



PEARL

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Published in:
Ocean acidification

Publication date:
2011

Link:
[Link to publication in PEARL](#)

Citation for published version (APA):
Barry, JP., Hall-Spencer, JM., & Widdicombe, S. (2011). Effects of ocean acidification on marine biodiversity and ecosystem function. In JP. Gattuso, & L. Hannsen (Eds.), *Ocean acidification* (Vol. 0)

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Effects of ocean acidification on marine biodiversity and ecosystem function

James P. Barry, Stephen Widdicombe, and Jason M. Hall-Spencer

10.1 Introduction

The biodiversity of the oceans, including the striking variation in life forms from microbes to whales and ranging from surface waters to hadal trenches, forms a dynamic biological framework enabling the flow of energy that shapes and sustains marine ecosystems. Society relies upon the biodiversity and function of marine systems for a wide range of services as basic as producing the seafood we consume or as essential as generating much of the oxygen we breathe. Perhaps most obvious is the global seafood harvest totalling over 100 Mt yr⁻¹ (82 and 20 Mt in 2008 for capture and aquaculture, respectively; FAO 2009) from fishing effort that expands more broadly and deeper each year as fishery stocks are depleted (Pauly *et al.* 2003). Less apparent ecosystem services linked closely to biodiversity and ecosystem function are waste processing and improved water quality, elemental cycling, shoreline protection, recreational opportunities, and aesthetic or educational experiences (Cooley *et al.* 2009).

There is growing concern that ocean acidification caused by fossil fuel emissions, in concert with the effects of other human activities, will cause significant changes in the biodiversity and function of marine ecosystems, with important consequences for resources and services that are important to society. Will the effects of ocean acidification on ecosystems be similar to those arising from other environmental perturbations observed during human or earth history? Although changes in biodiversity and ecosystem function due to ocean acidification have not yet been widely observed, their onset may

be difficult to detect amidst the variability associated with other human and non-human factors, and the greatest impacts are expected to occur as acidification intensifies through this century.

In theory, large and rapid environmental changes are expected to decrease the stability and productivity of ecosystems due to a reduction in biodiversity caused by the loss of sensitive species that play important roles in energy flow (i.e. food web function) or other processes (e.g. ecosystem engineers; Cardinale *et al.* 2006). In practice, however, most research concerning the biological effects of ocean acidification has focused on aspects of the performance and survival of individual species during short-term studies, assuming that a change in individual performance will influence ecosystem function. By their nature, controlled experimental studies are limited in both space and time, and thus may not capture important processes (e.g. acclimatization and adaptation, multispecies biological interactions, chronic low-level impacts) that can ultimately play large roles in the response of marine systems to ocean acidification. This 'scaling up' from individual- to ecosystem-level effects is the most challenging goal for research on the potential effects of ocean acidification.

To plan for the future, society needs information to understand how ocean acidification and other environmental changes will affect fisheries, aquaculture, and other services deriving from the efficient function of marine ecosystems. The influx of fossil fuel CO₂ into the upper ocean from the atmosphere is altering the chemistry of ocean waters at a faster rate and greater magnitude than is thought to have

occurred on earth for at least a million years and perhaps as much as 40 Myr (Pelejero *et al.* 2010; see Chapter 2). In this chapter, the influence of this important change in ocean chemistry on the biodiversity and function of marine ecosystems is considered, from basic physiological responses of individual organisms and species, to the potential changes in various ocean environments.

10.2 Biodiversity and ecosystem function

The term biodiversity is broadly defined, and used to characterize aspects of the biological complexity of natural systems. Often cast simply as the number of species in a region (i.e. *species richness*), biodiversity has a far larger scope that spans the variation within and among systems and organisms over multiple scales and levels of genetic, organismal, ecological, or ecosystem diversity. Measures of biodiversity attempt to estimate the richness and evenness of biological characteristics at different levels, such as *species richness* and *species diversity* (the number and evenness of species in a region), *taxonomic diversity* (not just species richness, but diversity at higher taxonomic levels), *genetic diversity* (genetic variation in a population or species), *habitat* or *ecosystem diversity* (range of habitats or ecosys-

tems in a region), or *functional diversity* (the number of functional roles performed by the species present) (see Fig. 10.1; Petchey and Gaston 2006). Biodiversity is a dynamic feature of natural systems, reflecting the continual evolutionary response of species in a region to selection across a broad range of environmental and ecological pressures. Biodiversity can expand and contract as species diversity or other elements of biological diversity are created, maintained, or lost to extinction.

The function of ecosystems is wholly dependent on biodiversity that allows energy to flow through trophic webs and biological networks. Moreover, the stability and resilience of ecosystem functions, from nutrient cycling and energy flow, to the population dynamics of species, are thought to be sensitive to the loss of biodiversity caused by perturbations of both human and non-human origin. This concept has long been considered theoretically, with more diverse and trophically complex systems expected to be more stable and resistant to perturbations. *Species complementarity* (different species have similar ecological roles) and *species redundancy* (different species perform the same function) are thought to provide ‘insurance’ for ecosystem function in diverse systems by promoting functional diversity and maintaining energy flow among trophic levels (i.e. ecosystem function)



Figure 10.1 Species diversity does not necessarily represent functional diversity. Note that both groups have equal species richness and diversity (a single individual from each of eight molluscan species), but the group on the right has greater taxonomic distinctness and functional diversity. Photo R. M. Warwick.

upon a reduction or loss of species in response to environmental variation or other factors (Loreau *et al.* 2001).

Field studies in terrestrial and marine ecosystems over the past two decades have provided both support (e.g. Steneck *et al.* 2002) and moderate controversy concerning the diversity–stability concept (Loreau *et al.* 2001; Cardinale *et al.* 2006). The controversy relates, in part, to the disproportionate role of key species in many systems studied, without which stability is reduced. This issue may be important in several marine ecosystems where key prey species (e.g. pteropods, krill, anchovies, and squid in coastal systems) or taxa that play an important structural role (e.g. habitat-forming corals) can be critical resources for other taxa. Thus, reduced biodiversity due to the loss of prey taxa or habitat-forming species may not have large effects on energy flow or ecosystem function and stability, so long as key species that maintain the functional diversity of the system are relatively unaffected (Tilman *et al.* 1997). Although this debate continues, a recent examination of experimental studies of nearshore marine communities (Duffy 2009) and long-term studies of large marine ecosystems (Worm *et al.* 2006) provides fairly strong support for the role of biodiversity in ecosystem function and stability. For many marine systems, however, the current understanding of the natural history and functional roles of most species is poor; thus it will be challenging to predict how ocean acidification may affect ecosystem function.

10.3 Acclimatization and adaptation

Organisms and species faced with ocean acidification or other environmental changes have four options—migration, acclimatization (i.e. tolerance), adaptation, or extinction. Migration, by individuals or by a population successively through generations, may be possible in some cases, but the global nature of ocean acidification coupled with range limitations imposed by other environmental parameters (e.g. temperature) may limit this option. For example, meridional gradients in aragonite saturation (see Fig. 14.5 in Chapter 14) may allow the ranges of some mid-latitude taxa to shift toward more saturated waters of the tropics as acidification intensifies, unless other factors (e.g. tempera-

ture) are intolerable. Range shifts along other gradients in pH or carbonate saturation (e.g. depth-related or horizontally in coastal regions) may also be possible.

Whether marine organisms, from microbes to long-lived megafauna, will be able to acclimatize or adapt to future ocean acidification is an important, but unresolved, question. Acclimatization is the process by which individuals adjust to environmental changes (i.e. physiological adjustment). This may result in a change in energy costs (positive or negative) associated with living. Adaptation is the adjustment of species to environmental change between generations, through natural selection of individuals tolerant of new conditions. Tolerance or acclimatization by at least some individuals in the population allows for adaptation, assuming that the tolerant traits are heritable and sufficient time is available for selection to increase the frequency of tolerant genotypes through multiple generations. If individuals in most populations are able to acclimatize to reduced ocean pH or carbonate saturation through the adjustment of physiological homeostasis, changes in ocean biodiversity could be mild—perhaps only a contraction in genetic diversity within species with minor effects on ecosystem functions.

Although it is expected that there will be ‘winners’ and ‘losers’ in response to ocean acidification, many vulnerable species (such as corals; see Kleypas and Yates 2009) may suffer from reduced performance and survival, and have limited scope for adaptation due to the expected pace and magnitude of ocean acidification in the future. Taxa with short generation times and immense population sizes such as phytoplankton and microbes (e.g. with one to three generations per day) have perhaps the greatest capacity to adapt, given that upwards of 35 000 to 100 000 generations are possible over the next 100 years as ocean acidification intensifies. Collins and Bell (2006), however, found little evidence of adaptation to high CO₂ levels in a pond alga (*Chlamydomonas*) after 1000 generations. In contrast, the scope for adaptation by species with long generation times (e.g. 10 to 30 yr for some fishes) and relatively small population sizes is expected to be limited when selection for tolerant genotypes is constrained to just a few generations.

