

3. Biological responses to ocean acidification

LEAD AUTHORS: HOWARD I. BROWMAN, SAM DUPONT, JON HAVENHAND, LISA ROBBINS

CONTRIBUTING AUTHORS: MICHAEL BEMAN, CARLOS DUARTE, MAOZ FINE, JAN HELGE FOSSÅ, JASON HALL-SPENCER, PAMELA HALLOCK-MULLER, THOMAS P. HURST, DEBORA IGLESIAS-RODRIGUEZ, PAUL KNORR, HARUKO KURIHARA, JOHN LISLE, CLARA MANNO, SOPHIE MCCOY, FRANK MELZNER, PHILIP MUNDAY, HANS-OTTO PÖRTNER, JUSTIN RIES, DOMINIQUE ROBERT, JEFFREY RUNGE, DAVID SCOTT, HEIN RUNE SKJOLDAL, KEITA SUZUKI, FREDERIK THINGSTAD, TIM WOOTTON

3.1 Introduction

This chapter presents an overview of what is known about the effects of ocean acidification on marine organisms and ecosystems. Information on Arctic species and ecosystem processes is extremely limited owing to the logistical difficulties of working in these environments (remoteness, ice cover, high cost, etc.) and in conducting experiments at very low temperatures (long generation times, working at below freezing temperatures for prolonged periods, etc.). This is clearly illustrated in Figure 3.1 using echinoderms as an example. Where possible, this report presents available data from Arctic and/or polar cases. However, for the reasons just stated, most of the material presented here is from studies on non-Arctic species and ecosystems, accompanied by an attempt to assess what this means in an Arctic context.

This chapter summarizes briefly the natural variability in pH and carbon dioxide (CO₂) in time and space (see Chapter 2 for further details) and presents an overview of the biological and physiological context for assessing the impact of ocean acidification on marine organisms and ecosystems (Section 3.2). This is followed by a description of Arctic ecosystems and food webs (Section 3.3). The chapter then reviews what is known about the effects of ocean acidification on different taxonomic groups; with each sub-section distilling what is known from non-Arctic species and then discussing how that may be relevant to Arctic species and to the key linkages in the Arctic food web (Section 3.4). Ecosystem-wide responses

to ocean acidification are addressed in Section 3.5. There is then a brief discussion of ocean acidification analogs (areas of naturally lower pH and/or high carbon dioxide regions) and their potential for research (Section 3.6). The chapter concludes with some general caveats to this work (Section 3.7), proposals for research priorities (Section 3.8) and a series of conclusions and recommendations (Section 3.9).

3.2 Biogeochemical, biological, and physiological context for assessing the impact of ocean acidification

3.2.1 Natural variability in pH and carbon dioxide in time and space

Uptake of atmospheric CO₂ by the oceans is driving changes in the carbonate chemistry of the Arctic Ocean – this is commonly referred to as ‘ocean acidification’ and is described in detail in Chapter 2. There is high spatio-temporal variability in these changes with, for example, rapid and large fluctuations on the continental shelves and more stable conditions in ancient deep waters that currently contain no anthropogenic carbon. Organisms living in shallow coastal waters may already experience transient changes in pH as great as 7.4–9.2 on a daily basis (e.g., Middelboe and Hansen, 2007). Pelagic organisms will be exposed to less pronounced diel fluctuations, but will encounter seasonal changes in pH of the order of 7.5–9.7



Figure 3.1. Number of published studies investigating the impact of ocean acidification on sea urchins. Source: Sam Dupont, University of Gothenburg.

(Hofmann et al., 2011). The range in pH to which organisms might be exposed is particularly large (7.1–9.7) in eutrophic coastal waters (e.g., Hansen, 2002). In the Arctic, large changes in pH may occur in sea ice, but in open waters pH will typically be in the 7.7–8.3 range. The highest pH values (9.7) have been recorded during algal blooms, whereas the lowest (7.1) occur where respiration lowers the pH, such as below the pycnocline or during winter after prolonged dark periods.

