An updated synthesis of the impacts of ocean acidification on marine biodiversity

Acknowledgements

[To be provided later]

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Executive summary

1. **Ocean acidification has increased by ~ 30% since pre-industrial times**
   Since pre-industrial times it is estimated that the oceans have absorbed at least a quarter of the carbon dioxide released by human activity. It now seems inevitable that within 50-100 years, anthropogenic carbon dioxide will increase ocean acidity such that by the end of the 21st century, seawater acidity is predicted to reach levels that may reduce the growth rates of marine calcifying organisms, or even cause their shells and skeletons to dissolve. This is because carbon dioxide dissolution directly alters the carbonate chemistry of seawater and reduces the availability of ions needed to form shells and skeletons.

Current awareness

2. **International awareness of ocean acidification and its potential consequences is increasing.**
   Many international research consortia are now investigating potential impacts of ocean acidification upon marine biodiversity and global human welfare. Among the marine calcifying organisms believed to be under most threat are commercial shellfish fisheries, calcifying algae that are important in biogeochemical cycling, and coral reefs both in the tropics and cold-water. It is estimated that the livelihoods of over 400 million people depend upon tropical coral reefs. Understanding how changing ocean chemistry will impact upon these key ecosystems is therefore of great importance.

Global status and future trends of ocean acidification

3. **Substantial natural seasonal and diurnal variability exists in seawater pH**
   This variability varies greatly between habitats, with coastal habitats experiencing greater variability than open oceans due to biological processes within relatively small areas.

4. **High latitude oceans will feel the effects of ocean acidification sooner than temperate or tropical regions**
   Regions at high latitudes are expected to be undersaturated with respect to aragonite (one form of calcium carbonate used by many calcifiers in their skeletons and shells) by the end of the century

5. **Ocean acidification monitoring networks are growing**
   This is crucial to understand current variability and to monitor ocean acidification rates at key sites across the globe. Emerging technologies and sensor development increase the efficiency of this evolving network.

What the past can tell us: palaeo-oceanographic research

6. **During ocean acidification which occurred ~56 million years ago over a period of 6000 years, a significant number of deep-sea calcifying organisms became extinct**
   By looking at ocean acidification events in geological history, we can increase our understanding of our present situation and what the future may hold. Some past events, such as the Palaeo-Eocene Thermal Maximum ~56 million year ago were similar in magnitude to predicted CO_2 levels for the end of this century, although changes in CO_2 occurred over thousands of years, rather than the rapid change as is the case presently. Despite this, sediment core archives from this period provide a valuable insight into potential impacts of ocean acidification, with some species being more tolerant than others, and some species going extinct.

7. **Even if CO_2 outputs are decreased now, impacts will be felt for thousands of years**
   The palaeo-record confirms that ocean acidification takes thousands of years to return to original levels following a CO_2 input event, such as following the Palaeo-Eocene Thermal

Maximum (PETM).

Impact of ocean acidification on biodiversity and ecosystem function:
Physiological responses

8. **Ocean acidification can lead to acid-base imbalance in many marine organisms such as fish, invertebrates and sediment fauna**
   Acid-base balance, or regulation, is an energetic process, so a disruption caused by changing external CO_2 levels will require energy to maintain the internal balance. This can lead to metabolic suppression, reduced protein synthesis and reduction in long-term fitness

9. **Impacts of ocean acidification upon fertilisation success are highly variable, and highlight the potential for genetic adaptation**
   Impacts of ocean acidification on fertilization range from none to very negative effects, which reflects biological reality that some species and individuals within species, are more tolerant than others.

10. **Ocean acidification is generally 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 morphology complexity, and decreased calcification.

11. **Ocean acidification can alter sensory systems and behaviour in fishes and some invertebrates**
    Impacts include the loss of ability to discriminate between important chemical cues, and may make individuals more active and liable to exhibit bolder and more risky behaviour.

12. **Impacts of ocean acidification upon immune responses and disease are of an emerging field, and only few studies have been performed to date.**
    Future ocean acidification has the potential to impact immune functions in marine organisms, but much more research is needed in this area. More research on the virulence and persistence of pathogens under future conditions is also needed.

Benthic communities

13. **Responses are highly variable, but many benthic species generally have lower growth rates and survival under projected future acidification**
    For corals, molluscs and echinoderms, many studies show reduction in growth and increased sensitivity with ocean acidification, but these responses are variable, with examples of species which live at low pH conditions.

14. **Many macroalgae and seagrass species are tolerant or may benefit from future ocean acidification**
    Non-calcifying species may benefit from future ocean acidification, and can be found near natural CO_2 seeps. High densities of seagrass and macroalgae can also significantly alter the local carbonate chemistry, with potential benefit for neighbouring ecosystems.

Pelagic communities

15. **Mesocosm experiments involving calcifying and non-calcifying plankton indicate increased community net carbon uptake under future ocean acidification**
    While non-calcifying phytoplankton may benefit from future ocean acidification, calcifying phytoplankton such as coccolithophores exhibit variable responses both between and within species. Mesocosm experiments include the dynamic between possible benefits for photosynthesis, and detriments to calcification as well as community shifts.

Bacterial response to ocean acidification has yet to be quantified fully, but altered communities may have implications for nutrient cycling.

16. **Planktonic foraminifera and pteropods will experience decreased calcification or dissolution under predicted future conditions**
Both of these groups are physiologically 'unbuffered' to changes in seawater carbonate chemistry, and as such, will experience dissolution if calcium carbonate saturation drops below 1. Decreases in planktonic Foraminifera shell thicknesses and sizes may also decrease efficiency of future carbon transport between the sea surface and seabed.

17. **Most fish are likely able to maintain sufficient O_2 delivery under future conditions, but squid metabolism may be reduced**
Fish are generally considered to be more resilient to ocean acidification that many other marine organisms because they do not have an extensive skeleton of calcium carbonate, and they possess well-developed acid-base regulation mechanisms. However, some squid species rely on a CO_2 sensitive oxygen transporter to sustain their high metabolic rates, and may thus be detrimentally impacted by future changes.

Impact on ecosystem services, livelihoods and biogeochemical cycles

18. **Impact of ocean acidification upon ecosystem services such as provisional, regulating, cultural, and supporting services can already be observed**
Ocean acidification has already impacted upon provisioning services of some oyster hatcheries in the Pacific Northwest, with up to 80% oyster mortalities since 2006 as ocean acidification is combined with deep-water upwellings.

19. **Rising CO_2 could impact net primary productivity, alter nitrogen and carbon ratios in exported particulate matter, and decrease iron bioavailability**
These impacts could also include a decrease in the amount of particulate organic carbon exported to the sea floor through a process called 'ballasting'. Impacts upon future trace gas emissions and how this would interact with biogeochemical processes largely remain to be determined.

Resolving uncertainties

20. **Existing variability in organism response to ocean acidification needs to be investigated further, and potential for adaptation over progressive generations identified**
Many gaps are now being investigated, but appreciating natural variability and capacity for adaptation are both needed to increase our understanding of future effects of ocean acidification from individuals to ecosystems.

21. **Research examining ocean acidification alongside other stressors (‘multiple stressor’) is needed, as acidification is taking place alongside other changes including temperature increase, altered seawater nutrients, and oxygen levels**
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, and increase our understanding of future impacts.

Synthesis

Research into ocean acidification has highlighted that not all organisms respond the same way, with some organisms being negatively impacted, some positively affected, and others not showing any apparent change. These variable results need to be understood to explain how ocean acidification affects whole communities, although it is always important to consider that impacts may not be detectable over the short time scales of most laboratory experiments. While we do not yet completely understand the impact of ocean acidification on biodiversity and ecosystems, historic archives and current experiments indicate that significant change is to be expected, with some species continuing as normal and some becoming more successful, while others may become locally or even globally extinct.

1. BACKGROUND AND INTRODUCTION

Key Messages:

1. Ocean acidification is a reaction involving increasing levels of carbon dioxide and seawater, with potentially deleterious consequences for marine calcifiers and ecosystems

2. The acidity of the oceans has increased by ~30% since pre-industrial levels

3. There has been increased international attention of ocean acidification, including in the CBD, which has catalysed research and the identification of 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 25% 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 already dropped by 0.1 units, a linear-scale increase in acidity of ~30%. Unless CO_2 emissions are rapidly curtailed, mean surface pH is predicted – with a high degree of certainty – to fall by a further ~0.3 units by 2100 [2, 3, 4].

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 in a negative way [4, 5, 6]. The consequences of ocean acidification for marine food webs, ecosystems, biogeochemistry and the human use of marine resources are, however, 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). The combined biological effects of several stressors are not readily predictable; together, impacts may be amplified or diminished, or there may be no interaction. Furthermore, there is now evidence that some – but not necessarily all – organisms may show genetically-mediated, adaptive responses to ocean acidification.

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, other Governments and organisations as well as experts who kindly peer-reviewed the report.

1.1. Mandate of this review

The CBD was one of the first international bodies to raise concern on the potential adverse impacts of ocean acidification. Attention was initially raised at its 9th meeting of the Conference of

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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.

Parties (COP 9; Bonn, 2008) that 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) [7], carried out jointly with the UNEP World Conservation Monitoring Centre. In response to that review, COP 10 (Nagoya, 2010) recognised 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; X/2).

Decision X/29 mandated a series of expert review processes, with partners, to assess ocean acidification impacts on biodiversity. To initiate implementation of that decision, an Expert Meeting on Ocean Acidification was held in Montreal in October 2011, involving experts fromParties, other Government and relevant organizations (the meeting report available at http://www.cbd.int/doc/meetings/mar/emioamcb-01/official/emioamcb-01-sbstta-16-inf-14-en.pdf). 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 group's report [8] 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.

The new review – this document – should provide "a targeted synthesis of the biodiversity implications of ocean acidification for marine and coastal systems, including information on the less reported palaeo-oceanographic research, building upon the synthesis provided in CBD Technical Report Series No 46" (XI/18, paragraphs 22-24). The new review would be considered by SBSTTA prior to COP 12 in 2014, with a view to forwarding it to Parties, other Governments and relevant organizations and transmitting 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 new review, through the UK Ocean Acidification programme, co-funded by the Natural Environment Research Council, the Department for Environment, Food and Rural Affairs, and the Department for 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.

The increasing international awareness of ocean acidification and its societal implications were demonstrated at the 14th meeting of the UN Open-ended Informal Consultative Process on Oceans and Law of the Sea (New York, 17-20 June 2013), that focussed on the development of appropriate policy responses [9]. An early draft of this CBD review was then presented and discussed at a CBD Secretariat side event, organized in collaboration with IOC/UNESCO, and valuable feedback was received.

1.2. What is ocean acidification?

Ocean acidification can be defined in relatively narrow terms, limiting its meaning to the global-scale, longterm decrease in seawater pH primarily due to human-driven increases in atmospheric CO_2. This process is underway, and it is near-certain that it will intensify. Such effects have now been observed at many locations, with the longest time series from the Mauna Loa observatory clearly demonstrating the CO_2-pH relationship (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), that 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 the dissolved carbon dioxide (pCO_2), the total dissolved inorganic cabon (DIC) and the total alkalinity (TA; the combined abundance of all negatively-charged ions).

One further chemical reaction is noteworthy. As the abundance of carbonate ions in seawater declines, it affects the stability of calcium carbonate ($CaCO_3$) in solid form, that 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 not only require more energy to produce $CaCO_3$ when carbonate levels in the surrounding water are low, but they may also need to cover their exoskeletons and carapaces with an organic layer, to prevent shell dissolution.

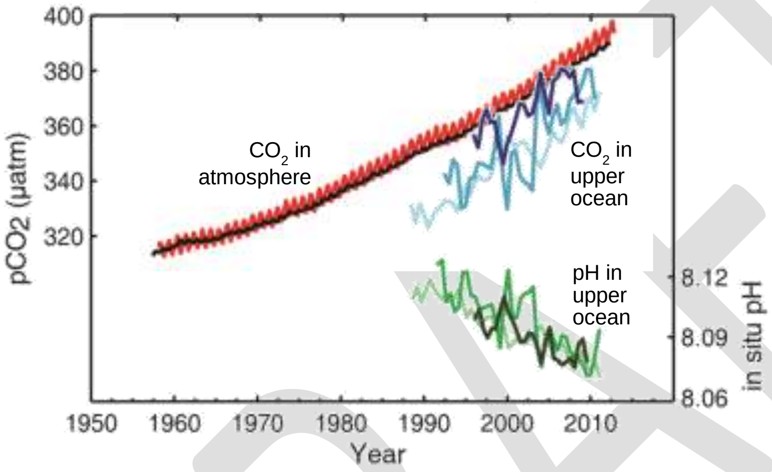

Figure 1.1. *Measured decreases in near-surface ocean pH in the central Pacific (light green) and two Atlantic sites (green, dark green) compared to dissolved CO_2 at those sites (light blue, blue, dark blue) and atmospheric CO2 at Mauna Loa, Hawaii (red) and the South Pole (black). From IPCC (2013) Twelfth Session of Working Group I, Summary for Policymakers; www.ipcc.ch* [10]

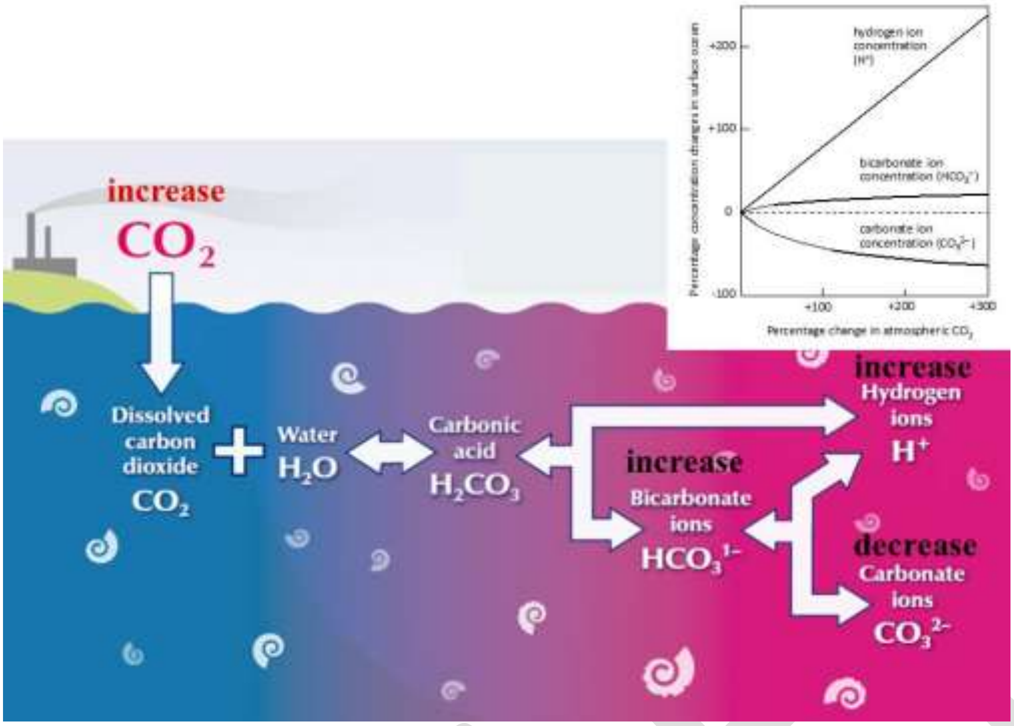

Figure 1.2. *Left: The chemical reactions that occur when additional carbon dioxide dissolves in seawater, with net effect of increasing the abundance of hydrogen ions and bicarbonate, whilst reducing carbonate. Right: Model-based global estimates of the percentage changes in hydrogen ions, bicarbonate 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 on the left hand part of this figure. Credits: left, redrawn from* (11)*; right,* (12) *based on data in* [6].

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. Ω >1.0. However, most of the deep ocean is unsaturated, with Ω <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 Ω = 1.0 is the saturation horizon, with most of the deep seafloor below that horizon and therefore corrosive to unprotected $CaCO_3$. Some calcareous material may be found below that horizon 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.

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 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 predicted to shallow from >2000 m to ~100 m in the North Atlantic, from ~150 m to the near-surface in the North Pacific [13], and to reach the surface in the Arctic and Southern Ocean [14]. Due to lower temperatures in polar regions, the shallowing of saturation horizons is more pronounced there, an effect described in more in 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, whilst bacteria, protists and rotifers can survive at pH values as high as 10.5 [15]. Nevertheless, all species have their individual optimal pH ranges and tolerance limits that usually closely match the range of variability naturally encountered in the species' habitats. As discussed in greater detail in Chapter 3, natural seawater pH values are generally between 7.9-8.2 in the upper open ocean, but can vary between 7.7-8.7 in shelf seas and coastal regions, and can be below 7.4 at ocean depths.

Given those ranges, it might be thought that the projected pH reductions of ~0.3 during the current century could be inherently unlikely to have substantive biological consequences, at least in coastal waters. However, that logic is invalid. An analogous situation applies to temperature tolerances and projected global warming: thus a global surface temperature increase of ~2°C is now generally recognised as having 'dangerous' climatic and ecological consequences, threatening extinction for many species – despite very many organisms experiencing seasonal (or even daily) temperature ranges that are 5-10 times greater, and the very wide temperature range (from -20°C to 115°C) within which life, of some kind, can survive. 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 carbonate and/or pH, occurring at the same time.

- 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 [16, 17] have helped to identify general trends, consistent patterns and life-cycle effects, discussed in greater detail in Chapter 5 and elsewhere in this review.

- 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, e.g. due to over-fishing, habitat loss/destruction, pollution, and enhanced nutrient loading (with associated eutrophication and low oxygen), and global-scale, climate-related impacts, 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), and de-oxygenation. Key issues relating to the three main global-scale stressors – acidification, warming, and de-oxgenation – are summarised in Table 1.1. Further information on our relatively limited understanding of the interaction of ocean acidification with other factors is given in subsequent chapters.

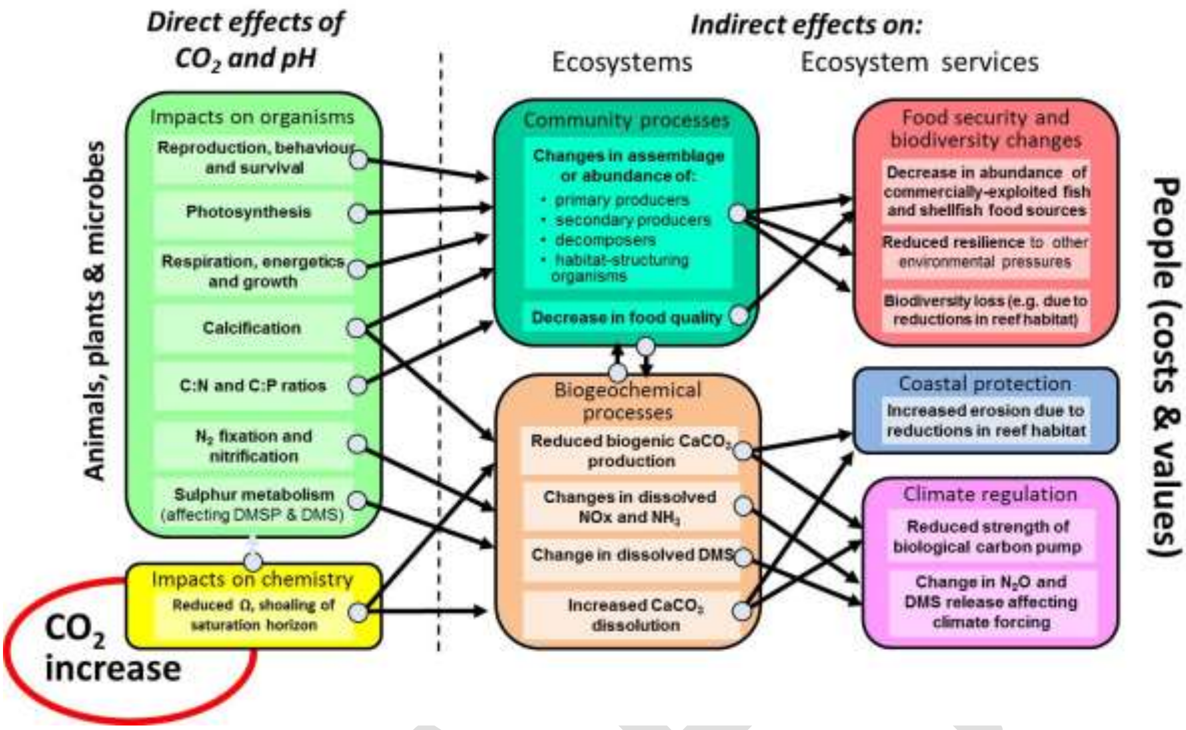

Figure 1.3. *Simplified summary of ocean acidification impacts upon organisms, ecosystems, ecosystem services and hence society. Impacts cascade through marine ecosystems with effects on human society including changes to food security, biodiversity, coastal protection and climate regulation (see Table 5.2 for further detail). DMS, dimethylsulphide; DMSP, dimethylsulphoniopropionate; Ω, $CaCO_3$ saturation state. Based on* [12].

