Data point given as black filled circle was considered to be a statistical outlier, and was not used in the regression analysis. From[53]. Copyright 2014 by the Association for the Sciences of Limnology and Oceanography, Inc

Nevertheless, some commercially important species may be able to adapt, or may be naturally resilient; for example, the mussel *Mytilus edulis* is reportedly thriving in the naturally CO_2-enriched waters of Kiel Fjord[57]. Some other species may be indirectly impacted by ocean acidification through changes in their food chain and habitat. Examples include finfish that feed on benthic or pelagic calcifying organisms (e.g., haddock feeding on echinoderms, or salmon feeding on pteropods)[58]. It is also important to consider the national impacts of altered provisioning services.

Regulating services. These include coastal defense and carbon storage. Many marine habitats and ecosystems (e.g., tropical coral reefs, mangroves, seagrass meadows and bivalve beds) significantly dissipate the energy in waves reaching the coast, increasing sedimentation rates and decreasing coastal erosion[59,60]. Changes in these natural communities resulting from ocean acidification would therefore affect their ability to protect the coast. While potential impacts of ocean acidification on corals and bivalves may be negative, this may not be true for seagrasses, which may benefit from higher levels of CO_2[61] in the water and may therefore afford greater protection of the coast.

Cultural services. The impact of ocean acidification on cultural ecosystem services is particularly difficult to assess. While impacts to tourism, leisure and recreation can be partially quantified, e.g., through potential degradation of reefs attracting fewer tourists due to dead coral and through decreased ancillary biodiversity, many cultural services, such as spiritual enrichment and aesthetic appreciation, are intangible in nature, and the role of biodiversity in these services is unclear. Nevertheless, where marine species and ecosystems are given high inherent worth (conservation value in developed countries) or are important to indigenous peoples' heritage and identity, their reduction in abundance may result in significant cultural loss. Understanding the potential impacts of ocean acidification on tourism, leisure and recreation is also challenging, and more research is required to quantify the scale of such effects.

8.3 ECONOMIC AND LIVELIHOOD IMPACTS

A quantitative assessment of the interactions of ocean acidification with socio-economics and human welfare requires that the full impact pathway is understood and modeled. This requires the coupling or integration of models that explain each step in the pathway linking: i) socio-economic activities responsible for CO_2 emissions, and resultant changes in water chemistry; ii) impacts on marine ecosystems; iii) changes in the provision of ecosystem services; and, finally, iv) impacts on human welfare.

The existing economic literature on ocean acidification has only assessed a partial set of the potentially impacted ecosystem services, with a focus on the direct-use values that are most easily addressed. Of the 13 studies reviewed here (Table 8.2), only five provide monetary estimates of the costs of ocean acidification. Three of these are for impacts on mollusc fisheries (two for the United States of America and one global estimate); one covers impacts on fisheries and carbon storage; and one is for impacts on coral reef services. Central estimates from each study are presented in Table 8.2 and standardized to annual values in the terminal year of each analysis in US $ at 2010 price levels. From the information currently available, impacts to tropical coral reef services dominate; these are examined in more detail below.

The economic impacts of ocean acidification on the fisheries industry are relatively understudied. However, models suggest that there may be a substantial reduction in fisheries catch potential under future conditions[62], affecting the quantity, quality and predictability of future harvests[63]. It is also important to consider projected impacts upon different societal components, i.e., indigenous and local communities as well as global markets. Coastal indigenous and local peoples catch large quantities of marine species, which may be consumed, or traded with inland groups in exchange for other foods or goods. This may also differ regionally, and it could be that coastal communities in the Arctic are likely to be affected disproportionally by ocean acidification due to the rapid environmental changes towards higher latitudes. Further research is thus needed to understand likely impacts in multiple coastal communities.