A comprehensive dataset of continuous pH observations spanning polar to tropical ecosystems, and open-ocean to kelp forests and coral reefs, shows that pH in the upper 15 m of the water column can vary by up to 1.43 units (Hofmann et al., 2011). Polar sites (Antarctica) showed low fluctuation (≤ 0.1 pH units), although measurements were only made for two weeks. The most extreme fluctuations were observed in natural CO₂ vent areas (Ischia, Italy), however, kelp-forest, estuarine, and upwelling ecosystems all showed fluctuations of 0.4–0.6 pH units over a period of four weeks (Hofmann et al., 2011). Similar magnitude pH variations have been observed diurnally in tide pools (Wootton et al., 2008; Moulin et al., 2011). In all cases, lower-bound recorded pH values can be below, or well below, those projected for the end of the 21st century for the average surface ocean (IPCC, 2007). This demonstrates that many organisms are already experiencing pH conditions that are lower than previously considered likely. The consequences of fluctuating pH conditions are only just beginning to be investigated. The variability in ocean acidification and Arctic Ocean carbonate chemistry will increase in both space and time as the process of acidification continues. This means that the biological and ecological effects of ocean acidification will vary regionally and with its increase over time. Consequently, as well as a need for more data detailing diurnal/seasonal/annual fluctuations in pH in Arctic habitats, experimental results are also required to consider local scenarios and take into account the effects of fluctuating pH on Arctic species (McElhany and Busch, 2012).

The interpretations and conclusions of the ocean acidification challenge experiments described in this chapter should be set within the context of this natural variability in pH.

3.2.2 General biological responses to lowered pH / elevated CO₂

Marine organisms with external shells made up of calcium carbonate obtain the raw material used to build them from seawater (e.g., Roleda et al., 2012). Therefore, the carbonate chemistry of seawater is an important factor for these organisms as it will, at least in part, affect the shell-building process and, for those organisms whose shells are not protected by a chemically resistant organic layer, also the rate of dissolution (e.g., Lischka et al., 2011). For heterotrophic marine metazoans, pH and the partial pressure of CO₂ ($p\text{CO}_2$) are the main ocean acidification-related variables that impact them: effective respiration requires a diffusion gradient of CO₂ from the extracellular body fluids (blood, haemolymph or coelomic fluid) to the seawater. Typically, $p\text{CO}_2$ in ectothermic marine animal body fluids is about 1000 to 4000 μatm higher than that of seawater (Melzner et al., 2009a). Increases in seawater $p\text{CO}_2$ typically increase body fluid $p\text{CO}_2$ by an equal amount, as

diffusion gradients must be maintained to guarantee constant rates of CO₂ excretion (see Melzner et al., 2013: Fig. 6). These unavoidable changes in body fluid $p\text{CO}_2$ impact physiology primarily through two mechanisms: (1) accumulation of bicarbonate ions in the body fluids in order to stabilize pH at higher levels (e.g., cephalopods, teleost fish, many decapod crustaceans), (2) no bicarbonate accumulation resulting in much larger decreases in pH (Seibel and Walsh, 2003; Melzner et al., 2009a). Both types of reaction can result in pathologies in short- to medium-term experiments (e.g., Melzner et al., 2013).

Many other direct effects of ocean acidification on organisms are possible; for example, sublethal effects on metabolism and energetics, growth rate, condition, reproductive success or behavior (e.g., see Chapters 4–10 in Gattuso and Hansson, 2011). There is also the possibility of indirect impacts through the food web (e.g., Eklof et al., 2012; Rossoll et al., 2012). To complicate matters further, these effects can be very different depending upon the life-history stage being evaluated (although essential, studies that consider the complete life cycle of an organism are rare).

3.2.2.1 Impact on calcification by marine organisms

The calcification rates of a wide range of marine organisms decline when subjected to the seawater pH values projected for the coming centuries due to atmospheric increases in CO₂. Review articles by Kleypas et al. (1999, 2006), Hoegh-Guldberg et al. (2007), Fabry et al. (2008), Doney et al. (2009), Gattuso and Hansson (2011), and Wicks and Roberts (2012) provide excellent summaries of many of the studies conducted to date. Ries et al. (2009) also found highly variable calcification responses of 18 species of benthic marine organisms to $p\text{CO}_2$ treatments of 400, 600, 900, and 2850 ppm. They observed linear negative responses (soft clam, oyster, scallop, periwinkle, whelk, serpulid tubeworm), threshold-negative responses (tropical urchin, temperate coral, conch, hard clam), no response (mussel), parabolic responses (coralline red alga, calcareous green alga, temperate urchin, limpet), a threshold-positive response (lobster), and linear positive responses (crab, shrimp). These disparate responses are attributed to differences in the organisms' ability to regulate pH at their site of calcification, the extent to which their outer shell is covered by an organic layer, the solubility of their biomineral polymorph, and whether they utilize CO₂ directly via photosynthesis. Numerous experimental studies have investigated the effect of CO₂-induced ocean acidification on rates of calcification within marine organisms (see reviews cited above). Far fewer, however, have investigated its effects on other properties of their skeletons (e.g., Cohen and Holcomb, 2009; Dissard et al., 2010), such as polymorph mineralogy, elemental composition, ultrastructure, and biomechanics.