Table 1.1. Summary of the causes and impacts of the three main, interacting global-scale stressors that will increasingly affect marine biodiversity, with severity of impacts depending on future emissions of greenhouse gases. Based on [18].

Stressor	Causes	Result	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 [7] identified five questions to assist in focussing research effort on important knowledge gaps. Table 1.2 below briefly re-visits these issues, summarising relevant progress and the current 'high level' status of our understanding of these topic areas. Additional detail, with supporting scientific citations, is given in subsequent chapters of this review.

Three more 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 (Figure 1.3) – whilst also recognising that the scale and importance of many of these additional impacts are still very uncertain. Second, these questions only indirect refer, through adaptation (Q3), to the relevance of genetic and evolutionary processes in determining the scale of future acidification impacts. Third, that none of the questions explicitly mention ecosystem services, societal impacts or possible policy responses. Whilst research and understanding in these areas are not yet well-developed, the current review does begin to address crucial aspects of such 'human dimensions' of ocean acidification and its effects on biodiversity.

Table 1.2. Knowledge gaps identified in 2009 [7] and subsequent relevant research developments.

Research question	Comments; current status
1. How is calcification affected in organisms at different stages of their life cycle?	Significant progress made on life-cycle experimental studies, particularly with echinoderms. For that group, acidification slows development of embryos/larvae (hence increasing mortality in field); juveniles may also be negatively affected, whilst adults generally more tolerant. Life-cycle changes in acidification sensitivity not limited to calcifiers. Also increased awareness that experimental life-cycle studies should be relevant to natural conditions, with need for 'realistic' yet well-controlled pH/carbonate system parameters; also controlled food availability. Potential impacts of multiple stressors (e.g. temperature, nutrients, 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 (giving potential for multi-generational adaptation, although that may be at cost of reduced fitness for other traits).
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 – that is difficult to determine, but can be informed by palaeo-studies - is dependent on reproductive strategy, existing genotypic variability (on which selection can operate), and generation time. 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 the future scale and influence of other environmental variables, and models are unable to take account of factors (e.g. adaptation) that have not yet been mechanistically quantified.

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2. SCIENTIFIC AND POLICY FRAMEWORK

2.1 Steps toward global recognition and international science 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 the ocean buffering capacity[1], and that this could decrease calcification[2, 3]. Scientific interest in ocean acidification has increased exponentially in the past few years, with a fifteen-fold increase in the number of publications from 2004 to 2012, and an increasing number of new researchers entering the field (Figure 2.1) [4, 5].

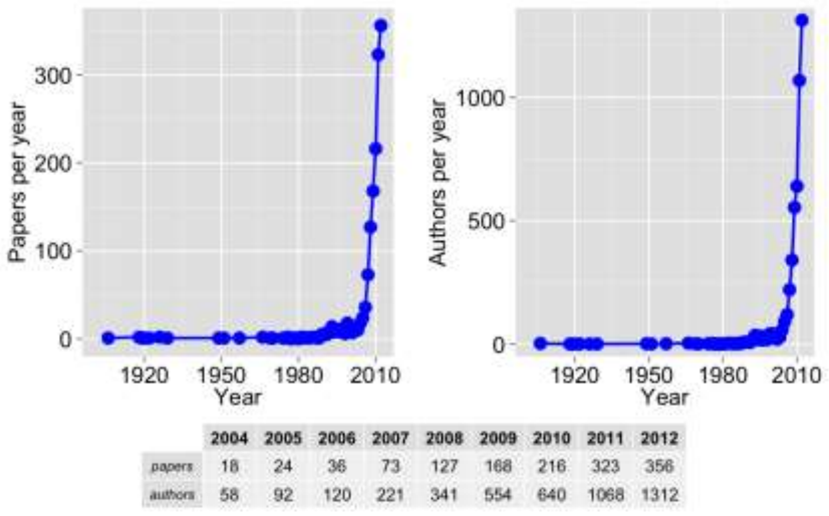
The prioritisation of ocean acidification as a research topic began around 2003-04, with its inclusion in the Science Plans of two global change research programmes, the Surface Ocean Lower Atmosphere Study (SOLAS) [6] and the Integrated Marine Biogeochemistry and Ecosystem Research project (IMBER) [7]. In a closely-related initiative, the first symposium on “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).

Key Messages:

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

2. Ocean acidification is best investigated in an interdisciplinary and international framework

3. Many intergovernmental bodies have a vested interest in this issue, currently without any one having a lead agency role



	2004	2005	2006	2007	2008	2009	2010	2011	2012
papers	18	24	36	73	127	168	216	323	356
authors	58	92	120	221	341	554	640	1068	1312

Figure 2.1. *The annual number of ocean acidification publications and the number of authors involved 1900-2012. Data from OA-ICC, and Gattuso & Hansson 2011* [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 subsequent policy-related publications attracted significant attention, including:

- The 2008 Monaco Declaration [9], signed by 155 scientists from 26 countries and endorsed by HSH Prince Albert 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 "The Ocean in a High CO_2 World"symposium series, held in Monaco and co-organised by the International Atomic Energy Authority (IAEA),

- The CBD's 2009 report "Scientific Synthesis of the Impacts of Ocean Acidification on Marine Biodiversity" [10], produced jointly with the United Nations Environment Programme (UNEP) World Conservation Monitoring Centre. 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.

The first large-scale, multi-national project on ocean acidification was the European Commission's "European Project on Ocean Acidification" (EPOCA) [12], 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" [13] in 2011 (Figure 2.2). A second EC project began in 2010, to study ocean acidification and climate change in the Mediterranean (MedSeA) [14], and a further call for proposals was made in 2012, for acidification studies in the context of other marine stressors, such as global warming and oxygen depletion.

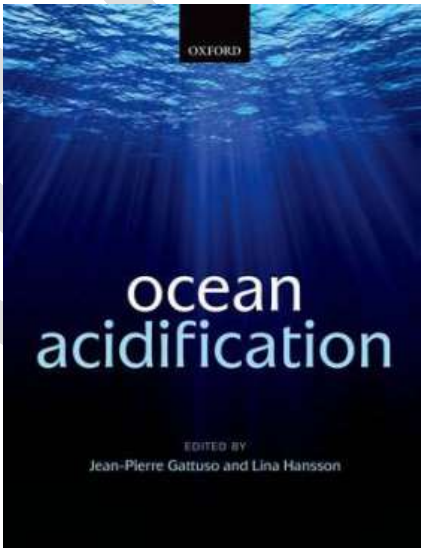


***Figure 2.2**. The first book on ocean acidification, with international authorship and arising from the European EPOCA project.*

National research efforts, with close linkages, were developed in parallel. These have included the German programme Biological Impacts of Ocean Acidification (BIOACID) [15], that started in 2009, and is now in its 2nd 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, projects and funding calls in Australia, China, Japan, Republic of Korea, Norway and elsewhere. The current breadth of international involvement in ocean acidification research is indicated in Figure 2.3.

Linkages between these worldwide research efforts on ocean acidification have been encouraged at the intergovernmental level (see 2.2 below), also by national funders and by non-governmental science bodies, particularly by the SOLAS-IMBER Ocean Acidification Working Group (SIOA-WG) [18]. The SIOA-WG helped to establish the Ocean Acidification International Coordination Centre (OA-ICC) [19] of the IAEA, hosted in Monaco. The OA-ICC became operational in 2012, supported by IAEA member states; its current and future OA-ICC 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 (with the OA-iRUG). The OA-ICC is primarily supported by IAEA member States.

OA-ICC liaison with policy-makers, the private sector and other stakeholders will be 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.

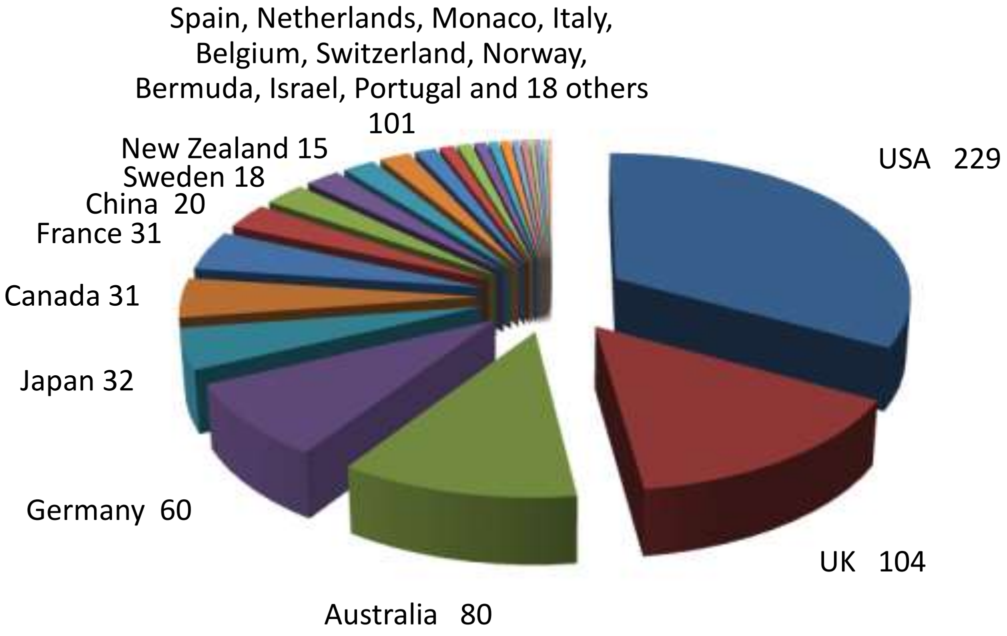


Figure 2.3. *International involvement in ocean acidification research, based on first authors' addresses for papers published in 2005-2011 (Web of Science data).*

2.2 Intergovernmental interest in ocean acidification and actions to date

Whilst some local and national measures can be taken to ameliorate 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. In addition to the interests and activities of the CBD and IAEA, already mentioned above, several other intergovernmental bodies, mostly within the UN system, have also included ocean acidification in their agendas, with both single-body and joint actions to inform policy makers and support policy development. These interests and activities are summarised in Table 3 below; more comprehensive references to UN agencies' decisions and recommendations on ocean acidification are given in a recent review of the policy context [22]. No single UN body currently has a designated lead role for policy development regarding ocean acidification, and there is an ongoing debate [23, 24] on this issue, particularly with regard to any regulatory framework. CBD's own 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 interests and activities of United Nations bodies, Conventions and other intergovernmental organizations in relation to ocean acidification, based on [22]. Not comprehensive

***Body, subsidiary body/agency or Convention*; interests and actions**			
United Nations General Assembly ***(UNGA)***	Deliberative assembly of all UN member states; receives reports from other UN bodies and makes recommendations		• Concern expressed in 2006 on “projected adverse effects of anthropogenic and natural climate change and ocean acidification on the marine environment and marine biodiversity”. Concern re-iterated in subsequent years, most recently in 2012 when need identified “to work collectively to prevent further ocean acidification”.
	Open-ended Informal Consultative Process on Law of the Sea	Forum for member states’ discussions on ocean affairs and law of the sea	• 14th meeting (June 2013) on Impacts of Ocean Acidification on the Marine Environment; report to 2013 UNGA [25]
United Nations Secretariat	Administrative organ of the UN, led by Secretary General		• Oceans Compact initiative [26], to deliver on marine components of “The Future we Want” (see below); objectives include reducing anthropogenic pressures on coral reefs and other vulnerable ecosystems impacted by climate change or ocean acidification.
United Nations Environment Programme ***(UNEP)***	Coordination of UN environmental activities		• 2010 publication: “Environmental Consequences of Ocean Acidification: a Threat to Food Security” [27]
	3rd United Nations Conference on Sustainable Development *(“Rio+20”; organised with UN Department of Economic & Social Affairs)*	Building green economy; improving international coordination	• Rio+20 outcome document “The Future we Want” [28] includes call for support of “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 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”
United Nations Educational, Scientific and Cultural Organization ***(UNESCO)***	*Inter-governmental Oceanographic Commission* *(IOC)*	The UN body for ocean science, observatories, data, information exchange and services	• Coordination of measurements of worldwide changes in ocean chemistry and biology through Global Ocean Observing System (GOOS) and International Ocean Carbon Coordination Project (IOCCP; co-supported by SCOR) • Lead UN agency for “A Blueprint for Ocean and Coastal Sustainability” [29] (with IMO, FAO and UNDP), including actions to mitigate and adapt to ocean acidification • Major role in developing Global Ocean Acidification Observing Network (GOA-ON)
World Meteor-ological Organization ***(WMO)***	*Inter-governmental 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) [30, 31]. 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 for research on ocean fertilization and other marine geoengineering relevant to ocean acidification

International Atomic Energy Authority ***(IAEA)***	Encourage peaceful uses of nuclear technology		• Convening of two workshops (in 2010 and 2012) on socio-economics of ocean acidification
	Ocean Acidification International Coordination Centre (OA-ICC)	Enhancing world-wide coordination of scientific study of ocean acidification	• Development of global network for to measure changes in ocean carbon chemistry and its ecological impacts (with GOA-ON) • Improving ocean acidification data management; capacity building, dissemination and outreach.
United Nations Framework Convention on Climate Change ***(UNFCCC)***	Policy 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 agreements, but discussed as '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
Convention on Biological Diversity ***(CBD)***	Treaty to promote conservation and sustainable use of biological diversity		• Concern on ocean acidfication raised at 9th Conference of Parties (COP 9) in 2008 • 2009 Review (with UNEP) "Scientific Synthesis of the Impacts of Ocean Acidification on Marine Biodiversity" [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 • Development of protocols for ocean acidification monitoring and assessment
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]
Arctic Council*	*Arctic Monitoring and Assessment Programme (AMAP)*	Provision of information on status of Arctic environment	• AMAP Arctic Ocean Acidification Assessment (2013) [33]
International Union for Conservation of Nature* ***(IUCN)***	Aim is to conserve biodiversity at global and local level		• Work with IOC, Ocean Acidification international Reference User Group and others to raise awareness of ocean acidification.

*body with government membership but not part of the UN

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3. GLOBAL STATUS AND FUTURE TRENDS OF OCEAN ACIDIFICATION

3.1 Variability

Regional and habitat natural variability of oceanic CO_2 and pH (diurnal to seasonal) is crucial to consider when projecting future changes, as variability could mask underlying anthropogenic ocean acidification trends [1]. Since this variability is very habitat-specific [2] (Figure 3.1), it is potentially simpler to detect an ocean acidification signal in the equatorial or open ocean than in a highly variable coastal system [1, 3]. For example, natural variability in ocean pH within shallow coastal and coral reef habitats can range between pH 6.5 – 8 [4], and could be affected by periodic up- or down-welling as is the case for the Mingulay cold-water coral reef complex off the coast of Scotland [5]. As demonstrated in the European coastal zone [6], the variability in pH increases dramatically when moving from the open-ocean towards shallow coastal waters, and for many coastal ocean sites, short-term natural variability has a greater range than the projected pH decline over the next century due to anthropogenic CO_2 emissions [3,7].

Temporal variability can also be significant [8], (Figure 3.2A), in both daily and seasonal timescales. Results taken over the course of a research expedition (Figure 3.2B), thus have to account for temporal, as well as regional, variability.

Key Messages:

1. Substantial natural seasonal and diurnal variability exists in seawater pH

2. Seawater pH variability differs between different habitats

2. High latitude oceans will feel the effects of ocean acidification sooner than temperate or tropical regions, as saturation horizons are already shallower than lower latitudes

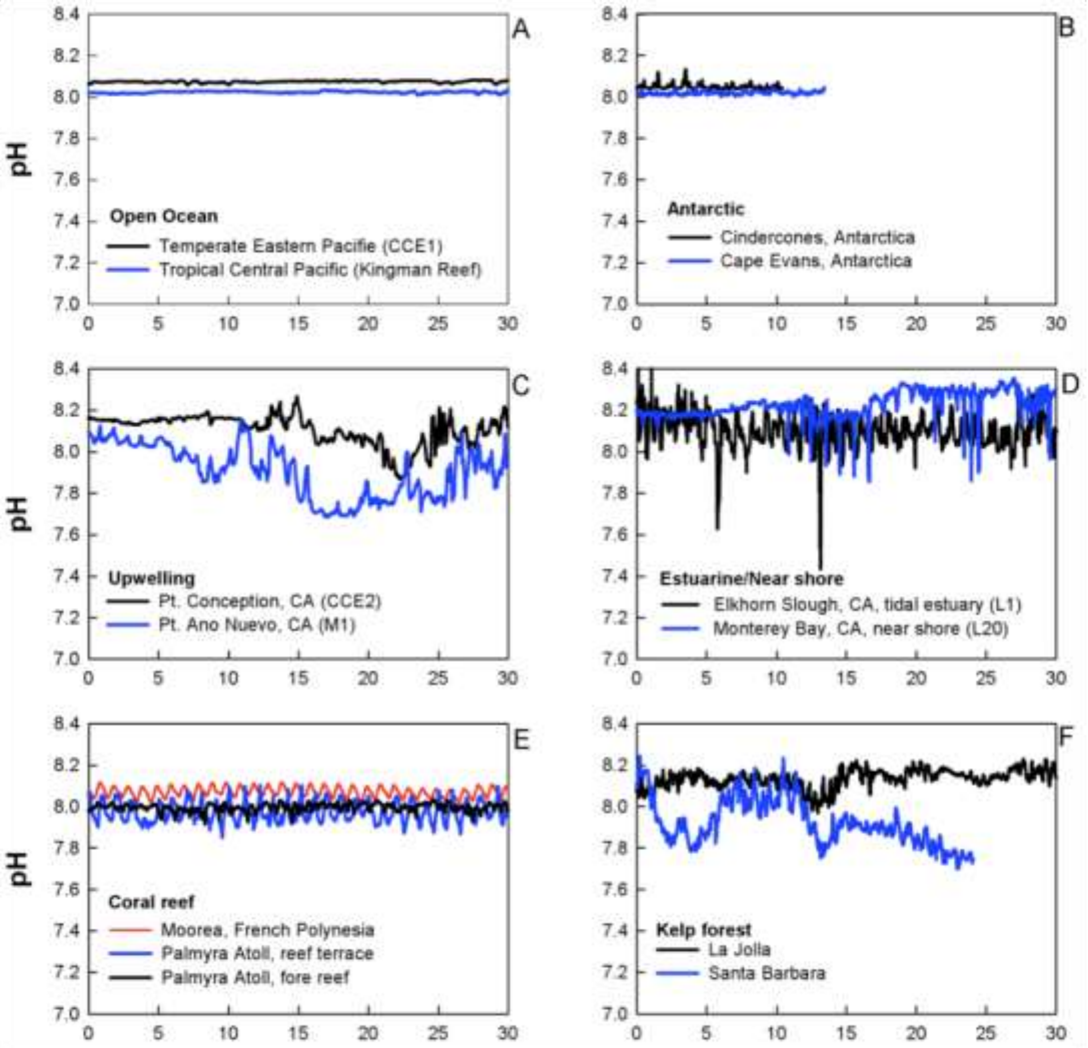

Figure 3.1. *Natural variability in pH dynamics at 15 locations worldwide over a period of weeks in 0–15 m water depth (Hoffman et al. 2011).*

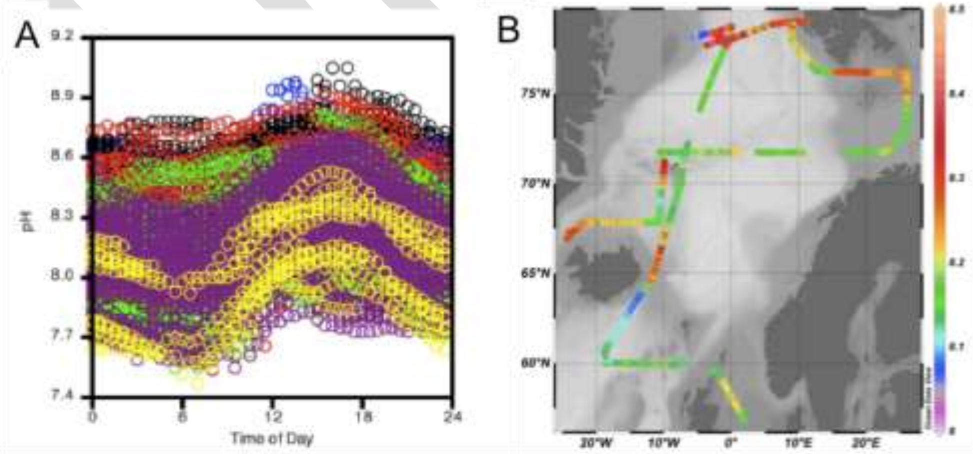

Figure 3.2. *The temporal and spatial variability in seawater pH: A) seasonal and daily variability in pH at Tatoosh Island, where colours indicate different months that data were collected* [8]*, and B) regional variability in the N Atlantic/ Arctic during the research cruise JR271 (UKOA Sea Surface Consortium, unpublished)*

Several national and international programmes are now working to provide high-quality, standardised observations to provide key knowledge of carbonate system changes within the marine environment, and global datasets of inorganic carbon and total alkalinity have now been built incorporating available, quality assured data through the Global Ocean Data Analysis Programme (GLODAP, (Key et al., [9]) and lately CARbon in the Atlantic Ocean (CARINA) efforts (Key et al. [10]).