10.4 Effects of environmental change

Environmental variation over space or time can have positive and negative effects on biodiversity and ecosystem function related to the rate, magnitude, duration, and spatial scale of environmental change (Knoll *et al.* 2007). Habitats with greater spatial heterogeneity provide variable environmental conditions that typically support higher biodiversity than relatively homogeneous habitats. Temporal environmental variation also plays a key role in regulating local diversity. Some level of change in environmental factors (e.g. physical disturbance or variability in temperature, oxygen, or other parameters) or biological factors (e.g. variation in the abundance of predators or competitors) can lead to enhanced local diversity (Connell 1978). Moreover, environmental variability can promote genetic diversity by selecting for a broad range of genotypes to match environmental patterns, or allowing for adaptive radiation as species emerge to fill new ecological space. Species, populations, or genotypes originate through evolutionary divergence to exploit novel habitats, or through specialization in response to environmental variation (temperature, habitat complexity, oxygen concentration, light, etc.) and biological interactions (trophic, competitive, or mutualistic).

Coral reef ecosystems, typified by high topographic complexity that promotes species-packing, have been shown to have been cradles of diversification throughout the Phanerozoic, with high rates of species origination that are often exported to offshore and deeper regions (Kiessling *et al.* 2010; see Chapter 4). For example, habitat complexity generated by highly branched scleractinian corals such as *Acropora* spp. provide habitat for a remarkably diverse array of fishes and invertebrates. Such branching corals are keystone functional groups, and are threatened by ocean acidification and other environmental changes (Bellwood *et al.* 2004). Reduced coral growth and weaker carbonate cementation will increase the probability of damage to most structurally complex corals during storms, probably leading to reef flattening and reduced reef biodiversity (Hofmann *et al.* 2010). Similar impacts on scleractinian corals, and perhaps other structure-forming groups in deep-sea systems (Guinotte *et al.*

2006), may also influence biodiversity and ecosystem function due to the loss of critical habitat for various coral-associated taxa.

Evidence for shifts in biodiversity during periods of environmental change is common in the fossil record. Mayhew *et al.* (2008) report significant positive correlations between variation in global temperature and the rates of origination and extinction of families and genera through the Phanerozoic. Correlations were higher for originations, but not for extinctions, when diversity lagged behind temperature by 10 Myr, suggesting that diversification occurs mainly after a period of extinction driven by global warming. For marine genera, the effect of variation in CO₂ levels on extinction rates was stronger than that of temperature, suggesting that ocean carbon levels have influenced marine species diversity throughout the Phanerozoic. Five major mass extinction events that caused the loss of 75% or more of all species (Jablonski and Chaloner 1994; see also Chapter 4) are the most striking features of the fossil record. For many (if not all) of these events, rapid change in environmental parameters, such as temperature, oxygen levels, and ocean pH, coupled with ecological factors, appear to have played a large role in the high extinction rates (Knoll *et al.* 2007; Chapter 4). Marine life recovered following each extinction event, but required millions of years, potentially due to slow rates of evolutionary diversification or persistently unfavourable environmental conditions, or both (Knoll *et al.* 2007).

Is it likely that ocean acidification will reduce the biodiversity of marine ecosystems and drive significant shifts in their function? The response of marine ecosystems will be linked to the rate and magnitude of changes in ocean chemistry in relation to the potential rates of acclimatization, adaptation, and evolution of marine organisms, from microbes to vertebrates. The ongoing large and rapid changes in ocean pH and carbonate saturation are expected to drive environmental changes unseen in the recent evolutionary history of marine organisms, posing an evolutionary challenge to acclimatize or adapt. At a minimum, the genetic diversity of various marine taxa is likely to change. It remains unknown whether ocean acidification will drive species to extinction, but it is possible, based on the growing literature concerning the sensitivity

and performance of marine organisms under future, high-CO₂ conditions (e.g. Fabry *et al.* 2008; Widdicombe and Spicer 2008; Doney *et al.* 2009).

Extinction is not required for ocean acidification to affect the function of marine ecosystems, since changes in the relative abundance and activities of species can affect biological interactions (e.g. food web function) and habitat quality. If calcifying taxa are indeed the most vulnerable to decreasing ocean pH and carbonate saturation (Orr *et al.* 2005; Hofmann *et al.* 2010), then potential impacts of ocean acidification on the abundance and productivity of calcifying species that play key roles in marine food webs or other elements of ecosystem function are likely to have broad cascading effects within the ecosystem. For example, pteropod molluscs sensitive to reduced aragonite saturation conditions (Feely *et al.* 2004; Orr *et al.* 2005; Comeau *et al.* 2009) may be less abundant under future ocean conditions, leading to reduced availability for their current predators, which must then find alternative prey. Likewise, species that may depend on pteropods in other ways (e.g. *Pteropagurus* sp., a hermit crab that depends upon pteropod shells as habitat; McLaughlin and Rahayu 2008), may suffer from reduced pteropod abundance. Simultaneously, pteropod prey (e.g. copepods, diatoms) and potential competitors (e.g. krill, salps) are likely to experience reduced predation and competition, respectively, and thus, may increase in abundance. Consequently, a significant reshuffling of the structure of marine communities and ecosystem function in response to ocean acidification is possible if there are marked shifts in the abundance of 'losers' and 'winners', particularly if key species are affected.

10.5 The effects of ocean acidification on organisms

Several physiological processes, such as photosynthesis, calcification, acid–base homeostasis, respiration and gas exchange, and metabolic rate, can be influenced by changes in ocean carbonate chemistry (Gattuso *et al.* 1999; Seibel and Walsh 2003; Melzner *et al.* 2009b; Chapter 8). High ocean carbon levels are expected to affect primary producers in different ways, perhaps leading to a shift in the

structure of phytoplankton populations (Hall-Spencer *et al.* 2008; Doney *et al.* 2009; see Chapters 6 and 7). Taxa that are currently carbon-limited (e.g. some cyanobacteria) may be among the 'winners' in a high-CO₂ ocean. For other autotrophs (e.g. coccolithophores), photosynthesis and growth, as well as calcification, may be affected, with complex responses among species. A suite of experiments on marine phytoplankton have shown that the responses of coccolithophorids (calcareous phytoplankton) to elevated CO₂ levels vary, but generally exhibit reduced rates of calcification (Ridgwell *et al.* 2009; Hendriks *et al.* 2010). Reduced calcification has been measured in a variety of taxa, particularly corals and molluscs (Michaelidis *et al.* 2005; Gazeau *et al.* 2007; Kuffner *et al.* 2008; Doney *et al.* 2009), and is the most widely observed and consistent effect of ocean acidification (Hendriks *et al.* 2010; Kroeker *et al.* 2010). Exposure times have typically been short for most calcification studies, and may often be too short to detect acclimatization, which has been shown to require about 6 weeks for a marine fish (Deigweier *et al.* 2008). In contrast, coccolithophores may acclimatize to high CO₂ levels within hours (Barcelos e Ramos *et al.* 2010). Increased rates of calcification in low-pH waters have been observed for a few taxa (e.g. crustaceans, Ries *et al.* 2009), but it appears that, at least for some species, higher calcification in low-pH waters may require energetic trade-offs that reduce overall performance (Wood *et al.* 2008).

Even for taxa tolerant of low-pH waters, the physiological 'cost of living' is expected to change the energy required for basic biological functions (Pörtner *et al.* 2000). Immersion in high-CO₂ waters can disrupt the acid–base status of many marine animals, leading to reduced respiratory efficiency, reduced enzyme activity, and metabolic depression, with potentially large effects on overall metabolic performance (Seibel and Walsh 2003; see Chapter 8). Assuming a constant total energy budget, a change in the 'cost of living' is expected to result in a reallocation of energy for growth and reproduction (Fig. 10.2). For taxa affected by ocean acidification, individual physiological stress can lead to reduced growth, size, reproductive output, and survival. On a population level, impaired individual performance and survival have consequences for

populations and species that may include reduced abundance, productivity, and resilience to disturbance, as well as increased likelihood of extinction. For taxa benefiting either directly or indirectly from high CO₂ levels, the opposite may be true. It is also important to consider the cumulative effects of environmental stressors on the demography and productivity of populations. Effects on different life stages can sum to significant impacts on population success. For example, during periods of low sea-surface temperature (<13.1°C), exposure to low-pH waters reduces the survival of early life stage barnacles along the coast of the south-west United Kingdom by 25%, potentially leading to reduced local population abundance (Findlay *et al.* 2010).

Sensitivity to ocean acidification is expected to be coupled primarily to fundamental physiological adaptations linked closely to phylogeny. Marine organisms with a natural capacity for gas exchange (i.e. organisms with well-developed respiratory and circulatory systems, as well as respiratory proteins allowing high O₂ and CO₂ fluxes) that support high metabolic rates and high aerobic scope (e.g. fishes, decapod crustaceans, and cephalopods) are pre-adapted for many of the stresses related to ocean acidification (Melzner *et al.* 2009b; see Chapter 8). This is due in part to the overlapping physiological challenges posed by metabolic CO₂ generation during intense aerobic activity (e.g. coping with internal acid–base disruption) and the effects of ocean

acidification. Many taxa in habitats with variable or low pH (e.g. vesicomyid clams, vestimentiferan tubeworms, mussels in vent or seep environments) also have adaptations that allow them to thrive in naturally hypoxic and low-pH waters (Goffredi and Barry 2002; Tunnicliffe *et al.* 2009). Mobile crustaceans and fishes may benefit somewhat in a high-CO₂ ocean, based on their generally higher rates of growth and calcification in low-pH waters (Ries *et al.* 2009; Kroeker *et al.* 2010). However, even taxa with the capacity to cope with activity-related hypercapnia can experience impaired physiological performance in high-CO₂ waters. Rosa and Seibel (2008) found that activity levels in jumbo squid declined by 45% under a 0.3 unit reduction in pH. In contrast, cod exposed to a large pH perturbation (–1 pH unit) for several months displayed no evidence of impaired maximal swimming speed (Melzner *et al.* 2009a).