The only study to provide values of the global economic impact of ocean acidification on tropical coral reefs estimates the potential annual value of lost ecosystem services to be up to ~US $1000 billion by 2100[64]. The value varies across scenarios due to i) differing projected rates of CO_2 emissions, ocean acidification and loss of coral cover; and ii) differing rates of population and income growth that determine the value of coral reef services per unit area of coral cover. The results show that the annual economic impact (loss of coral reef service value) escalates rapidly over time, essentially because the scenarios have high economic growth in countries with coral reefs, and because demand for coral reef services increases more than proportionately with income. Nonetheless, the annual value of foregone ecosystem services from coral reefs in 2100 is still only estimated to be a small fraction of total global income (0.14% or US $870 billion in 2100; 2000 price levels; Special Report on Emissions Scenario A1B based on rapid and integrated world economic growth).

The estimated impacts are, however, considered to be partial since the underlying value data is largely focused on recreational values and includes limited information on the value of other services such as coastal protection or non-use values for biodiversity. Results of a sensitivity analysis show that the estimated impact is highly uncertain, with a confidence interval spanning one order of magnitude. It is important to note that other threats to the health of coral reefs and the provision of reef services are not included (e.g., over-fishing, sedimentation, eutrophication, sea level and temperature rise)[75].

Table 8.2. Summary of studies that examine the economic impacts of ocean acidification. From[64]

Study	Impacts	Geographic scope	Emissions scenario	Period of analysis	Welfare measure*	Annual value (US $; billions)**
Armstrong et al.(2012)[65]	Fisheries Carbon storage	Norway Norway	0.5 pH decrease 0.5 pH decrease	2010 – 2110 2010 – 2110	Revenue Damage Cost	0.01 3
Brander et al. (2012)[66]	Coral reefs	Global	SRES A1B	2000 - 2100	Mixed	1,093
Cheung et al. (2011)[62]	Fish and invertebrates	N-E Atlantic	SRES A1B	2005 - 2050	-	-
Cooley & Doney (2009)[67]	Molluscs	United States	IPCC A1F1	2007 - 2060	Revenue	0.07
Cooley et al. (2012)[54]	Molluscs	Global	CCSM3	2010 - 2060	-	-
Finnoff (2010)[68]	Fisheries; non-use values	Bering Sea	-	-	-	-
Harrould-Kolieb et al. (2009)[69]	Coral reefs; fisheries	Global	SRES A1B	2009 - 2050	-	-
Hilmi et al. (2012)[70]	All	Global	-	-	-	-
Kite-Powell (2009)[71]	Coral reefs; fisheries	Global	IS92a	-	-	-
Moore (2011)[72]	Molluscs	United States	RCP8.5; RCP6	2010 - 2100	CV	0.31
Narita et al. (2012)[73]	Molluscs	Global	IS92a	2000 - 2100	CS, PS	139
Rodrigues et al. (2013)[74]	Use and non-use values	Mediterranean	-	-	-	-
Sumaila et al. (2011)[63]	Capture fisheries	Global	-	-	-	-

* CV: compensating variation; CS: consumer surplus; PS: producer surplus

** Impact estimates are standardised to annual values for the terminal year in each analysis (i.e., 2060 for Cooley and Doney[67] and 2100 otherwise) in US $2010 price level

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9. FUTURE CONSIDERATIONS

KEY MESSAGES

1. A true multidisciplinary approach involving technological advances is needed
2. Research should be oriented toward a quantitative understanding at all levels from chemistry to socio-economics
3. Research should be solution–oriented, covering the scale from local to global, and should prioritize the ecosystems and societies most at risk
4. A high density of measurements in space and time is required to identify variability and anthropogenic ocean acidification
5. Autonomous systems will remove the need for operators and encourage the development of low-cost, low-power, long-term measurement techniques