3.2 Modelled simulations of future ocean acidification

Special Report on Emission Scenarios (SRES)

A1 – Integrated world, rapid economic growth, limited population growth

A2 – Divided world, regional economic growth and continuous population growth

B1 – Integrated world, rapid economic growth, limited population growth with global movement towards economic, social and environmental stability

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

The future change in ocean carbon chemistry is closely linked to increasing future atmospheric CO_2 levels [11,12, 13] (Figure 3.3), and the changes in pH and carbonate chemistry will vary with latitude (Figure 3.4) [14] as temperature variation and CO_2 solubility increases at lower temperatures. Under the "business as usual" scenario, which assumes little CO_2 emission abatement, atmospheric CO_2 levels could increase from ~390 to ~1000 ppm by the end of the century [15], lowering the average surface ocean pH from about 8.2 in preindustrial times to be about 7.8 [14,16,17]. The degree of ocean acidification will also depend on the model and carbon emission scenario used. The aragonite saturation horizon, below which aragonite, the more soluble form of calcium carbonate dissolves, is projected to rise from a few thousand meters to just a few hundred metres in many temperate and tropical oceans by 2100 [16]. Temperature effects on carbonate chemistry means that many high latitude areas will experience larger declines in 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 [18]. Similarly, surface waters of Polar Regions of the Northern Hemisphere are projected to become under-saturated by the middle of the century under most scenarios [13,19] (Figure 3.5).

The presence of sea-ice in the Arctic acts to limit the exchange of CO_2 between the atmosphere and ocean, but with predicted climate change, the reduction in sea-ice cover exposes the surface ocean to the atmosphere. This enhances the air-sea CO_2 exchange, which, when coupled with the freshening of the surface water, is causing acceleration of the under-saturation of the surface water and decreases the Ca^{2+} ion concentration such that some regions are already under-saturated with respect to aragonite [20].

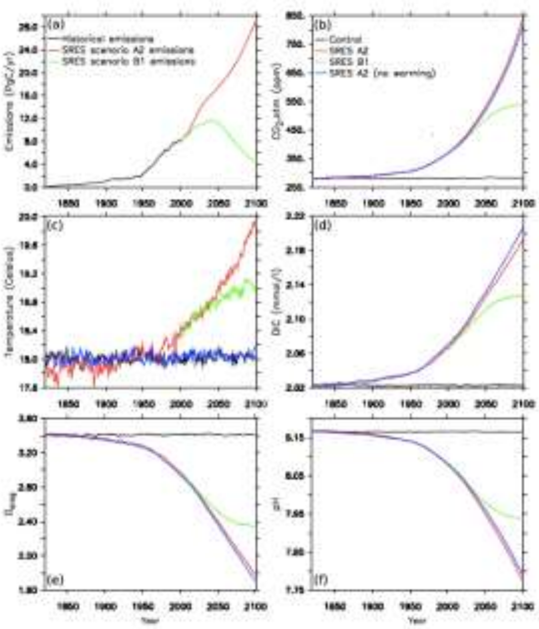

Figure 3.3. *Prescribed fossil fuel and land use CO_2 emissions (a) based on historical data (1820-2000, black) and the SRES-A2 (red) and B1 (green) scenarios (2000-2100). Simulated global annual mean atmospheric CO_2 (b), sea surface temperature (SST) (c), dissolved inorganic carbon (DIC) (d), aragonite saturation (e) and pH (f) at the ocean surface.* Steinacher et al. 2009 [13]. *Seek permission*

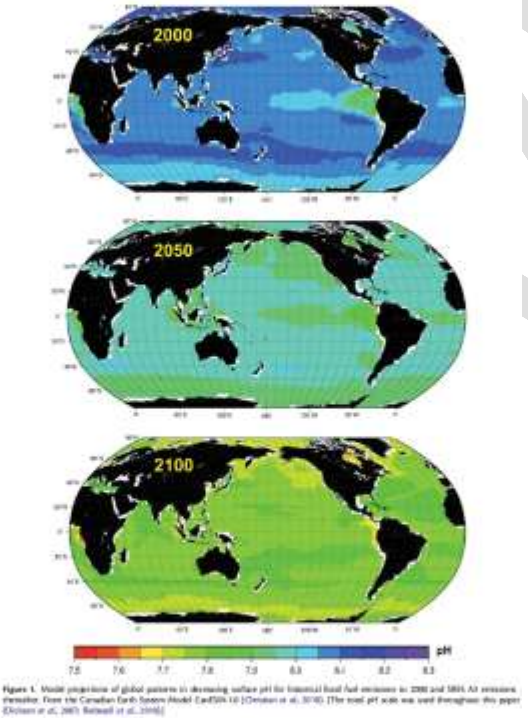

Figure 3.4. *Model projections of global patterns in decreasing surface pH for historical fossil fuel emissions to 2000 and SRES A2 emissions therafter. From the Canadian Earth System Model CanESM-1.0.* Denman et al. 2011 [14]. *Seek permission*

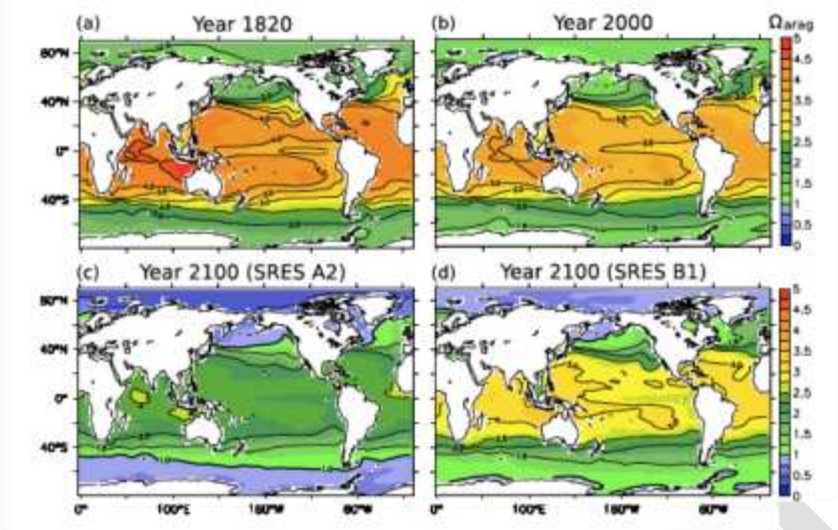

Figure 3.5. *Simulated aragonite saturation at the surface by the years 1820 (a), 2000 (b), and 210 (c) (c,d) for SRES scenarios A2 and B1.* Steinacher et al. 2009 [13]. *Seek permission*

Beneath the surface, the detectable signal of ocean acidification is already penetrating into the ocean interior due to entrainment, mixing, and deep-water formation. In the North Atlantic and Southern Ocean, signals of decreasing pH have already been observed at the ocean floor [21,22] (Figure 3.6). These changes are resulting in a shoaling of the aragonite and calcite saturation horizons, and amplification of natural carbonate chemistry variability. In the Pacific and the South Atlantic, signals of anthropogenic carbon are seen in the intermediate waters [23,24], and model predictions maintain that ocean acidification will occur throughout the water column.

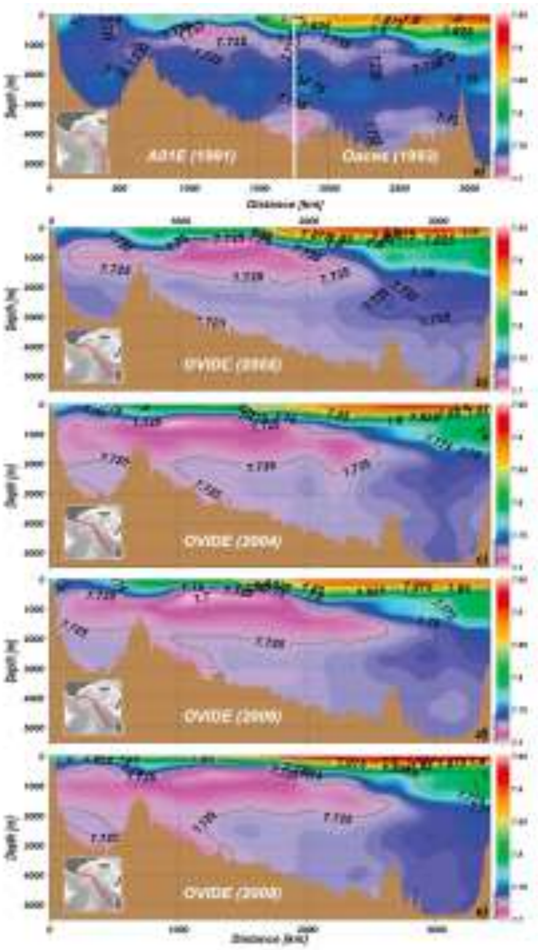

Figure 3.6. *Measured pH gradients and sequential temporal changes along a trasect from the SE tip of Greenland towards the Iberian Basin. Data from A01E, OACES and OVIDE cruises. Vasquez-Rodriguez et al. 2009* [21]. *Seek permission*

An important factor to recognize is the longevity of ocean acidification: long after carbon emissions are curtailed, ocean acidification will remain. Current increases in CO_2 may take tens to hundreds of thousands of years to return to pre-industrial values [25], as CO_2 will be slowly buffered by the dissolution of calcium carbonate sediments and continental weathering of silicates to promote the return of carbon back into the geological reservoir (Figure 3.7).

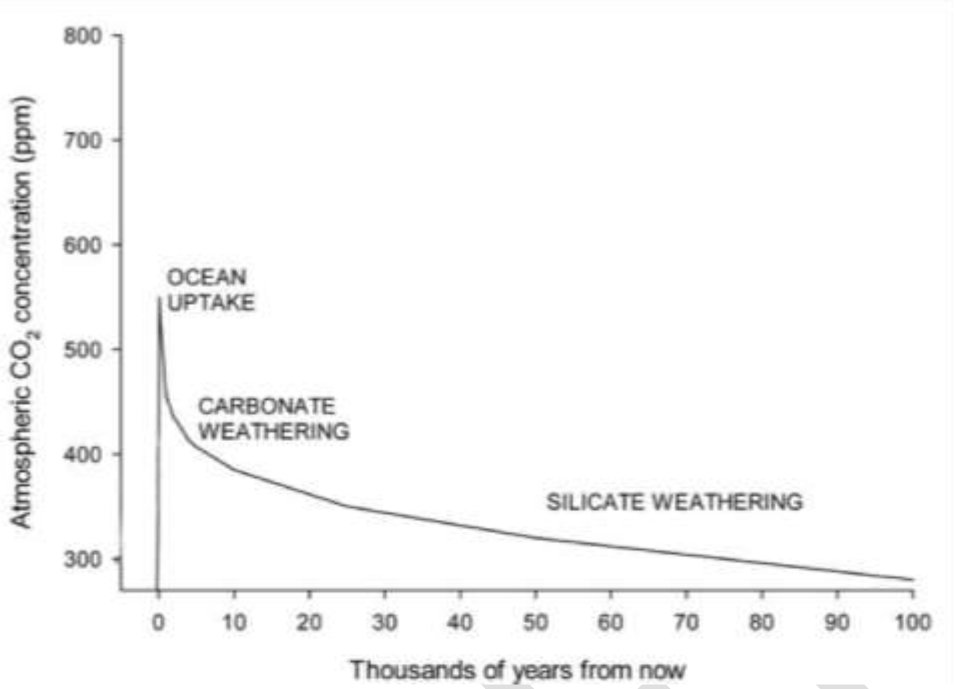

Figure 3.7. *The lifetime of atmospheric CO_2. Archer, 2005* [25]*; Stager, Nature Education, 2012* [26]. *Atmospheric CO_2 levels reached 400ppm in 2013.* *Seek permission*

3.3 Current status of global observations

Ocean observations are not yet on a truly global scale due to the traditionally complex logistics and costs of ocean-going expeditions, and the inaccessibility of many regions of the expansive global ocean partly due to limits of autonomous monitoring vehicles and sensors. However, there are some significant examples of how long time series have documented the changing marine carbon dioxide system in the Atlantic (Bermuda Atlantic Time-series Study, BATS), Pacific (Hawaii Ocean Time series, HOT), and North-east Atlantic (European Station for Time-series in the Ocean, ESTOC). These time series have documented the averaged-surface pH decline over the last several decades as -0.0016 to -0.0019 yr^{-1} [27,28,29] [Dore et al. 2009; Bates et al. 2012; Santana-Casiano 2007]. The observed decline in surface pH at these three open-ocean stations is consistent with a surface ocean that is tracking the increase in atmospheric CO_2 levels over the past three decades.

Driven by recognition that ocean acidification is an important environmental issue, international effort is exploiting new and existing platforms (e.g. ship surveys, moorings, floats, and gliders) to provide an Ocean Acidification Observing Network (Figure 3.8), as documented following the recent International Workshop to Develop an Ocean Acidification Observing Network (St Andrews, July 2013). Part of the need to expand the network is the recognition that the natural variability in key ocean acidification parameters (e.g. pH) can be highly variable in both time and space.

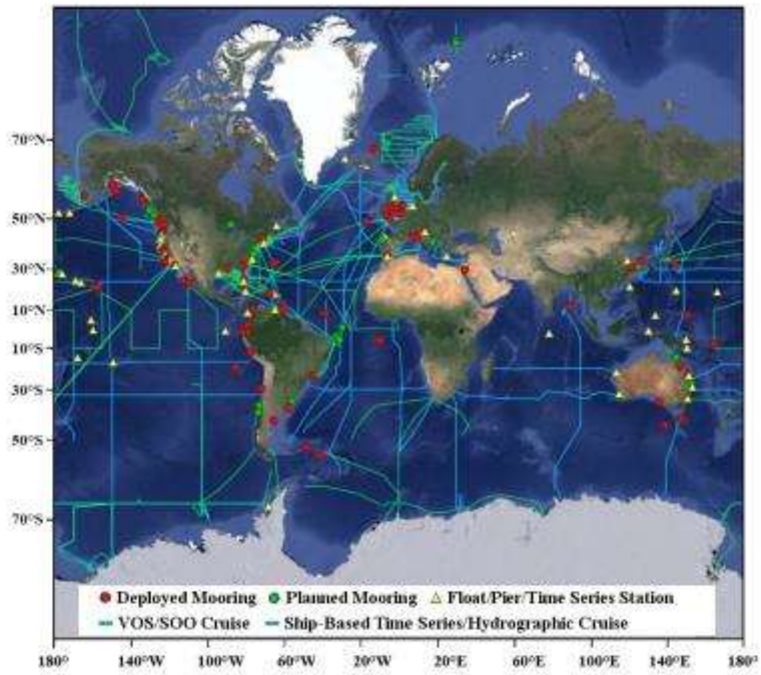

Figure 3.8. *Current network of ocean acidification observing platforms, moorings, ship surveys and gliders as identified in the International Workshop to Develop an Ocean Acidification Observing Network (Seattle, June 26-28, 2012). Map courtesy of Catherine E. Cosca, NOAA/ PMEL.*

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4. WHAT THE PAST CAN TELL US – PALAEO-OCEANOGRAPHIC RESEARCH

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 section), the average state of the ocean can also change through time in response to 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, corals and algae, or of ocean sediments which are accessible by drilling into the sea-bed. 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 palaeo-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 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.

Key Messages:

1. During ocean acidification which occurred ~56 million years ago over a period of 6000 years, a significant number of deep-sea calcifying organisms became extinct

2. Current ocean acidification is projected to reach similar levels over 500 years

3. It is possible that ocean acidification was a contributing factor to four out of five coral reef crises in the last 500 million years

4. The palaeo-record confirms that ocean acidification takes thousands of years to return to original levels following a CO_2 input event

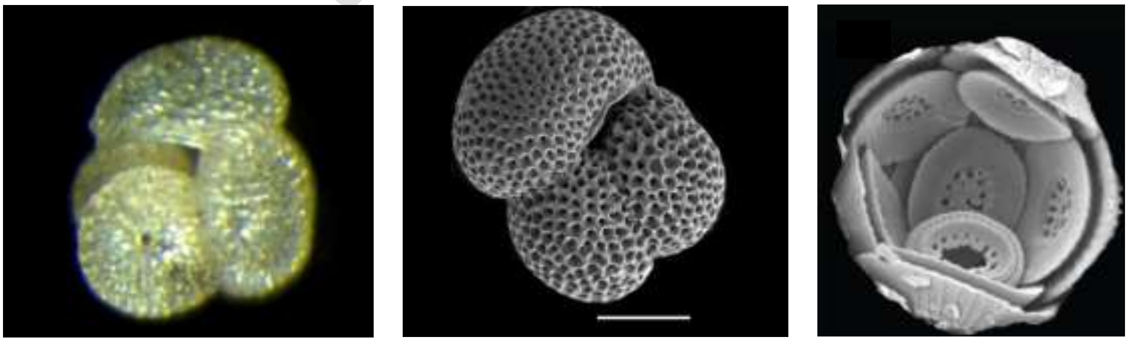

Figure 4.1. *A light microscope and scanning electron microscope image of planktonic Foraminifera specimens from Paleocene-Eocene Thermal Maximum (PETM, ~56 million years ago) sediments from Tanzania. Geochemical analysis of Foraminifera shells can provide information about oceanic chemistry millions of years ago. Scale bar 100 µm. The far right panel is a well preserved cossosphere. Source: P. Pearson.*

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 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. Trace element to calcium ratios of 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 Paleocene (~65-33 million years ago) 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 characterised 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 was released into the Earth's atmosphere over thousands of years [4] and global temperatures increased by about 5°C [5]. Coincident with this climatic shift was a lowering of oceanic pH, as evidenced by dissolution of carbonate at the seafloor [6] (Figure 4.2).

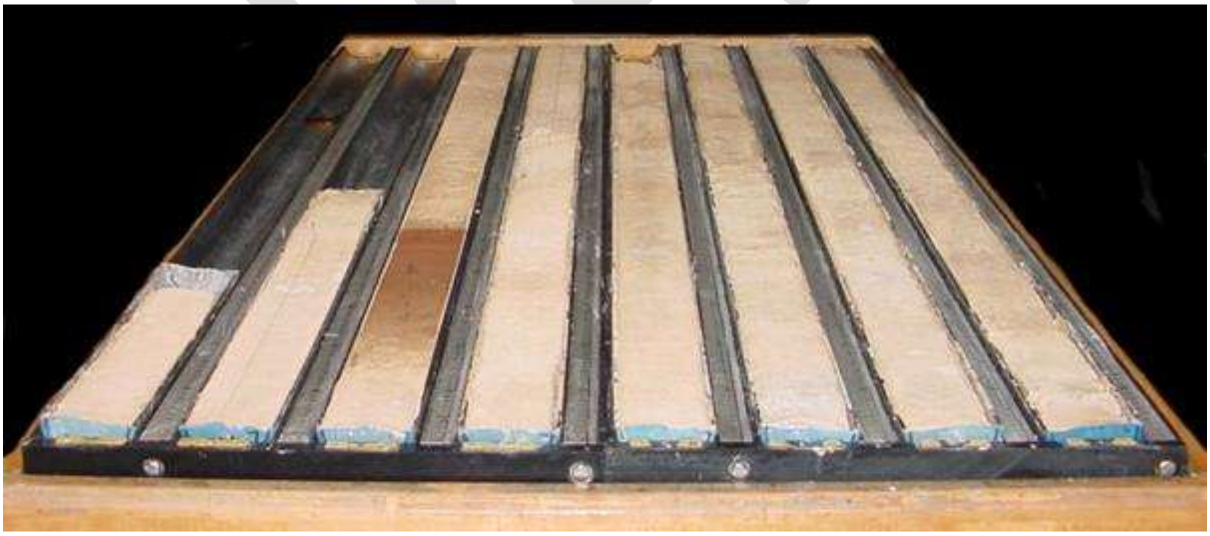

Figure 4.2. *Deep-sea core from the Integrated Ocean Drilling Program. Note the brown section of the core that represents the disappearance of deep-sea benthic calcifying organisms such as Foraminifera at the Paleocene-Eocene Boundary. This could represent a lack of calcifiers during that time period or the dissolution of dead shells. Source: James Zachos.*

4.3. The impact of past ocean acidification upon calcifiers

Good geological records can be collected of corals and calcifying plankton due to their progressive structures 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 [7] investigated whether 1) reef crises (declines in carbonate production) and 2) reef mass extinctions (Figure 4.3), were contributed to by ocean acidification, and concluded that it was likely that four out of five global reef crises in the last 500 million years were partially governed by ocean acidification and rapid global warming (Table 4.1). However, two of the five mass extinctions were not just detrimental to calcifying habitats, but general marine biodiversity; the late-Ordovician and the end-Cretaceous [7].