Taxa with weaker control over internal fluid chemistry may be at greater risk from ocean acidification. For example, echinoderms, brachiopods, and lower invertebrates (e.g. sponges, cnidarians, and ctenophores) lack respiratory organs and exchange gases with seawater by molecular diffusion across various body tissues. Although physiological tolerance to ocean acidification has not been examined closely in most of these groups (other than rates of calcification, see below), their postulated weak control of internal fluid chemistry (e.g. sea urchins, Miles *et al.* 2007) is expected to increase their sensitivity to changing ocean chemistry. Echinoderms appear less tolerant of low-pH waters than many groups, as indicated by their conspicuous absence from habitats with naturally high CO₂ levels such as hydrothermal vents (Grassle 1986) and low-pH areas near shallow CO₂ vents off Italy (Hall-Spencer *et al.* 2008). Notably, various taxa with limited physiological capabilities (many cnidarians and sponges) appear to tolerate low or variable pH, due to their occurrence in low-pH habitats such as hydrothermal vents and other natural CO₂ venting sites. Moreover, generalities based on short-term studies of organism physiology or survival, as are most common in the literature, may differ from the eventual long-term consequences of ocean acidification.

For calcifying taxa, the type of carbonate minerals formed can influence their vulnerability to ocean

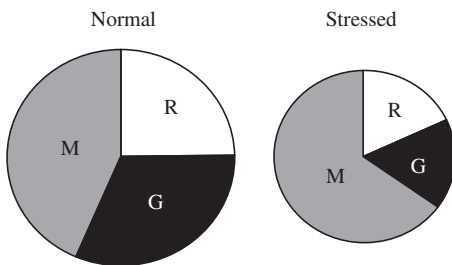


Figure 10.2 Hypothetical energy budget for normal and stressed organisms. Under normal conditions, the energetic cost of maintenance (M) is a significant portion of the total energy budget. If ocean acidification or other environmental changes are stressful, maintenance costs (e.g. ion regulation) can increase, leaving less energy available for growth (G) or reproduction (R). In addition, if metabolic depression is induced by ocean acidification, the total energy budget may decrease, hence the smaller pie size for the energy budget of the stressed organism.

acidification. Carbonate skeletal structures of marine taxa vary considerably both in terms of how much calcium carbonate (CaCO_3) is included, from nearly 100% CaCO_3 to mixtures of chitin and CaCO_3 (e.g. many crustacean shells). The form of CaCO_3 also varies, with most taxa precipitating aragonite or calcite, the latter which may include some percentage of magnesium. Of these, high-Mg calcite is the most soluble in seawater, and thus most susceptible to dissolution by ocean acidification, followed by aragonite and calcite (see Box 1.1 in Chapter 1).

Although calcification rates by organisms are generally impaired under low-pH conditions, there is considerable variation among the responses of major taxonomic groups (Hendriks *et al.* 2010; Kroeker *et al.* 2010). Scleractinian corals (aragonite) exhibit the largest reduction in calcification and most consistent response to low-pH waters. Coccolithophores (calcite) and molluscs (mostly calcitic) had somewhat weaker, variable, and non-significant changes in calcification. Individual studies have reported generally reduced rates of calcification for bivalve and gastropod molluscs under high- CO_2 conditions (Gazeau *et al.* 2007; Doney *et al.* 2009; Ries *et al.* 2009; Hendriks *et al.* 2010). In contrast, echinoderms (calcite) are highly variable in response, mainly due to the great variability in degree of calcification within the phylum (e.g. Wood *et al.* 2008). Crustaceans (chitin, calcite, amorphous carbonate) are the single group showing a significant increase in calcification rate under high- CO_2 conditions (Kroeker *et al.* 2010).

Reef-building corals in particular, due to their aragonitic skeletons, are perceived to be at high risk from ocean acidification, based on the projected future reduction in aragonite saturation throughout the world's oceans (Kleypas *et al.* 1999). These projections are consistent with the existing global distribution of deep-sea aragonitic corals, which are most abundant in the Atlantic and relatively rare in habitats with low aragonite saturation, such as the Pacific Basin (Guinotte *et al.* 2006; Manzello 2010). Surprisingly, some corals may survive acidic conditions without carbonate skeletons. Two Mediterranean species (*Oculina patagonica* and *Madracis pharencis*) survived a 12-month exposure to acidic ($\text{pH}_T = 7.3\text{--}7.6$) waters but lost their carbonate skeletons, which dissolved in the corrosive

waters (Fine and Tchernov 2007). Upon immersion in ambient pH waters ($\text{pH}_T = 8.3$) the corals recalcified. This type of recovery is unlikely for many other coral taxa with modes of life linked strongly to their structural framework.

Calcified shells and skeletons can play important roles for organisms coping with environmental variability. In some cases, more robust calcification may increase the survival (and presumably the fitness) of organisms, which can affect the biodiversity and function of marine communities. For example, the intertidal snail *Littorina littorea* thickens its shell after exposure to chemical cues produced by its main predator, the green shore crab, *Carcinus maenas*, in effect increasing its defence against predation (Bibby *et al.* 2007). Such shell thickening does not occur under high- CO_2 conditions, presumably due to the increased energetic cost of calcification at lower-pH, less saturated conditions, thereby increasing their risk of predation. Very few studies have examined the effects of ocean acidification on behavioural responses that mediate interactions between interacting species and populations.

10.6 Habitats

The risk of changes in the biodiversity and function of marine ecosystems due to ocean acidification is likely to vary considerably among habitats. Seawater carbonate chemistry is affected by temperature and biological processes, leading to significant patterns in carbonate chemistry across zonal and meridional gradients (Kleypas *et al.* 1999; Feely *et al.* 2004), with depth, and in relation to biological productivity. Colder high-latitude regions have naturally lower saturation states for aragonite and calcite due to the higher solubility of CO_2 at low temperatures, and will be the first surface waters to be persistently undersaturated with respect to aragonite (Orr *et al.* 2005; see Chapter 2), with potentially significant effects on marine calcifiers. The influence of ocean acidification on sediment ecosystems is considered in Chapter 9.

10.6.1 Upper ocean

Changes in environmental conditions through this century, including ocean acidification and warming,

could lead to a restructuring of phytoplankton assemblages with consequences that would reverberate throughout marine communities. For example, the composition of phytoplankton assemblages in the north-east Atlantic changed as waters warmed during the latter half of the last century, with a poleward expansion of warm-temperate plankton and recession of colder forms (Hays *et al.* 2005). In the English Channel, coccolithophores and dinoflagellates have become more abundant and dominant over the past ~20 yr, while diatoms and *Phaeocystis* have decreased (Widdicombe *et al.* 2010). The expansion of dinoflagellates may be expected based on the emergence of these groups during warmer, high-CO₂ periods in earth's history (Beardall and Raven 2004). Cyanobacteria, which thrived under high CO₂ levels earlier during earth's history, are also expected to benefit from ocean acidification. Photosynthetic rates of two dominant oceanic cyanobacterial genera (*Synechococcus* and *Trichodesmium*) were observed to increase markedly under expected future climate conditions, so long as nutrient levels were sufficiently high, while other closely related taxa (*Prochlorococcus* and *Nodularia*) showed little change or even lower rates (Fu *et al.* 2007). An increase in the diversity, abundance, or productivity of cyanobacteria could increase rates of global nitrogen fixation (Hutchins *et al.* 2009), which would be likely to drive responses in primary production by other groups. High CO₂ levels have also been shown to cause enhanced production of dimethyl sulphide by natural phytoplankton assemblages, which could promote climate homeostasis by stimulating cloud formation (see Chapter 11).

Elevated pCO₂ can also affect phytoplankton communities and the entire water column community through changes in elemental uptake or calcification by major groups. Increased C:N and C:P ratios have been measured in mixed phytoplankton assemblages in response to high CO₂ levels (Riebesell *et al.* 2007; see Chapter 6), potentially changing their nutritional value to consumers and leading to changes in growth and reproduction of zooplankton. Reduced rates of calcification for coccolithophores and foraminifera, two major planktonic calcifying groups, may also affect the flux of organic debris to deeper waters, due to changes in

ballasting of organic aggregates (Fabry *et al.* 2008; Ridgwell *et al.* 2009).