9.1 TECHNICAL CHALLENGES: FROM INDIVIDUALS TO ECOSYSTEMS

A large body of scientific information about ocean acidification has rapidly been generated during the past few years, contributing to increased political and wider societal awareness. The field evolved from an exploratory phase leading to several key proof-of-concepts, toward more hypothesis-driven research[1,2]. Key factors modulating responses of species, ecosystems and their services have been identified and include environmental variability[3], ecological interactions[4], species potential for acclimation and adaptation[5] and multiple drivers. Ideally, an experiment assessing the impact of ocean acidification on a given species, community or ecosystem should include realistic changes for all environmental drivers (CO_2, temperature, salinity, food concentrations, light availability), and be long term (i.e., several years) to allow for natural variability[6] and multiple generations of each species under consideration. Multiple end-points from physiological response to biodiversity and socio-economic impacts should also be considered (Table 9.1). Such experiments should be replicated several times in different areas to account for spatio-temporal variability. However, it is obvious that such an approach is usually unrealistic, and it is impossible to test all species and ecosystems in the world using such an experimental design. To address this, future ocean acidification research should develop and implement new technology and experimental designs, and elucidate a greater mechanistic understanding at all levels from chemistry to socio-economics.

Single experimental approaches on single organisms often do not capture the true level of complexity of *in situ* marine environments, and multi-disciplinary approaches involving technological advancements and development are critically needed. This includes combining natural variability and monitoring with organismal biology[7]. Below are some examples at differing complexity levels of what we know to date, and of some challenges and focuses for future research. These are summarized in Table 9.1.

Ocean acidification at the individual level. Research to date has highlighted individual species variability in response to ocean acidification[8], due in part to differing organismal capacity to tolerate ocean acidification. The capacity for acid-base regulation is an important example, and species that show developed

Table 9.1. Some key research gaps and challenges for future ocean acidification research

Ocean acidification process	Research question(s)
Biogeochemical	Will future OA provide significant feedback to the global carbon cycle and climate change, through global-scale changes in calcification, ocean productivity, particle sinking in the ocean, and effects on other climatically active gases, e.g., DMS and N_2O? Will the ocean become a less important CO_2 sink in the future, exacerbating atmospheric changes?
Physico-chemical	What is the current variability of ocean carbonate chemistry at ecologically significant temporal and spatial scales, and how will this change under future climate change scenarios, with associated additional changes in temperature, oxygen, stratification, ocean circulation, and river inputs? Which areas of the ocean (e.g., polar regions, upwelling zones, and shelf seas) will experience greatest and most rapid change? Will chemical changes also impact sound transmission in future oceans, with impacts on organism communication[41]?
Physiological and behavioural	What are the unifying mechanisms linking species' molecular, metabolic and behavioural responses to ocean acidification? (e.g., based on energy metabolism and acid-base regulation). Does this explain the high taxonomic variability observed in response to ocean acidification and complex interactions with other stressors (e.g., temperature, low oxygen and food/nutrient availability, ultraviolet radiation)? How would different scenarios of ocean acidification affect the immune system resilience of various species to pathogens?
Genetic	How can information from relatively short-term studies (weeks to months) on individual species be applied to long-term (decadal), multi-generational responses by populations, involving adaptation and evolution? Does genetic variation confer population resilience? How will this impact marine biodiversity?
Ecological	How can experimental studies on ocean acidification impacts be best scaled-up to the ecosystem level where interacting multi-species communities are subject to other environmental changes, i.e., allowing for multi-stressor effects, and recognising that negative (or positive) impacts of ocean acidification on one species may indirectly benefit (or disadvantage) another and thus community composition and biodiversity? How will impacts on one species impact upon others (trophic interactions), and how will this affect food security through the food chain?
Socio-economic	What future socio-economic impacts will arise from ocean acidification? How can we best quantify the risks to non-market ecosystem services (e.g., storm protection provided by tropical coral reefs) as well as to aquaculture and fisheries? Can adaptation strategies be identified for the most vulnerable people and industries? How are various types of communities (from indigenous and local communities to global markets) differentially vulnerable to the impacts of ocean acidification? How can ocean acidification science best contribute to risk management, the sustainable use of natural resources and national/international policy development?

