

## **Chapter 5.6 The Risk Of Ocean Acidification To Ocean Ecosystems**

### **Lead Author:**

Carol Turley, Plymouth Marine Laboratory, Prospect Place, The Hoe, Plymouth PL1 3DH, UK

### **Chapter Citation:**

Turley, C. (2016). Chapter 5.6: The Risk of Ocean Acidification to Ocean Ecosystems. In UNESCO IOC and UNEP (2016). The Open Ocean: Status and Trends. United Nations Environment Programme, Nairobi, pp. 193-205.



## 5.6 The Risk of Ocean Acidification to Ocean Ecosystems

### 5.6.1 Summary and Key Messages

Ocean acidification is a process that refers to major changes to the ocean's carbonate chemistry, mainly caused by ocean uptake of anthropogenic emissions of carbon dioxide. This process involves a decrease in ocean pH (important for regulation of the internal acid balance and physiological health of many organisms) carbonate ions and calcim carbonate minerals such as aragonite and calcite (important for shell and skeleton builders) and an increase in bicarbonate ions (important for algal photosynthesis).

To understand what marine ecosystems may look like in the future if carbon emissions continue unabated, it is necessary to know the severity of the perturbation that different ecosystems will be exposed to and their ability to adapt within the time-scales of change. The severity and speed of ocean acidification, the exposure and vulnerability of the component organisms of an ecosystem to ocean acidification and their role in an ecosystem contribute to the risk of impacts to ecosystem structure and function. Although there are great uncertainties moving from impacts on individual organisms to impacts on complex marine ecosystems, these basic changes to marine chemistry pose a substantial risk to marine ecosystem structure and function through the impacts on the growth, physiology, behaviour, predator-prey interactions, competitiveness and population dynamics of individual species and how these may cascade through the rest of the ecosystem. Some organisms are able to adapt to ocean acidification, especially if food resources are high, by trading-off energy from one physiological function to another, although this may impact their long-term survival and ecosystem function.

Foodwebs where vulnerable organisms provide key trophic links, especially those exposed to undersaturated waters in polar, sub-polar and upwelling regions where severity will be greatest, will be at *high* risk of impact from ocean acidification. However, ecosystems formed by the aragonitic skeletons of deep-sea or tropical corals are also at *high* risk of impact from ocean acidification, either due to *high* severity, exposure or vulnerability or a combination of all three. Risk increases further when ocean acidification acts in concert with other global and/or local ocean stressors.

Predicting impacts of changing biodiversity or community dynamics on ecosystem structure and function also requires expanding the scope of current experimental research to examine multi-stress impacts in multi-level foodwebs and complex ecosystems.

### Key Messages

- Basic changes to marine chemistry pose a substantial risk to marine ecosystem structure and function through the impacts on the growth, physiology, behaviour, predator-prey interactions, competitiveness and population dynamics of individual species and how these cascade through the rest of the ecosystem;
- Though some organisms may be able to adapt to ocean acidification by trading-off energy from one physiological function to another, this may impact their long-term survival and ecosystem function;
- *Risk* of impacts will depend on the *severity* (of which strength and speed are components) of ocean acidification, and the *exposure* and *vulnerability* of organisms to ocean acidification especially those playing key roles in ecosystems. The higher the *severity*, *exposure* and *vulnerability* the greater the *risk* of impact to numbers of organisms and therefore to foodwebs and ecosystems; and
- Foodwebs where *vulnerable* organisms provide key trophic links, especially those *exposed* to undersaturated waters in polar, sub-polar, deep sea and upwelling regions where *severity* will be greatest, will be at *high risk* of impact from ocean acidification. However, as ocean acidification progresses with increasing anthropogenic CO<sub>2</sub> emissions, ecosystems across the whole ocean will be at *risk*.

### 5.6.2 Main Findings, Discussion and Conclusions

#### *The stressor – ocean acidification*

The ocean absorbs 24 million tonnes of CO<sub>2</sub> every day, around 27 per cent of that emitted to the atmosphere mainly through burning of fossil fuels (Le Quéré et al 2013). When CO<sub>2</sub> enters the surface ocean it rapidly undergoes a series of chemical reactions, which produce hydrogen ions [H<sup>+</sup>] resulting in an increase in the acidity (lowered pH), a decrease in the concentration of calcium carbonate ions and an increase in the concentration of bicarbonate ions.

Three oceanic sites have monitored ocean carbonate chemistry over 20 years and show decreasing seawater pH and carbonate ion concentration concurrent with rising atmospheric CO<sub>2</sub> (IPCC 2013). Mean ocean pH has decreased by 0.1 since the start of the 'Industrial Revolution', a decline of around 30 per cent.

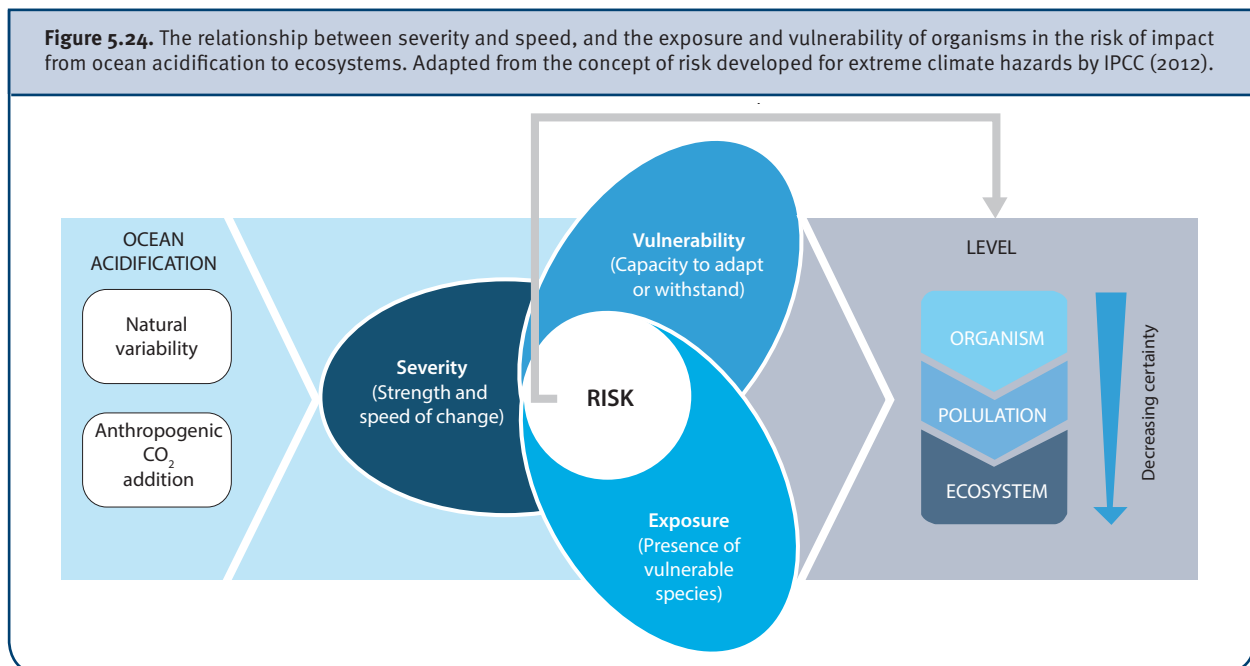
IPCC (2013) projects a global increase in ocean acidification for all "Representative Concentration Pathways" (RCP) scenarios, with decreases in mean surface ocean pH by the end of the 21st century in the range of 0.06 - 0.07 (RCP 2.6), 0.14 - 0.15 (RCP 4.5), 0.20 - 0.21 (RCP 6.0) and 0.30 - 0.32 (RCP 8.5). The RCP 8.5 outcome represents an increase in acidity of >150 per cent compared with pre-industrial values (IPCC 2013; Bopp et al. 2013, Joos et al. 2011; van Hooidonk 2015) (See Glossary Box 2).

#### *Risk to ecosystems from ocean acidification*

Such fundamental and rapid changes to basic ocean chemistry represent a great challenge for many marine organisms and complex marine foodwebs and ecosystems. Over the last decade there has been a dramatic increase in research on impacts of ocean acidification, initially involving simple short-term experiments on single processes in single species. However, experiments have become increasingly more complex; carried out over a long-term, looking at multiple processes, different life stages, multiple species or communities and the combined effect of other stressors.