Holoplankton can also be affected by changing ocean chemistry, perhaps especially in weakly saturated waters of high-latitude systems. Euphausiids and thecosomatous pteropods, two key planktonic groups thought to be critical linkages in global food webs, may be affected differently by ocean acidification. Pteropods (e.g. *Limacina* sp. and *Clio* sp.) are important planktonic calcifiers in open-ocean food webs and represent major prey taxa for higher predators (e.g. many salmon species), and thus are a key link in open-ocean food webs and energy flow (Fabry *et al.* 2009). Immersion of shelled pteropods in high-CO₂, low-CO₃²⁻ waters is known to weaken their aragonitic shells (Orr *et al.* 2005) and is expected to reduce their survival and productivity (Comeau *et al.* 2009, 2010). To date, only minor decadal-scale changes have been observed globally in these groups. In the California Current ecosystem, pteropod abundance has not declined, and may have increased over the past 50 yr (Ohman *et al.* 2009). In the Southern Ocean, where aragonite undersaturation is predicted to begin as early as 2030 (McNeil and Matear 2008), ocean acidification may already be affecting pteropod populations. Roberts *et al.* (2008) reported that the shell weights of pteropods collected in sediment traps deployed in sub-Antarctic waters (47°S) have decreased over the past decade. This decrease was not correlated with chlorophyll abundance or temperature, but was consistent with changes in aragonite saturation, and thus the potential influence of ocean acidification cannot be rejected. The loss of *Limacina* or other key pteropod taxa in undersaturated waters due to reduced calcification (e.g. Comeau *et al.* 2009, 2010) could have significant implications for their predators and energy flow through open-ocean food webs.

Euphausiids, copepods, and other planktonic crustaceans are dominant elements of food webs worldwide, and are often suitable alternative prey for many oceanic pteropod predators (Cooley *et al.* 2009). In contrast to pteropods, krill and other crustaceans may not be strongly affected by ocean acidification, and some taxa may even benefit, but few studies have examined this topic. Kroeker *et al.* (2010) report that the literature available to date

indicates significantly higher calcification rates and marginally higher growth for crustaceans in low-pH waters, though survival was somewhat reduced. Kurihara (2008) found lower hatching success for krill exposed to low-pH waters and mixed effects on other crustacean taxa. It remains questionable how krill populations will be affected by ocean acidification, and how the effects, if any, will influence marine biodiversity and food web function.

Sparingly few studies are available to assess the effects of ocean acidification on gelatinous taxa. Jellyfish outbreaks have been reported more commonly over the past decades, with several factors (warming, overfishing, habitat modification, eutrophication, species introductions) being implicated (Richardson *et al.* 2009). Several gelatinous groups are important elements of open-ocean food webs from the tropics to the poles, including larvaceans, chaetognaths, salps, and siphonophores. It remains unclear how these taxa will respond to ocean acidification.

Meroplankton, taxa that live only part of their lives (often early life-history phases) in open waters, are expected to be particularly sensitive to ocean acidification. Recent reviews have shown generally negative or mixed results concerning the effects of ocean acidification on early life stages (Dupont *et al.* 2010; Kroeker *et al.* 2010). Kurihara (2008) reports generally negative effects on eggs, larvae, and other early phases for a variety of marine calcifiers. The vulnerability of early life-history stages can have large effects on population survival and demography, even though adults are somewhat unaffected. For some taxa, the development and survival of early life stages are impaired, and in others delayed, but the larvae develop fully in low-pH waters, albeit more slowly than in control treatments (Dupont *et al.* 2010). Slow development can put early life-history phases at prolonged risk to predators. Although the literature remains sparse concerning the impacts of ocean acidification or climate-related environmental change on the survival and development of meroplankton in general, changing ocean conditions could drive important changes in the population dynamics of various species, with indirect effects throughout marine food webs.

10.6.2 Deep-sea ecosystems

Deep-sea ecosystems may experience some of the most profound changes in biodiversity and ecosystem function in response to ocean acidification. Dramatic shoaling of the aragonite and calcite saturation boundaries (see Chapter 2) will cause very large shifts in habitat quality for deep-sea calcifiers. Aragonite and calcite undersaturation of deep-sea waters is likely to restrict deep-sea aragonitic corals (and perhaps many calcitic forms) from much of their existing bathymetric ranges (Tittensor *et al.* 2010). As the saturation states for aragonite (Ω_a) and calcite (Ω_c) drop, it becomes energetically more costly to precipitate CaCO_3 (Cohen and Holcomb 2009), and where Ω drops below 1, exposed CaCO_3 is subject to dissolution (Hall-Spencer *et al.* 2008; Manzello *et al.* 2008). Recent surveys of the global distributions of aragonitic scleractinian corals indicate that few taxa are currently found below the saturation depth for aragonite (Guinotte *et al.* 2006). *Lophelia* sp., a common aragonitic deep-sea coral, has been shown to calcify 30 to 56% more slowly in waters with pH perturbations 0.15 to 0.3 units lower than ambient (Maier *et al.* 2009). Although calcification proceeds even when Ω_a drops below 1, continued reductions in CaCO_3 saturation appear very likely to have an effect on deep-sea corals in the future. Many other deep-sea corals (e.g. gorgonians) precipitate less soluble calcite, but could be affected as the calcite saturation depth rises with increasing ocean CO_2 .

Changes in the biodiversity of deep-sea corals are likely to affect the function of deep-sea ecosystems. Deep-sea coral communities are often considered to be hot spots for biodiversity, with high species diversity of structure-forming corals (often dominated by octocorals) as well as many other taxa associated with the heterogeneous habitat structure (Roberts *et al.* 2006). Such communities are common on many seamounts, which number upwards of 50 000 worldwide. Impacts on deep-sea corals could also require long periods for recovery, even in suitable habitats, considering the slow growth rates and high longevity of many species, with ages reaching from decades to centuries (Roberts *et al.* 2006) or longer (Roark *et al.* 2009).

Abyssal sedimentary habitats are not immune to the potential effects of ocean acidification. Echinoderms, including a diverse assemblage of ophiuroids, echinoids, and holothurians, commonly form a dominant guild of abyssal benthic invertebrates, along with decapod crustaceans and fishes. The weakly calcified tests of deep-sea urchins suggest that calcification is either unimportant as a protection against predators, or is energetically costly, or both. Some taxa, such as *Tromikosoma* sp. in the North Pacific, have little or no carbonate in their test, which is proteinaceous. As anthropogenic CO₂ penetrates to the abyss in the future, seawater will become corrosive to aragonite and calcite, presumably making it even more difficult for many echinoids and other carbonate-bearing taxa to form their skeletons. The absence of echinoderms from areas in the Okinawa Trough exposed continuously to high-CO₂ vent fluids (A. Boetius, pers. comm.), suggests that ocean acidification could act selectively against this often dominant abyssal phylum. Weaker calcification under more acidic conditions could affect the survival of a variety of taxa. Mussels (*Bathymodiolus brevior*) inhabiting low-pH hydrothermal vent systems in the western Pacific survive and grow, but have poorly calcified shells, making them more vulnerable to predation by decapod crabs (*Paralomus* sp.) than are conspecifics with thickly calcified shells that inhabit less corrosive sites (Tunncliffe *et al.* 2009).

The strong link between communities at the surface and in the deep sea suggests that changes in biodiversity in the upper ocean due to ocean acidification could initiate shifts in biodiversity and ecosystem function in the deep sea. Changes in the export of organic debris from surface waters due to ocean acidification, perhaps in combination with other environmental changes, could affect bathypelagic, abyssal, and benthic ecosystems in the deep sea. Recycling of organic material in the upper water column may increase due to increased dissolution of coccolithophores and foraminifera, leading to a reduction in carbonate ballast within organic aggregates and reduced export of organic carbon to deep waters. These potential effects of ocean acidification on the rate of carbonate rain and the biological pump are not yet well understood (see Chapter 6). For the food-limited deep sea, however, changes

in sinking organic flux, in addition to altered pH and carbonate saturation, may drive important changes in ecosystem function.

10.6.3 Coastal ecosystems

Coastal ecosystems, including coastal upwelling zones, coral reefs, mangroves, kelp forests, seagrass beds, estuaries, and other nearshore systems, are by far the most important ecosystems that humans depend upon for finfish and shellfish fisheries and aquaculture, as well as recreation, and thus are critically important with respect to future impacts from ocean acidification and other environmental changes (Cooley *et al.* 2009). Coastal systems span a wide range of physical and oceanographic regimes from high to low latitudes, upwelling systems to western boundary currents, and both benthic and pelagic assemblages. The seawater chemistry and biological processes in these disparate environments vary greatly, and thus their sensitivity to ocean acidification is also expected to vary. Anthropogenic changes in oceanographic and ecological processes in coastal systems related to fossil fuel emissions and other human activities (e.g. coastal nutrient loading) are not fully understood (e.g. Feely *et al.* 2010), but will probably also differ among ecosystems. Considering the diversity of coastal ecosystems, it is beyond the scope of this chapter to provide a comprehensive treatment of their vulnerability to ocean acidification. Instead, we touch on several features of ocean acidification in coastal systems, using upwelling systems and coral reefs as examples.