3.2.2.2 Physiological effects

The effect of ocean acidification on phytoplankton and primary production has been one of the main foci of research. Inorganic carbon is one of the essential building blocks of photosynthesis and, therefore, increases in $p\text{CO}_2$ might be expected to increase primary production. This pattern is generally seen in macroalgae

(see Section 3.4.5); however, no consistent pattern of response to ocean acidification has emerged in phytoplankton. This may be related to highly efficient carbon capture systems in many phytoplankton species, however different groups, different species, and even different clones within species show divergent responses to ocean acidification, revealing a highly contextually dependent pattern of photosynthesis, growth, carbon fixation, nutrient usage, and calcification. Phytoplankton blooms are appearing earlier (Kahru et al., 2011) and increased dominance of blooms by picophytoplankton has been attributed to ocean acidification (Newbold et al., 2012) and freshening (Li et al., 2009) of the Arctic Ocean. The extent to which these changes will have flow-on effects in the Arctic food web is unknown but could be substantial. These patterns and their likely consequences are dealt with in more detail in Section 3.4.3. Other work suggests that the harmful algal diatom *pseudo-nitzschia* produces more toxin (domoic acid) under high CO₂ conditions (Sun et al., 2011).

Assessing the sensitivity of Arctic marine animals to ocean acidification must consider the special circumstances and functional characteristics of life in Arctic waters. The Arctic Ocean is an open system in which variability in ambient conditions is driven partly by the influence of waters from the North Atlantic and North Pacific. In these areas, as well as the sub-Arctic, temperatures are low but variable. This contrasts with the more constant temperatures in Antarctic oceans due to its near isolation by the circum-Antarctic current. Understanding the evolution and adaptations of marine polar fauna to changing climate and ocean acidification requires an understanding of the key mechanisms and driving forces involved. The key driving force presently is temperature, although enhanced solubility of CO₂ in cold waters and body fluids may also shape their future sensitivity. High solubility of CO₂ decreases aragonite and calcite saturation states and lowers the pH of the water (see Chapter 2, Section 2.2), which has been hypothesized to threaten calcifying organisms at the poles (Orr et al., 2005; but see Roleda et al., 2012, who argued that calcifying organisms that do not rely on carbonate may not be affected). Multi-year ice melt, increased river input and associated salinity decreases exacerbate the extent of acidification in surface layers of the Arctic Ocean (Denman et al., 2011). The combined effects of warming, acidification, and freshening, on marine ecosystems have not yet been estimated (Ainsworth et al., 2011).

Understanding key physiological and life-history characteristics is critical to estimating the sensitivity of species to climate change. In the Antarctic, such efforts are based on the concept of oxygen- and capacity-limited thermal tolerance (OCLTT; Pörtner, 2006). This concept integrates molecular, cellular, whole organism and ecological characteristics with responses to climate change (Pörtner, 2001, 2002, 2010; Pörtner and Knust, 2007). In general, polar marine ectotherms ('cold-blooded' animals) minimize baseline energy costs in order to maximize growth potential in the cold, especially in the Antarctic. Similar patterns can also be seen in some ectotherms from the High Arctic (e.g., crustaceans, Walther et al., 2010) and sub-Arctic. The temperature variability that characterizes large sections of the sub-Arctic Ocean causes elevated levels of energy turnover in the cold-eurythermal fauna (animals that can tolerate a wide