There have been recent reviews, meta-analysis and assessments of the impacts of ocean acidification mostly on individual isolated species under laboratory conditions which are drawn upon here (Wicks and Roberts 2012; Williamson and Turley 2012; Kroeker et al. 2013; Whittmann and Portner 2013; Gattuso et al. 2014; IPCC 2014; CBD 2014). However, how impacts at the organism level are reflected in the real world, at the population and ecosystem level, is far from clear and more challenging to determine due to the complex nature of marine ecosystems. This Chapter will explore the ways in which ocean acidification might pose a risk to the structure and function of marine ecosystems.

**Figure 5.24.** The relationship between severity and speed, and the exposure and vulnerability of organisms in the risk of impact from ocean acidification to ecosystems. Adapted from the concept of risk developed for extreme climate hazards by IPCC (2012).

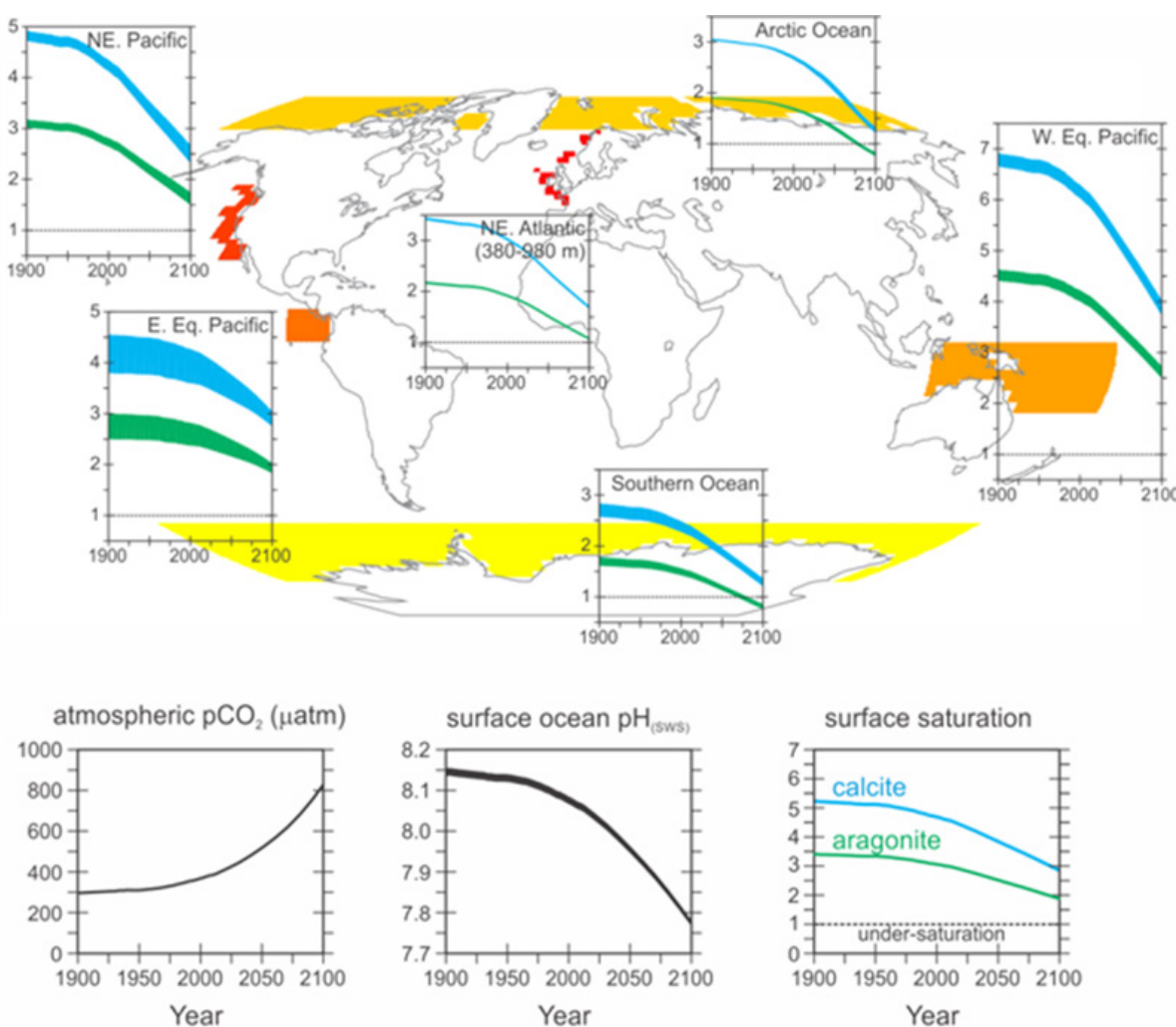


Here *risk* from ocean acidification is defined as the likelihood of severe alterations in the normal functioning of an ecosystem and will depend on the *severity* (of which strength and speed are components) of ocean acidification, and the *exposure* and *vulnerability* of organisms to ocean acidification especially those playing key roles in ecosystems (for example: ecosystem engineers, key trophic links) (Figure 5.24). The higher the *severity*, *exposure* and *vulnerability* the greater the *risk* of impact at organism to ecosystem levels. The arrow on the right shows the decreasing certainty of impacts on an organism through to complex ecosystems.

### Severity and timescale

The strong coupling between atmospheric CO<sub>2</sub> and surface ocean acidification means that further and rapid emission of CO<sub>2</sub> to the atmosphere will inevitably increase the *severity* of ocean acidification (with >150 per cent increase in ocean acidification projected with RCP 8.5 by 2100 (IPCC 2013)). It is not just the magnitude of the carbon input that is important: the timescale over which this carbon perturbation occurs is also critical to the ocean's carbonate

**Figure 5.25.** Projected regional changes in ocean chemistry (top map and graphs), likely to be experienced by particularly vulnerable ecosystems and global-scale surface ocean changes (bottom three graphs) using SRES A2 scenario. For each of the six illustrative high risk marine ecosystems (Arctic Ocean, Southern Ocean, Northeast Pacific margin, intermediate depth Northeast Atlantic (500–1500 m), western equatorial Pacific, eastern equatorial Pacific) the blue shaded band indicates the annual range in ocean saturation state with respect to aragonite, while the green shaded band indicates the range for calcite saturation. Area average surface ocean conditions are calculated for all regions with the exception of the NE Atlantic where area average benthic conditions between 380 and 980 m have been used. The thickness of the line indicates the projected seasonal range, with the threshold of undersaturated environmental conditions marked as a horizontal dash line.



Source: Turley et al. (2010).

chemistry. The time-scale for the current perturbation is just a few hundred years and too short for the natural capacity of the ocean to buffer it. If this anthropogenic carbon input was spread over a timescale of thousands of years, the ocean's buffering system would decrease the *severity* of change to the ocean's carbonate chemistry (Zeebe and Ridgwell 2011). The current speed of ocean acidification is unprecedented within the last 65 million years (IPCC 2013; Ridgwell and Schmidt 2010), possibly the last 300 million years (IPCC 2013; Hönisch et al. 2012) and it will take tens of thousands of years for future ocean pH to return to near pre-industrial conditions (Archer 2005). Such *severity* and speed of change increases *risk* to marine foodwebs and ecosystems.

Although ocean acidification is happening across the whole global ocean, the *severity* of ocean acidification will be highest in cold waters because they absorb more CO<sub>2</sub> than warmer waters (Figure 5.25). Polar and sub-polar waters will therefore experience the lowest pH and carbonate ion concentrations (Figure 5.25, with aragonite reaching undersaturation in about 50 per cent of the Arctic Ocean around 2050, although large areas will achieve undersaturation within the next two decades (Steinacher et al. 2009, Turley et al. 2010). Undersaturation in the Southern Ocean and sub-polar waters will follow shortly after this (Orr et al. 2005). Upwelling waters already rich in CO<sub>2</sub> will also be affected early, with some already experiencing periods of undersaturation (Feely et al. 2008; Hauri et al. 2013). The deep-sea is not immune to anthropogenic ocean acidification with the aragonite saturation horizon moving towards the sea surface at a pronounced rate of 1-2 myr<sup>-1</sup> (Feely et al. 2004; Orr et al. 2005). On the Icelandic Sea it is shoaling at a faster rate of about 4 myr<sup>-1</sup> so that each year another 800 km<sup>2</sup> of seafloor becomes exposed to waters that have become undersaturated with respect to aragonite (Olafsson et al. 2009). Earth system models project for three out of four RCPs, that by 2100 over 17 per cent of the seafloor area below 500m depth in the North Atlantic sector will experience pH reductions exceeding -0.2 units by 2100 (Gehlen et al. 2014). Tropical waters will never experience undersaturation, however they will experience a rapid fall in saturation state (Figure 5.25).