10.6.3.1 Upwelling zones

Upwelling zones off the western US coast, along most eastern boundary currents, and several other regions worldwide typically have a wider range in oxygen, pH, and other carbonate system parameters than most open-ocean systems, due largely to the boom and bust productivity of surface waters and remineralization of organic material at depth. Surface pH and carbonate saturation vary through these cycles, and waters in the oxygen minimum zone (OMZ) several hundred metres below the surface can be suboxic and corrosive to CaCO₃. Estuaries can also have quite strong gradients in

oxygen, pH, and carbonate saturation (Miller *et al.* 2009). Along the Californian coast (and eastern Pacific margin) the concentration of oxygen can approach anoxia (less than 5% saturation, $\sim 10 \mu\text{mol kg}^{-1}$) in the core of the OMZ near a depth of 700 m. Wind-driven coastal upwelling and other processes can transport hypoxic, low-pH waters from the upper OMZ toward the surface, creating conditions of undersaturation with respect to CaCO_3 for surface organisms and coastal benthic communities (Feely *et al.* 2008, 2010). The highly variable conditions found in coastal upwelling zones act as a physiological filter, allowing species to thrive only if all of their life stages can tolerate the variable local conditions. Natural environmental variability has been shown to have large effects on the structure and function of the California Current ecosystem (e.g. Chavez *et al.* 2003), which may mask or interact with the effects of ocean acidification or other anthropogenic changes. Increasing acidification of coastal environments through this century due to elevated CO_2 emissions or other factors is likely to pose new physiological challenges for coastal taxa.

The response of coastal species to future ocean chemistry has been examined in various recent studies indicating mixed, but generally negative, responses (Kroeker *et al.* 2010). As noted above, some photosynthetic taxa may benefit from ocean acidification (e.g. some seagrasses; Hall-Spencer *et al.* 2008; Hendriks *et al.* 2010). However, even though they thrive in highly variable environments, coastal heterotrophs have generally responded to low-pH or low-carbonate-saturation waters with impaired performance (e.g. acid-base balance, calcification, growth, or survival), including adults (e.g. barnacles, Findlay *et al.* 2010; bivalves, Gazeau *et al.* 2007; ophiuroids, Wood *et al.* 2008; urchins, Miles *et al.* 2007) and early life-history phases (barnacles, Findlay *et al.* 2010; echinoderms, Dupont *et al.* 2010; molluscs, Kurihara 2008). Not all coastal fauna respond strongly or negatively to ocean acidification. Adults of some higher taxa have shown little sensitivity to acidification (e.g. Dungeness crab, Pane and Barry 2007; cod, Melzner *et al.* 2009a), and Ries *et al.* (2009) observed mixed responses to ocean acidification for juveniles of various taxa, including enhanced calcification and growth for a lobster and a shrimp.

Changes in the biodiversity and function of coastal ecosystems due to ocean acidification are likely to be linked to the vulnerability of key intermediate prey taxa, with broader effects driven indirectly through trophic dependences. Top predators in these systems, including fishes, cephalopods, birds, and mammals, are expected to have greater physiological capacities (at least as adults) to cope with elevated CO_2 levels, than many of their prey. Large, active cephalopods, especially those inhabiting suboxic habitats, may experience respiratory problems with future acidification (e.g. Rosa and Seibel 2008), but most vertebrates, especially air-breathing birds and mammals, are not expected to be affected directly by ocean acidification. However, the indirect effects of ocean acidification for these higher predators could be substantial. Impacts on highly sensitive taxa (e.g. thecosomatous pteropods) could cascade through food webs, as has been observed in relation to other environmental changes (warming). For example, the breeding success of planktivorous and piscivorous seabirds along the central California coast varies among warm and cold periods, but is linked directly to the availability of key prey taxa rather than specific physical parameters (Sydeman *et al.* 2001). It remains unknown whether the potentially negative effects of ocean acidification on some groups (e.g. pteropods) will be balanced by positive responses in other groups with similar functional roles (e.g. krill). In coastal systems with generally reduced functional redundancy among species (Micheli and Halpern 2005), the likelihood of indirect food web effects due to ocean acidification and other environmental changes may be high.

Benthic communities in coastal systems and seabed habitats throughout the world's oceans are centres of biodiversity where much of the species richness of the oceans is found. These communities include a wide range of organisms that play key roles as ecosystem engineers, providing habitat for other taxa (e.g. corals, kelp, seagrasses, burrowing taxa, and oyster beds), and play important roles in elemental fluxes of carbon and nitrogen through bioturbation and other effects of burrowing (Widdicombe and Spicer 2008). Benthic systems in coastal zones may be more vulnerable to ocean acidification than some more offshore sites because

they are likely to contain waters that are corrosive to CaCO_3 (at least along coastal areas with strong oxygen minimum zones) earlier than many surface communities (e.g. Feely *et al.* 2008), with potentially important impacts for calcification and survival. Other chapters in this volume give a more thorough discussion of benthic (Chapter 7) and sedimentary (Chapter 9) habitats.

10.6.3.2 Coral reefs

Coral reefs are perhaps the ecosystems understood the best in terms of potential impacts of ocean acidification for marine biodiversity. Precipitation of CaCO_3 by corals and calcifying algae forms the physical structure and much of the habitat complexity of coral reefs upon which additional biodiversity develops. Tropical reef systems have also been shown to be 'cradles of evolution', where more species have originated during earth's history than any other region (Kiessling *et al.* 2010). Likewise, tropical reefs have been shown to disappear from the fossil record during several mass extinctions (Veron 2008), indicating that they are also vulnerable to environmental change (see Chapter 4).

Ocean acidification, coupled with ocean warming, can pose important risks for the biodiversity and function of coral reef systems in several ways, ranging from basic changes in the biomineralization and erosion of the physical foundation of reefs, to less understood changes in biological interactions among species. Numerous studies have documented a reduction in calcification by corals and coralline algae in response to ocean acidification (Doney *et al.* 2009). De'ath *et al.* (2009) documented a recent decline in calcification rates on the Great Barrier Reef attributable to warming, ocean acidification, or both. In addition to reduced calcification rates, the strength of cementation may also be reduced in waters with a lower pH, promoting higher rates of physical and bio-erosion (Manzello *et al.* 2008). Processes other than calcification are also affected by ocean acidification. Competition between corals and other taxa, particularly non-calcifying macroalgae, may also be mediated by reduced rates of calcification or other physiological processes linked to ocean acidification, which are likely to reduce the ability of corals to compete for space (Kuffner *et al.* 2008). Reproduction and recruit-

ment of corals can be affected by low-pH waters (Cohen and Holcomb 2009). Reduced calcification coupled with poor cementation can promote erosion and reef flattening, which severely reduces the structural heterogeneity of reefs and lowers its potential to support biodiversity (Alvarez-Filip *et al.* 2009). Reefs experiencing a loss of structural complexity also experience a loss or change in fish assemblages, lower densities of commercially important species, and lower rates of larval fish recruitment (Feary *et al.* 2007). Weaker reef cementation also increases the potential for reef damage as storm frequency and intensity increases with continued global warming, leading to further reef degradation. Eventually, erosion of poorly cemented (and non-accreting) forereef habitats will open lagoon and backreef areas to erosion and provide less effective shoreline protection for coastal communities.

The effect of ocean acidification on the function of entire communities has been addressed only rarely. In a mesocosm-based study of a temperate rocky shore community in the UK, Hale *et al.* (2011) observed a reduction in the species diversity and evenness of the faunal assemblage with reduced pH, with a general ranking of vulnerability from echinoderms (most sensitive), to molluscs, crustaceans, and polychaetes (least sensitive). Nematode abundance increased as pH was reduced, most likely due to a release from biological disturbance (predation and competition) rather than a direct benefit from ocean acidification. The effects of elevated temperature differed among pH treatments, highlighting the difficulty of extrapolating from studies involving single species or single environmental factors, to predict the effects of future environmental changes on natural communities.

Natural CO_2 venting sites offer perhaps the strongest evidence of shifts in the biodiversity of entire communities in response to high ocean CO_2 levels. Benthic communities along a persistent gradient in pH and carbonate saturation near CO_2 vents in intertidal to shallow subtidal depths adjacent to the island of Ischia off the southern coast of Italy show dramatic faunal and floral patterns that are apparently a result of differential tolerance to ocean acidity (Hall-Spencer *et al.* 2008). Continuous seafloor venting of nearly pure CO_2 alters seawater

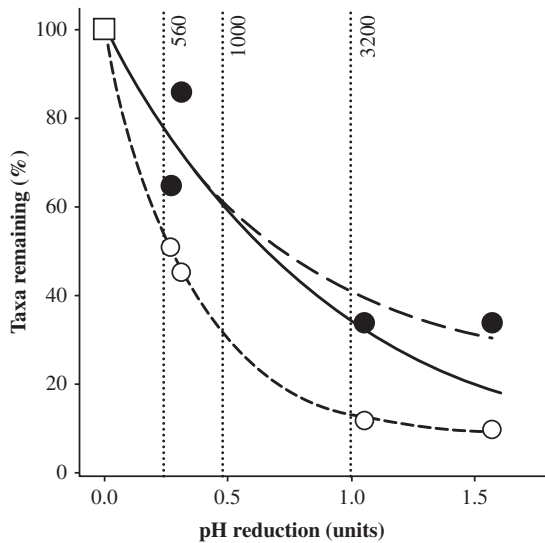


Figure 10.3 Change in diversity as a function of pH reduction for organisms living near the Ischia CO_2 vents. The biodiversity remaining (per cent of taxa that occur in areas with no pH reduction, open square) is shown for calcifying taxa (51 taxa total, white circles) and non-calcifying taxa (71 taxa total, black circles). Atmospheric $p\text{CO}_2$ levels (ppmv CO_2) that would be required to cause pH changes in ocean surface waters equivalent to those observed at three locations along the pH gradient at Ischia are indicated by dotted vertical lines. For calcifiers (short dashed curve), non-calcifiers (long dashed curve), and all taxa combined (solid curve, data not shown), exponential regressions explained 99%, 90%, and 88% of the variance, respectively. Fitted regressions indicate a loss of biodiversity of ~40% for non-calcifiers and all taxa, and ~70% for calcifiers, for a pH reduction corresponding to the atmospheric $p\text{CO}_2$ level expected by 2100. Data from Hall-Spencer *et al.* (2008).