capacity are in general expected to be more resilient to ocean acidification[9,10]. Other studies have demonstrated that tolerance to ocean acidification can even differ between closely related species, or even within species, as shown in coccolithophores[11]. Variability within species may indicate the potential for organisms to adapt to ocean acidification, and indeed adaptation has been documented in metazoan species near natural CO_2 vents[12]. Physiological plasticity of organisms and the potential to adapt to changing conditions thus remains an important area for future research[5], supported by observed long-term acclimatization and adaptation in fast-growing microalgae in response to ocean acidification[13].

However, it is not feasible to measure this adaptation potential in all species due to differing life history requirements and limitations within laboratory experiments. A key focus for future work may therefore be for taxa and systems involved in ecosystem services, such as coccolithophores[5].

Organism response to ocean acidification may be different for the short term relative to the long term, or may even differ seasonally as found in one of the longest experiments to date (542 days)[3]. Long-term effects of ocean acidification may therefore be buffered or exacerbated at different times of year. Thus while experiments can give us a crucial insight into how organisms respond to ocean acidification, much more may be unaccounted for. Other factors that may lead to variability and hence uncertainty are projected values for temperature, light, salinity and nutrients, and even methodological differences[8]. Light availability is particularly relevant to photosynthetic calcifiers such as tropical coral species, and food availability has been demonstrated to be important in organism response to ocean acidification[14], as well-fed organisms might have more energy to compensate for regulatory changes. Ocean acidification may alter the behaviour of (and organism response to) sediment-bound metals by altering their bioavailability, as demonstrated by DNA damage and acute toxity in amphipods[15]. This could affect both population and community levels.

Ocean acidification at the population level. To assess the potential impacts of ocean acidification at the population level, it is critical to evaluate different life cycle stages of organisms, such as fertilization, dispersal larval stages and recruitment. Various studies have demonstrated that early life stages may be (but are not always) particularly vulnerable to ocean acidification. Taking into account that many marine invertebrates show high mortality rates during planktonic larval stages, detrimental impact at these stages can mean critical differences to the population level. The impact of ocean acidification on gametogenesis is a knowledge gap to be addressed across more species and different timescales. Future work capable of determining the effect of ocean acidification on several life phases, and of subsequent generations of the same species combined with population dynamic models, is therefore required. Building on research at different life stages, evolutionary adaptation could be assessed at population levels by correlating ecology, physiology and taxonomy with evolutionary capacity, using known population sizes and recombination rates[5].

Ocean acidification at the community level. The impact of ocean acidification on species interactions remains relatively unstudied, but is a key area to focus on if whole ecological communities are to be considered[16]. These interactions include changing food quality and how this constrains trophic transfer[17,18], predator-prey relationships[19-21] and feeding rates[22,23]; how the presence of one species (e.g., coralline algae) may directly impact upon the recruitment or success of another (coral juveniles) [24-26]; resource competition[27,28]; and how all the above will have "knock on" effects through competitive interactions[29] and food webs. However, quantifying species interactions will be complicated, as interactions will also be affected by conditioning time, biotic interactions, and initial community compositions[30]. Embedded within this is the need to understand the adaptation potential of different species, and taxa sensitivity to ocean acidification[31]. A number of major experiments have been conducted on pelagic communities over several weeks using mesocosm approaches[32], but there are few such experiments for benthic systems. While mesocosm experiments are an extremely valuable tool for assessing community responses to manipulated variables, there remain scale-dependent challenges in extrapolating results to ecosystems[33].