range of temperatures). This elevation can be seen in species that extend from temperate to Arctic regions (e.g., Atlantic cod, *Gadus morhua*) compared to temperate zone conspecifics (Pörtner and Farrell, 2008). Elevated baseline metabolic costs in cold-adapted eurytherms have been related to their broad thermal tolerance to cold. True polar characteristics as seen in animals from the Antarctic or High Arctic only develop under highly stable, extremely low temperatures around and below 0 °C. Low-energy costs of maintenance at low temperatures are also mirrored in low turnover rates of transmembrane ion exchange and in a lower capacity for acid-base regulation than seen in temperate to warm-water species (Pörtner, 2010). Life-stage and lifestyle dependent capacity for acid-base regulation has been suggested as an over-arching principle that shapes sensitivity to ocean acidification (Pörtner, 2008; Melzner et al., 2009a). Pre-adaptation to climatic regimes will thus influence these patterns, with a decreasing capacity for ion and acid-base regulation in polar species.

Insight into the biochemistry of cold adaptation in Arctic versus Antarctic species confirms these generalizations. Low metabolic rates found in Antarctic marine stenotherms (organisms that only function well within a narrow range of temperatures) contrast with the more costly patterns of metabolic regulation at elevated rates in cold-adapted (sub-Arctic) eurytherms. In light of very limited data, these principles would support the extrapolation that sub-Arctic eurytherms are likely to be more resistant to ocean acidification while Antarctic and High Arctic stenotherms may be more sensitive. Whether calcification processes are also more resistant to ocean acidification in eurythermal Arctic than in stenothermal Antarctic and Arctic species requires further investigation.

Various other environmental factors, such as CO₂ or pollution, have been suggested to constrain aerobic performance and fitness and to thereby narrow the thermal window (Pörtner and Farrell, 2008). They thus act as additional stressors that interact with extreme temperatures. By narrowing the window of aerobic scope, CO₂ elicits passive rather than active tolerance to thermal extremes. The extent to which species are able to acclimate to such challenges over long time scales is as yet unexplored, however recent examples from laboratory and field studies confirm the hypothesis of a reduced thermal window under elevated CO₂ for crustaceans (Metzger et al., 2007; Walther et al., 2009; Findlay et al., 2010b), fishes (Munday et al., 2009a), and corals (via enhanced bleaching; Anthony et al., 2008). Pollutants can also enhance thermal sensitivity (Lannig et al., 2008). These effects, while most likely representing unifying principles, remain to be quantified in Arctic species.

3.3 Arctic marine food webs

The Arctic Ocean is characterized by marine ecosystems in which a small number of taxa channel a large percentage of the energy from zooplankton to vertebrate predators including seabirds, seals, whales, and polar bears (*Ursus maritimus*). As such, the effects of ocean acidification on these ecosystems will depend greatly – and far more so than for ecosystems with a more complex food web – upon the susceptibility of the keystone taxa to ocean acidification and other stressors.

3.3.1 Arctic habitats and biogeography

The Arctic can be broadly divided into High Arctic, Low Arctic, and sub-Arctic (Dunbar, 1968; see also Chapter 1, Figure 1.4). The High Arctic corresponds to areas of the central Arctic Ocean with more or less permanent (multi-year) ice cover and persistently cold water, while the Low Arctic corresponds broadly to the zone with seasonal ice cover on the shelves surrounding the Arctic Ocean basin. The sub-Arctic zone is comprised of the adjacent areas which have little sea ice but relatively low winter temperatures. The Arctic Ocean basins (Canada and Eurasian basins separated by the Lomonosov Ridge) are connected to the deep basins of the Nordic Seas through the deep Fram Strait. The basin of Baffin Bay is separated from the Arctic Ocean by passages through the Canadian Arctic Archipelago with sill depths of about 150 m. The Bering Sea basin is separated from the Arctic Ocean by roughly 1000 km of very shallow areas, mostly <50 m deep.

The Arctic Ocean is in some sense a warm ocean with its deeper waters filled with Atlantic water from about 200–1000 m depths and temperatures of 0–3 °C. However, at the surface, cooling and formation of sea ice lead to seawater at near freezing point under the ice. This cold water may extend to the bottom of shallow shelf areas (100–200 m depths). When the sea ice melts in summer, the lighter meltwater floats as a buoyant upper layer and shields the deeper layer from seasonal warming (also see Chapter 2, Section 2.3.1). Cold Arctic water therefore prevails over shelves as a seasonally persistent layer at depths from about 25 m to 100–150 m. Shallower than this the nearshore waters may be warmed to some degree in summer, while at greater depths warmer water from the intermediate layer in the Arctic Ocean may intrude onto the outer shelf.