chemistry at this site. CO_2 mixes as it is advected downstream to produce a spatial gradient in ocean pH from normal ($\text{pH}_T \sim 8.2$) to acidic ($\text{pH}_T \sim 6.6$). Hall-Spencer *et al.* (2008) documented patterns of species richness at sites along the pH gradient created by the venting CO_2 , finding a general decrease in biodiversity with pH for all floral and faunal taxa examined. Over all taxa, biodiversity declined exponentially with pH ($R^2 = 0.88$; $P < 0.001$), with a slope indicating a 65% loss in taxa richness for a 1 unit decrease in pH (Fig. 10.3). Taxa richness for calcifiers declined more rapidly with pH than non-calcifying taxa with a ~60% loss of species under a ~0.5 unit pH reduction. Of 12 calcifying algal taxa, 10 were lost with just a 0.27 unit pH reduction, and none were present in the lower-pH sites. Calcifying animals were also less diverse in lower-pH areas,

but 62% of 39 taxa were still present in the mildly acidic sites (reduction of 0.27 pH units). In contrast, the pattern of diversity loss with pH was similar for non-calcifying fauna and algae. Although this system and other natural CO_2 venting sites do not completely mimic the scale and effects of global ocean acidification, they are strong indicators of its potential effects on biodiversity and ecosystem function, as well as natural laboratories that complement other efforts to understand the effects of a changing ocean.

10.7 Implications of biodiversity loss

Although studies available to date do not provide a clear picture of future changes in ecosystem function due to ocean acidification, much evidence suggests that ocean acidification could have increasingly profound effects in several marine ecosystems (coral reefs, deep-sea systems, high-latitude systems), particularly in combination with other anthropogenic environmental changes. Some reshuffling of dominance in phytoplankton communities appears likely, but it is still not known if the long-term effects of higher ocean CO_2 levels will cause a decrease or increase in primary production (see Chapter 6). If key species in intermediate trophic levels (e.g. thecosomatous pteropods) are affected either positively or negatively by ocean acidification, food webs may be destabilized to some extent, perhaps altering the path and efficiency of energy transfer to upper trophic levels. If biodiversity is reduced within food webs, it is expected that the productivity and predictability of fisheries will be reduced (Worm *et al.* 2006). It is also possible, however, that a simpler food web structure and potentially higher primary production will enable greater trophic transfer from the base to the top of food webs, thereby increasing fisheries yields.

Changes in biodiversity could have important effects on ecosystem services for society, with the greatest impacts being on island nations which rely heavily on seafood harvests and have less opportunity for agriculture (Cooley *et al.* 2009). Expected declines in coral reefs will affect coastal fisheries as well as tourism, an economic base for many tropical island nations. Reduced calcification, growth, and survival of calcifying organisms, especially molluscs,

could compromise aquaculture efforts around the world, reducing production as demand for seafood rises with population. In addition, negative impacts on larvae could place a greater reliance on cultured larvae rather than natural seeding. For example, recent failures of oyster reproduction for both natural and cultured larvae in the Pacific Northwest appear to be linked strongly to low-pH waters (Feely *et al.* 2010). Chapter 13 gives a broader discussion of the societal impacts of ocean acidification.

Will the effects of ocean acidification on ecosystem function be comparable to those of other anthropogenic environmental changes? Overfishing has had very large effects on the distribution and abundance of marine fish communities across the globe (Pauly *et al.* 2003) and, at least at present, is exerting greater influence on the function of marine ecosystems than ocean acidification. In terrestrial systems, the effects of climate change are expected to be second only to land-use changes in the projected rapid decline in terrestrial biodiversity by 2100, with somewhat smaller effects of elevated CO₂ levels (Sala *et al.* 2000). Anthropogenic activities including fossil fuel emissions, pollutants, and nutrient additions to coastal and open-ocean waters are all expected to increase through much of this century and drive increasingly negative impacts on the function of ocean ecosystems (Doney 2010).

Ecologists are now developing innovative methods to move forward from short-term, single-species studies that have provided important information on species' responses to ocean acidification, to experimental approaches that capture longer-term, ecosystem-level effects and provide predictions of future ecosystem responses useful for resource managers and other stakeholders (Fig. 10.4). The design of experiments that integrate the effects of multiple environmental factors (e.g. warming, ocean acidification, eutrophication) on population and ecosystem performance is challenging, but is essential to gain an understanding of the real-world effects of ocean acidification. Multispecies responses to ocean acidification, in combination with other stressors, may be considerably different from results extrapolated from single-species, single-factor studies. For example, experimental approaches that examine linkages between physiological responses to ocean acidification and long-term organism performance and activity, particularly in the context of multispecies interactions would move beyond simpler mechanistic studies of physiological performance. A greater understanding of the potential for adaptation by individual species and entire communities are also important elements of future research programmes. Longer-term experiments, preferably including multiple factors and encompassing multispecies com-

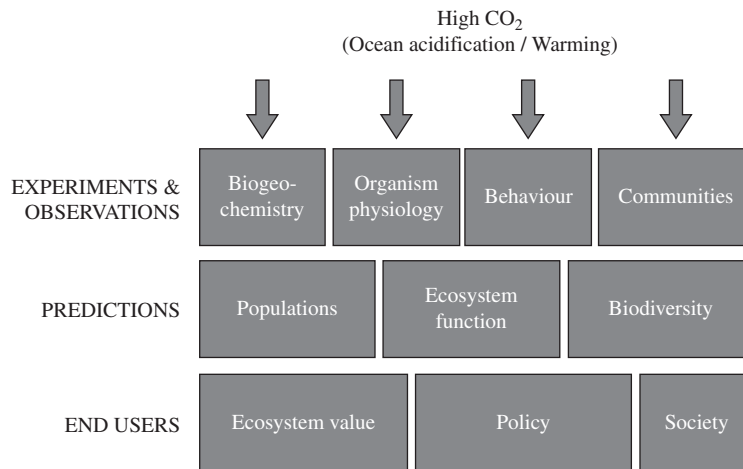


Figure 10.4 Integration of ocean acidification research activities. Experimental studies concerning the effects of ocean acidification and warming, or other environmental changes, on individuals to communities will provide input for understanding and modelling the effects on population processes and ecosystem function. Ultimately, integrated research and outreach will provide information for various stakeholders and society.

munities, will be essential for examining the effects of chronic ocean acidification. One important goal of such studies will be to understand if and how ocean acidification and other anthropogenic environmental changes will ultimately affect the function of marine communities. Will ocean acidification drive communities past 'tipping points' with dramatic shifts in ecosystem function and ecosystem services, as has been proposed for coral reef systems (Hoegh-Guldberg *et al.* 2007)? New experimental approaches to evaluate the response of organisms to ocean acidification and other concurrent environmental changes and human influences, including (1) the potential for acclimatization and adaptation by key taxa, (2) scaling up from individuals to populations, multispecies assemblages, and communities over long timescales and in various ecosystems, and (3) effects on energy flow through marine food webs and the eventual consequences for top predators, including marine fisheries, will provide society with new tools and understanding concerning how the resources and services society depends upon may be affected in a changing ocean.

10.8 Conclusion

Ocean acidification represents a large and very rapid change in the chemistry of the ocean, with the potential to affect the biodiversity and function of a variety of marine ecosystems. Although broad effects of anthropogenic ocean acidification have not yet been observed, they may be difficult to detect amid the influence of other factors, and are expected to emerge and increase through this century. Ocean acidification is considered a threat mainly due to the expected reduction in calcification in various species as the pH of ocean waters decreases. Reduced calcification, growth, and survival by corals in coral reef habitats and deep-sea coral-dominated communities are expected in response to ocean acidification, with ecosystem-wide impacts due to the indirect effects on coral-associated taxa. Shifts in phytoplankton communities and intermediate prey groups due to differential responses to ocean acidification may drive changes in energy flow through marine food webs, ultimately influencing the productivity and stability of marine fisheries. Ocean acidification is currently considered to have lesser impacts on the

function of marine ecosystems than other anthropogenic activities, but its influence in various communities is expected to increase as ocean acidification intensifies through this century. In some ecosystems, it is possible that ocean acidification, along with other anthropogenic environmental changes, may alter ecosystem function by reducing biodiversity and either approaching or potentially crossing ecological tipping points, with unpredictable effects on ecosystem function and services for society.

10.9 Acknowledgements

J.P.B. is grateful for support from the David and Lucille Packard Foundation, and to F. Melzner and W. Fischer who provided important and very helpful comments on the manuscript.