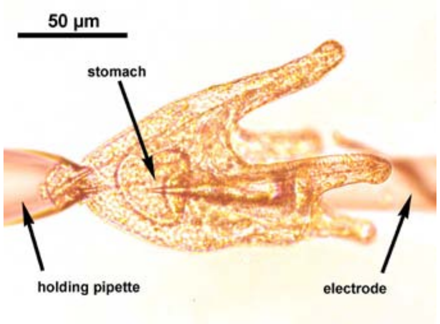
Ocean acidification at the ecosystem level. Natural volcanic CO_2 vents have provided new insights on the effects of ocean acidification at the ecosystem level and are a good opportunity to document species-species and species-environment interactions under low pH conditions. These species-environment interactions are very important to consider, as simple impacts upon key species may have cascading effects through the ecosystem[10]. For example, ocean acidification can modify the relationship between the burrowing shrimp *Upogebia deltaura* and ammonia-oxidising microorganisms inhabiting their burrows, potentially negating positive impacts of shrimp bioturbation[4]. This could impact benthic-pelagic nitrogen cycling, which is fundamental to the food web and the ecosystem dynamics as a whole[4,16]. While these natural systems are extremely useful in the present, further examination of the past (see Chapter 4), can also increase our understanding of how calcifying communities and ecosystems changed under similar past events.

9.2 THEORETICAL CHALLENGES AND FUTURE PRIORITIES

Whatever technological advances are made, it will still be impossible to assess the effect of ocean acidification on all species, all ecosystems and all services in all parts of the world. Thus information from specific studies will still need to be generalised. But there is currently another fundamental limitation: the lack of theoretical background regarding the overarching principles of ocean acidification effects, applicable

Box 9.1 Examples of approaches and technical challenges

Laboratory-based perturbation experiments: Understanding of mechanisms in action is needed to improve our predictive power. This will be possible through a better understanding of the biological responses at molecular and physiological levels. This is often associated with technological challenges. For example, new *in vivo* techniques have been developed to measure extra- and intra-cellular acid-base regulation and digestion in sea urchin larvae[34,35].

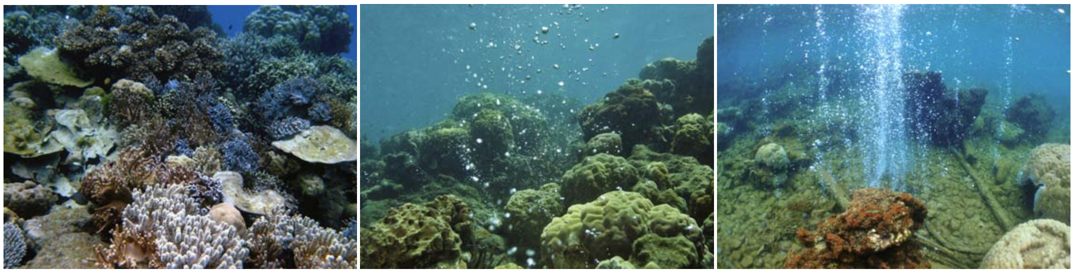


In vivo measurements of larval stomach pH using ion-selective micro-electrodes. Adapted from[34]. Reprinted by permission from Macmillan Publishers Ltd: *Nature Climate Change 3*: 1044-1049, © 2013

Field-based perturbation experiments: Free Ocean CO_2 Enrichment (FOCE) systems have been developed in order to study the effects of ocean acidification on benthic communities by controlling, for several months, the pH to which a natural community is exposed. While the original system was designed for a deployment in the deep-sea, worldwide projects are presently adapting the system to study shallow water areas in temperate and polar environments[36]. The usefulness of this approach was recently demonstrated in a tropical coral reef setting.

The coral proto – free ocean carbon enrichment system (CP–FOCE) deployed on Heron Island, Great Barrier Reef, Australia. Source: David Kline, Scripps.

Natural CO_2 vents case studies: From studying ecosystems near natural CO_2 vents it is clear that acidification can cause fundamental changes at the ecosystem level: calcifying communities may shift to algal-dominant ecosystems[37], or undergo a change in species dominance such as in Papua New Guinea[38], or shift community type[39]. A consistent feature of these studies is that species diversity decreases near CO_2 vents. Importantly, natural CO_2 vent ecosystems include non-calcifying organisms, which can strongly contribute to species competition and ecosystem function[40].