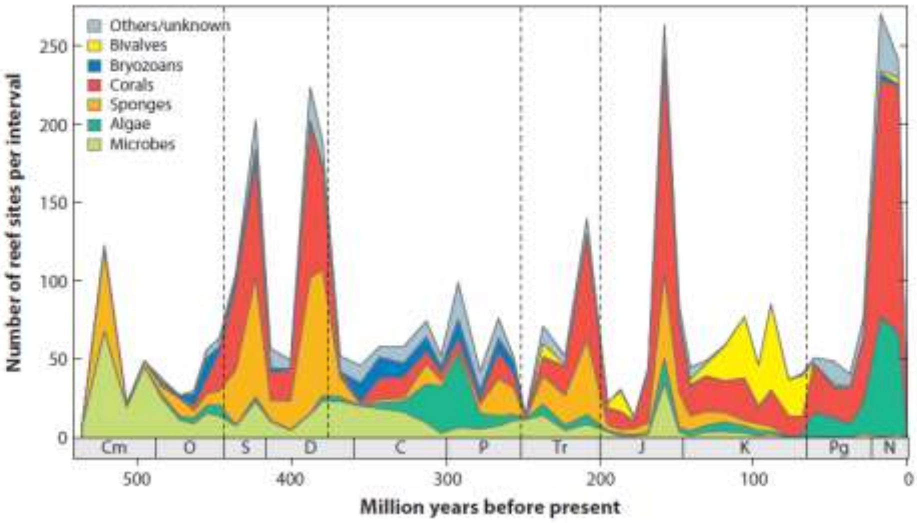

Figure 4.3. Number of reef sites and their biotic components plotted by 10-million year bins. A reef site often lumps several reef structures of the same age and environement within 20km. Vertical dashed lines indicate mass extinction episodes. Abbreviations of geological periods: Cm, Cambrian; O, Ordovician; S, Silurian; D, Devonian; C, Carboniferous; P, Permian; Tr, Triassic; J, Jurassic; K, Cretaceous; Pg, Paleogene; N, Neogene. Kiessling [8]. Seek permission

Table 4.1. Summary of results from Kiessling and Simpson [7], and assessment of ocean acidification as a probable cause. Biotic changes include impacts on physiologically buffered and unbuffered organisms. Seek permission

Time	Reef crisis	Biotic change	Evidence for OA*
Late Ordovician (445.6-443.7 Ma)	Not evident	Mass depletion of biodiversity during double mass extinction. Unselective with respect to buffering	None
Late Devonian (374.5 Ma)	Mostly metazoan (especially for corals and sponges)	Mass depletion of biodiversity. Selective extinction of corals and sponges over prolonged period of time	Weak
Middle - Late Permian (260.4 Ma)	Coral-sponge reef crisis only	Substantial extinction, weakly selective with respect to buffering	None
Permian - Triassic (251 Ma)	Massive for all reef types	Mass depletion of biodiversity and mass extinction, especially for unbuffered organisms	Strong
Triassic – Jurassic	Massive for all reef	Mass depletion of biodiversity and mass	Strong

(199.6 Ma)	types	extinction selective against corals, sponges, and unbuffered organisms	
Early Jurassic (183 Ma)	Coral reef crisis	Modest but selective extinction of corals and other unbuffered organisms	Strong
Cretaceous – Paleogene (65.5 Ma)	Not evident	Mass depletion of biodiversity and mass extionction, selective against buffered organisms	Weak
Palaeocene – Eocene	Coral reef crisis	Background extinction, except for benthic foraminifers	Strong

*OA=ocean acidification

However, this does not reflect the full story of coral history, and to fully understand the geological history of coral reefs, it seems likely a combined environment and evolutionary approach may be needed. Indeed, the modern Scleractinia (the framework forming corals as we know them 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, and not 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 'Sandburg curve' [11] which details the dominance of calcitic and aragonitic biomineralisation 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 assemblages [5]. 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 biomineralisation 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. 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 also 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].

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. However distinguishing the effects of acidification from associated environmental variables in the past is difficult 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 it the case today. Even so it provides an invaluable test-bed for studying the overall impact and subsequent recovery of the earth system and biotic communities, and potential biotic sensitivity to abrupt climate change.

4.5. Timescales of ocean acidification

The onset of the PETM occurred over a timescale of approximately 6000 years, and released ~2000-3000 petagrams of carbon into the Earth's atmosphere [14]. 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 [15, 16]. In Figure 4.4A, carbon released into the atmosphere during the PETM, and projected carbon outputs from human activities have been overlaid to provide perspective on the timescales involved. As a result of the carbon released in 4.4A, the saturation state of calcite (one of the mineral forms of calcium carbonate) decreases (Figure 4.4B). 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, 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.

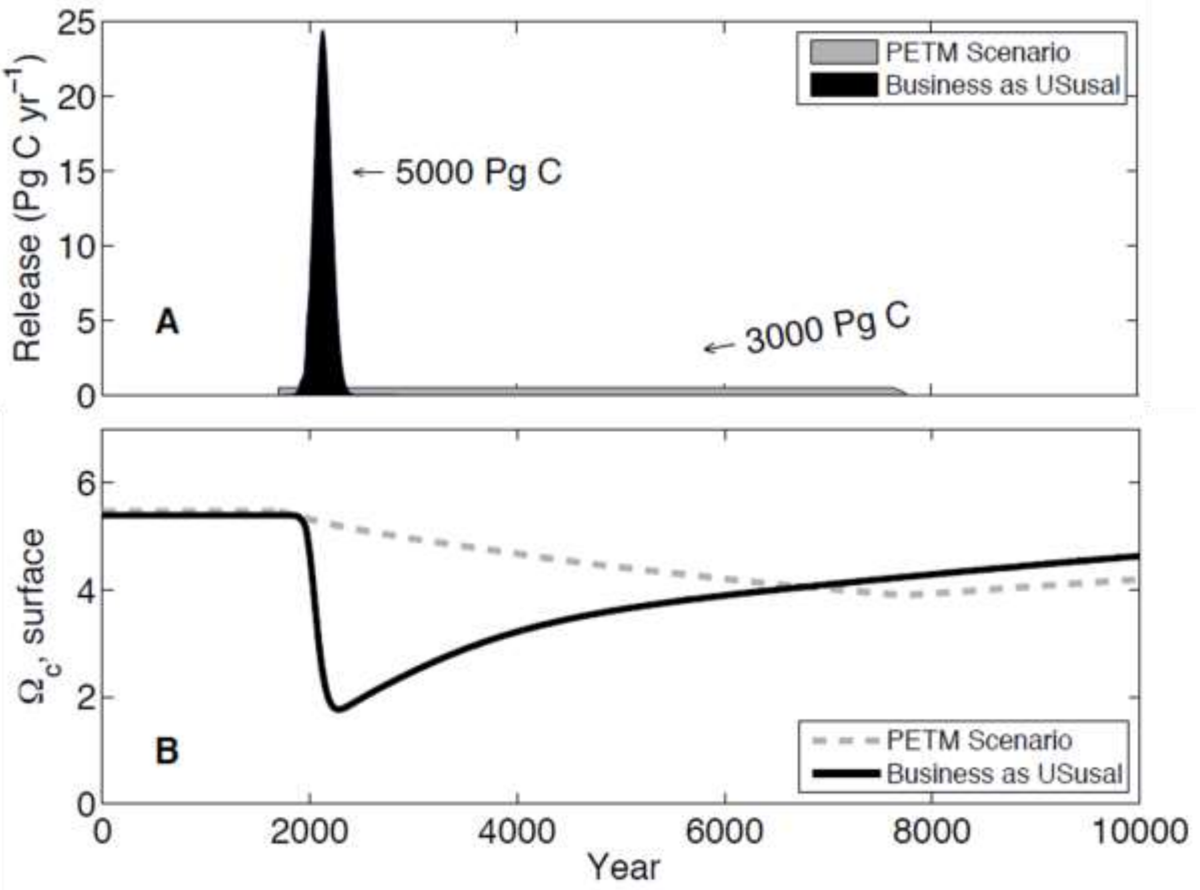

Figure 4.4. *Palaeocene-Eocene Thermal Maximum (PETM) versus present day time scales.(A) Carbon emission scenarios as projected for the future (5000 petagrams carbon over ~500 years;*

Zeebe et al. 2008) and the PETM (3000 petagrams of carbon over ~6000 years; Zeebe et al. 2009). The onset of the PETM has been aligned with the onset of industrialisation. (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 (Ocean Acidification). Seek permission

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5. IMPACT OF OCEAN ACIDIFICATION ON BIODIVERSITY AND ECOSYSTEM FUNCTION

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 summarises the interaction between direct effects of CO_2 and pH (non-comprehensive) and ecosystem services.

5.1. Physiological responses

5.1.1. Ocean acidification cellular processes

Many organisms regulate their internal pH, either for calcification purposes, or because their metabolic activity requires some level of internal 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 the internal balance. This has been observed in many marine organisms such as deep sea invertebrates [1], and fish [2, 3] (see later sections for more detail). If a constant total energy budget is assumed, then increasing energetic investment into acid-base regulation will decrease allocation from elsewhere, such as reproduction or growth (Figure 5.1). However, if this acid-base balance is not achieved, metabolism can become depressed as a short-term response in order to suppress ATP demand to extend potential tolerance [4]. However, this is not advantageous as it is typically at the expense of processes such as protein synthesis [4, 5, 6].

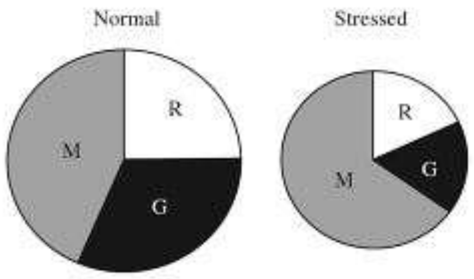

Figure 5.1. *Hypothetical energy budget for normal and stressed organisms. M = maintenance costs, R = reproduction and G = growth. If metabolic depression is also induced by ocean acidification, the total energy budget may also decrease (hence the smaller pie on the right). Barry et al. 2011* [7]*.Seek permission.*

Key Messages:

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. As seawater becomes more acidic, calcification may become less efficient

Many marine organisms produce shells and other structures composed of calcium carbonate ($CaCO_3$), and the very widespread use of biocalcification by organisms reflects the fact that the oceans are in large part supersaturated with a variety of calcium carbonate minerals. Future ocean acidification will lower the saturation state of calcium carbonate (aragonite and calcite) and if the water is undersaturated, dissolution of unprotected calciul carbonate will occur. While the chemistry involved is well-established [8, 9], the biological responses of different groups are very much harder to predict.

However, the response of biocalcifying organisms to changing saturation states may be affected not simply by whether the seawater is saturated or undersaturated, but also by reductions in the degree of oversaturation. 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 will need to becom more efficient. Thus, even if biocalcification is possible at low saturation values, it may be slower and less efficient. The degree to which different groups of organisms are sensitive to changes in carbonate saturation states was not a topic of particular interest before the concern over ocean acidification, but it 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 media (ECM) semi-isolated from the surrounding seawater environment [10] (Figure 5.2). 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 [11]. 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 [12]. However, the passage of seawater is restrictive [12] and coral tissues protect the skeleton from potential dissolution [13] (Rodolfo-Metalpa et al, 2012). One way for corals to exert biological control to buffer against the effects of ocean acidification is to increase pH in the calcifying fluid [14], effectively increasing $\Omega_{aragonite}$ at the site of calcification [15, 16]. It is thought that this process requires greater investment into acid-base regulation of calcifying cells and fluid under ocean acidification at an energetic cost to the coral [15, 16, 17, 18]. 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 [18, 19].

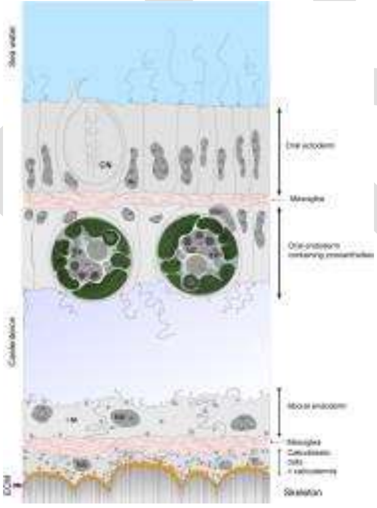

Figure 5.2. *Schematic representation of the histology of coral tissue (drawn from a picture in transmission electronic microscopy of the coral* Stylophora pistillata*) showing the tissue layers between the seawater and the site of calcification. CL = Chloroplast. CN = Cnidocyte. M = Mitochondria. NA = Nucleus of animal cell. NZ = Nucleus of zooxanthella. PY = Pyrenoid. ECM = Extracellular Calcifying Medium. Tambutte et al. 2011* [10]. Seek permission.

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5.1.2. Fertilisation, early life and settlement

Key Messages:

1. Impacts of ocean acidification upon fertilisation 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 in which different developmental stages inhabit benthic and pelagic environments. The persistence and success of these species therefore requires 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 [1]. Consequently, a comparative understanding of the sensitivities of all life-stages, from planktonic (fertilisation, embryos, larvae) to benthic (juveniles, adults), to life in a changing ocean is vital if we are to identify vulnerabilities that can threaten species persistence in the future.

5.1.2.1. Fertilization in benthic marine invertebrates

Reported effects 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 [2, 3]. This includes potentially different source populations [3, 4], the concentration of gametes [6], the number of parents [7], and the dominance of different parental genotypes in mass spawnings [8]. Importantly, fertilizations using gametes pooled from multiple parents, mimicking the multiple spawner scenario in the field, can show some resilience to near-future (ca. pH 7.8) ocean acidification conditions, (e.g. Byrne et al. [9]) as opposed to single crosses [10, 11, 12, 13, 14]. High variability in responses of single crosses to ocean acidification also highlight the potential for selection and genetic adaptation, supporting the concept of winners and losers in the face of changing ocean conditions [11, 12].

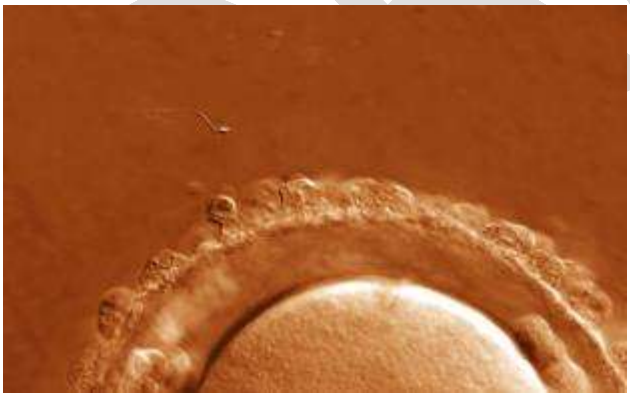

***Figure 5.3.** Sperm and egg of* Ascidia mentula. *Image courtesy of Jon Havenhand.*

The responses 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 [12], increases sperm swimming speed in a different echinoid species [15], has variable and non-linear effects on both sperm motility and swimming speed in a polychate worm [4], and no effect on sperm swimming speed in an oyster [11]. 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 [16, 17]. Overall, ocean acidification causes a reduction in fertilization at low sperm concentrations, but this response varies markedly among both populations and species.

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 [18, 19, 20]. Additional work is required to illuminate the possibility that acidification (and warming) are selecting a robust subset of progeny that possess phenotypic/genetic variation appropriate to changing 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 [20, 21, 22, 23, 24, 25, 26]. Increased pCO_2 within the range of near future projections is generally negative to calcifying larvae, including mollusc veligers and sea urchin echinoplutei [20, 27, 28, 29, 30], (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 (-0.3-0.4 pH units below ambient). One study reported reduced growth in bivalve larvae with just a slight decrease to pH 8.0 [28]. 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% [31]. 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 [32, 33]. 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 [30, 34, 35, 36].

In general, non-calcifying larvae, including coral and some sea star larvae, are more resilient to near future acidification [37, 38, 39, 40]. However, non-calcifying species (e.g., polychaetes) also show negative responses to acidification (Lewis et al [4]), 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 [38, 40]. Interestingly, crustacean larvae with poorly calcified exoskeletons (e.g. amphipods, barnacles, crabs) appear tolerant to acidification [35, 41, 42, 43, 44].

We have less information on the impact of increased ocean pCO_2 and temperature on the metamorphic transition to a benthic life in marine invertebrates, or on the early juvenile stages. The transition to the benthos may be affected by the negative effect of high CO_2, as shown for reduced coral larvae settlement [45]. Deleterious effects of ocean acidification (through smaller or lower weight juveniles) have also been reported for corals, bivalves, polychaetes and echinoderms [4, 46, 47, 48, 49, 50, 51], with emerging evidence that current CO_2 values compared to pre-industrial levels could already have caused a reduction in some larval sizes [51]. 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* [49], or *Mytilus edulis* [52]. Tolerance of these species to acidification may reflect the adaptation to life in low pH and highly variable environments [52]. Juvenile crustaceans are comparatively tolerant of acidification [43, 44] (Arnberg et al. 2013; Pansch et al. 2013), although again there is variability [53, 54].

Understanding how effects at early life-stages can "carry-over" [1] to influence growth and reproduction of the adult remains a significant challenge and knowledge gap.

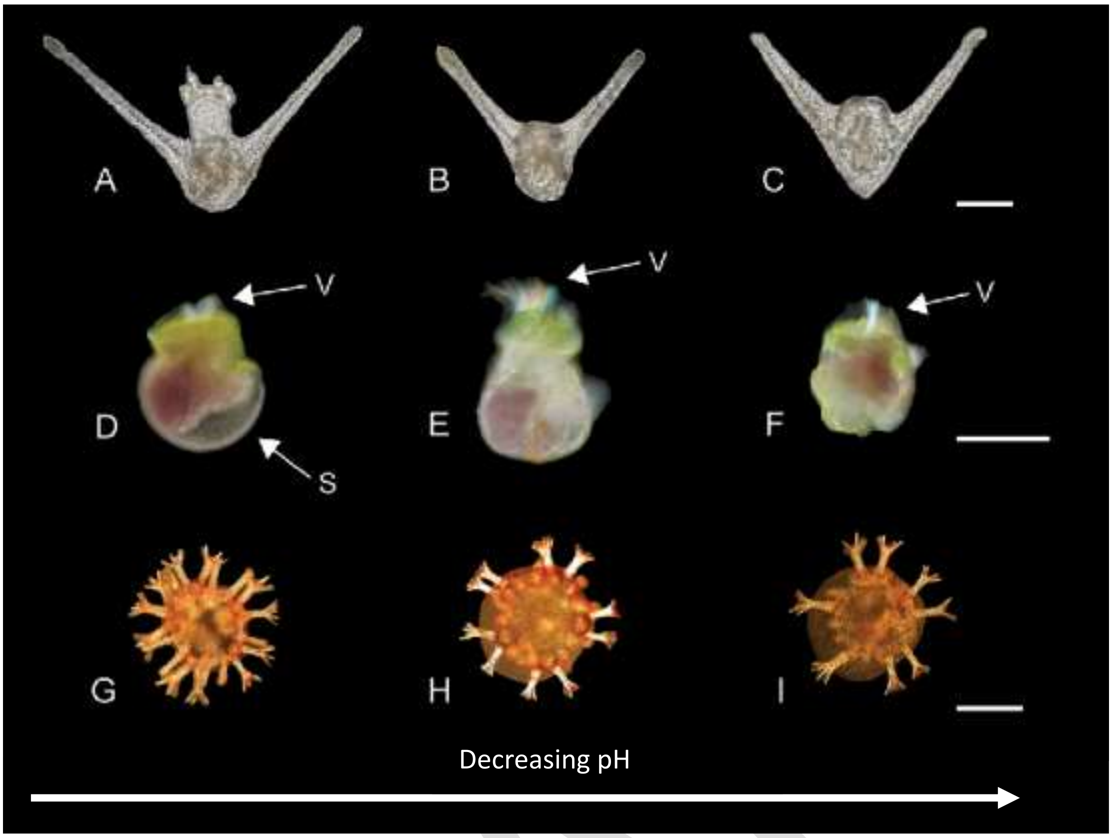

Figure 5.4. *A-C. Two-armed echinoplutei of the sea urchin* Centrostephanus rodgersii *reared in controls (A, pH 8.2/21°C) and smaller larvae from experimental (B, pH 7.8/21°C, C, pH 7.6/21°C) conditions. D-F. Veliger larvae of the abalone* Haliotis coccoradiata *reared in control (A, pH 8.2/20°C) conditions with a well-developed shell (arrow) and larvae reared in experimental (B-C, pH 7.8/20°C - pH 7.8/22°C) conditions lacking a shell. G-I Juvenile* Heliocidaris erythrogramma *reared in control (G, pH 8.2/20°C) and experimental (H, I pH 7.6/ 24°C) treatments, the latter showing abnormal calcification as seen in the reduced number of spines. Scales 100 µm. Source: Byrne et al. 2012. Seek permission - Elsevier*

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5.1.3. Sensory capacity and behaviour

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 fishes and some invertebrates [1, 2] (Figure 5.5). 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, and the smell of predators [3,4]. Response to auditory cues is altered [5], behavioural lateralization is lost [6] and fish are no longer able to learn [7]. 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, leading to higher mortality from predators [8, 9]. 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 [10, 11], habitat selection [12] and homing to resting sites [13]. A wide range of reef fish species appear to be affected [9], including important fisheries species such as the coral trout *Plectropomus leopardus* [14]. Impaired behaviour at all life stages occurs as a result of permanent exposure to CO_2 levels $\geq$ 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.