Persistently cold waters are found over the deeper slopes and basins of the Arctic Ocean (below about 1000 m) and over relatively shallow shelves surrounding the central Arctic Ocean, which are extensive on the Eurasian side from the northern Barents Sea to the Chukchi Sea, and also in large portions within the Canadian Arctic Archipelago. The Chukchi Sea differs from other Arctic shelf regions by the strong through-flow of Pacific water (Bering slope water) that pushes away the cold water during the summer season.

This temperature regime determines the distribution and biogeography of species. Endemic Arctic species are found mainly in the permanently cold shelf areas and in the deep basins. The number of endemic Arctic species is limited, and the majority of species in the Arctic is comprised of Arctic-boreal species or boreal species with northern ranges that extend into the Arctic. For example, of 242 marine fish species that have been recorded from the ice-covered Arctic, 25% (62 species) were classified as Arctic (or predominantly Arctic), 16% (38 species) as Arctic-boreal, while more than half (53%, 128 species) were boreal or predominantly boreal (Mecklenburg et al., 2011).

Many Arctic species have wide distributions, often circumpolar or near-circumpolar. This is the case for invertebrates as well as for fish, birds, and mammals. For invertebrates and fish, the majority of species is of Atlantic origin. For example, among the 62 species of fish classified as Arctic, 34 species are

found in the Atlantic sector, six in the Pacific sector, and 29 in both. Arctic-boreal species are distributed more evenly, with 15 species in the Atlantic, 13 in the Pacific, and 13 in both sectors. The situation is very different among boreal species of marine fish if the Bering Sea is included as part of the sub-Arctic zone. For this category, the greatest number of species occurs in the Pacific sector with 286 species (out of 375), compared to 85 species in the Atlantic sector. Only four species are identified as amphiboreal (occurring in both Atlantic and Pacific sectors). However, there are many examples of closely related species in the two sectors, for example, twin Atlantic and Pacific species of cod (*Gadus morhua* and *G. macrocephalus*), halibut (*Hippoglossus hippoglossus* and *H. stenolepis*), and herring (*Clupea harengus* and *C. pallasii*) as examples among commercially (and ecologically) important species.

3.3.2 Arctic ecosystems and food webs

Broad species distributions, many closely related species, and similar physical regimes create a large element of commonality in the structure and function of Arctic marine ecosystems. However, marked differences in sea ice, bathymetry, and oceanography also lead to pronounced zonal patterns between the High, Low and sub-Arctic.

Very strong seasonal changes in light and ice conditions between summer and winter are key features that are reflected in the patterns of primary production and its utilization in the food web. The extensive migrations of birds and mammals into the Arctic to breed and feed during the short and hectic Arctic summer benefit from this production: the Arctic provides major breeding – and staging – grounds for most global populations of shorebirds and geese and many populations of ducks (e.g., eiders and scoters) and seabirds (e.g., Arctic tern *Sterna paradisaea*, gulls, and jaegers or skuas). Large populations of many species such as auk and eider migrate between breeding areas in the High or Low Arctic and wintering areas in the sub-Arctic or boreal zones. The three ice-associated whales, bowhead (*Balaena mysticetus*), beluga (*Delphinapterus leucas*), and narwhal (*Monodon monoceros*), also have migratory populations that move into the High Arctic to feed and nurse their calves in summer and back to wintering areas in the southern extent of drift ice. Walrus and seals (e.g., harp seal *Pagophilus groenlandicus* and hooded seal *Cystophora cristata*) undertake similar seasonal migrations. At lower latitudes many species of birds and mammals use sub-Arctic seas for breeding and feeding in summer, while spending the winter at lower latitudes (e.g., northern fur seals *Callorhinus ursinus* and humpback whales *Megaptera novaeangliae*).

Although birds and mammals are not likely to be affected by ocean acidification directly, they might be through the food web if their forage base is affected.

Arctic marine food webs include food chains of different types and lengths, characterized by their basis in the water column, ice, and seabed, respectively. Phytoplankton comprise the dominant primary producers in Arctic marine ecosystems, however ice algae also contribute to production – especially in High Arctic areas with multiannual ice. Benthic macroalgae such as kelp do occur in Arctic waters, but ice scour, suitable substrate, and high turbidity from large Arctic rivers limit their growth.