### Exposure

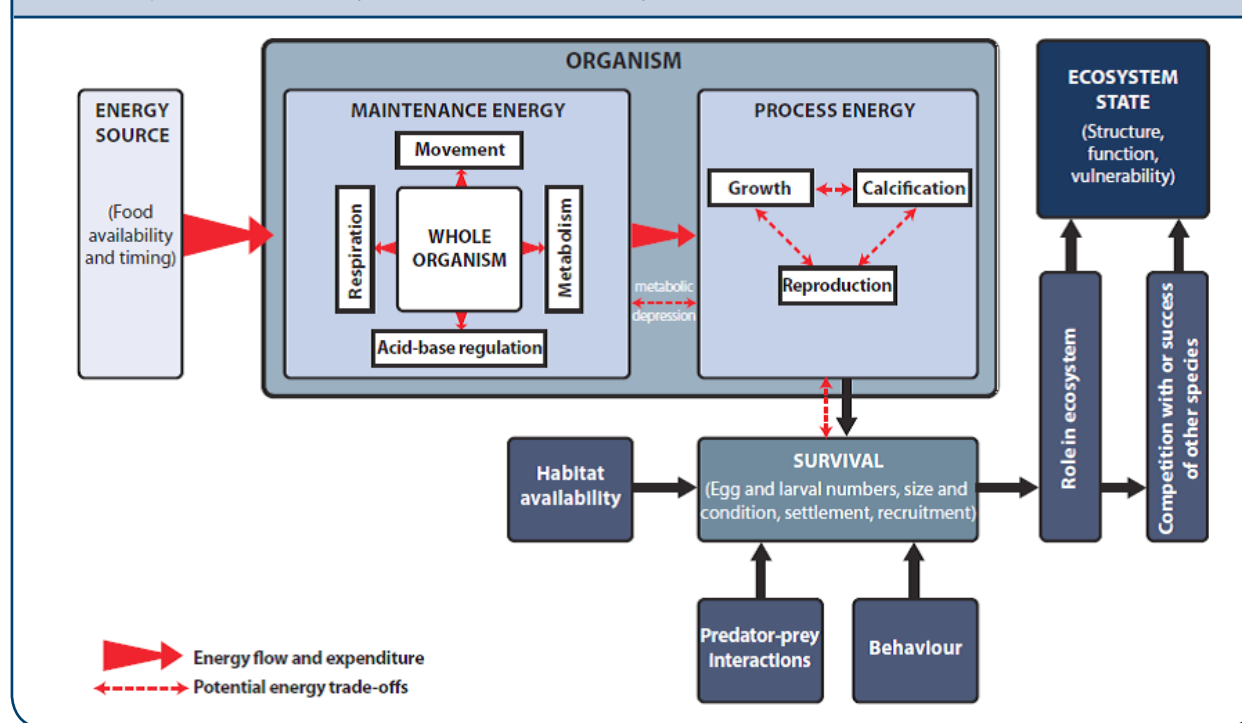
*Exposure* is the presence of organisms, communities or ecosystems to ocean acidification (Figure 5.24). As ocean acidification is a global phenomenon and all marine systems contain large biodiverse and often complex ecosystems, *exposure* will be omnipresent as CO<sub>2</sub> emissions increase through this century. Ecosystems present in areas of current low pH or calcium carbonate undersaturation, or those where low pH or undersaturation is projected to occur relatively rapidly such as polar, upwelling and deep-sea waters, will have increased *exposure* to ocean acidification and hence increased *risk*. The presence of ecosystems dependent on high concentrations of calcium carbonate to build reef like structures, such as those produced by calcifying cold water and tropical corals also increases risk.

### Vulnerability

*Vulnerability* is the propensity or predisposition of a species, population or ecosystem to be adversely affected by ocean acidification (Figure 5.24). *Vulnerability* encompasses a variety of concepts and elements including sensitivity or susceptibility and the ability of an ecosystem and its component parts to withstand or adapt to the effects ensuring the preservation of its essential basic structures and functions. Adaptation to ocean acidification could influence the degree to which ocean acidification translates into impacts but is also influenced by the *severity* of change. Adaptation ability is *likely* to be higher in some species than others. For example, trans-generational or evolutionary adaptation has been shown in some rapidly-reproducing species (Sunday et al. 2014), reducing impacts of projected CO<sub>2</sub> emission scenarios. However, the speed of current change is unlikely to allow widespread adaptation, especially in slower growing species (IPCC 2014).

Some organisms can withstand periods of acidification if food availability is high or they can trade-off energy flow to different physiological or metabolic processes in the organism (Figure 5.26). An organism requires energy gained from the food it ingests to maintain itself (for example: for metabolism, respiration, acid-based regulation and movement). It must also expend energy in processes such as calcification, growth and reproduction and ensure eggs and larvae are produced in sufficient size, numbers and condition for species recruitment and survival (Figure 5.26). Trade-offs between different energy requirements have been observed in organisms when placed in low pH conditions in order to withstand ocean acidification but this can impact their survival (reviewed by Wicks and Roberts 2012). How the impact of ocean acidification scales up from impact on the individual organism level to the ecosystem level depends

**Figure 5.26.** Energy flow and energy requirement of different processes within an organism and potential energy trade-offs that can occur in order to withstand ocean acidification. Potential ecosystem level impact depends on the role of the organism in the ecosystem, its food availability and whether it can manage its energy flow and expenditure to ensure its survival to propagate successfully and maintain its competitive advantage over other species.



on the role of the organism in the ecosystem, and whether changes to its energy flow (caused by, for example, changes to food availability and/or increased energy requirements for a physiological process) will ensure its survival and long-term fitness and competitiveness within an ecosystem framework (Figure 5.26). However, there is currently no understanding of how food availability in different levels of a foodweb will change in a future ocean.

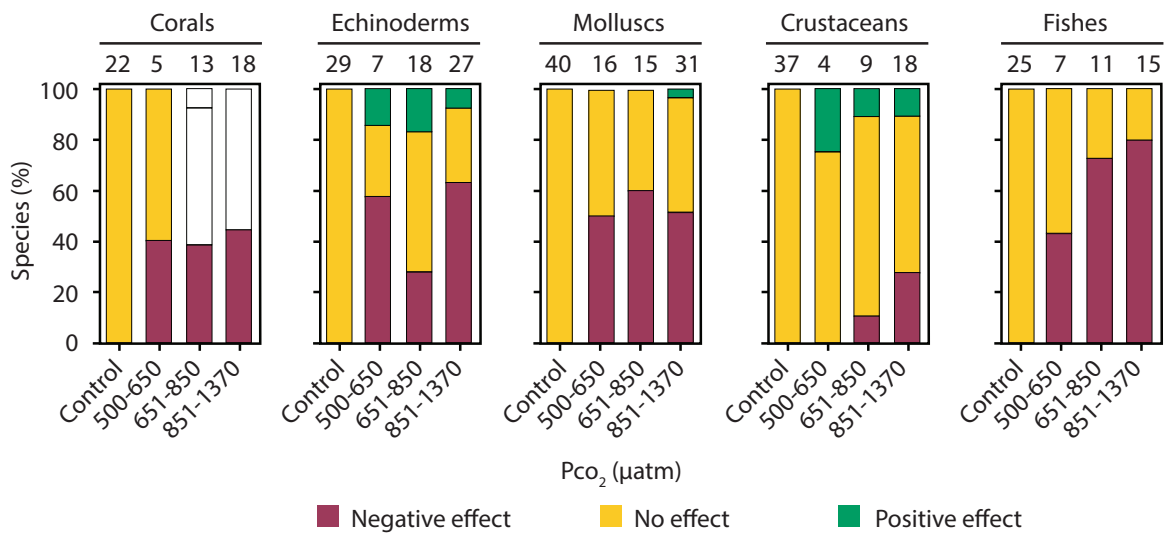
It is therefore important during the assessment of possible impacts to study the weakest link in an organism's physiology and life cycle. A *vulnerability* to lower pH and carbonate saturation state in any of these functions at any life stage could result in loss of competitive fitness, narrowing of a species ecological niche or its demise (Wicks and Roberts 2012).

#### **Risk to organisms**

*Vulnerability* to ocean acidification has been mainly tested on single species, often in short-term experiments but increasingly in longer-term experiments. A synthesis of the results of 228 studies examining biological responses to ocean acidification reveal decreased survival, calcification, growth, development and abundance in response to acidification when the broad range of marine organisms is pooled together (Kroeker et al. 2013). This meta-analysis showed that early life history stages were particularly vulnerable in some but not all taxa. The magnitude of responses varies among taxonomic groups, for example crustaceans seem less vulnerable than echinoderms, molluscs, corals and fish (Wittmann and Pörtner 2013; Figure 5.27).