Figure 5.5. *Altered behaviour of larval damselfish when exposed to elevated CO_2; individuals were more active and ventured further from shelter. Munday et al. 2012a* [2]. *Seek permission.*

Key Messages:

1. Ocean acidification can alter sensory systems and behaviour in fishes and some invertebrates

2. Impacts include the loss of ability to discriminate between important chemical cues

Similar behavioural effects have been discovered in some marine invertebrates. An intertidal snail exhibited increased predator cue avoidance [15], and hermit crabs reduced their antennular flicking in response to food and altered their shell exchange behaviour, when exposed to ~12,000 µatm CO_2 [16, 17]. Whether similar behavioural abnormalities occur at near-future CO_2 levels is currently unknown.

Elevated pCO_2 alters fish behaviour, and possibly invertebrate behaviour, by interfering with brain neurotransmitter function [18]. 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, especially those that use Cl^- and/or HCO_3^- to maintain their acid-base balance when exposed to elevated CO_2. Some invertebrates are weak acid-base regulators and suffer metabolic depression when exposed to high CO_2 [19, 20]. 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 population 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 [8]. These individuals have much higher survivorship when exposed to predators compared with the individuals that are significantly affected by 700 µatm CO_2 [21]. 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.

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5.1.4. Immune responses and disease

Key Messages:

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

2. Future ocean acidification has the potential to impact immune functions in marine organisms

3. It is unknown whether future environmental change 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 realisation 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 (argued in Stentiford et al., [1]).

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 [2], and it has been speculated that even chronic moderate reductions in pH [3] 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 identified that there is a significant impact upon bivalve haemocyte functionality [4], acidosis and phagocyte numbers in echinoderms (variable between species) [5] and that over 6 months, immunity was impaired in sea stars as evidenced by reduced phagocytic capacity [6]. As environmental factors play a significant role in determining the course of infection [7], climate change has the potential to increase susceptibility to disease [8]. From the limited number of examples that are available above it can be concluded that there is the *potential* for future OA to 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 well 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 [9].

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5.2 Benthic communities

Benthic ecosystems comprise some of the key ocean communities that we rely upon for food and ecosystem services, and occur throughout the world's ocean from the splash zones of all shores to the deepest waters. While none will be immune to ocean acidification, it remains unclear how growing changes in ocean conditions will affect the composition and function of benthic communities in different environments.

Although environmental conditions are largely constant through time in the deep waters of the sea, there is considerable spatial variability, as carbonate chemistry of deep-sea waters is strongly related to large scale thermohaline circulation patterns. Consequently, abyssal pH is ca. 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 N.E. Pacific it shoals to ca. 200 m depth. Deep-sea benthic communities are, by far, the most widespread and abundant benthos in the world's oceans, and 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 highlighted lower rates of growth, survival, or other performance measures for many benthic organisms in acidified waters. Meta-analyses by Wittmann and Pörtner [2] demonstrated differing sensitivity of different marine taxa to ocean acidification, but a general negative or no effect was observed across the taxa in Figure 5.6.

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 examples exist of species living in low pH

4. For adult echinoderms, many studies show reduced growth, calcification and reproduction under elevated CO_2

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

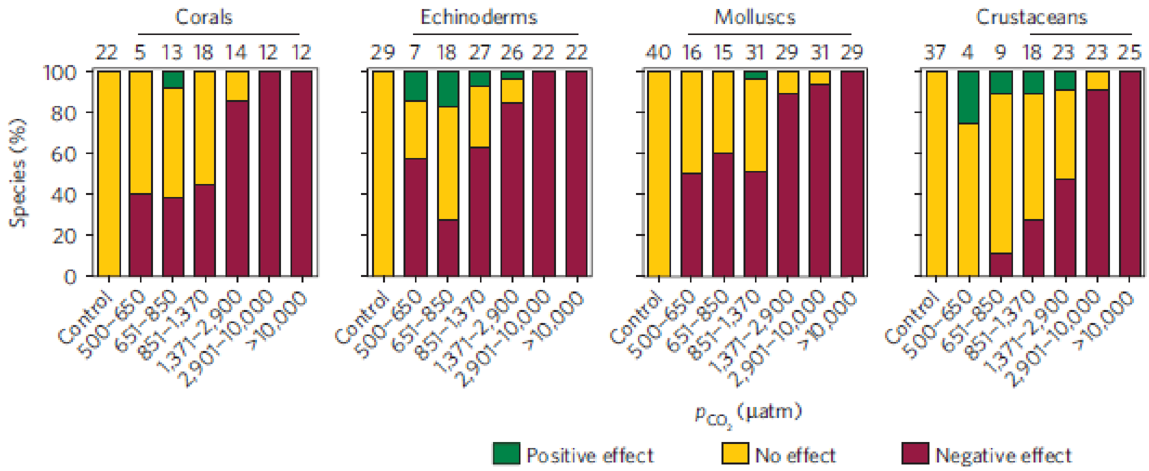

Figure 5.6. *Sensitivity of animal taxa to ocean acidification. Fractions (%)of coral, echinoderm, mollusc and crustacean exhibiting negative, no or positive effects on performance indicators reflecting individual fitness in response to increased* CO_2 *Bars above columns denote count ratios significantly associated with* pCO_2*. Modified from Wittmann and Pörtner* [2]*. Seek Permission.*

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 vast differences in the magnitude of variation among areas [5]; compared to the very mild variation (<0.1 pH units) in the open ocean over 30 days, pH at coastal sites can vary from ca. 0.2 to 0.8 pH units 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 (Figure 5.7).

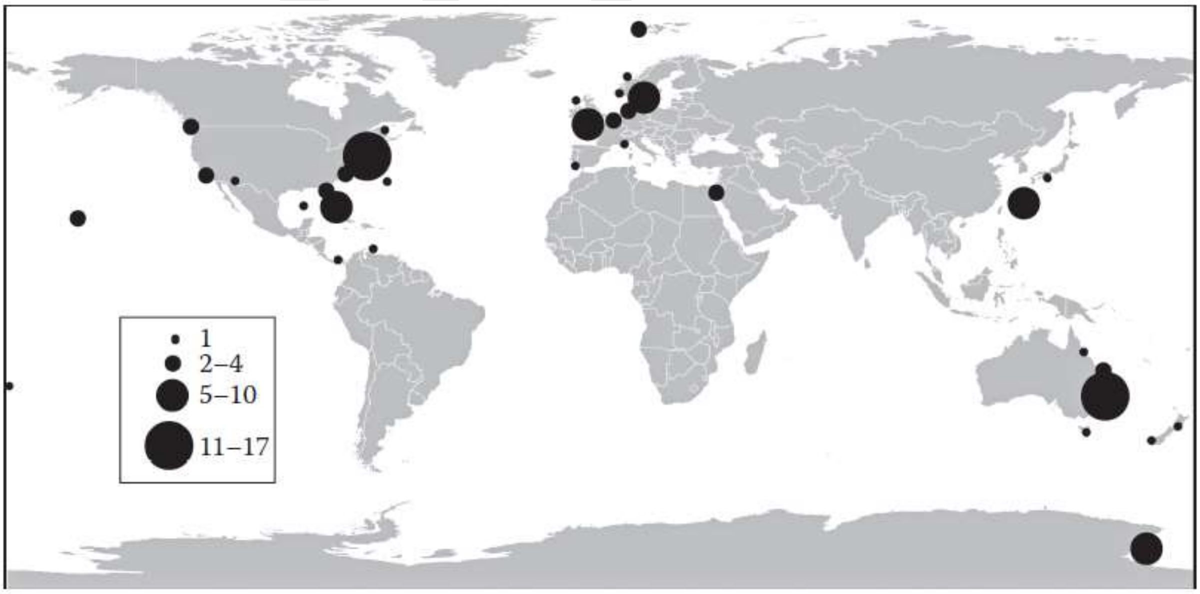

Figure 5.7. *Locations of experimental ocean acidification simulations on benthic organisms, using realistic pH values up to the end of the century. Size of circles represent number of organisms studied. Source: Wicks and Roberts 2012 Seek permission*

5.2.1. Coral Reefs

Tropical coral reef ecosystems represent one of the most biodiverse habitats in the oceans, being home to about a third of all marine species [6, 7]. 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 [8]. 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.

5.2.1.1. Cold-water corals (CWCs)

Cold-water corals, also often referred to as deep-water corals, are found in all of the world oceans, and overviews of their distribution can be found in Rogers [9], Freiwald et al.[10] and Roberts et al. [11], with new information on their distribution being updated through national mapping programmes such as MAREANO in Norway (www.mareano.no), The Deep Sea Coral Research and Technology Program (USA), and through European Community projects including HERMES, HERMIONE and CoralFISH. Figure 5.8 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.

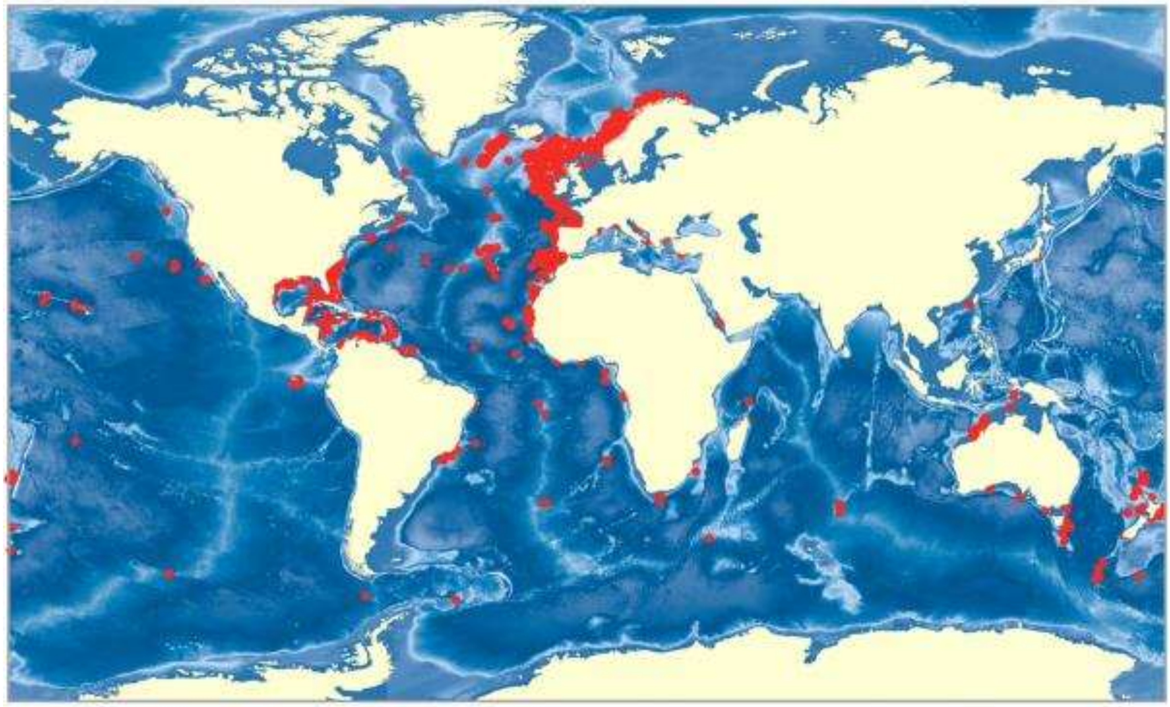

Figure 5.8. *Global distribution of reef framework–forming cold-water corals. Source: AAAS, Science.*

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-Artcic [12, 13], and are defined as vulnerable marine ecosystems (VMEs). Impact or damage to these VMEs may lower the local biodiversity and diminish the possibility for many species to find shelter and feeding grounds.

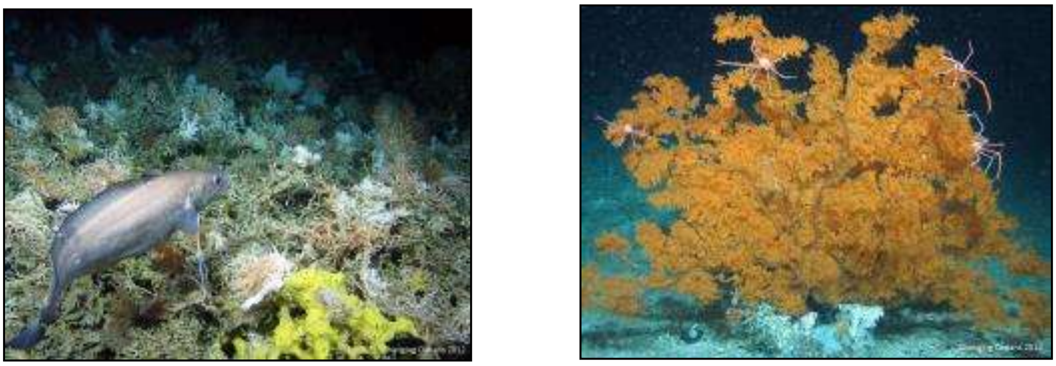

***Figure** 5.9. Deep-sea coral habitats. Source: Changing Oceans 2012*

Due to the uptake of anthropogenic CO_2 in the ocean both the aragonite saturation horizon (ASH) and calcite saturation horizon (CSH) (see sections 1 and 3) are becoming shallower. In places, *Lophelia pertusa* already lives very close to the ASH, for example in the Gulf of Mexico [14]. By the end of the century, many deep-sea corals are predicted to be in calcium carbonate undersaturated water [15, 16]. Guinotte et al. [15] 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 (Figure 5.10).

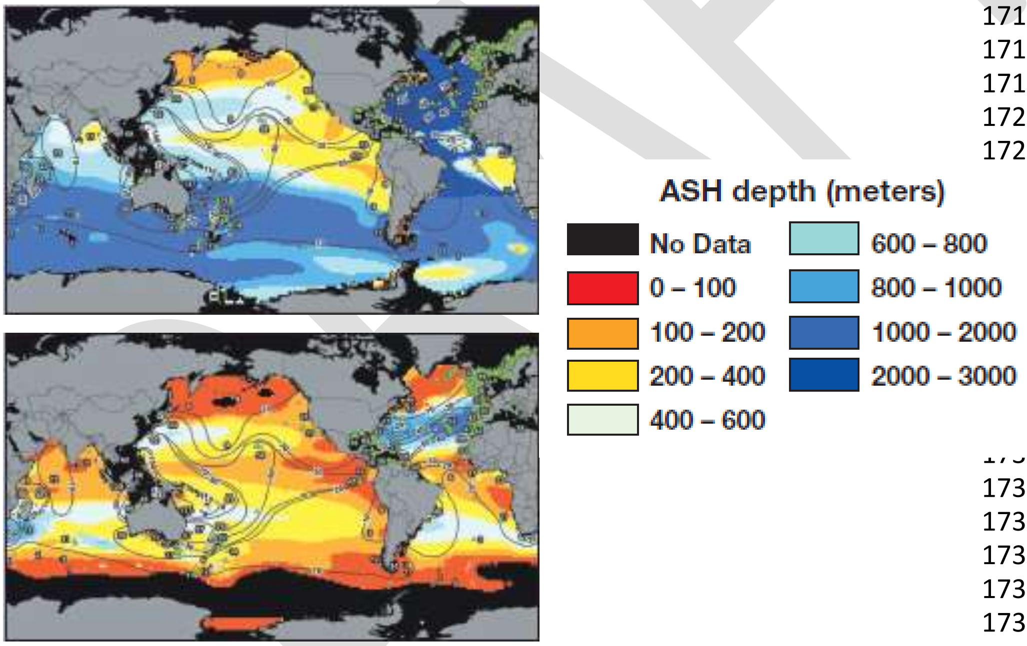

***Figure 5.10.** Depth of aragonite saturation horizon (ASH) and locations of deep-sea corals (green triangles). Top: Projected ASH depth for year 1995; pCO_2 = 365 ppmv. Bottom: Projected ASH for the year 2099; pCO_2 = 788 ppmv. Black areas appearing in Southern Ocean and North Pacific in bottom panel indicate where ASH depth has reached the surface. Contours indicate diversity for 706 species of azooxanthellate (without microalgal symbiont) corals. Numerals not fallinf on diversity contours indicate number of azooxanthellate coral species. Guinotte et al. 2006 [15]*. Seek permission

The limited evidence available for how ocean acidification will impact CWCs indicates that in the short term, projected decreases in pH can decrease metabolism and growth [17, 18, 19] (Maier et al. 2009; Form and Riebesell 2012; Hennige et al. 2013), but over 6-12 months, *L. pertusa* does not display reductions in growth when subjected to predicted end of the century CO_2 conditions [18, 20] (Form & Riebesell 2012, Maier et al. 2013). 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, and that potential increased energetic demands for living below the ASH cannot usually be met.

The ability and long-term sustainability of cold-water corals to survive and thrive below calcium carbonate saturation depths such as those noted by Thresher et al. [21] thus remain debated. Although scleractinian corals can up-regulate their internal pH at the sites of calcification through energy intensive processes [22,23,24, 25], the regulation only applies for coral skeleton that is covered by living coral tissue. CWC framework reefs are typically composed of a significant amount of bare, dead skeleton beneath the living material (Figure 5.11), which would start to dissolve in undersaturated conditions, and be eroded with increased efficiency by bio-eroding sponges [26]. Thus future changing conditions are likely to have large impacts upon current CWC habitats and associated biodiversity.

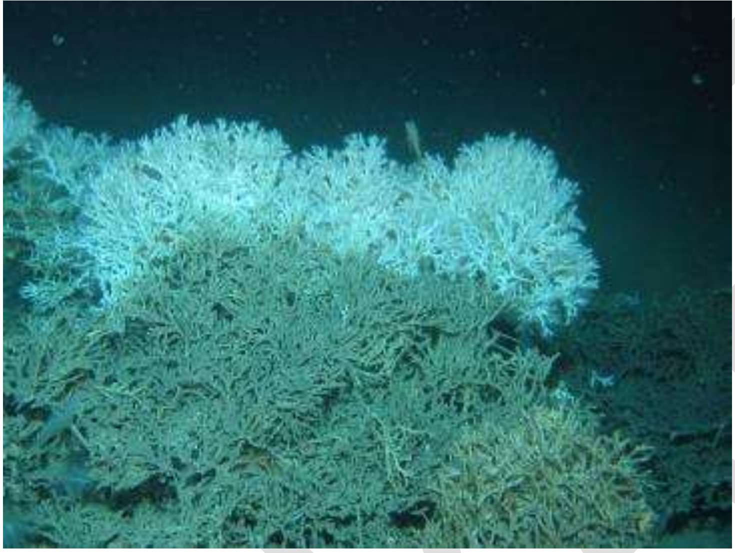

Figure 5.11. *Image of live Lophelia pertusa with underlying dead framework (Rockall Bank, NE Atlantic). Source: Changing Oceans 2012.*

5.2.1.2. Tropical corals

For tropical corals, many studies demonstrate a reduction in growth (net calcification rates) in response to ocean acidification [27, 28, 29, 30, 31]. However, this is not a ubiquitous response, with different species exhibiting negative [32], no measureable response [33], or variable responses [27] to reduced pH [34]. Furthermore, responses may be non-linear, such that there may be no response until a 'tipping point' is reached [35].

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 [1,36, 37, 38]. The general conclusion of these analyses and other reviews (e.g. Hoegh-Guldberg et al., Pandolfi et al., Erez et al., Andersson et al. [39, 40, 41, 42]), is that corals are sensitive to ocean acidification, with declines in coral calcification associated with declining aragonite saturation state and seawater pH (see Figure 5.12). 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.