Primary production spans two orders of magnitude over the Arctic area, with maxima of $> 500 \text{ g C/m}^2/\text{y}$ in the northern Bering Sea and southern Chukchi Sea, and minima of $< 5 \text{ g C/m}^2/\text{y}$ in the central Arctic Ocean under dense pack-ice. The very high production in the northern Bering Sea reflects the northward flow of nutrient-rich North Pacific water in what has been described as a horizontal upwelling system (Sambrotto et al., 1984; Walsh et al., 1989; Springer and McRoy, 1993; Springer et al., 1996). Nutrients are not fully depleted en route through the Bering Strait, and the Pacific water that forms a layer in the upper halocline in the Canada Basin is still nutrient-rich compared to Atlantic water in the Arctic Ocean.

Ice limits light for photosynthesis and thereby limits the length of the season of primary production, although perhaps not as much as previously thought (e.g., Fortier et al., 2002; Mundy et al., 2009; Arrigo et al., 2012). Melting ice forms a surface layer of low salinity water, which effectively restricts the transport of nutrient-rich water from deeper layers, although upwelling events and wind-induced mixing can break down surface stratification and thus foster blooms (Brugel et al., 2009; Tremblay et al., 2011). This leads to a distinct seasonal and vertical pattern in the distribution and production of phytoplankton in ice-covered Arctic seas (Sakshaug and Skjoldal, 1989; Sakshaug, 2004). The annual primary production on the Arctic shelves with seasonal ice cover is typically rather low, in the range of $20\text{--}50 \text{ g C/m}^2$, while production in the sub-Arctic seas in the North Atlantic sector is typically $100\text{--}150 \text{ g C/m}^2$.

The growth of ice algae is strongly light limited: 2 m of sea ice with some snow cover transmits 1% or less of the incoming sunlight to the surface (Bergmann et al., 1991; Cota et al., 1991; Mundy et al., 2005). Ice algae are adapted to low light and start to grow in spring (April) at these low light levels (Michel et al., 1988; Smith et al., 1988; Bergmann et al., 1991). Successive accumulation of algal biomass absorbs more of the transmitted light, limiting further growth of ice algae (and underlying phytoplankton) through self-shading (Smith et al., 1988; Welch and Bergmann, 1989). The onset of melting improves light conditions, but ice algae are also sloughed from the underside of the ice by the meltwater. Extensive studies in the Canadian Arctic have found annual production of ice algae in the range $1\text{--}20 \text{ g C/m}^2$, with a typical mean value of 5 g C/m^2 (Smith et al., 1988; Bergmann et al., 1991; Welch et al., 1992; Michel et al., 2006). After the culmination of the ice-algae bloom, phytoplankton dominate and usually far exceed the ice algae in terms of annual primary production (Welch et al., 1992; Michel et al., 2006).

While heterotrophic and mixotrophic protists, such as ciliates and dinoflagellates, are important grazers in marine Arctic waters (Levinsen et al., 2000), the predominant herbivores in Arctic marine ecosystems are large calanoid copepods. Three species of *Calanus* (*C. finmarchicus*, *C. hyperboreus*, and *C. glacialis*) are important in the Atlantic sector (Conover, 1988; Melle et al., 2004). *Calanus finmarchicus* dominates the sub-Arctic seas (Norwegian and Labrador seas), while *C. hyperboreus* is dominant in Baffin Bay, the Greenland Sea, and the central Arctic Ocean (Østvedt, 1955; Dawson, 1978; Hirche, 1997; Melle and Skjoldal, 1998; Sundby, 2000). *Calanus glacialis* is a shelf species with a circumpolar distribution extending to

the Chukchi and northern Bering seas (Mathisen et al., 1996; Melle and Skjoldal, 1998). *Neocalanus* species (*N. cristatus*, *N. plumchrus*, and *N. flemingeri*) are dominant herbivores in the Bering Sea basin and are advected with the currents up through the Bering Strait region into the Chukchi Sea (Conover, 1988; Springer et al., 1989, 1996; Mathisen et al., 1996). Pteropods also play important roles in Arctic food webs and *Limacina helicina* is a common species in Arctic surface waters after the spring (ice-edge) bloom and is a food source for several species of fish.