#### **Risk to communities, foodwebs and trophic interactions**

Experiments using multi-species assemblages revealed enhanced variability in species' responses suggesting that it is important to consider indirect effects and exercise caution when forecasting abundance patterns from single species laboratory experiments (Kroeker et al. 2013). Furthermore, the results suggest other factors, such as nutritional status or source population, could cause substantial variation in organisms' responses and enhanced vulnerability to acidification to occur when taxa are concurrently exposed to elevated seawater temperature. For example, the blue

**Figure 5.27.** Synthesis of experimental results on impacts of ocean acidification taxaSource: *Nature Climate Change Journal*; Wittmann and Pörtner (2013)

mussel (*Mytilus edulis*) tolerates low pH when food supply is abundant (Thomsen et al. 2013). However, low food concentrations and low pH each significantly decreased shell length growth and the magnitude of inner shell surface dissolution (Melzner et al. 2011). This illustrates that under food limited conditions, this species allocates energy to more vital maintenance processes rather than to shell conservation. High food availability was also found to offset the negative consequences of elevated CO<sub>2</sub> on larval shell growth and total dry weight in the larvae of the Olympia oyster (*Ostrea lurida*) (Hettinger et al. 2013).

Some organisms prosper in more acidic waters. With the exception of those that calcify, most sea grass, macroalgae and microalgae respond positively to elevated bicarbonate ion concentrations by increasing photosynthesis and growth (Raven et al. 2005). Observations of natural CO<sub>2</sub> vents in coral reef systems off Papua New Guinea show increased algal growth but declining coral reef biodiversity and loss of reef structure that provides homes to many reef dependent species as pH decreases close to the vents (Fabricius et al. 2011). Other vents in the Mediterranean Sea also show declining biodiversity and loss of shelled organisms but increases in sea grass meadows and alien species as pH declines closer to the vents (Hall-Spencer et al. 2008).

Some non-calcifying algae may do better than others and thereby change the structure and functioning of an ecosystem. For example, profound effects of ocean acidification were found at the productive base of the pelagic foodweb in the Arctic using mesocosm CO<sub>2</sub>-enrichment experiments, which enclose large volumes of seawater containing the whole plankton community (Brussaard et al. 2013). The composition and growth of the two smallest (picophytoplankton and nanophytoplankton) components of the phytoplankton community increased at the expense of the growth and biomass of the larger diatoms but were also found to be prone to viral lysis. A shift towards the smallest primary producers and increased viral lysis as a result of acidification would have direct consequences for the structure and functioning of pelagic ecosystems by shunting more carbon through the microbial loop rather than to grazing zooplankton and on higher trophic levels. This is an example of how responses (even positive ones) to ocean acidification could have a bottom-up impact on ecosystem dynamics and how it is important to consider multiple organisms or levels. For instance, isolated research on diatom species in the laboratory would not have revealed that they could be out-competed by the smaller members of the phytoplankton community with a conclusion that diatoms may do well in a high CO<sub>2</sub> ocean.

Organisms higher up the foodweb are not just at risk from “bottom-up” impacts. Evidence is accumulating that CO<sub>2</sub> projected to occur by 2100 impairs sensory performance and alters the behaviour of larval teleost fishes (Munday et al. 2009; Dixon et al. 2010), impairing decision-making (Domenici et al. 2012) and the response to auditory (Simpson et al. 2011) and olfactory cues (Munday et al. 2009; Dixon et al. 2010). Trans-generation acclimation does not seem to reduce such impacts, implying that genetic adaptation will be necessary to overcome the effects of ocean acidification on behaviour (Welch et al. 2014). Projected future CO<sub>2</sub> levels impair odour tracking behaviour of the smooth dogfish (*Mustelus canis*) an Elasmobranch fish (Dixon et al. 2014). A highly sensitive sense of smell is considered particularly important for these apex predators to detect chemical cues emanating from distant prey. If other sharks are affected similarly to the smooth dogfish, the consequences of a decrease in their effectiveness as apex predators could have cascading effects throughout ocean ecosystems (Myers et al. 2007). Elimination or decreased effectiveness of top predators can be far-reaching and include release of intermediate predator prey populations from predatory control and induction of subsequent cascades of indirect trophic interactions (Pace et al. 1999). Changes to apex predators by ocean acidification may result in top-down impact on ecosystems dynamics.

### **Risk to key links in foodwebs**

Some species represent key links in foodwebs. For example, sea butterflies (Pteropoda) contribute on average 25 per cent to total phytoplankton grazing and consume up to 19 per cent of daily primary production in the Southern Ocean. In addition they are also an important prey item for many predators, such as larger zooplankton as well as herring and salmon (Hunt *et al.* 2008). Laboratory experiments show great sensitivity of Arctic pteropods to ocean acidification (Comeau et al. 2009 and 2010a; Lischka et al. 2011; Comeau 2015, see Chapter 5.5 of this Report). Natural populations of the shelled pteropod *Limacina sp.* are already showing shell thinning in the Southern Ocean and the California Current Ecosystem where pH and carbonate levels are lowest (Bednaršek et al. 2012; 2014). These shelled molluscs seem at *high risk* from ocean acidification due to their high levels of *exposure*, *vulnerability* and the *severity* and early onset of acidification in their habitat (Bednaršek et al. 2012 and 2014; Comeau 2015, See Chapter 5.5 of this Report). Some pteropod species that naturally migrate for short periods into oxygen minimum zones, where pH is low, are not affected but it is unlikely that they will be able to withstand the longer time-scales associated with ocean acidification (Maas et al. 2012). Juveniles of the species *Cavolinia inflexa* held in low pH seawater for 5–13 days were viable but completely shell-less (Comeau et al. 2010b). If this were to happen in their natural habitat it is *likely* that there would be long-term effects on population fitness through loss of swimming efficiency and defensive capacity. As important links in the foodweb, a reduction in pteropod survival in polar, sub-polar and upwelling waters could have implications to ecosystem structure and function through changes in predator-prey interactions.

To maintain a shell when exposed to more acidic conditions an organism may have to divert energy from other metabolic processes to up regulate calcification in order to compensate for dissolution of this calcified structure (Findlay et al. 2009). Other metabolic processes may also be impacted by the higher CO<sub>2</sub> so this compensation may be a useful adaptive response for only short periods of time and may not be helpful over the timescale associated with ocean acidification. The physiological adaptations to combat the effects of decreasing pH may themselves reduce survival and fitness as much as acidification itself. An extreme example of this is the brittlestar (*Amphiura filiformis*), a key link in benthic foodwebs, which exhibited a trade-off between maintaining skeletal integrity and arm function by using the muscle as an energy source (Wood et al. 2008). Such adaptive responses may be helpful to cope with the natural daily or even seasonal variability of ocean pH but may be less effective on the timescale of ocean acidification resulting in reduced long-term fitness and survival. This highlights the need to place short-term acclimation responses, sometimes seen in short-term experiments, in perspective when interpreting them in the long-term timescale of ocean acidification.

In the Southern Ocean extensive krill (*Euphausia superba*) populations support many predators and it is therefore a keystone species for this ecosystem. Shifts in krill metabolism have been observed when exposed to low pH and are consistent with increased physiological or energy costs associated with internal acid-base regulation (Saba et al. 2012). Such trade-offs may hamper growth and reproduction, which could negatively impact the krill population and cascade through the ecosystem (Figure 5.26).

### **Risk to ecosystem builders**

Organisms forming three dimensional structures on a sufficient scale create some of the most diverse ecosystems on the planet and can occur in the warm sunlit upper or deeper darker waters of the ocean.

Scleractinian cold-water corals, also known as deep-sea corals, may form one of the most vulnerable ecosystems to ocean acidification (Guinotte et al. 2006). They are found at depths from 200–>1,000 m throughout the ocean and are several 100s of years old. Their reef-like structures can be sizable, extending 10s of kilometres and reach heights of 10s of metres and may cover a similar proportion of the ocean as tropical coral reefs (Freiwald and Roberts 2005; Guinotte et al. 2006). These *Lophelia* reefs and giant carbonate mounds are biodiversity hotspots acting as a refuge, feeding ground and nursery for deep-sea organisms (CBD 2014, Roberts et al. 2006). It has been estimated that about 70 per cent of known cold-water coral ecosystems will experience under-saturated conditions with respect to aragonite, the form of calcium carbonate used to form their skeletons, within this century (Orr et al. 2005; Guinotte et al. 2006; Turley et al. 2007). Locally, down-welling of food rich, high pH water from the upper ocean may facilitate the short-term survival of some communities (Findlay et al. 2013) but with increased warming of surface waters the down-welling would be bringing warm waters that may elicit a negative response.