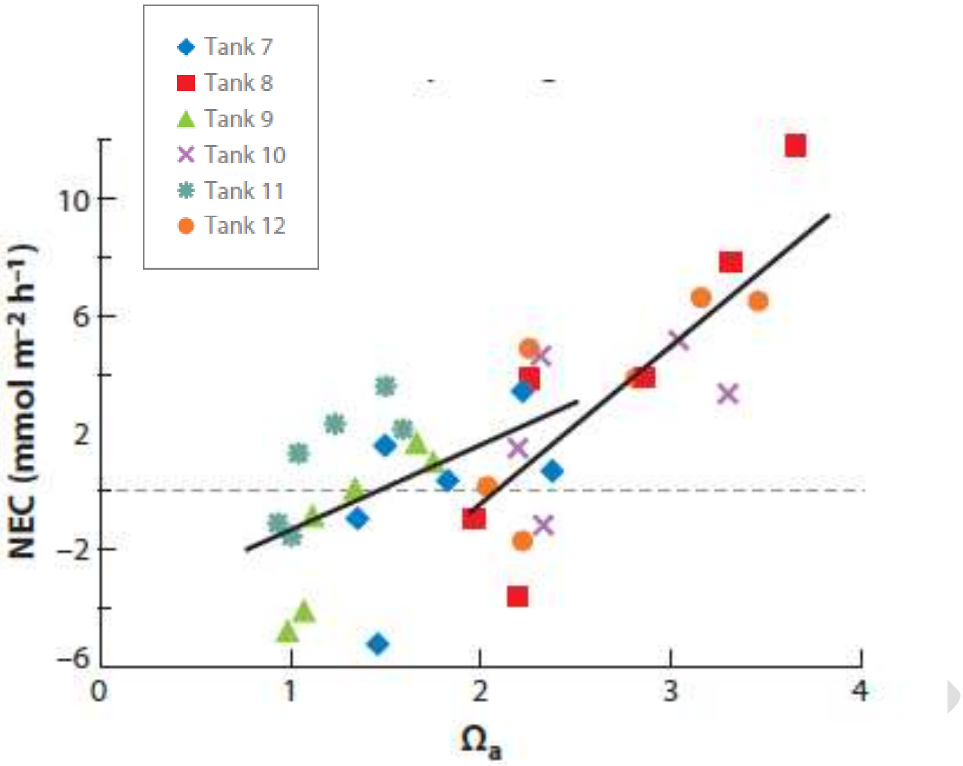

Figure 5.12. *Net ecosystem calcification as a function of aragonite saturation state of experimental sub-tropical coral mesocosms dominated by the coral* Montipora capitata *over a 24h period. Tanks 7, 9 and 11 were exposed to ambient conditions, and tanks 7, 9 and 11 were exposed to double ambient* pCO_2. *Growth rates decline with decreasing aragonite saturation, even though saturation states are >1. Andersson et al. 2012* [42] *with data from Andersson et al. 2009* [43]. *Seek permission*

There are lots of unanswered questions still to address with respect to the impact of ocean acidification on corals, and recent studies that have analysed coral gene expression highlighted that many more changes (including ion transport and cytoskeletal organisation) may be occurring than we currently quantify [44]. These changes in gene expression emphasize the need to expand future studies of ocean acidification to include a wider spectrum of cellular processes, many of which may occur before impacts on calcification.

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. For example variation in the capacity to regulate ions/ pH under ocean acidification may be a defining physiological trait that facilitates future survival, and there is emerging evidence in corals skeletons that suggests that the extent to which corals can upregulate pH varies from species to species [24]. Additionally, research has already indicated that temperature and ocean acidification can act synergistically for some species to reduce calcification rates more than ocean acidification acting alone [45], so future studies have to consider multiple stressors to determine the future fate of these key ecosystems.

5.2.2. Molluscs

Bivalve molluscs were identified in early ocean acidification research to be particularly challenged by ocean acidification (see Gazeau et al. 2013 [46] for a review), and indeed a large fraction is negatively impacted by even relatively low levels of ocean acidification (Figure 5.6); similar to echinoderms Wittmann and Pörtner [2]. However, for some species, while acute experiments without an acclimation period result in strong reductions in calcification [47], longer-term incubations with realistic food regimes demonstrated that significant calcification can be maintained even when the seawater is undersaturated with respect to calcium carbonate, such as for adult mytilid mussels [48,49,50]. In fact, mussels (*Bathymodiolus brevior*) have been found close to deep-sea hydrothermal vents, growing at pH values between 5.36-7.29. While this feature indicates great biological control over the calcification process, Tunnicliffe et al.[51] also suggest a fundamental role of the external organic cover, the periostracum, in enabling persistence at such stressful locations. A similar role of the periostracum has been suggested for coastal *Mytilus edulis*, which can also calcify at very high rates when calcium carbonate is undersaturated [49]. Results from a coastal enriched CO_2 habitat, the Western Baltic Sea, indicate that successful settlement and dominance of mytilid mussels and other calcifying invertebrates is possible at seawater pCO_2 values similar to those projected for the end of the century [49,52]. Where reductions in growth and calcification are observed, energy budget reallocation may be the cause [53], or potentially increased oxidative stress [54]. Future research should thus focus on determining cellular energy budgets to analyze energetic trade-offs.

Of course, the impact of ocean acidification to larval stages of bivalves is also of great importance to their continued survival, especially since larval bivalves and heavily calcified pelagic larvae of other molluscs have been shown to be sensitive to ocean acidification [55, 56, 57]. This topic is covered in more depth in section 5.1.2.

Figure 5.13. *The blue mussel* Mytilus edulis *shell (Left) and cultured on ropes (Right). Images courtesy of the Atlantic Marine Aquaculture Center, University of New Hampshire.*

5.2.3 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 5.1.2 for more details on echinoderm larval stages). Briefly, while early life stages of some species have been shown to react with severely increased mortality to ocean acidification (e.g. Dupont et al. 2008 [58]), most species respond with slight reductions in larval growth and calcification performance [59,60].

When exposed to simulated ocean acidification, adult echinoderms suffer from energy budget reallocation, with only few examples of increased mortality (e.g. Shirayama & Thornton 2005 [61]). While moderately elevated pCO_2 (<1,000 µatm) has led to increased feeding and growth rates in intertidal sea stars [62], other studies identified reduced investment in growth, calcification, reproduction or immunity (e.g. Appelhans et al., Wood et al., Findlay et al., Hernroth et al., Stumpp et al. 2012 [63,64,65,66,67]). Most of these studies have been conducted using shallow-dwelling species. However, deep-sea and polar species that live close to calcium carbonate saturation horizons might be more at risk, and deserve more future research attention [68]. As with studies on molluscs, little research attention has been devoted to understanding long-term, trans-generational and adaptive responses of echinoderms to ocean acidification [59], and future studies should reflect this.

Figure 5.14. *Echinoderms- The sea urchin* Strongylocentrotus droebachiensis *(Left) and brittlestars* Ophiothrix fragilis *(Right). Source Robert Cook.*

5.2.4 Seagrass and macroalgae

Macroalgae can be calcareous or non-calcareous and form an important component of many coastal ecosystems [69], and many macroalgae species are known to be tolerant to or benefit from future ocean acidification [4,69,70,71,72] (Figure 5.15). While ocean acidification can be detrimental to the calcifying species, the enhanced CO_2 can also increase productivity in calcareous and non-calcareous species alike (See Johnson et al. [72]). It is also important to note that seagrass dominated areas, can also substantially modify their own seawater carbonate chemistry environment through primary productivity. This leads to substantial diel variability in seawater pH [73,74]. In the case of tropical seagrasses, they could potentially benefit adjacent coral reef systems by elevating pH by up to 0.38 at tidal intervals [73].

Although ocean acidification is generally detrimental to calcareous algae [75, 76], some species like *Padina* spp. have been found to thrive under naturally high CO_2 conditions even after decalcification [72], although this may be due in part to a concurrent decrease in grazers. The role of grazers and species interactions may thus be an important aspect for future studies to consider in more depth, as there is also emerging evidence that high CO_2 can decrease the production of protective phenolic substances used to deter grazers [77].

Figure 5.15. *Seagrass and a natural CO_2 seep. Source: Giorgio Caramanna.*

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5.3 Pelagic communities

5.3.1. Plankton

Plankton play an important role in marine ecosystems, and comprises of phytoplankton (photosynthetic plankton), zooplankton (which includes organisms that spend their whole life in the water column as well as juveniles and gametes of many benthic organisms), and bacteria. These plankton (calcifiers and non-calcifiers) form a key component of the marine food chain and also in biogeochemical cycling.

Biocalcification by plankton (phyto- and zoo-) is thought to have a special role in the carbon cycle through assisting export of organic matter out of the upper ocean and its burial in deep-sea sediments. Sedimentologists studying the flux of particles collected in deep-sea sediment traps have inferred that “ballasting” of organic matter aggregates by biominerals is likely a key factor in facilitating export 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 section 5.4.3 for more detail).

5.3.1.1 Phytoplankton and bacteria

Non-calcifying phytoplankton - These organisms form a significant proportion of the phytoplankton and can include diatoms, cyanobacteria and dinoflagellates. Many Harmful Algal Bloom species (HAB) are included in this group. Stimulating effects of increased CO_2 on photosynthesis and carbon fixation have been noted in all of these groups [3, 4, 5, 6]. It is hypothesised that an increase in CO_2 will be of benefit to phytoplankton, as the increased CO_2 in external seawater will reduce CO_2 diffusion leakage from biological cells (where the CO_2 is concentrated) to the surrounding seawater [3]. However, photosynthetic mechanisms vary widely between photosynthetic organisms [7], and this may lead to a shift in community composition in the future [8]. Assessing whether HAB species will be among those which will benefit from future environmental change remains a key focus for future research [9].

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 demonstrate enhanced net carbon uptake by phytoplankton under elevated CO_2

4. Bacterial response to ocean acidification has yet to be quantified fully, but any changes will have implications for nutrient cycling

5. Planktonic Foraminifera and pteropods will experience decreased calcification or dissolution under predicted future conditions

6. Decreases in planktonic Foraminifera shell thicknesses and sizes may decrease efficiency of future carbon transport between the sea surface and floor

Calcifying phytoplankton - Of the calcifying algae, coccolithophores are perhaps the group which have received most interest, as they form a major component of the phytoplankton in more oligotrophic waters. They are biogeochemically important as carbonate producers, and are extensively studied by geologists. Chalk is predominantly formed of fossil coccoliths. Coccolithophores are a group of unicellular phytoplankton which produce calcite plates called coccoliths (Figure 5.16), and cells are typically 5 to 20 µm across but are present in abundances of tens of thousands to millions per litre in most seawater from the photic zone.

Unlike some planktonic zooplankton, some species of coccolithophores (such as *Emiliania huxleyi*) can readily be grown in laboratory cultures and at least 40 significant 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 that there was a clear reduction in calcification with increasing $p\mathrm{CO}_2$ [10, 11, 12, 13]. They did, however, note that other effects such as growth rate and cell size changes could obscure this response. This may be due to shifting balances in potential positives and negatives for photosynthesis and calcification. Building on these initial indications of a distinct influence of carbonate chemistry on coccolithophores, several ecological studies suggested that variations in carbonate saturation state might influence aspects of the distribution of modern coccolithophores, such as the timing of blooms [14], and absence of coccolithophores from the Baltic Sea [15] and from parts of the Antarctic [16]. Most strikingly it has been suggested that coccolith mass in *E. huxleyi* and closely related species is controlled by saturation state in both the modern ocean and historically [17].

However, culture work on species other than *E. huxleyi* can show very different responses, with some species showing negligible response to elevated $p\mathrm{CO}_2$ [18]. Moreover it has been shown that even within *E. huxleyi*, the response of different laboratory strains is highly variable, with responses varying from no calcification to increased calcification in response to strongly elevated $p\mathrm{CO}_2$ conditions [19]. Importantly, Lohbeck and colleagues [20] suggested that coccolithophores may be able to adapt to changing conditions even on the relatively rapid timescales at which they are occurring.

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 [19, 21].

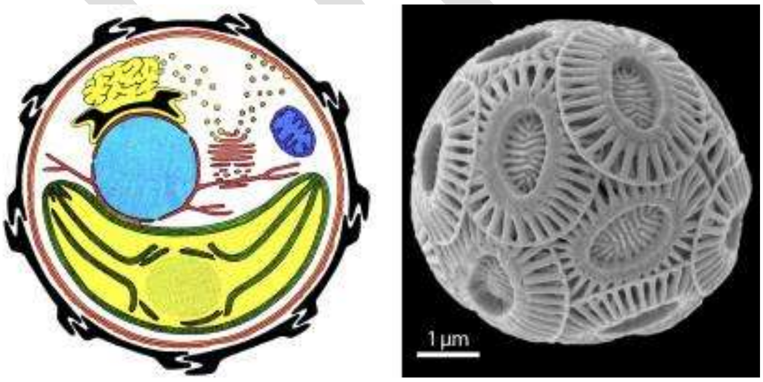

***Figure 5.16**. Left: Drawing of a single cell of* Emiliania huxleyi *showing coccoliths (black) forming within an intracellular vesicle before being extruded to form the extracellular coccosphere (image courtesy of Peter Westbroek). Right: Scanning electron micrograph of an* E. huxleyi *coccosphere.*

Bacteria - While some bacteria are counted among the phytoplankton (*Synechoocuccus* and *Prochlorococcus*), many do not photosynthesise but can play a key role in nutrient cycling, being 'free-living' or associated with some of the other plankton such as Foraminifera. 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 bacteria which associate as biofilms suggests that future changes will alter bacterial community composition [22]. Future nutrient cycling may also change depending upon whether bacterial communities change significantly as pH decreases, which could have direct impacts upon nutrient cycling between benthic and pelagic ecosystems [23].

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 and used in Svalbard, Norway, to assess impacts of ocean acidification over ecologically relevant timescales under close-to-natural conditions. Results indicated that under high CO_2/ low pH, phytoplankton community composition changed but the microzooplankton community exhibited high tolerance (Aberle et al.[24]). Importantly, net carbon uptake by phytoplankton was enhanced, but the systems were pushed towards overall negative effects on export potential (Czerny et al.[25]).

Experimental ocean acidification mesocosms in Svalbard, Norway. Photo: Maike Nicolai, GEOMAR. Seek permission

5.3.1.2. 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 gastropods (i.e. snails) 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 is also often elaborately modified [26] (Figure 5.17). Pteropods occur throughout the global ocean but they are but are most abundant in sub-Arctic and sub-Antarctic to Antarctic waters where they can form a significant part of the zooplankton and are important foodstocks for fish and other predators [27]. Pteropods have shells formed of aragonite rather than calcite. The combination of thin aragonitic shells and 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 since undersaturation will first occur at high latitudes, a combination of the direct effect of low temperatures on solubility as well as concomitant decreases in carbonate ion concentrations [28].

Early shipboard incubations demonstrated that pteropod shell dissolution could indeed easily occur, which has now been replicated in the Antarctic at $\Omega_{\text{aragonite}} < 1$ [28, 29, 30]. In addition to no calcification occurring when seawater is undersaturated ($\Omega_{\text{aragonite}} < 1$), it has now also been demonstrated that calcification is inhibited at significantly higher levels of $\Omega_{\text{aragonite}}$ [31, 32, 33]. The vulnerability of pteropods to ocean acidification and warming has been demonstrated for the Arctic pteropod *Limacina halicina*, in which shell growth was reduced and degradation increased at moderately elevated temperature and $p\text{CO}_2$ (1100 µatm) [34] despite some regulatory capacity to ameliorate these effects [35]. This has been further confirmed by a modeling study combining predicted aragonite saturation states for the end of the century, with data on the likely impact on pteropod calcification, which concluded that "there appears little future for high-latitude shelled pteropods" [36].

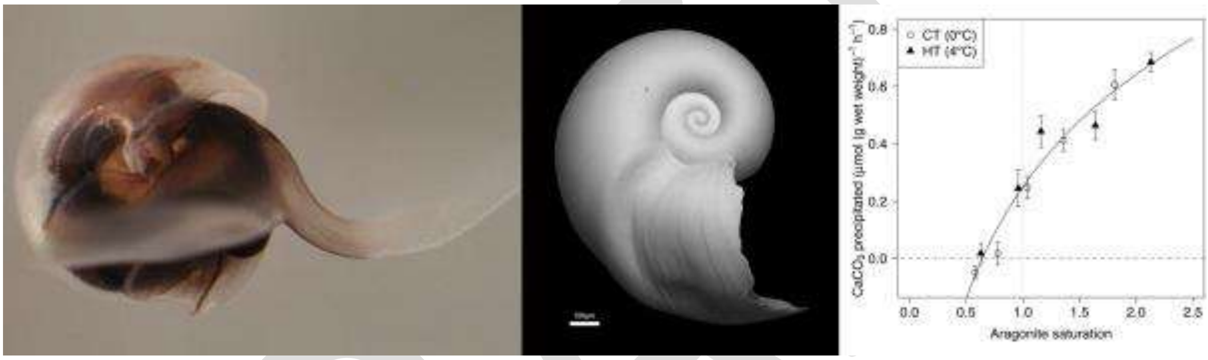

Figure 5.17. *Left: A living pteropod from the Arctic (image Vicky Peck, BAS). Centre: The shell of a juvenile pteropod from the South Atlantic. Right: Data from laboratory culture experiments on shell growth rate of* Limacina helicina *incubated under aragonite saturation states equivalent to those seen in the Artic at present day (ca 2.0) to the year 2100 (<1.0), from Comeau et al* [33].

Planktonic foraminifera are a group of unicellular zooplankton forming chambered calcite shells. The shells are elegant structures typically about 0.1 to 0.5 mm across and many species have a halo of delicate radial spines supporting a mass of protoplasm, gas bubbles, and symbiotic algae. 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 [37]. This makes them important contributors to the ballasting effect, and makes them 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 $\Omega_{\text{(calcite)}} = 1$ [38, 39, 40, 41, 42] (Figure 5.18). This is also confirmed through geological studies [43, 44]. Perhaps most remarkably, 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 [44, 45].

However, shell mass and thickness is also controlled by other factors such as temperature, depth and gametogenic calcite formation, and to date only a few studies exist on foraminiferal shell mass and thickness. Despite this, and that recent work on pre-Quaternary fossil records of planktonic Foraminifera failed to find predicted effects of carbonate chemistry [46], 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.

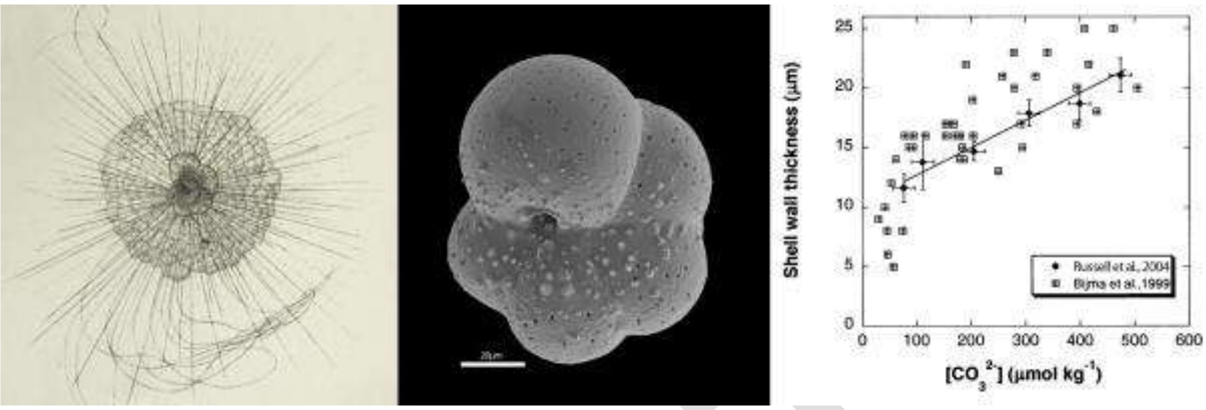

Figure 5.18. *Left: Drawing of a modern planktonic Foraminifera surrounded by a halo of bubbles and symbiotic algae supported by spines (Brady, 1884* [47]*, Permission: David C. Bossard, 19thcenturyscience.org). Centre: Scanning electron micrograph of the shell of juvenile planktonic Foraminifera. Right: Laboratory culture data variation in shell wall thickness in* Orbulina universa *cultured under bicarbonate conditions equivalent to those from the modern ocean (ca. 250µmol kg^{-1}) to those anticipated in 2100 (ca. 100 µmolkg^{-1}), and under rather more extreme conditions (from Russell et al. (2004)* [40] *incorporating data from Bijma et al. (1999* [39]*)). Seek permission for graph-Elsevier*

Copepods - Direct effects of elevated pCO_2 on copepods have only recently gained attention, and our knowledge on 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 forming the predominant link in pelagic food webs between primary production and higher trophic levels [48, 49]. 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 [50, 51, 52, 53, 54, 55]. However, in Arctic mescosm experiments over thirty 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 [56], although the grazing rates of *Calanus* spp. decreased with increasing CO_2 [57]. Other, more sensitive species such as *Centropages tenuiremis* had increased respiration and grazing rates at 1000 µatm.

Direct effects of CO_2 on copepods and other non-calcifiying heterotrophic plankton may not be as potentially severe as for calcifying organisms. However, 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 [58]. Thus, non-calcifying organisms may also be impacted by ocean acidification via trophic interactions.

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5.3.2. Fish, squid and cuttlefish

Key Messages:

1. Most fish are likely able to maintain sufficient O_2 delivery under future conditions, but squid 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 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, squid are also important in terms of abundance and economic value.