Left to right: healthy coral reef at Papua New Guinea control site, pH 8.1, unaffected by CO_2 seep; seascape showing moderate seeps, pH 7.8-8.0; and barren seascape showing intense venting of CO_2 and a pH of <7.7, when all coral growth stops. Images courtesy of Katharina Fabricius.

across many domains. Conceptual, analytical, and computational models are invaluable to explain pattern in nature. The theoretical frameworks and unifying principles that explain many other topics and themes in ocean science (e.g., in chemistry, physiology, ecology, evolution, and socio-economics) need to be much better developed for ocean acidification, to assist with prediction and anticipation of its effects, from global to local scales.

Ocean acidification is already underway, and it is now inevitable that it will, in combination with other stressors, have significant effects on marine ecosystems and their services to humankind. Ultimately, only the reduction of atmospheric CO_2 levels provides the "solution" to ocean acidification; nevertheless, there may be ways in which ocean acidification research can become more "solution-oriented" – rather than only "documenting the disaster". To prioritize research efficiently, sensitivity should be assessed at all levels: i) chemistry (e.g., regions experiencing the greatest and fastest changes, such as polar regions, upwelling zones, and shelf seas); ii) biology (e.g., sensitive species or ecosystem, biodiversity at risk, etc.), and iii) socio-economics (e.g., less-developed countries or high dependence on ocean). By improving our understanding of the impacts of ocean acidification, we will be able to identify the organisms and ecosystems most at risk that deserve the most urgent attention.

Experiments investigating how biota will respond to ocean acidification have, until recently, largely focused only on the manipulation of the carbonate system. However, marine organisms and ecosystems are increasingly stressed by other changes in their physical, chemical and biological environments. For global variables, there has been considerable progress in model projections in the past two years, in conjunction with the preparation of the 5th Assessment Report of the Intergovernmental Panel on Climate Change (AR5). Recent simulations performed in the framework of the Coupled Model Intercomparison Project 5 have assessed how several drivers will evolve during the 21st century[42]. For the "business-as-usual" scenario, the model-mean changes in 2090s (compared to 1990s) for sea surface temperature, sea surface pH and global O_2 content amount to +2.7°C, ~-0.33 pH unit, and -3.5%, respectively. For the "high mitigation efforts now" scenario, corresponding changes are +0.7°C, -0.07 pH unit and -1.8%.

Ocean acidification can interact with other variables synergistically (amplified stress), additively (no additional stress), or antagonistically (reduced stress)[43]. In 2012, only around a third of the 225 papers that reported on the biological response to ocean acidification also manipulated at least one other environmental property. This is a large increase compared to previous years but knowledge of the impacts of multiple drivers is still insufficient to provide reliable projections of biodiversity and ecosystem function. The challenges associated with conducting more complex manipulation experiments that include combined temperature, O_2 stressors, and ultraviolet radiation in conjunction with ocean acidification are technological, but also include experimental design (e.g., replication vs. regression approach, pseudo-replication, number of treatments for each driver). However, even then, controlled experiments may not capture the full complexity of ecosystems. To fully address the need for multiple-driver approaches, comparative ecosystem analyses that combine both experimental observations and models are needed[44].

9.3 ADVANCES IN SENSING, MONITORING AND EMERGING TECHNOLOGIES

Measuring pH and the other variables of the marine carbonate system has traditionally been challenging due to inconsistent pH scales and measurement routines, as well as non-standardized instrumentation that required skilled technical expertise and experience. Consequently, inter-comparison exercises between laboratories revealed large discrepancies[45]. Over the last 30 years, great strides have been taken in standardizing our understanding of what exactly the marine carbonate system is, how to measure it and how to report the results, the availability of very high quality reference material, and the standardization of the pH scale for the reporting of ocean acidification – the total hydrogen ion scale[46].