While short-term experiments assessing the effects of ocean acidification on cold-water coral species showed the vulnerability of their growth and metabolism to low pH (Maier et al. 2009; Hennige et al. 2014), relatively long-term laboratory experiments of 6–9 months duration found no apparent impacts (Form and Riebesell, 2012; Maier et al. 2013; Movilla et al. 2014). This implies their resilience to acidification, at least for the time-scales of these experiments, possibly through energy intensive up-regulation of their internal pH at the sites of calcification (McCulloch et al. 2012) or through reallocation of energy from other processes (CBD 2014). This underlines the need to carry out energy budgets to determine whether this apparent acclimation comes at a cost to long-term fitness. However, the carbonate mounds, which create the three dimensional habitat of these reef-like ecosystems, are comprised of dead skeletons unprotected by living tissue and these will be susceptible to dissolution as the waters around them become undersaturated with respect to aragonite (CBD 2014). It is noteworthy that few cold water framework forming corals currently exist below the saturation horizon or in the North Pacific where this horizon is shallow (50–600 m) (Feely et al. 2004). There is therefore a *high risk* that ocean acidification may have substantial impacts on the structure and function of these deep-water ecosystems due to *high severity, exposure and vulnerability*.

Deep-sea fauna has evolved under conditions of relative environmental stability (Yu et al. 2010) and may therefore be particularly vulnerable to the current rapid changes in seawater chemistry (Figure 5.25). The past stability of their habitat and their lower metabolic processes due to lower temperature and sparse and sporadic food availability (Gooday and Turley 1990) may indicate a lower adaptive capacity to future environmental variability. This contrasts to organisms that inhabit warmer, food rich and environmentally dynamic shallow coastal waters where adaptive capacity may be inherently greater due to this environmental instability (Barry et al. 2011; Somero, 2012).

Tropical coral reefs support diverse and productive ecosystems and exist in warm waters with high saturation states of aragonite that are used by reef-building organisms such as corals and calcareous red algae to construct the reef. Healthy coral reefs form three-dimensional calcium carbonate structures that provide habitats for about one million species. The projected rate of change of ocean acidification in tropical waters is greater than that seen in polar waters (Figure 5.25 although tropical waters are very unlikely to reach undersaturation, so acidification could arguably be less severe. However, *exposure* is *high* due to the high density of coral reefs and the large number and diversity of organisms they support. Coral reefs also seem very *vulnerable* to ocean acidification, with declines in coral calcification associated with declining aragonite saturation state even though saturation states are >1 (Kleypas and Langdon, 2006; Andersson and Gledhill 2013). Although not all corals species exhibit negative responses to reduced pH (CBD 2014) studies have already shown a 16 per cent decrease in reef calcification rates over the last two decades which may be attributed to increasing acidification (De'ath et al. 2009). A year-long *in situ* experiment net community calcification in a Great Barrier coral reef is depressed compared with values expected for preindustrial conditions, indicating that ocean acidification may already be impairing coral reef growth (Albright et al. 2016) If reef growth declines faster than natural physical and biological reef erosion there will be a net loss in reef over time.

An examination of coral reef biodiversity in the vicinity of a natural CO<sub>2</sub> vent revealed notable loss of coral diversity, recruitment and abundance and reef integrity when pH decreased from 8.1 to 7.8, with reef development stopping below pH 7.7 (Fabricius et al. 2011). The loss of habitat complexity and its provision of essential refugia had indirect impacts on larger reef-associated invertebrates that may not be directly vulnerable to ocean acidification (Fabricius et al. 2014).

Coral reef communities can alter their own seawater chemistry, through processes of photosynthesis, respiration, calcification, and dissolution (Kleypas et al. 2011; Anthony et al. 2013). Coral reefs located within or immediately downstream of seagrass or eelgrass beds, for example, may find refuge from ocean acidification (Palacios and Zimmerman 2007; Manzello et al. 2012). On the other hand, the rate of acidification in some coral reef ecosystems may be more than three times faster than in the open ocean due to local or regional disturbances to drivers of seawater carbonate chemistry (Cyronak et al. 2014).

Tropical coral reefs are also *vulnerable* to ocean warming, with episodes of warming leading to coral bleaching, as well as local stressors such as pollution, sedimentation, invasive species and poor fisheries practices. The combined action of these multiple stressors raises the *risk* of the loss of the majority of tropical coral reefs globally (Gattuso et al. 2014; IPCC 2014; Burke et al. 2015,).

### **Research needs and gaps**

Future coastal conditions are more difficult to project in models due to greater heterogeneity (Artioli et al. 2014) than found in the open ocean (Figure 5.6.2) because of the interactions with sediment processes and input from rivers or melting sea-ice (Salisbury et al. 2008; Hoffmann et al. 2011; Yamamoto et al. 2012). Increased understanding of these more dynamic coastal systems and their influences on the severity and variability of coastal pH is essential to assess the risk to coastal ecosystems and the provision of food resources to society (Turley and Gattuso 2012; Mathis et al. 2014).

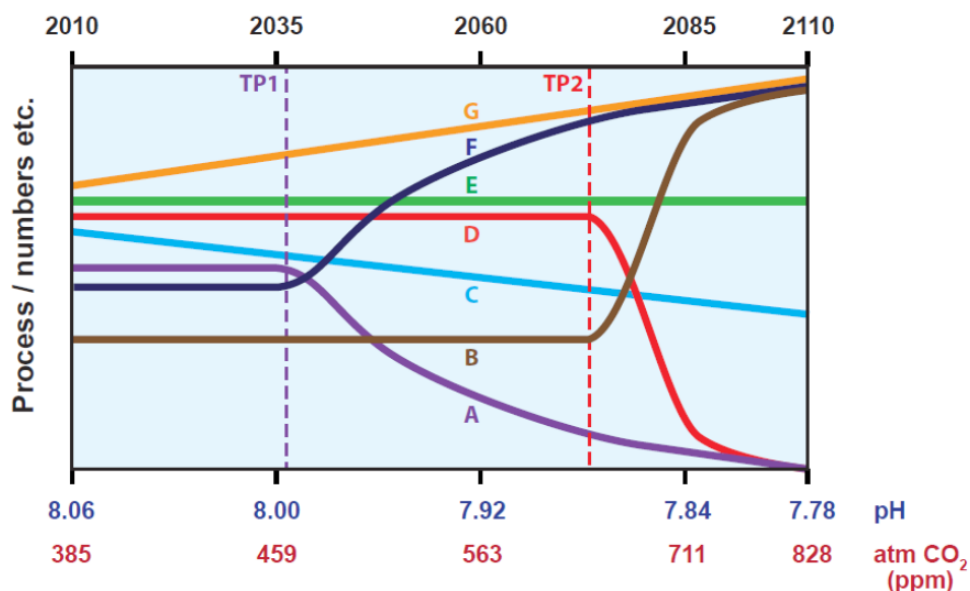
Understanding the long-term ecosystem-level consequences of ocean acidification is critical. However, scaling up understanding of the impact of ocean acidification on complex ecosystems from controlled experiments on single species is a formidable challenge requiring deep understanding of the role of the different species within an ecosystem, the dependency and interaction between the large number of species comprising the ecosystem and how these community dynamics may alter over time as ocean acidification progresses.

For instance, different species will react differently and at different time-scales. Some organisms could decline gradually but others could reach non-linear shifts - thresholds or “tipping points” - at different times. Some species could increase gradually; others could increase rapidly taking advantage of the vacant niches, while others may not change (Figure 5.28). How these responses and interactions are played out within a complex foodweb or ecosystem is difficult to predict and is a multidisciplinary research challenge.

It also requires a better understanding of how different organisms can control their internal pH, including pH at the site of calcification and how trade-offs of energy supply to different processes may enable them to either withstand or succumb to ocean acidification (Figure 5.26). It is also important to study the weakest link in an organism’s physiology and life cycle. A better understanding of which organisms are capable of long-term acclimatization or adaptation is required and whether there is sufficient phenotypic plasticity in a population to enable their survival in a future ocean, is required.

Predicting impacts of changing biodiversity or community dynamics on ecosystem function also requires expanding the scope of current experimental research to multi-level foodwebs and complex ecosystems (for example: Brussaard et al. 2013). Of this, a central challenge is to evaluate the importance of trophic cascades, the distribution of interaction strengths within natural communities and how they change with community composition.