References

- Alvarez-Filip, L., Dulvy, N.K., Gill, J.A., Côté, I.M., and Watkinson, A.R. (2009). Flattening of Caribbean coral reefs: region-wide declines in architectural complexity. *Proceedings of the Royal Society B: Biological Sciences*, **276**, 3019–25.
- Barcelos e Ramos, J., Müller, M.N., and Riebesell, U. (2010). Short-term response of the coccolithophore *Emiliania huxleyi* to abrupt changes in seawater carbon dioxide concentrations. *Biogeosciences*, **6**, 177–86.
- Beardall, J. and Raven, J.A. (2004). The potential effects of global climate change on microalgal photosynthesis, growth and ecology. *Phycologia*, **43**, 26–40.
- Bellwood, D.R., Hughes, T.P., Folke, C., and Nyström, M. (2004). Confronting the coral reef crisis. *Nature*, **429**, 827–33.
- Bibby, R., Cleall-Harding, P., Rundle, S., Widdicombe, S., and Spicer, J. (2007). Ocean acidification disrupts induced defences in the intertidal gastropod *Littorina littorea*. *Biology Letters*, **3**, 699–701.
- Cardinale, B.J., Srivastava, D.S., Duffy, J.E. *et al.* (2006). Effects of biodiversity on the functioning of trophic groups and ecosystems. *Nature*, **443**, 989–92.
- Chavez, F.P., Ryan, J., Lluch-Cota, S.E., and Niquen, M. (2003). From anchovies to sardines and back: multidecadal change in the Pacific Ocean. *Science*, **299**, 217–21.
- Cohen, A.L. and Holcomb, M. (2009). Why corals care about ocean acidification: uncovering the mechanism. *Oceanography*, **22**, 117–27.
- Collins, S. and Bell, G. (2006). Evolution of natural algal populations at elevated CO₂. *Ecology Letters*, **9**, 129–35.

- Comeau, S., Gorsky, G., Jeffree, R., Teyssié, J.-L., and Gattuso, J.-P. (2009). Impact of ocean acidification on a key arctic pelagic mollusc (*Limacina helicina*). *Biogeosciences*, **6**, 1877–82.
- Comeau, S., Jeffree, R., Teyssié, J.-L., and Gattuso, J.-P. (2010). Response of the arctic pteropod *Limacina helicina* to projected future environmental conditions. *PLoS One*, **5**, e11362.
- Connell, J.H. (1978). Diversity in tropical rain forests and coral reefs. *Science*, **199**, 1302–10.
- Cooley, S.R., Kite-Powell, H.L., and Doney, S.C. (2009). Ocean acidification's potential to alter global marine ecosystems services. *Oceanography*, **22**, 172–81.
- De'ath, G., Lough, J.M., and Fabricius, K.E. (2009). Declining coral calcification on the Great Barrier Reef. *Science*, **323**, 116–19.
- Doney, S.C. (2010). The growing human footprint on coastal and open-ocean biogeochemistry. *Science*, **328**, 1512–16.
- Doney, S.C., Fabry, V.J., Feely, R.A., and Kleypas, J.A. (2009). Ocean acidification: the other CO₂ problem. *Annual Review of Marine Science*, **1**, 169–92.
- Deigweier, K., Koschnick, N., Pörtner, H.-O., and Lucassen, M. (2008). Acclimation of ion regulatory capacities in gills of marine fish under environmental hypercapnia. *American Journal of Physiology – Regulatory, Integrative and Comparative Physiology*, **295**, R1660–R1670.
- Duffy, J.E. (2009). Why biodiversity is important to the functioning of real-world ecosystems. *Frontiers in Ecology and the Environment*, **7**, 437–44.
- Dupont, S., Ortega-Martinez, O., and Thorndike, M. (2010). Impact of near-future ocean acidification on echinoderms. *Ecotoxicology*, **19**, 449–62.
- Fabry, V.J., Seibel, B.A., Feely, R.A., and Orr, J.C. (2008). Impacts of ocean acidification on marine fauna and ecosystem processes. *ICES Journal of Marine Science*, **65**, 414–32.
- Fabry, V.J., McClintock, J.B., Mathis, J.T., and Grebmeier, J.M. (2009). Ocean acidification at high latitudes: the bellwether. *Oceanography*, **22**, 160–71.
- FAO (2009). *The state of world fisheries and aquaculture (2008)*, 178 pp. Food and Agriculture Organization of the United Nations (FAO), Rome, Italy.
- Feary, D.A., Almany, G.R., McCormick, M.I., and Jones, G.P. (2007). Habitat choice, recruitment and the response of coral reef fishes to coral degradation. *Oecologia*, **153**, 727–37.
- Feely, R.A., Sabine, C.L., Lee, K. *et al.* (2004). Impact of anthropogenic CO₂ on the CaCO₃ system in the oceans. *Science*, **305**, 362–6.
- Feely, R.A., Sabine, C.L., Hernandez-Ayon, J., Ianson, D. and Hales, B. (2008). Evidence for upwelling of corrosive 'acidified' water onto the continental shelf. *Science*, **320**, 1490–2.
- Feely, R.A., Alin, S.R., Newton, J. *et al.* (2010). The combined effects of ocean acidification, mixing and respiration on pH and carbonate saturation in an urbanized estuary. *Estuarine, Coastal, and Shelf Science*, **88**, 442–9.
- Findlay, H.S., Burrows, M.T., Kendall, M.A., Spicer, J.L., and Widdicombe, S. (2010). Can ocean acidification affect population dynamics of the barnacle *Semibalanus balanoides* at its southern range edge? *Ecology*, **9**, 2931–40.
- Fine, M. and Tchernov, D. (2007). Scleractinian coral species survive and recover from decalcification. *Science*, **315**, 1811.
- Fu, F.-X., Warner, M.E., Zhang, Y., Feng, Y., and Hutchins, D.A. (2007). Effects of increased temperature and CO₂ on photosynthesis, growth and elemental ratios in marine *Synechococcus* and *Prochlorococcus* (cyanobacteria). *Journal of Phycology*, **43**, 485–96.
- Gattuso, J.-P., Allemand, D., and Frankignoulle, M. (1999). Photosynthesis and calcification at cellular, organismal and community levels in coral reefs: a review on interactions and control by carbonate chemistry. *American Zoologist*, **39**, 160–83.
- Gazeau, F., Quiblier, C., Jansen, J.M., Gattuso, J.-P., Middelberg, J., and Heip, C.H.R. (2007). Impact of elevated CO₂ on shellfish calcification. *Geophysical Research Letters*, **34**, L07603, doi:10.1029/2006GL028554.
- Goffredi, S.K. and Barry, J.P. (2002). Species-specific variation in sulfide physiology between closely related vesicomyid clams. *Marine Ecology Progress Series*, **225**, 227–38.
- Grassle, J.F. (1986). The ecology of deep-sea hydrothermal vent communities. *Advances in Marine Biology*, **23**, 301–62.
- Guinotte, J.M., Orr, J., Cairns, 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**, 141–6.
- Hale, R., Calosi, P., McNeill, L., Mieszkowska, N., and Widdicombe, S. (in press). Predicted levels of future ocean acidification and temperature rise could alter community structure and biodiversity in marine benthic communities. *Oikos*, **120**, 661–674.
- Hall-Spencer, J.M., Rodolfo-Metalpa, R., Martin, S. *et al.* (2008). Volcanic carbon dioxide vents show ecosystem effects of ocean acidification. *Nature*, **454**, 96–9.
- Hays, G.C., Richardson, A.J., and Robinson, C. (2005). Climate change and marine plankton. *Trends in Ecology and Evolution*, **20**, 337–44.