Fish are generally considered to be more resilient to 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 [1]. Fish compensate for acidosis (increased acidity in blood or tissues) by transport of acid-base relevant ions, mostly across the gills [2, 3]. In most species studied to date, almost complete compensation of acidosis occurs within a few hours or days of exposure to elevated CO_2 [3, 4, 5, 6]. 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 [7].

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 [8]. Although aerobic scope in two tropical cardinalfishes declined significantly at projected future CO_2 levels [9], Atlantic cod 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 [10]. Furthermore, studies on freshwater and estuarine fishes exposed to CO_2 levels many times greater than end-of-century predictions for ocean pCO_2 have generally found no effect on oxygen uptake or swimming performance [3, 7, 11]. 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.

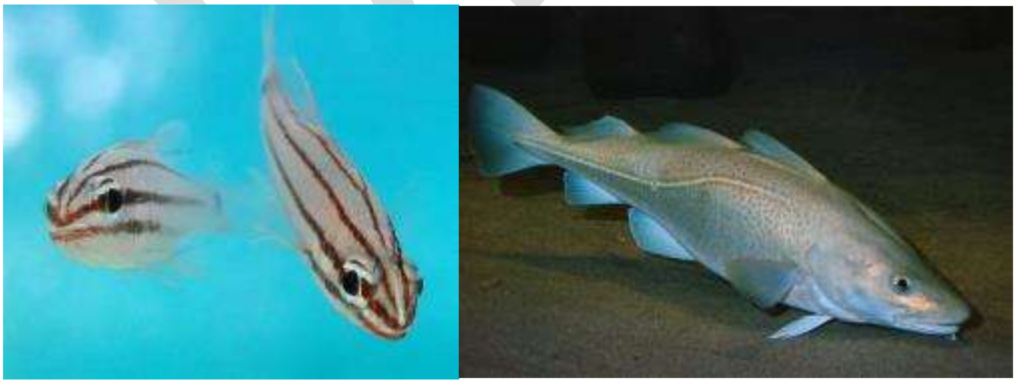

Figure 5.19. *Left – The cardinalfish* Ostorhinchus doederleini. *Right – Atlantic cod* Gadus morhua. *Image source Goran Nilsson and animalspot.net*

CO_2 effects on cellular energy budgets have scarcely been studied to date, yet it has been shown for Antarctic fish (*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 [6]. Increased intracellular levels of bicarbonate, due to both increased pCO_2 and active pH buffering by bicarbonate uptake [3] can lead to competitive inhibition of enzymes of the Krebs cycle (citrate synthase, succinate dehydrogenase) and elicit transcriptional changes and functional modifications of mitochondrial proteins by activation of a soluble adenylyl cyclase and subsequent action of protein kinase A (PKA) [12].

The effects of ocean acidification on development, growth and survival of marine fishes has largely focused on larval and juvenile stages, because they are predicted to be more sensitive to elevated pCO_2 than adults [1, 7]. Despite this prediction, recent studies have found that the early life-history stages of some fishes are resilient to projected future levels of ocean acidification. Development, growth and survival of larvae and juveniles of several reef fish species [13, 14], the pelagic cobia [15] and walleye pollock [16] appear relatively robust to near-future CO_2 levels (≤1000 µatm CO_2). In contrast, larval growth declined and mortality increased in the estuarine species *Menidia beryllina* at similar CO_2 levels [17] (Figure 5.20), and tissue development was disrupted in Atlantic cod *Gadus morhua* reared at higher CO_2 levels (1,800 and 4,200 µatm CO_2) [18]. These studies suggest that the sensitivity of larval and juvenile fishes to rising CO_2 levels is highly variable and that some species will be negatively impacted. However, 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 [19]. Therefore, it is premature to conclude that near-future CO_2 levels will have significant negative effects on the growth, development or survival of marine fishes until studies include exposure to high CO_2 during both the parental and offspring generations.

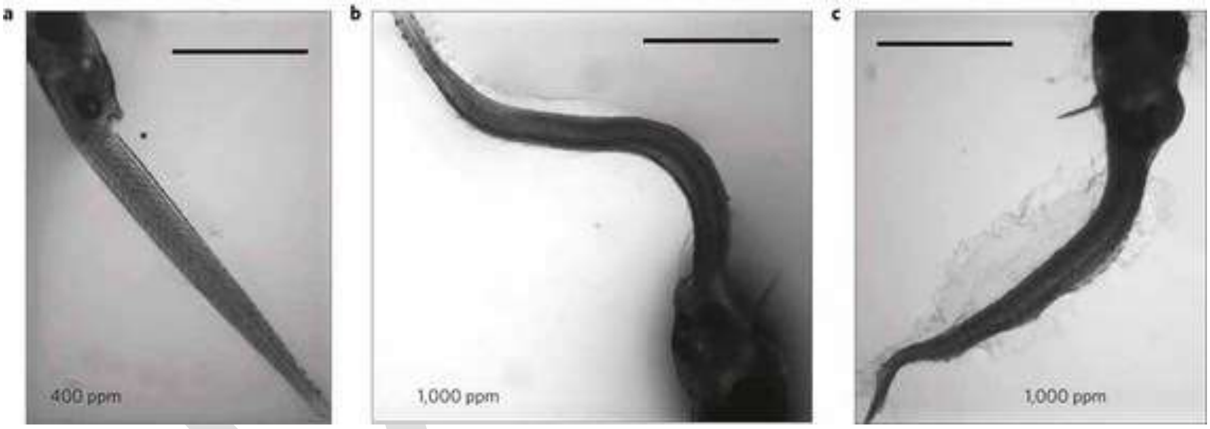

***Figure 5.20.* *a*–*c*, *Larvae with curved or curled bodies were significantly more common at increased (**b**,**c**) when compared with control (**a**) CO_2 levels. Scale bar=1 mm. Adapted by permission from Macmillan Publishers Ltd: Nature Climate Change (Baumann et al.), copyright (2012).*

The effects of chronic exposure to high CO_2 on fish reproduction has been little studied, but preliminary studies have not detected substantial impacts. Sperm motility is arrested by mild increases in pCO_2 in some flatfishes [20], but not in Baltic cod, *Gadus morhua* [21], or 11 other species from a range of families [20]. 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 [22]. 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 [7], which is 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, exposure to elevated CO_2 causes sensory and behavioural impairment in a range of marine fish [23]. Second, otolith (earbone) size is consistently larger in larval and juvenile fishes reared under elevated CO_2. Larger ear bones have been observed in larval seabass [24] (Figure 5.21), clownfish [25], cobia [15] and Atlantic cod [26] 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 [27].

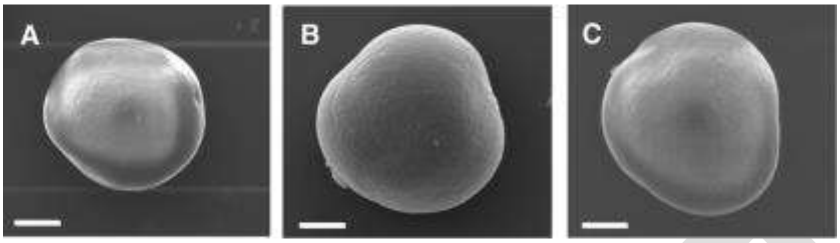

Figure 5.21. *Dorsal view of sagittal otoliths of 7-day-old white sea bass grown at (**A**) 430, (**B**) 1000, and (**C**) 2500 µatm $p(CO_2)_{seawater}$. Scale bars indicate 10 µm. Source: Seek permission*

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. The 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 [28]. Haemocyanin is very sensitive to CO_2 and as such, blood oxygen transport can be easily disturbed to reduce activity [29, 30] 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 [31]. Importantly, 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 [32].

More research is needed to characterise the effects of ocean acidification and warming on the cuttlefish *Sepia officinalis*, one of the most common in Europe. While it does not appear detrimentally impacted by ocean acidification during some development studies, and even displays increased calcium uptake into its cuttlebone [33], when combined with temperature *S. officinalis* displayed shorter embryonic periods, lower survival rates and enhanced premature hatching [34].

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5.4 Impacts on ecosystem services, livelihoods, and biogeochemical cycles

5.4.1 Impacts on ecosystem services

The previous sections show how pH affects different organisms and ultimately biodiversity, but what do these changes mean for society? The implications for society will become apparent if ocean acidification causes changes in the health, abundance or distribution of economically and socially important marine species and the ecosystems that support them [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 (e.g. Hall-Spencer et al. [3]).

To examine the societal implications of ocean acidification in more depth, an ecosystem services framework can be used. Ecosystem services are the components of nature that are used (actively or passively) to create human well-being and economic wealth [4]. They result from ecological processes, functions and biodiversity [5], and society is dependent upon them as a life support system as well as for enhancing its well-being [6]. At a general level, ecosystem services can be categorised into four distinct groups [7]: **provisioning services** (e.g. food and fibres); **regulating services** (e.g. gas and climate regulation and bioremediation of waste); **cultural services** (e.g. education, recreation and inspiration); and **supporting services** (e.g. nutrient cycling, primary production and ecosystem resilience) (Figure 5.22).

Key Messages:

1. Ocean acidification has already impacted the provisioning services of some oyster hatcheries

2. Impact of ocean acidification on ecosystem services can on provisional, regulating, cultural, and supporting services.

3. Estimated impacts of ocean acidification are estimated to be over $1000 billion annually for molluscs and coral reefs by 2100

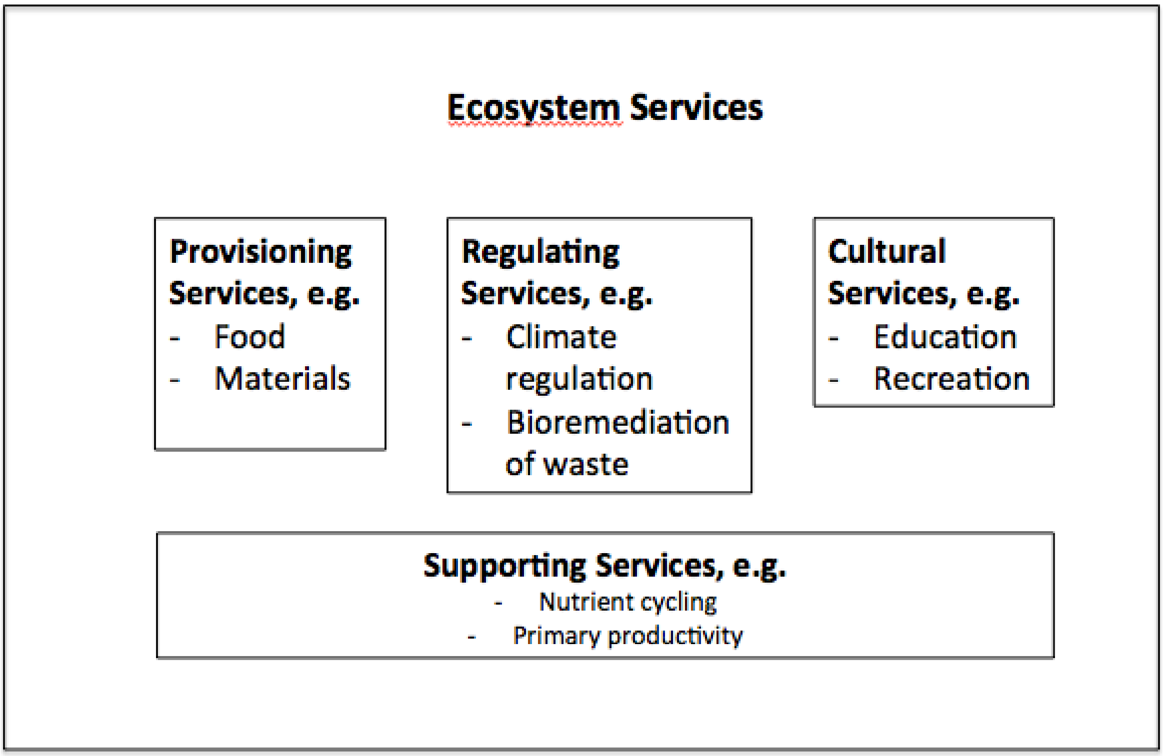


Figure 5.22. *Simplified summary of ecosystem services with selected examples given*

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. many calcifiers) are habitat-forming organisms providing shelter, food and nursery functions to many marine species, including commercially important fish species. They also contribute to coastal protection, leisure, recreation and other cultural benefits. Nutrient cycling e.g. changes in N-fixation [8, 9], or changes in bioturbator and bioirrigator communities will also change the fundamental processes within ecosystems [2].

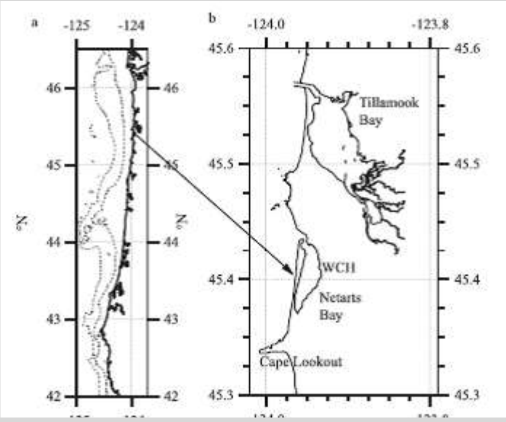
Provisioning services - Evidence supporting the impacts on provisioning services is variable. Molluscs and crustaceans harvested for food are likely to be affected as they have calcareous shells and exoskeletons. Non-experimental evidence of the impact of OA on molluscs has been reported at sites along the Pacific North West of the USA where the failure of oyster reproduction in hatcheries has been attributed to high levels of CO_2 in the water that upwells along that coast [10, 11]. Impacts such as these may have different implications depending upon their location. For example, small island states that are reliant upon shellfish aquaculture for export and for protein intake would be particularly vulnerable to ocean acidification in this instance [12]. However, adaptation of organisms may also be possible, as seems to be the case for molluscs reportedly thriving in naturally CO_2 enriched waters (e.g. Kiel Fjord [13]). Some other species may be indirectly impacted by ocean acidification by changes in their food chain and habitat. Examples include finfish, [14] such as haddock, which feed on calcifying organisms like echinoderms. It is also important to consider the national impacts of altered provisional services

Regulating services - This includes coastal defense and carbon storage. Many marine communities (e.g. tropical coral reefs, mangroves, seagrass meadows and bivalve beds) can dissipate the energy in waves reaching the coast, influence sedimentation rates and affect levels of erosion at the coast [15, 16]. Changes in these communities resulting from ocean acidification will therefore affect their ability to protect the coast. In addition, 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 [17] 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 to reefs attracting less tourism 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 are important to, for example, people’s heritage and identity (e.g. in some native Australian communities) any loss of these species may lead to further erosion of their heritage and identity. Understanding the impacts of ocean acidification on tourism, leisure and recreation is also challenging, and more research is required to quantify this.

Impact of ocean acidification upon oyster hatcheries

On the North West coast of the USA, established oyster hatcheries have suffered up to 80% larval mortalities since 2006. While it is understood that predicted ocean acidification is detrimental for many larval stages (see early life section), the conditions on the coast of Oregon mean that effects are being felt now. The threats to this key industry in the Pacific Northwest could impact upon its total economic value of $278 million (as of 2009; Pacific Coast Shellfish Growers Association 2010). Barton et al. [11] documented the variable carbonate chemistry and pH of the water due to the periodic upwellings, and noted that waters already in transit to the upwelling locations could be more corrosive due to exposure to the recent higher CO_2 atmosphere. The oyster hatcheries have now adapted their working practices so that they avoid using corrosive seawaters by recirculating their seawater systems during upwelling events.



a) map of Oregon coast from California border to the mouth of the Columbia River. Dotted contours offshore show the portion of the 100- and 200-m isobaths. b) expanded view of Netarts Bay, where 'WCH' denote the position of the Whiskey Creek Hatchery. Barton et al. 2012.
Seek Permission

5.4.2 Economic/livelihood impact

Assessing the impacts of ocean acidification on economic welfare requires that the full impact pathway is understood and modeled. This demands the coupling or integration of models that explain each step in the pathway linking (1) socio-economic activities, CO_2 emissions, ocean acidification, (2) impacts on marine ecosystems, (3) changes in the provision of ecosystem services, and finally (4) impacts on human welfare.

Reviewing the existing economic literature on ocean acidification, only a partial set of the potentially impacted ecosystem services have been assessed, with a focus on the direct use values that can be more easily addressed. Of the thirteen studies reviewed in Table 5.1 only five provide monetary estimates of the costs of ocean acidification. Three of these are for impacts on mollusc fisheries (two for the US 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 5.1 and standardized to annual values in the terminal year of each analysis in US$ at 2010 price levels. From the limited information that is currently available, it appears that impacts to tropical coral reef services dominate, so 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 potential fisheries catch in more acidic waters [18]. This would impact upon quantity, quality and predictability of future catches [19]. It is also important to consider projected impacts upon different communities i.e. indigenous communities as well as global markets. Coastal indigenous peoples catch large quantities of marine species, which may be consumed, or traded with some with inland groups in exchange for other indigenous foods like plants, berries, and terrestrial mammals. 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. Urgent research is thus needed to understand likely impacts in multiple coastal communities (http://www-crp.iaea.org/html/rifa-show-activecrp.asp).

Table 5.1. *Summary of studies that examine the economic impacts of ocean acidification. Brander et al.* [20]

Study	**Impacts**	**Geographic scope**	**Emissions scenario**	**Period of analysis**	**Welfare measure**[1]	**Annual value (US$; billions)**[2]
Armstrong et al. (2012) [21]	Fisheries	Norway	pH decrease 0.5	2010 – 2110	Revenue	0.01
	Carbon storage	Norway	pH decrease 0.5	2010 – 2110	Damage Cost	3
Brander et al. (2012) [22]	Coral reefs	Global	SRES A1B	2000 - 2100	Mixed	1,093
Cheung et al. (2011) [18]	Fish and invertebrates	N-E Atlantic	SRES A1B	2005 - 2050	-	-
Cooley & Doney (2009) [23]	Molluscs	United States	IPCC A1F1	2007 - 2060	Revenue	0.07
Cooley et al. (2012) [12]	Molluscs	Global	CCSM3	2010 - 2060	-	-
Finnoff (2010) [24]	Fisheries; non-use values	Baring Sea	-	-	-	-
Harrould-Kolieb et al. (2009) [25]	Coral reefs; fisheries	Global	SRES A1B	2009 - 2050	-	-
Hilmi et al. (2012) [26]	All	Global	-	-	-	-
Kite-Powell (2009) [27]	Coral reefs; fisheries	Global	IS92a	-	-	-
Moore (2011) [28]	Molluscs	United States	RCP8.5; RCP6	2010 - 2100	CV	0.31
Narita et al. (2012) [29]	Molluscs	Global	IS92a	2000 - 2100	CS, PS	139
Rodrigues et al. (2013) [30]	Use and non-use values	Mediterranean	-	-	-	-
Sumaila et al. (2011) [19]	Capture fisheries	Global	-	-	-	-

[1] CV: compensating variation; CS: consumer surplus; PS: producer surplus

[2] Impact estimates are standardised to annual values for the terminal year in each analysis (i.e., 2060 for Cooley and Doney (2009) and 2100 otherwise) in US$ 2010 price levels

5.4.2.1 Tropical coral reefs

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 ~$1000 billion by 2100 [20] (Brander et al. 2012). The value varies across scenarios due to (1) differing projected rates of CO_2 emissions, ocean acidification and loss of coral cover; and (2) differing rates of population and income growth that determine the value of coral reef services per unit area of coral cover. The results show that the annual economic impact (loss of coral reef service value) escalates rapidly over time, essentially because the scenarios have high economic growth in countries with coral reefs, and because demand for coral reef services increases more than proportionately with income. Nonetheless, the annual value of foregone ecosystem services from coral reefs in 2100 is still only estimated to be a small fraction of total global income (0.14% or US$ 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) (e.g., Noone et al. [31]).

5.4.3 Projected impacts on ocean biogeochemical cycles

In the previous section, the impact of ocean acidification upon ecosystem services and human livelihoods was discussed. However, ocean acidification also has the potential to affect major biogeochemical cycles [32] and be of global concern. In assessing the potential impacts of ocean acidification on biogeochemical cycles it is important to recognise that ocean acidification impacts do not occur in isolation, but will occur in conjunction with other stressors including ocean warming, and these changes might significantly modulate future impacts [33].

Acidification has the potential to modify the ocean's biogeochemical cycles in a number of ways, which could alter the climate. We use the term biogeochemical climate feedback to denote biogeochemical processes in the ocean that could either enhance (positive feedback) or reduce (negative feedback) future global warming due to rising greenhouse gases. To investigate these feedbacks, we primarily focus on biogeochemical processes in the ocean that are impacted by ocean acidification, and that can alter ocean uptake and storage of carbon. To help simplify the discussion of the potential

Key Messages:

1. Rising CO_2 will affect net primary productivity, alter nitrogen and carbon ratios in exported particulate matter, and decrease iron bioavailability

2. Ocean acidification could decrease particulate organic carbon export to the deep ocean

3. Net effect of ocean acidification on ocean productivity and carbon storage is uncertain

4. Decreased DMS production could lead to exacerbated global warming impacts of ocean acidification on biogeochemical cycles, a summary is provided in Table 5.2, and some processes that 1) alter **biological production** in the photic zone (where light penetrates), and 2) alter the **remineralisation** (or breakdown) of sinking particulate organic and inorganic carbon are discussed in more detail below.