**Figure 5.28.** A conceptual representation and simplification of potential different reactions of different species (A-G) comprising an ecosystem to increasing acidification (decreasing pH) with time. Some organisms could decline gradually (C) but others (A and D) could reach non-linear shifts - tipping points (TP1 and TP2) - at different times. Others could increase gradually (G), others could increase rapidly (B and F) taking advantage of the vacant niches, and others may not change (E). The time-scales of such tipping points and the implication on ecosystem structure and function are largely unknown.



Other stressors acting at the same time as ocean acidification, such as ocean warming and deoxygenation, and non-climate related local stressors such as pollution, nutrient runoff from land, and over-exploitation of marine resources, will increase *risk* to marine ecosystems (Gattuso et al. 2015; See Chapter 5.41, 4.2, 4.3, Section 6 and 7 for further context). This underlines the need to carry out multi-stress impact assessments on whole communities. That is, changes in ecosystem structure and function cannot be projected by investigating individual-level impacts in isolation, or by considering stressors separately. Scaling up to ecosystem impacts requires approaches that account for long-term, multi-scale responses to multiple stressors, in an ecosystem context (Queros et al. 2014).

Policy-makers, decision-makers, marine managers, industry and other stakeholders need to understand the *risk* posed to marine ecosystems, and the goods and services they provide society, of different concentrations and rates of anthropogenic CO<sub>2</sub> emissions and therefore the progression of ocean acidification. *Risk* of impacts from ocean acidification will depend on the likelihood of severe alterations in the normal functioning of an ecosystem. This will depend on the *severity* (of which strength and speed are components) of ocean acidification, and the *exposure* and *vulnerability* of organisms to ocean acidification especially those playing key roles in ecosystems. The higher the *severity*, *exposure* and *vulnerability* the greater the *risk* of impact to numbers of organisms and therefore to ecosystems.

#### Acknowledgements

This author would like to thank the UK Ocean Acidification (UKOA) research programme, funded jointly by the Natural Environment Research Council (NERC), the Department for Environment, Food, and Rural Affairs (Defra) and the Department of Energy and Climate Change (DECC) (grant no. ME5201) and the EU funded projects, the European Project on Ocean Acidification (EPOCA), the Mediterranean Sea Acidification in a Changing Climate project (MedSea.) sincere thanks also to Dr Sebastian Hennige for his helpful comments on a draft manuscript.

# References:

- Albright, R., Caldeira, L., Hosfelt, J., Kwiatkowski, L., Maclaren J.K., Mason, B.M., Nebuchina, Y., Ninokawa, A., Pongratz, J., Ricke, K.L., Rivlin, T., Schneider, K., Sesboué, M., Shamberger, K., Silverman, J., Wolfe, K., Zhu, K. and K.Caldeira (2016) Reversal of ocean acidification enhances net coral reef calcification. *Nature*, published online 24 February 2016. doi:10.1038/nature17155
- Andersson, A.J. and Gledhill, D. (2013) Ocean acidification and coral reefs: effects on breakdown, dissolution, and net ecosystem calcification. *Annual Review of Marine Science* 5, 321-348.
- Anthony, K.R.N., Diaz-Pulido, G., Verlinden, N., Tilbrook, B. and Andersson A.J. (2013). Benthic buffers and boosters of ocean acidification on coral reefs. *Biogeosciences Discussions* 10, 1831-1865.
- Archer, D. (2005) Fate of fossil fuel CO<sub>2</sub> in geologic time. *Journal of Geophysical Research* 110, C09S05, doi:10.1029/2004JC002625.
- Artoli, Y., Blackford, J., Nondal, G. et al. (2014) Heterogeneity of impacts of high CO<sub>2</sub> on the North Western European Shelf. *Biogeosciences* 11, 601-612.
- Barry, J.P., Widdicombe, S. and Hall-Spencer, J.M. (2011). Effects of ocean acidification on marine biodiversity and ecosystem function. In: Ocean acidification (eds J.-P. Gattuso & L. Hansson), Oxford University Press, Oxford.
- Bednaršek, N., Feely, R. A., Reum, J. C. P., Peterson, B., Menkel, J., Alin, S. R., and Hales, B. (2014). *Limacina helicina* shell dissolution as an indicator of declining habitat suitability owing to ocean acidification in the California Current Ecosystem. *Proceedings of the Royal Society B*, 281(1785), 20140123.
- Bednaršek, N., Tarling, G. A., Bakker, D. C. E., Fielding, S., Jones, E. M., Venables, H. J., and Murphy, E. J. (2012). Extensive dissolution of live pteropods in the Southern Ocean. *Nature Geoscience* 5(12), 881-885.
- Bopp, L., Resplandy, L., Orr, J.C., et al. (2013). Multiple stressors of ocean ecosystems in the 21st century: Projections with CMIP5 models. *Biogeosciences* 10(10), 6225-6245.
- Brussaard, C.P.D., Noordeloos, A.A.M., Witte, H., Collenteur, M.C.J., Schulz, K., Ludwig, A. and Riebesell, U. (2013) Arctic microbial community dynamics influenced by elevated CO<sub>2</sub> levels, *Biogeosciences* 10, 719–731, doi:10.5194/bg-10-719-2013.
- Burke, L. (2015). Warm-water corals at risk: local and future impact. Chapter 5.4 of this report.
- CBD (2014). An Updated Synthesis of the Impacts of Ocean Acidification on Marine Biodiversity (Eds: S. Hennige, J.M. Roberts & P. Williamson). T. Aze, J. Barry, R. Bellerby, L. Brander, M. Byrne, S. Dupont, J.-P. Gattuso, S. Gibbs, L. Hansson, C. Hattam, C. Hauton, J. Havenhand, J.H. Fossa, C. Kavanagh, H. Kurihara, R. Matear, F. Mark, F. Melzner, P. Munday, B. Niehoff, P. Pearson, K. Rehdanz, S. Tambutte, C. Turley, A. Venn, M. Warnau, J. Young. Secretariat of the Convention on Biological Diversity, Montreal, Technical Series No. 75, 99 pages.
- Comeau, S., Gorsky, G., Jeffree, R., Teyssié, J.-L., Gattuso, J.-P. (2009). Impact of ocean acidification on a key Arctic pelagic mollusc (*Limacina helicina*). *Biogeosciences* 6, 1877-1882.
- Comeau, S., Jeffree, R., Teyssié, J.-L. and Gattuso, J.-P. (2010a) Response of the Arctic pteropod *Limacina helicina* to projected future environmental conditions. *PLoS one* 5, e11362.
- Comeau, S., Gorsky, G., Alliouane, S. and Gattuso, J.-P. (2010b) Larvae of the pteropod *Cavolinia inflexa* exposed to aragonite undersaturation are viable but shell-less. *Marine Biology* 157, 2341-2345.
- Comeau, S. (2015) Pteropods at risk: ocean acidification. Chapter 5.5 of this report.
- Cyronak, T., Schulz, K.G., Santos, I.R. and B.D. Eyre (2014). Enhanced acidification of global coral reefs driven by regional biogeochemical feedbacks. *Geophysical Research Letters* 41, doi:10.1002/2014GL060849.
- De'ath, G., Lough, J.M. and Fabricius, K. E. (2009). Declining coral calcification on the Great Barrier Reef. *Science* 323(5910), 116-119.
- Dixon, D.L., Munday, P.L. and Jones, G.P. (2010). Ocean acidification disrupts the innate ability of fish to detect predator olfactory cues. *Ecology Letters* 13, 68–75.
- Dixon, D. L., Jennings, A. R., Atema, J. and Munday, P. L. (2014). Odor tracking in sharks is reduced under future ocean acidification conditions. *Global Change Biology* doi: 10.1111/gcb.12678
- Domenici, P., Allan, B., McCormick, M.I. and Munday, P.L. (2012). Elevated carbon dioxide affects behavioral lateralization in a coral reef fish. *Biology Letters* 8, 78–81
- Fabricius, K. E., Langdon, C., Uthicke, S., Humphrey, C., Noonan, S., De'ath, G., Okazaki, R., Muehllehner, N., Glas, M.S. and Lough, J. M. (2011). Losers and winners in coral reefs acclimatized to elevated carbon dioxide concentrations. *Nature Climate Change* 1(3), 165-169.
- Fabricius, K.E., De'ath, G., Noonan, S. and Uthicke, S. (2014). Ecological effects of ocean acidification and habitat complexity on reef-associated macroinvertebrate communities. *Proceedings of the Royal Society B* 281(1775), 20132479.
- Feely, R.A., Sabine C.L., Lee K., Berelson W., Kleypas J., Fabry, V.J. and Millero, F.J. (2004). Impact of anthropogenic CO<sub>2</sub> on the CaCO<sub>3</sub> system in the ocean. *Science* 305, 362–366.
- Feely, R.A., Sabine, C.L., Hernandez-Ayon, J.M., et al. (2008) Evidence for upwelling of corrosive “acidified” water onto the continental shelf. *Science* 320, 1490-1492.
- Findlay, H.S., Wood, H.L., Kendall, M.A., Spicer, J.I., Twitchett, R.J. and Widdicombe, S. (2009). Calcification, a physiological process to be considered in the context of the whole organism. *Biogeosciences Discussions* 6(1), 2267-2284.
- Findlay, H.S., Artioli, Y., Moreno Navas, J., Hennige, S.J., Wicks, L.C., Huvenne, V.A., Woodward, E.M.S. and Roberts, J.M. (2013). Tidal downwelling and implications for the carbon biogeochemistry of cold-water corals in relation to future ocean acidification and warming. *Global change biology* 19(9), 2708-2719.
- Form, A.U. and Riebesell, U. (2012). Acclimation to ocean acidification during long-term CO<sub>2</sub> exposure in the cold-water coral *Lophelia pertusa*. *Global change biology* 18, 843-853.
- Freiwald, A. and Roberts, J. M. (2006). *Cold-water corals and ecosystems*. Springer.
- Gattuso, J.-P., Hoegh-Guldberg, O. and Pörtner H.-O. (2014). *Coral Reefs*. In: Field C et al. (Eds.), *Climate Change 2014: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge: Cambridge University Press.
- Gattuso J-P, Magnan A, Billé R, Cheung WWL, Howes EL, Joos F, Allemand D, Bopp L, Cooley S, Eakin CM, Hoegh-Guldberg O, Kelly RP, Pörtner H-O, Rogers AD, Baxter JM, Laffoley, Osborn D, Rankovic A, Rochette J, Sumaila UR, Treyer S & Turley C (2015) Contrasting futures for ocean and society from different anthropogenic CO<sub>2</sub> emissions scenarios. *Science*, 3 July 2015, 349(6243).
- Gehlen, M., Séférian, R., Jones, D. O. B., Roy, T., Roth, R., Barry, J., ... and Tjiputra, J. (2014). Projected pH reductions by 2100 might put deep North Atlantic biodiversity at risk. *Biogeosciences Discussions* 11(6), 8607-8634.