The majority of established long-term ocean acidification time series have used standard, shipboard and laboratory instrumentation for measurements of the four marine carbonate system variables: pH, total alkalinity, total inorganic carbon and the partial pressure (or fugacity) of carbon dioxide in seawater[47]. Using any two of these variables enables the calculation of the other two, plus the speciation of the marine carbonate system, calcium carbonate saturation states, buffer capacity and the major contributions to the total alkalinity.

As indicated in Chapter 3, a high density of measurements in both time and space are required if the fine details of local, regional and global ocean acidification are to be routinely identified. New approaches include the adaption of existing techniques, such as ion selective field effect transistors (ISFETs)[48] and the development of approaches to enable remote measurements, thus removing the need for an operator. These include measurements from autonomous systems, voluntary observing ships (or ship of opportunity[49]), buoys, profiling floats[50], and wave-riders[51] and landers[52] (Figure 9.1). Adapting these methods have led to the development of novel combinations[53] and lower-cost, low-power, long-term measurement techniques[54] that are approaching, and sometimes excelling, the accuracy of traditional methods. By incorporating new approaches into the expanding range of monitoring platforms, through initiatives such as the Global Ocean Acidification Observing Network (GOA-ON, see chapters 2 and 3), the current knowledge of natural variability across space and time will be improved. Experimental studies can then be better placed into context (natural variability versus projected changes), and projections of future conditions will become more accurate and reliable.

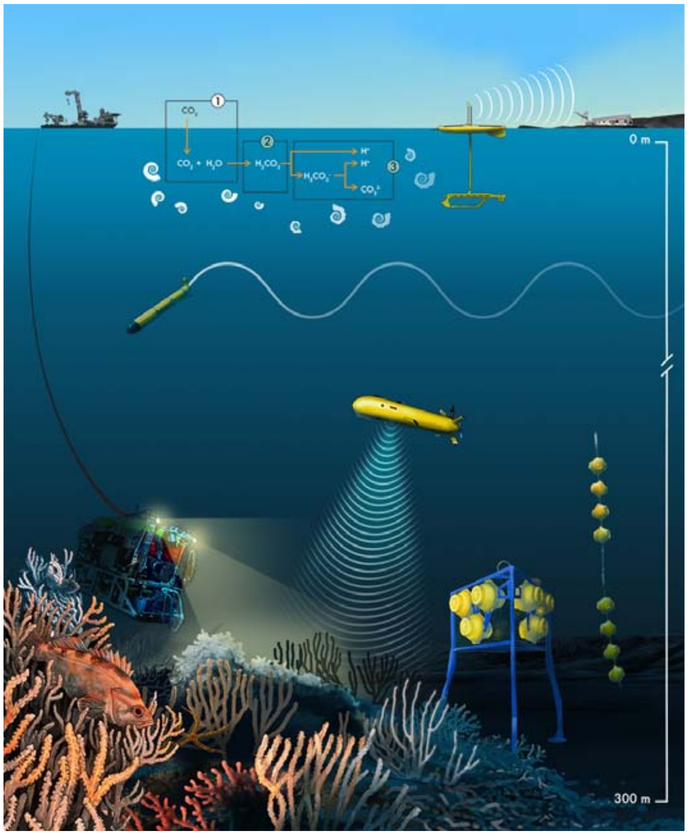


Figure 9.1. A cartoon of various platforms for environmental sensors. These include autonomous and remotely controlled underwater vehicles, wave gliders, moorings and benthic landers. Data from these sensors can be used to record physical properties of ecosystems. Source: Heriot-Watt University.

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10. 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"[1]. 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.