5.4.3.1 Biological production

Rising CO_2 concentrations in the upper ocean have the potential to affect biological production in several ways:

- Increase net primary productivity and Particulate Organic Carbon (POC) production by making photosynthesis more efficient [34, 35]. However, increased water stratification could also limit nutrient supply to surface algae, and inhibit phytoplankton growth [36].
- Alter the stoichiometric nitrogen to carbon ratio in exported particulate organic matter (POM), as observed in mesocosm experiments by Riebesell et al. [37] and Bellerby et al., [38]: C/N ratio increased from 6.0 at 350 µatm to 8.0 at ~1050 µatm. This would increase the storage of carbon in the ocean [39].
- Enhance dinitrogen (N_2) fixation by cyanobacteria, which could also increase primary production in nitrogen-limited areas. Larger cyanobacteria have consistently shown a significant increase in nitrogen fixation under elevated CO_2 [40], although this is not the case for unicellular cyanobacteria [41, 42].
- Impede the ability of organisms to calcify [43]. This is anticipated to reduce the production of calcium carbonate.
- Decrease the bioavailability of dissolved iron (Fe). Acidification of seawater decreases the Fe uptake rate of diatoms and coccolithophores [44].

5.4.3.2. Remineralisation (breakdown) of particulate material

Dissolution of $CaCO_3$ is driven largely by thermodynamics, and will increase in response to projected declines in saturation state [45]. Most of the exported organic carbon is broken down in the upper 1000 m, but roughly 10% escapes 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 [46]. 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 [47]. Armstrong et al. [47] proposed that $CaCO_3$ acts as "'ballast" for transporting POC at the surface to deeper waters, thereby increasing its sinking speed. It is also 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 exoenzyme activity may increase under elevated CO_2 [48, 49]. 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.

Table 5.2. *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 Gehlen et al. (2011)[32] 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); and iii) text for processes (7) and (8) is based on*

Hopkins et al. (2011)[50] and Six et al. (2013) [51]. Level of understanding: H, high; M, medium; L, low.

Process	Effect of future OA	Feed-back	Magnitude	Level of under-standing
1. CO_2 buffer factor	Decreased ocean uptake capacity	+ ve	Large	H
2. Photo-synthesis	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 DMS production	+ ve*	Medium?	L
8. Organo-halogens	Contradictory evidence: both enhancement and reduction may occur	?	Small?	L
9. Nitrogen fixation	Enhanced N_2 fixation – with enhanced biological production	– ve	Medium	M
10. Oxygenation	Shallower remineralization increases O_2 demand; expansion of low O_2 regions	+ ve	Medium	L
11. Nitrification	Reduced nitrification	?	Small	L
12. Nitrous oxide production	Decreased O_2 levels will increase N_2O production	+ ve	Medium	L

*feedback via cloud formation

Looking to the end of the century, Matear et al. [52] used an Earth System Model (ESM) to explore the potential consequences of ocean acidification on the marine biogeochemical cycles identified in Table 5.1, and identified that key biogeochemical parameters in the ocean will be significantly altered [52]. 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 [53, 54] 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 [52, 55]. This would affect the flow of energy through ecosystems, and could have significant impacts on marine ecosystem productivity and biodiversity.

In addition, large changes in PIC and POC export could significantly alter ocean interior oxygen levels. Oceanic oxygen levels are expected to decline under global warming (e.g. Matear et al. [56] 2000); Bopp et al. [57] 2002), and the latest ESMs project a small decrease in the total ocean inventory of dissolved oxygen (2% to 4%) by the end of 2100 [53]. However, the projections vary regionally, and the total volume of hypoxic and suboxic waters remain 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 [58].

Other gases - While CO_2 is the most important greenhouse gas modulated by the ocean, 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 [59, 60]. Declining oxygen levels should be associated with increased production of both these gases [61, 62], 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 [52]. However, increased warming could also potentially destabilise methane hydrates stored in sediments along continental margins, leading to additional release of CH_4 [63] (Biastoch et al. 2011).

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 [64] and provides 90% of the biogenic sulfur in the marine atmosphere [65]. 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 2100 [66,67, 68], but elevated CO_2 predictions in isolation of other environmental change suggest a significant decrease in future concentration of DMS [50], as summarised by Six et al. [51] (Figure 5.22).When combined in Earth System Models to simulate future climate change, decreased DMS production could lead to exacerbated global warming [51]. However, DMS responses measured to date are variable and 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 and potential magnitude.

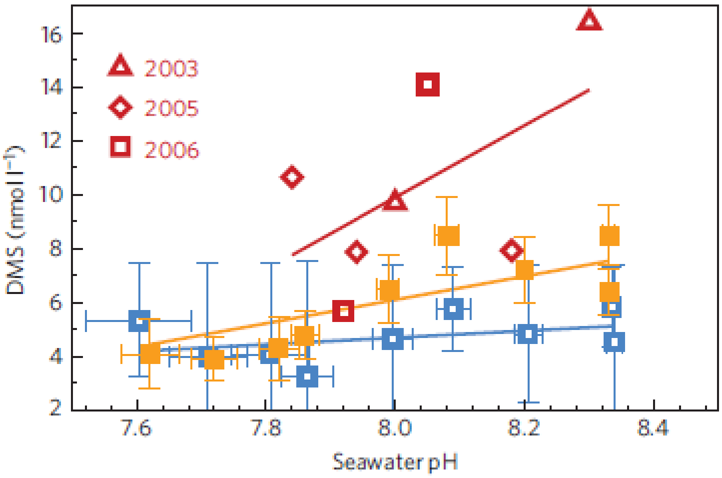


Figure 5.23. *Relationship between DMS concentration and pH based on data from mesocosm experiments. Measurements of DMS and seawater pH are averaged from the mid-phase of Svalbard experiments (orange) and over the entire experiment (blue). Red denotes measurements from Norwegian mesocosm experiments from three different years. Source: Six et al. 2013* [51]. *Seek Permission.*

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6 FUTURE CONSIDERATIONS

6.1. Resolving uncertainties

A large body of scientific information about ocean acidification was rapidly generated during the past few years, contributing to increased political awareness. However, gaps in our knowledge remain. Although based in marine chemistry, ocean acidification is an inherently interdisciplinary research problem, covering many scientific fields and connections between them. It involves observational, monitoring, experimental, palaeo- and modelling studies – linking interactions of processes that are physico-chemical, physiological/behavioural, genetic, ecological, biogeochemical and socio-economic. The major knowledge gaps to be addressed in these areas are identified in Table 6.1. Many of these gaps are starting to be investigated, but significant challenges remain.

Table 6.1. *Some key research gaps in ocean acidification.*

OA topic area	Research question(s)
Physico-chemical processes	What is the current variability of ocean carbonate chemistry at ecologically-significant temporal and spatial scales? 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?
Physiological and behavioural processes	What are the unifying mechanisms linking species' molecular, metabolic and behavioural responses to ocean acidification? (e.g. based on energy metabolism and internal acid-base regulation). Does this explain the high taxonomic variability observed in response to OA - and complex interactions with other stressors (e.g. temperature, low oxygen and food/nutrient availability)? How would different scenarios of ocean acidification affect the immune system resilience of various species to pathogens?
Genetic processes	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?
Biogeochemical processes	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?
Socio-economic processes	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 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?
Ecological processes	How can experimental studies on OA 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 OA on one species may indirectly benefit (or disadvantage) another and thus community composition and biodiversity.

6.1.1 From individuals to ecosystems

To consider the ecological consequences of ocean acidification, the impacts have to be investigated at a number of different levels, each of which have challenges for future research.

Key Messages:

1. Existing variability in organism response to ocean acidification needs to be investigated further, and potential for adaptation over progressive generations identified

2. Impacts of ocean acidification on different life cycles need to be determined

3. Relationships and interactions between species need to be assessed under projected future conditions

Ocean acidification at the individual level - Research to date has highlighted the variability in organism response to ocean acidification (reviewed by Wicks & Roberts 2012 [1]). One reason that might explain this variability is that species differ in their capacity to tolerate ocean acidification. The capacity for acid-base regulation is an important example, and species that show developed capacity are in general expected to be more resilient to ocean acidification [2, 3]. Other studies have demonstrated that tolerance to ocean acidification can even differ between closely related species, or even within species as shown in coccolithophores [4]. 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 [5]. Physiological plasticity of organisms and the potential to adapt to changing conditions thus remains an important area for future research [5], further supported by observed long-term acclimatization and adaptation in fast growing microalgae in response to ocean acidification [6].

Importantly, organism response to ocean acidification may be different for the short term relative to the long term, for example as an organism acclimates to new conditions, or to laboratory aquarium conditions [6]. However, even long-term experiments of a year or more may not give the whole story, as acclimation may come at a cost to reproductive output, which remains unmeasured in many studies. To compound this further, the longest experiment to date (542 days) [8] has highlighted that organism response may also change seasonally, and so long-term effects of ocean acidification may 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 [1]. 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 [9], as well-fed organisms might have more energy to compensate for regulatory changes.

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. To date various studies have demonstrated that early life stages are one of the most vulnerable to ocean acidification. Taking into account that many marine invertebrates show high mortality rate during planktonic larval stages, detrimental impact at these stages can mean critical differences to the population level. A knowledge gap to be addressed across more species and different timescales is the impact of ocean acidification upon gametogenesis. Future work capable of determining the effect of ocean acidification on several life phases, and of subsequent generation of the same species combined with population dynamic models are therefore required.

Ocean acidification at the community level – The impact of ocean acidification upon species interactions remains relatively unstudied, but is a key area to focus on if whole ecological communities are to be considered [10]. These interactions include predator-prey relationships [11, 12, 13], feeding rates [14, 15], how the presence of one species (e.g. coralline algae) may directly impact upon the recruitment or success of another (coral juveniles) [16, 17, 18] and resource competition [19, 20]. However, quantifying species interactions remains complicated, as interactions will also be effected by conditioning time and biotic interactions [19, 20]. Embedded within this is the need to understand the adaptation potential of different species, and taxa sensitivity to ocean acidification [21].

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 (see Natural CO_2 vent case study box), and provides a good opportunity to document species-species and species-environments 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, Laverock et al. [22] demonstrated how 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. This could impact bentho-pelagic nitrogen cycling, which is fundamental to the food web and the ecosystem dynamics as a whole [10, 22].

Natural CO_2 vents case studies

From studying ecosystems surrounding natural CO_2 vents it is clear that fundamental changes do happen on the ecosystem level, as calcifying communities may shift to algal-dominant ecosystems [23], undergo a change in species dominance such as in Papua New Guinea [24], or shift community type [25]. A consistent feature of these studies is that species diversity decreases near CO_2 vents. Importantly, natural CO_2 vent ecosystems also include non-calcifying organisms, which could nonetheless play a very important role in species competition and ecosystem function [26].

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.

6.2. From laboratory to environment: importance of 'multiple stressor' experiments

Most experimental data on the impacts of ocean acidification were initially gathered in the laboratory on isolated organisms for short periods of time. In recent years several major experiments were conducted on pelagic communities over several weeks using open water mesocosm approaches [27], but there are few such experiments for benthic systems.

To close this gap, two approaches are particularly promising: (1) community-level studies in natural high-CO_2 environments and (2) CO_2 perturbation experiments at the community and ecosystem level. The best know example for a natural high CO_2 environment is a CO_2 venting site in the Gulf of Naples, where a community shift has been observed along a pCO_2 gradient, with calcifying organisms successively disappearing from the community approaching the CO_2 venting site [23]. Such natural high CO_2 environments capture the full scope of ecosystem interactions over long time scales, thereby providing crucial information on the effects on ocean acidification on trophic and competitive interactions and the potential for adaptation. However, the high spatial and temporal variability in pCO_2 and pH makes it difficult to determine a reliable dose-response relationship, complicating the use of this information in projecting future high CO_2 scenarios. The interpretation is also complicated by the uncontrolled advection and recruitment from unperturbed adjacent areas. Last but not least, the number of these sites is obviously limited and does not allow assessing the effects of ocean acidification on a large variety of communities and ecosystems.

Key Messages:

1. Multiple stressor research is needed, as ocean acidification will not be the only potential stressor in the future

2. In situ experiments on whole communities (using natural CO_2 vents or CO_2 enrichment) need to be conducted and compared to laboratory work

Recently, 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 (Figure 6.1). 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. The usefulness of this approach was recently demonstrated in a tropical coral reef setting [28].

Figure 6.1. The coral proto-free ocean carbon enrichment system (CP-FOCE) deployed on Heron Island, Great Barrier Reef, Australia. Source: David Kline, Scripps. Seek Permission.

Need for a multiple drivers approach - Experiments investigating how biota will respond to ocean acidification have, until recently, largely focused on the manipulation of the carbonate system only. However, marine organisms and ecosystems are increasingly stressed by human-induced changes of their physical, chemical and biological environment. For global variables, there has been considerable progress in model projections in the past two years, in conjunction with the preparation of IPCC AR5 report. Bopp et al. [29] used the most recent simulations performed in the framework of the Coupled Model Intercomparison Project 5 to assess how several drivers will evolve during the 21st century. 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 these other variables synergistically (amplified stress), additively (no additional stress), or antagonistically (reduced stress). In 2012, only 1/3 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 on 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 are technological, but also include experimental design (replication vs. regression approach, pseudo-replication, number of treatments for each driver etc.).

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6.3. Advances in sensing, monitoring, and emerging technologies

Key Messages:

1. A high density of measurements in space and time are required to identify variability and anthropogenically induced ocean acidification

2. Autonomous systems will remove the need of operators and encourage the development of low cost, low power, long-term measurement techniques

Measurements of the pH and the marine carbonate system have traditionally been challenging due to inconsistent pH scales, measurement routines and custom instrumentation that required the expertise and experience of a particular technician to operate. Consequently, inter-comparison exercises between laboratories revealed large discrepancies [1]. Over the last thirty 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 [2].

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) [3]. 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 Section 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 and the development of approaches to enable remote measurements, thus removing the requirements for an operator. These include measurements from autonomous systems voluntary observing ships (or ship of opportunity Hardman-Mountford et al.[4]), buoys, wave-riders (http://www.pmel.noaa.gov/co2/story/Carbon+Wave+Glider) and landers [5] (Figure 6.2). Adapting these methods have led to the development of novel combinations [6] and lower-cost, low power, long term measurement techniques [7] that are approaching, and sometimes excelling, the accuracy of traditional methods.

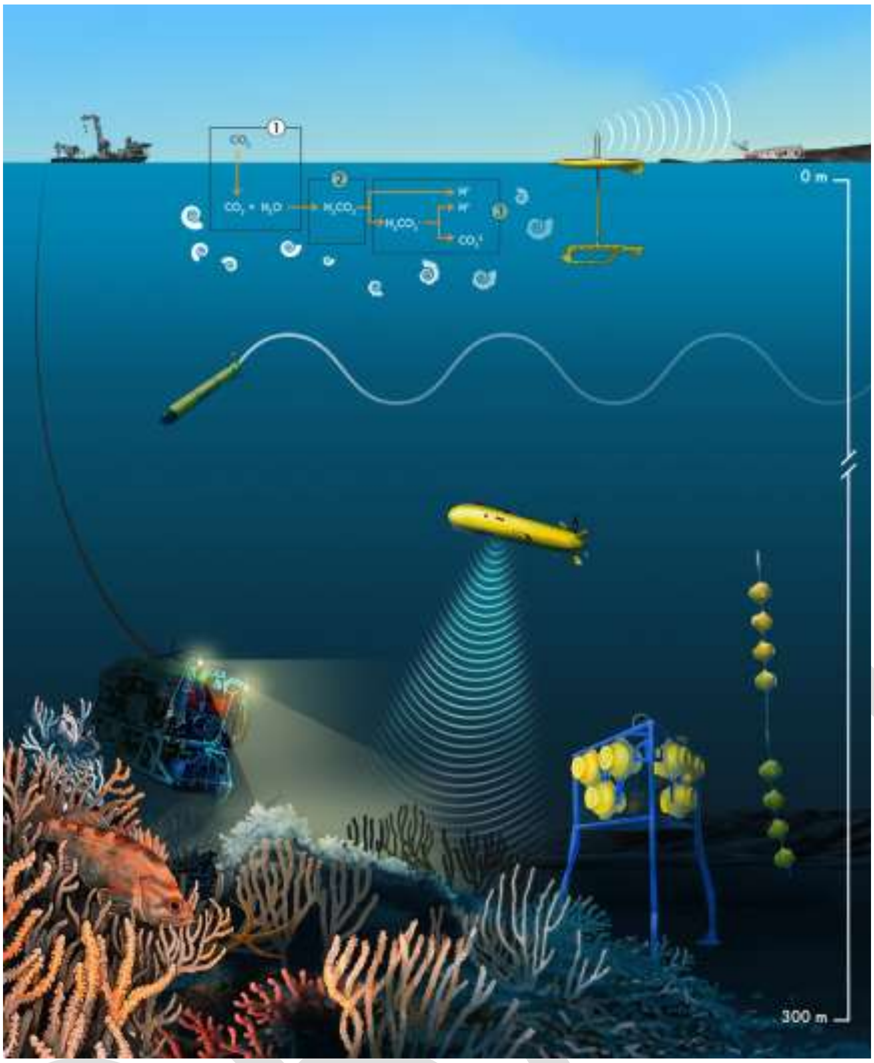

Figure 6.2. A simplified cartoon of various approaches to assessing marine habotats; including autonomous and remotely controlled underwater vehicles, wave gliders, moorings and benthic landers. Source: Heriot-Watt University.

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7. CONCLUSIONS

The level of ocean acidification that we have experienced since pre-industrial times, and the projected acidification by the year 2100 is occurring far faster than any similar ocean acidification events in the past 300 million years [1]. As such, current ocean acidification represents a new and unprecedented chapter of marine ecosystem change that could have a significant impact on marine species and ecosystems (including economically important species), on various industries and communities, and on global food security.

From the Palaeo-Eocene Thermal Maximum (56 million years ago), believed to be the closest historical analogue to present-day ocean acidification, geological records indicate that a significant number of deep-sea organisms went extinct, and many underwent habitat shifts. The speed at which ocean acidification is currently happening precludes the option of habitat shifts for many benthic species such as shellfish and corals, 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 meters to just a few hundred metres in many oceans 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 pH will decrease by ~0.33 units and sea surface temperature increase by 2.7°C [3].

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, but also highlights that experiment length is important as well in determining future long-term responses.

However, 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, algae important in biogeochemical cycling, and coral reefs [6, 7, 8, 9, 10], although adequate food supplies may ameliorate some negative responses [11, 12]. It has been demonstrated that 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, 17, 18], but non-calcifying larvae are more resilient [19, 20, 21]. The impacts of ocean acidification on fertilization success are highly variable, and highlight the potential for selection and genetic adaptation, 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 latitudes and low temperatures, and evidence has emerged from a three-year research programme, the Arctic Monitoring and Assessment Programme (AMAP), that acidification will not be uniform across Arctic environments. The research programme also showed that, that while impacts may be positive for some species, other species may face extinction, and that acidification may contribute to an alteration in fish species, with potential impact upon the livelihoods of local communities [24].

When considering how ocean acidification will affect global populations, the response of tropical coral ecosystems to ocean acidification is understandably much scrutinised, as over

400 million people worldwide live within 100km of reefs, and a vast majority rely upon them for their livelihoods and food security [25, 26]. The fact that over 95% of the world's calcifying corals currently live above the saturation horizon [27], and that coral growth ceases near natural CO_2 vents [28], indicates that in the long-term, it is not 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 rely upon them.

The economic costs of ocean acidification are only partially known, with many studies focussing on local costs rather than global. However, of the studies that focus on global costs, the impact to molluscs and tropical coral reefs will cost over $1000 billion annually by the end of the century [29, 30]. However, these calculations are inherently difficult and are 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, especially as it only considers ocean acidification, and not 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 oceans [31]. As such, varying conditions (exacerbated by diel community metabolism, local phytoplankton blooms and watershed processes) could complicate the predictions we can currently make, and force rapid (relatively) selection of tolerant individuals.

Looking to the immediate future, it is vital to increase our understanding of how multiple stressors will affect marine biodiversity and ecosystems [32], as ocean acidification will be accompanied by changes in oxygen saturation and temperature [3]. Currently, our knowledge on the impacts of multiple drivers is still insufficient to provide reliable projections of biodiversity and ecosystem function and this must 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 arctic 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. 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. Even if emissions are significantly curtailed now, however, acidification will still last tens of thousands of years. Significant ocean ecosystem change, and learning to live with those changes, therefore seems a certainty.

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