- Gooday, A.J. and Turley, C.M. (1990). Responses by Benthic Organisms to Inputs of Organic Material to the Ocean Floor: A Review. *Philosophical Transactions of the Royal Society of London A* 331(1616), 119-138.
- Guinotte, J.M., Orr, J.C., Cairns, S.S., Freiwald, A., Morgan, L. and George, R. (2006). Will human-induced changes in seawater chemistry alter the distribution of deep-sea scleractinian corals? *Frontiers in Ecology and the Environment* 4, 141-146.
- Hall-Spencer, J.M., Rodolfo-Metalpa, R., Martin, S., Ransome, E., Fine, M., Turner, S.M., Rowley, S. J., Tedesco, D. and Buia, M.C. (2008). Volcanic carbon dioxide vents show ecosystem effects of ocean acidification. *Nature* 454(7200), 96-99.
- Hauri, C., Gruber, N., Vogt, M., et al. (2013). Spatiotemporal variability and long-term trends of ocean acidification in the California Current System. *Biogeosciences* 10, 193-216, doi:10.5194/bg-10-193-2013.
- Hennige, S., Wicks, L.C., Keamenos, N., Bakker, D.C.E., Findlay, H.S., et al. (2014) Short term metabolic and growth responses of the cold-water coral *Lophelia pertusa* to ocean acidification. *Deep Sea Research II* 99, 27-35.
- Hettinger, A., Sanford, E., Hill, T. M., Russell, A. D., Sato, K. N., Hoey, J., Forsch, M., Page, H.N. and Gaylord, B. (2012). Persistent carry-over effects of planktonic exposure to ocean acidification in the Olympia oyster. *Ecology* 93(12), 2758-2768.
- Hofmann, G.E., Smith, J.E., Johnson, K.S., Send, U., Levin, L.A., Micheli, F., ... and Martz, T.R. (2011). High-frequency dynamics of ocean pH: a multi-ecosystem comparison. *PLoS one* 6(12), e28983. doi:10.1371/journal.pone.0028983.
- Hönisch, B., Ridgwell, A., Schmidt, D.N., et al. (2012) The geological record of ocean acidification. *Science* 335, 1058-1063. doi: 10.1126/science.1208277.
- Hunt, B.P.V., Pakhomov, E.A., Hosie, G.W., Siegel, V., Ward, P. and Bernard, K. (2008). Pteropods in Southern Ocean ecosystems. *Progress in Oceanography* 78, 193-221, doi:10.1016/j.pocean.2008.06.001.
- IPCC (2012). *Managing the Risks of Extreme Events and Disasters to Advance Climate Change Adaptation*. A Special Report of Working Groups I and II of the Intergovernmental Panel on Climate Change [Field, C.B., V. Barros, T.F. Stocker, D. Qin, D.J. Dokken, K.L. Ebi, M.D. Mastrandrea, K.J. Mach, G.-K. Plattner, S.K. Allen, M. Tignor, and P.M. Midgley (eds.)]. Cambridge University Press, Cambridge, UK, and New York, NY, USA, 582 pp.
- IPCC (2013). Summary for Policymakers. In: *Climate Change 2013: The Physical Science Basis*. Contribution of Working Group I to the *Fifth Assessment Report of the Intergovernmental Panel on Climate Change* [Stocker, T.F., D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and P.M. Midgley (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.
- IPCC (2014) *Technical summary*. In: Field C et al. (Eds.), *Climate Change 2014: Impacts, Adaptation and Vulnerability*. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change Cambridge: Cambridge University Press.
- Joos, F., Frölicher, T.L., Steinacher, M. and Plattner, G.-K. (2011) Impact of climate change mitigation on ocean acidification projections. In: *Ocean acidification* (eds J.-P. Gattuso and L. Hansson), Oxford University Press, Oxford.
- Kleypas, J.A., Anthony, K.R.N. and Gattuso, J.-P. (2011). Coral reefs modify their seawater carbon chemistry – case study from a barrier reef (Moorea, French Polynesia). *Global change biology* 17, 3667-3678. doi: 10.1111/j.1365-2486.2011.02530.x
- Kroeker, K.J., Kordas, R.L., Crim, R., Hendriks, I.E., Ramajo, L., Singh, G.S., Duarte, C.M. and Gattuso, J.P. (2013). Impacts of ocean acidification on marine organisms: quantifying sensitivities and interaction with warming. *Global change biology* 19, 1884-1896.
- Langdon, C., and Atkinson, M.J. (2005). Effect of elevated pCO<sub>2</sub> on photosynthesis and calcification of corals and interactions with seasonal change in temperature/irradiance and nutrient enrichment. *Journal of Geophysical Research: Oceans* (1978-2012), 110(C9).
- Le Quéré, C., Andres, R.J., Boden, T., et al. (2013) The global carbon budget 1959-2011, *Earth System Science Data* 5, 165-185, doi:10.5194/essd-5-165-2013.
- Lischka, S., Buedenbender, J., Boxhammer, T. and Riebesell, U. (2011). Impact of ocean acidification and elevated temperatures on early juveniles of the polar shelled pteropod *Limacina helicina*: mortality, shell degradation, and shell growth. *Biogeosciences* 8, 919-932.
- Maas, A.E., Wishner, K.F. and Seibel, B.A. (2012). The metabolic response of pteropods to acidification reflects natural CO<sub>2</sub>-exposure in oxygen minimum zones, doi: 10.5194/bg-9-747-2012
- Maier, C., Hegeman, J., Weinbauer, M.G. (2009). Calcification of the cold-water coral *Lophelia pertusa* under ambient and reduced pH. *Biogeosciences* 6, 1671-1680.
- Maier, C., Schubert, A., Berzunza-Sanchez, M.M., Weinbauer, M.G., Watremez, P. and Gattuso, J.P. (2013). End of the century pCO<sub>2</sub> levels do not impact calcification in Mediterranean cold-water corals. *PLoS one* 8: 10.1371/journal.pone.0062655.
- Manzello, D.P., Enochs, I.C., Melo, N., Gledhill, D.K. and Johns, E.M. (2012). Ocean acidification refugia of the Florida reef tract. *PLoS one* 7, e41715.
- Mathis, J.T., Cooley, S.R., Lucey, N., Colt, S., Ekstrom, J., Hurst, T., Hauri, C., Evans, W., Cross, J.N. and Feely, R.A. (2014). Ocean Acidification Risk Assessment for Alaska's Fishery Sector, *Progress in Oceanography*, ISSN 0079-6611, <http://dx.doi.org/10.1016/j.pocean.2014.07.001>.
- McCulloch, M., Trotter, J., Montagna, P., Falter, J., Dunbar, R., et al. (2012). Resilience of cold-water scleractinian corals to ocean acidification: Boron isotopic systematics of pH and saturation state up-regulation. *Geochimica et Cosmochimica Acta* 87, 21-34.
- Melzner, S., Stange, P., Trübenbach, K., Thomsen, J., Casties, I., Panknin, U., Gorb, S.N. and Gutowska, M.A. (2011). Food supply and seawater pCO<sub>2</sub> impact calcification and internal shell dissolution in the blue mussel *Mytilus edulis*. *PLoS one* 6, e24223.
- Movilla, J., Gori, A., Calvo, E., Orejas, C., Lopez-Sanz, A., Dominguez-Carrio, C., Grinyo, J. and Pelejero, C. (2014). Resistance of two Mediterranean cold-water coral species to low-pH conditions. *Water* 6, 59-67.
- Munday, P.L., Dixon, D.L., Donelson, J.M., Jones, G.P., Pratchett, M.S., Devitsina, G.V. and Døving, K.B. (2009). Ocean acidification impairs olfactory discrimination of homing ability of a marine fish. *Proceedings National Academy Science USA* 106, 1848-1852.
- Myers, R.A., Baum, J.K., Shepherd, T.D., Powers, S.P. and Peterson, C.H. (2007). Cascading effects of the loss of apex predatory sharks from a coastal ocean. *Science* 315, 1846-1850.
- Ohde, S. and Hossain, M. (2004). Effect of CaCO<sub>3</sub> (aragonite) saturation state of seawater on calcification of *Porites* coral. *Geochemical Journal* 38, 613-621.
- Olafsson, J., Olafsdottir, S. R., Benoit-Cattin, A., Danielsen, M., Arnarson, T.S. and Takahashi, T. (2009). Rate of Iceland Sea acidification from time series measurements. *Biogeosciences* 6(11), 2661-2668.
- Orr, J.C., Fabry, V.J., Aumont, O., Bopp, L., Doney, S.C., Feely, R.A., ... and Yool, A. (2005). Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. *Nature* 437(7059), 681-686.
- Pace, M.L., Cole, J.J., Carpenter, S.R. and Kitchell, J.F. (1999). Trophic cascades revealed in diverse ecosystems. *Trends in ecology & evolution* 14(12), 483-488.