- Hendriks, I.E., Duarte, C.M., and Alvarez, M. (2010). Vulnerability of marine biodiversity to ocean acidification: a meta-analysis. *Estuarine, Coastal and Shelf Science*, **86**, 157–64.
- Hoegh-Guldberg, O., Mumby, P.J., Hooten, A.J. *et al.* (2007). Coral reefs under rapid climate change and ocean acidification. *Science*, **318**, 1737–42.
- Hofmann, G.E., Barry, J.P., Edmunds, P.J. *et al.* (2010). The effect of ocean acidification on calcifying organisms in marine ecosystems: an organism to ecosystem perspective. *Annual Review of Ecology, Evolution and Systematics*, **41**, 127–47.
- Hutchins, D.A., Mulholland, M.R., and Fu, F. (2009). Nutrient cycles and marine microbes in a CO₂-enriched ocean. *Oceanography*, **22**, 128–45.
- Jablonski, D. and Chaloner, W.G. (1994). Extinctions in the fossil record. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **344**, 11–17.
- Kiessling, W., Simpson, C., and Foote, M. (2010). Reefs as cradles of evolution and sources of biodiversity in the Phanerozoic. *Science*, **327**, 196–8.
- Kleypas, J.A., Buddemeier, R.W., Archer, D., Gattuso, J.-P., Langdon, C., and Opdyke, B.N. (1999). Geochemical consequences of increased atmospheric carbon dioxide on coral reefs. *Science*, **284**, 118–20.
- Kleypas, J.A. and Yates, K.K. (2009). Coral reefs and ocean acidification. *Oceanography*, **22**, 108–17.
- Knoll, A.H., Bambach, R.K., Payne, J.L., Pruss, S., and Fischer, W.W. (2007). Paleophysiology and the end-Permian mass extinction. *Earth Planetary Science Letters*, **256**, 295–313.
- Kroeker, K.J., Kordas, R.L., Crim, R.N., and Singh, G.G. (2010). Meta-analysis reveals negative yet variable effects of ocean acidification on marine organisms. *Ecology Letters*, **13**, 1419–34.
- Kuffner, I.B., Andersson, A.J., Jokiel, P.L., Rodgers, K.S., and Mackenzie, F.T. (2008). Decreased abundance of crustose coralline algae due to ocean acidification. *Nature Geoscience*, **1**, 114–17.
- Kurihara, H. (2008). Effects of CO₂-driven ocean acidification on the early developmental stages of invertebrates. *Marine Ecology Progress Series*, **373**, 275–84.
- Loreau, M., Naeem, S., Inchausti, P. *et al.* (2001). Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science*, **294**, 804–8.
- McLaughlin, P.A. and Rahayu, D.L. (2008). *Pteropagurus* and *Catapagurus* (Decapoda, Anomura, Paguidae): resource sharing or 'any port in a storm'? *Zoosystema*, **30**, 899–916.
- McNeil, B.I. and Matear, R.J. (2008). Southern ocean acidification: a tipping point at 450-ppm atmospheric CO₂. *Proceedings of the National Academy of Sciences USA*, **105**, 18860–4.
- Maier, C., Hegeman, J., Weinbauer, M.G., and Gattuso, J.-P. (2009). Calcification of the cold-water coral *Lophelia pertusa* under ambient and reduced pH. *Biogeosciences*, **6**, 1671–80.
- Manzello, D.P. (2010). Ocean acidification hot spots: spatiotemporal dynamics of the seawater CO₂ system of eastern Pacific coral reefs. *Limnology and Oceanography*, **55**, 239–48.
- Manzello, D.P., Kleypas, J.A., Budd, D.A., Eakin, C.M., Glynn, P.W., and Langdon, C. (2008). Poorly cemented coral reefs of the eastern tropical Pacific: possible insights in reef development in a high-CO₂ world. *Proceedings of the National Academy of Sciences USA*, **105**, 10450–5.
- Mayhew, P.J., Jenkins, G.B., and Benton, T.G. (2008). A long-term association between global temperature and biodiversity, origination and extinction in the fossil record. *Proceedings of the Royal Society, B, Biological Sciences*, **275**, 47–53.
- Melzner, F., Göbel, S., Langenbuch, M., Gutowska, M., Pörtner, H.-O., and Lucassen, M. (2009a). Swimming performance in Atlantic Cod (*Gadus morhua*) following long-term (4–12 months) acclimation to elevated seawater Pco₂. *Aquatic Toxicology*, **92**, 30–7.
- Melzner, F., Gutowska, M.A., and Langenbuch, M. (2009b). Physiological basis for high CO₂ tolerance in marine ectothermic animals: pre-adaptation through lifestyle and ontogeny? *Biogeosciences*, **6**, 2313–31.
- Michaelidis, B., Ouzounis, C., Paleras, A., and Pörtner, H.O. (2005). Effects of long-term moderate hypercapnia on acid-base balance and growth rate in marine mussels *Mytilus galloprovincialis*. *Marine Ecology Progress Series*, **293**, 109–18.
- Micheli, F. and Halpern, B.S. (2005). Low functional redundancy in coastal marine assemblages. *Ecology Letters*, **8**, 391–400.
- Miles, H., Widdicombe, S., Spicer, J.I., and Hall-Spencer, J. (2007). Effects of anthropogenic seawater acidification on acid-base balance in the sea urchin *Psammechinus miliaris*. *Marine Pollution Bulletin*, **54**, 89–96.
- Miller, A.W., Reynolds, A.C., Sobrino, C., and Riedel, G.F. (2009). Shellfish face uncertain future in high CO₂ world: influence of acidification on oyster larvae calcification and growth in estuaries. *PLoS One*, **4**, e5661.
- Ohman, M.D., Lavaniegos, B.E., and Townsend, A.W. (2009). Multi-decadal variation in calcareous holozooplankton in the California Current system: thecosome pteropods, heteropods and foraminifera. *Geophysical Research Letters*, **36**, L18608, doi:10.1029/2009GL033901.
- Orr, J.C., Fabry, V.J., Aumont, O. *et al.* (2005). Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. *Nature*, **437**, 681–6.

- Pane, E.F. and Barry, J.P. (2007). Inefficient acid-base regulation in the deep-sea decapod crab (*Chionoecetes tanneri*) during short-term hypercapnia. *Marine Ecology Progress Series*, **334**, 1–9.
- Pauly, D., Alder, J., Bennett, E., Christensen, V., Tyedmers, P., and Watson, R. (2003). The future of fisheries. *Science*, **302**, 1359–61.
- Pelejero, C., Calvo, E., and Hoegh-Guldberg, O. (2010). Paleo-perspectives on ocean acidification. *Trends in Ecology and Evolution*, **25**, 332–44.
- Petchey, O.L. and Gaston, K.J. (2006). Functional diversity: back to basics and looking forward. *Ecology Letters*, **9**, 741–58.
- Pörtner, H.-O., Bock, C., and Reipschläger, A. (2000). Modulation of the cost of pHi regulation during metabolic depression: a ³¹P-NMR study in invertebrates (*Sipunculus nudus*) isolated muscle. *Journal of Experimental Biology*, **203**, 2417–28.
- Richardson, A.J., Bakun, A., Hays, G.C., and Gibbons, M.J. (2009). The jellyfish joyride: causes, consequences and management responses to a more gelatinous future. *Trends in Ecology and Evolution*, **24**, 213–322.
- Ridgwell, A., Schmidt, D.N., Turley, C. *et al.* (2009). From laboratory manipulations to earth system models: predicting pelagic calcification and its consequences. *Biogeosciences*, **6**, 2611–23.
- Riebesell, U., Schulz, K.G., Bellerby, R.G.J. *et al.* (2007). Enhanced biological carbon consumption in a high CO₂ ocean. *Nature*, **450**, 545–8.
- Ries, J.B., Cohen, A.L., and McCorkle, D.C. (2009). Marine calcifiers exhibit mixed responses to CO₂-induced ocean acidification. *Geology*, **37**, 1131–4.
- Roark, E.B., Guilderson, T.P., Dunbar, R.B., Fallon, S.J., and Mucciarone, D.A. (2009). Extreme longevity in proteinaeous deep-sea corals. *Proceedings of the National Academy of Sciences USA*, **106**, 5204–8.
- Roberts, D., Howard, W.R., Moy, A.D. *et al.* (2008). Interannual variability of pteropod shell weights in the high-CO₂ Southern Ocean. *Biogeosciences Discussions*, **5**, 4453–80.
- 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**, 543–7.
- Rosa, R. and Seibel, B.A. (2008). Synergistic effects of climate-related variables suggest future physiological impairment in a top oceanic predator. *Proceedings of the National Academy of Sciences USA*, **105**, 20776–80.
- Sala, O.E., Chapin, F.S. III, Armesto, J.J. *et al.* (2000). Global biodiversity scenarios for the year 2100. *Science*, **287**, 1770–4.
- Seibel, B.A. and Walsh, P.J. (2003). Biological impacts of deep-sea carbon dioxide injection inferred from indices of physiological performance. *Journal of Experimental Biology*, **206**, 641–50.
- Steneck, R.S., Graham, M.H., Bourque, B.J. *et al.* (2002). Kelp forest ecosystems: biodiversity, stability, resilience and future. *Environmental Conservation*, **29**, 436–59.
- Sydeman, W.J., Hester, M.M., Thayer, J.A., Gress, F., Martin, P., and Buffa, J. (2001). Climate change, reproductive performance and diet composition of marine birds in the southern California Current system, 1969–1997. *Progress in Oceanography*, **49**, 309–29.
- Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M., and Siemann, E. (1997). The influence of functional diversity and composition on ecosystem processes. *Science*, **277**, 1300–2.
- Tittensor, D.P., Baco, A.R., Hall-Spencer, J.M., Orr, J.C., and Rogers, A.D. (2010). Seamounts as refugia from ocean acidification for cold-waters stony corals. *Marine Ecology*, **31**(Suppl. 1), 212–25.
- Tunncliffe, V., Davies, K.T.A., Butterfield, D.A., Embley, R.W., Rose, J.M., and Chadwick, W.W. Jr (2009). Survival of mussels in extremely acidic waters on a submarine volcano. *Nature Geoscience*, **2**, 344–8.
- Veron, J.E.N. (2008). Mass extinctions and ocean acidification: biological constraints on geological dilemmas. *Coral Reefs*, **27**, 459–72.
- Widdicombe, C.E., Eloire, D., Harbour, D., Harris, R.P., and Somerfield, P.J. (2010). Long-term phytoplankton community dynamics in the western English Channel. *Journal of Plankton Research*, **32**, 643–55.
- Widdicombe, S. and Spicer, J.I. (2008). Predicting the impact of ocean acidification on benthic biodiversity: what can animal physiology tell us? *Journal of Experimental Marine Biology and Ecology*, **366**, 187–97.
- Wood, H.L., Spicer, J.I., and Widdicombe, S. (2008). Ocean acidification may increase calcification rates, but at a cost. *Proceedings of the Royal Society B: Biological Sciences*, **275**, 1767–73.
- Worm, B., Barbier, E.B., Beaumont, N. *et al.* (2006). Impacts of biodiversity loss on ocean ecosystem services. *Science*, **314**, 787–90.