At the Paleo-Eocene Thermal Maximum (56 million years ago), believed to be the closest historical analogue to present-day ocean acidification, geological records indicate that several deep-sea organisms became extinct. The speed at which ocean acidification is currently happening precludes the option of habitat shifts for many benthic species, and may exceed their ability to adapt.

At current rates, aragonite saturation horizons, below which aragonite dissolution occurs, are projected to rise from a few thousand metres to just a few hundred metres, or to the surface, in many ocean regions by the end of the century[2]. If CO_2 emissions continue on a "business as usual scenario," it is projected that by the end of the century global mean surface pH will further decrease by ~0.33 units (with H^+ concentrations more than doubling), and sea surface temperature will increase by 2.7°C[3], although with considerable regional variability.

Our understanding of ocean acidification and its consequences has increased tremendously in the past 10 years[4], and research to date, from both laboratory and *in situ* work, has highlighted that organism responses to ocean acidification can be very mixed, even between similar species[5]. This variability reflects that some species may be better adapted for projected future conditions than others; it also highlights that experiment conditions (particularly duration) are important in assessing future long-term responses.

Some general trends are emerging. Ocean acidification will have a negative effect on calcification or growth at different life cycle stages in many key organisms, such as commercial shellfish and corals[6-10], although adequate food supplies may ameliorate some negative responses[11,12]. Most fish are probably able to maintain sufficient oxygen delivery under predicted future CO_2 levels[13], but increased CO_2 can have significant impacts upon fish behaviour[14].

Sensitivity to ocean acidification varies at different life stages, so understanding how negative impacts can "carry-over"[15] from larval to adult stages remains a significant challenge. Ocean acidification is generally detrimental to calcifying larvae[16-18]; non-calcifying larvae are more resilient[19-21]. The impacts of ocean acidification on fertilization success are highly variable highlighting the potential for selection and genetic adaptation, and supporting the concept of "winners and losers" in the face of changing ocean conditions[22,23].

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[24].

When considering how ocean acidification will affect human society, the response of tropical coral ecosystems is understandably of great concern – since over 400 million people worldwide live within 100 km of coral reefs, with very many reliant on them for their livelihoods and food security[25,26]. The fact that over 95% of the world's calcifying corals currently occur above the saturation horizon[27], and that coral growth is much reduced near natural CO_2 vents[28], indicates that in the long-term, it is unlikely to be energetically feasible for corals to grow and thrive below the saturation horizon. Any reduction in coral growth (tropical or cold-water) in the future will have repercussions for the communities that directly or indirectly rely upon them.

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[29,30]. 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.

It is important to note that the response to ocean acidification in coastal regions will be influenced by more variable conditions than in the open ocean[31]. Such varying conditions (caused by diel community metabolism, local phytoplankton blooms and watershed processes) could complicate the predictions we can currently make, e.g., by forcing (relatively) rapid selection of tolerant genotypes.

Looking to the immediate future, it is vital to increase our understanding of how multiple stressors may affect marine biodiversity and ecosystems[32], as ocean acidification will be accompanied by, *inter alia*, changes in oxygen saturation, temperature[3], and ultraviolet radiation in surface waters[33]. Our current knowledge of the impacts of multiple drivers is still insufficient to provide reliable projections of biodiversity and ecosystem function; this should be a priority for future work. Increased monitoring capacity is also crucial to understand the current variability in ecosystems and the rate of change they are experiencing. This should include advances in autonomous underwater vehicle (AUV) sensing technology to monitor key benthic and polar ecosystems currently near to aragonite and calcite saturation horizons.

The incorporation of ocean acidification into governmental planning, environmental conservation and sustainable living has started to accompany growing awareness of the problem[34-36]. This is a very positive step that has been accompanied by several international research consortia involved in addressing key questions to inform policy-making decisions. However, even if CO_2 emissions are significantly curtailed now, anthropogenic ocean acidification will still last tens of thousands of years. Significant ocean ecosystem changes, and the need to learn to live with those changes, therefore seem certain.

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ANNEX

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