- Palacios, S. and Zimmerman, R.C. (2007). Response of eelgrass (*Zostera marina* L.) to CO<sub>2</sub> enrichment: Possible impacts of climate change and potential for remediation of coastal habitats. *Marine Ecology Progress Series* 344, 1-13
- Queirós, A.M., Fernandes, J.A., Faulwetter, S., Nunes, J., Rastrick, S.P.S., Mieszkowska, N., Artioli, Y., Yool, A., Calosi, P., Arvanitidis, C., Findlay, H.S., Barange, M., Cheung, W.W.L. and Widdicombe, S. (2014). Scaling up experimental ocean acidification and warming research: from individuals to the ecosystem. *Global Change Biology*, doi: 10.1111/gcb.12675
- Raven, J., Caldeira, K., Elderfield, H., Hoegh-Guldberg, O., Liss, P., Riebesell, U., Shepherd, J., Turley, C. and Watson, A. (2005). *Ocean acidification due to increasing atmospheric carbon dioxide*. The Royal Society.
- Ridgwell, A. and Schmidt, D.N. (2010). Past constraints on the vulnerability of marine calcifiers to massive carbon dioxide release. *Nature Geoscience* 3: 196-200.
- Roberts, J.M., Wheeler, A.J. and Freiwald, A. (2006). Reefs of the deep: the biology and geology of cold-water coral ecosystems. *Science* 312, 543-547.
- Saba, G.K., Schofield, O., Torres, J.J., Ombres, E.H. and Steinberg, D.K. (2012). Increased Feeding and Nutrient Excretion of Adult Antarctic Krill, *Euphausia superba*, Exposed to Enhanced Carbon Dioxide (CO<sub>2</sub>). *PLoS one* 7(12), e52224. doi: 10.1371/journal.pone.0052224
- Salisbury, J., Green, M., Hunt, C. and Campbell, J. (2008). Coastal acidification by Rivers: a threat to shellfish? *Eos, Transactions American Geophysical Union* 89, 513.
- Simpson, S.D., Munday, P.L., Wittenrich, M.L., Manassa, R., Dixon, D.L., Gagliano, M. and Yan, H.Y. (2011). Ocean acidification erodes crucial auditory behavior in a marine fish. *Biology Letters* 7, 917-920.
- Somero, G.N. (2012). The physiology of global change: linking patterns to mechanisms. *Annual Review of Marine Science* 4, 39-61.
- Steinacher, M., Joos, F., Frolicher, T.L., Plattner, G.K. and Doney, S.C. (2009). Imminent ocean acidification in the Arctic projected with the NCAR global coupled carbon cycle-climate model. *Biogeosciences* 6, 515-533.
- Sunday, J.M., Calosi, P., Dupont, S., Munday, P.L., Stillman, J.H. and Reusch, T.B. (2014). Evolution in an acidifying ocean. *Trends in ecology and evolution* 29 (2), 117-125.
- Thomsen, J., Casties, I., Pansch, C., Körtzinger, A. and Melzner, F. (2013). Food availability outweighs ocean acidification effects in juvenile *Mytilus edulis*: laboratory and field experiments. *Global change biology* 19 (4), 1017-1027.
- Turley C. and Gattuso J-P (2012), Future biological and ecosystem impacts of ocean acidification and their socioeconomic-policy implications. *Current Opinion in Environmental Sustainability* 4, 1-9 <http://dx.doi.org/10.1016/j.cosust.2012.05.007>.
- Turley, C.M., Roberts, J.M. and Guinotte, J.M. (2007). Corals in deep-water: will the unseen hand of ocean acidification destroy cold-water ecosystems? *Coral reefs* 26 (3), 445-448.
- Turley, C., Eby, M., Ridgwell, A.J., Schmidt, D.N., Findlay, H.S., Brownlee, C., Riebesell, U., Gattuso, J.-P., Fabry, V.J. and Feely, R.A. (2010). The societal challenge of ocean acidification. *Marine Pollution Bulletin* 60, 787-792. doi: 10.1016/j.marpolbul.2010.05.06
- Van Hoodonk, R. (2015). Ocean acidification: projections of future state under 2 scenarios. Chapter 4.5 of this report.
- Welch, M.J., Watson, S.-A., Welsh, J.Q., McCormick, M.I. and Munday, P.L. (2014). Effects of elevated CO<sub>2</sub> on fish behaviour undiminished by transgenerational acclimation. *Nature Climate Change*, PUBLISHED ONLINE: 5 OCTOBER 2014 | DOI: 10.1038/NCLIMATE2400.
- Whittmann, A.C. and Pörtner H.-O. (2013). Sensitivities of extant animal taxa to ocean acidification. *Nature Climate Change* 3, 995-1001, <http://dx.doi.org/10.1038/nclimate1982>
- Wicks, L.C. and Roberts, J.M. (2012). Benthic invertebrates in a high-CO<sub>2</sub> world. *Oceanography and Marine Biology: An Annual Review* 50, 127-188.
- Williamson, P. and Turley, C. (2012). Ocean acidification in a geoengineering context. *Philosophical Transactions of the Royal Society A* 370(1974), 4317-4342. doi:10.1098/rsta.2012.0167
- Wood, H.L., Spicer, J.I. and Widdicombe, S. (2008) Ocean acidification may increase calcification, but at a cost. *Proceedings of the Royal Society B*. 275, 1767-1773.
- Zeebe, R.E. and Ridgwell, A. (2011). Past changes of ocean carbonate chemistry. In: *Ocean acidification* (eds J.-P. Gattuso & L. Hansson), Oxford University Press, Oxford.
- Yamamoto, A., Kawamiya, M., Ishida, A., Yamanaka, Y. and Watanabe, S. (2012). Impact of rapid sea-ice reduction in the Arctic Ocean on the rate of ocean acidification. *Biogeosciences* 9, 2365-2375.
- Yu, J., Broecker, W.S., Elderfield, H., Jin, Z., McManus, J. and Zhang, F. (2010). Loss of carbon from the deep sea since the Last Glacial Maximum. *Science* 330, 1084-1087, doi:10.1126/science.1193221