The omnivorous euphausiids or krill are important components in sub-Arctic seas and form important prey for fish and whales. *Thysanoessa inermis* and *T. raschii* have amphiboreal distributions and are found both in the Bering Sea and the North Atlantic (Mauchline, 1980). These species are advected into the Low Arctic where they can play important roles in food webs (e.g., for bowhead whales, Lowry et al., 2004; Ashjian et al., 2010). Pelagic amphipods also play important roles in Arctic food webs, feeding on small copepods and other zooplankton prey. *Themisto libellula* can grow to 5–6 cm and is perhaps the single most important link between zooplankton and higher trophic-level consumers including many seabirds and seals (Dunbar, 1946; Welch et al., 1992; Melle et al., 2004).

Several small fish species play a similar linking role to higher trophic levels. Arctic cod (*Arctogadus glacialis*) can be an abundant pelagic species in the central Arctic Ocean (Walters, 1961; Aschan et al., 2009). There is little ecological knowledge about this species, which may fall prey to migratory stocks of beluga (e.g., Suydam et al., 2001, 2005). Polar cod (*Boreogadus saida* – termed ‘Arctic cod’ in North America) has a circumpolar distribution mainly in the Low Arctic. It probably exists with several large migratory (Welch et al., 1992, 1993; Gjørseter, 1998; Benoit et al., 2008) populations. Polar cod is a pillar of Arctic marine ecosystems, where it constitutes a major prey for many piscivores. Capelin (*Mallotus villosus*) has a similar distribution (Stergiou, 1989; Vilhjalmsen, 1994; Gjørseter, 1998; Dodson et al., 2007; Praebel et al., 2008; Mecklenburg et al., 2011).

The extensive pelagic and sea-ice associated food webs of Arctic ecosystems are based upon phytoplankton and herbivorous zooplankton. Large copepods, notably *Calanus hyperboreus* and *C. glacialis*, are major prey for bowhead whales, which also consume other crustaceans such as amphipods and epibenthic mysids. In sub-Arctic waters, krill are an important food for other baleen whales such as fin (*Balaenoptera physalus*), humpback, and minke (*B. acutorostrata*) whales that also eat small fish such as capelin. Beluga and narwhal dive deep and feed mainly on fish and squid. Beluga eats a wide variety of prey (both pelagic and benthic) but probably targets polar cod as its main prey for their seasonal migrations into the Arctic (Bradstreet et al., 1986; Frost and Lowry, 1990; Welch et al., 1992, 1993; O’Corry-Crowe, 2002, 2009). Narwhal also eats polar cod (and Arctic cod) but is considered to be a specialist to feed on deep-water prey including Greenland halibut (*Reinhardtius hippoglossoides*) and the squid *Gonatus fabricii* (Laidre and Heide-Jørgensen, 2005). Narwhal is perhaps the only species of Arctic mammal for which winter feeding is more important than summer feeding: satellite-tracking has revealed that they dive 15–20 times a day to depths of around

1000 m or more, for a duration of 5–6 months during winter (Laidre et al., 2003, 2004,a,b; Dietz et al., 2008).

Pelagic crustaceans such as *Themisto libellula*, and small fish (capelin and polar cod) are the primary prey for large stocks of harp seal, and ringed seal (*Pusa hispida*) – the most strongly ice-associated of the seals and the primary prey of polar bears. In contrast, hooded seal dives deep to feed on squid (mainly *Gonatus fabricii*) and various deep-water fish (e.g., *Sebastes* spp. and Greenland halibut). Bearded seal (*Erignathus barbatus*), also an ice-associated seal, mainly feeds on benthic invertebrates, as does the walrus (*Odobenus rosmarus*) that specializes on burrowing bivalves (e.g., *Mya truncata*, *Serripes groenlandicus*, and *Hiattella arctica*). Pacific walrus (subsp. *O. r. divergens*) is the most numerous subspecies (~ 200 000 individuals) and supported by the extensive productive shallow benthic habitats of the Chukchi Sea. Declining summer ice has deprived the walruses of haul-out platforms, forcing them to change to coastal haul-outs, which has reduced their foraging opportunities. Atlantic walrus (subsp. *O. r. rosmarus*) number around 20 000–25 000 individuals. Their lower numbers reflect strong overexploitation in the past as well as less productive and less extensive feeding grounds in the Atlantic sector of the Arctic. Historically, the largest population of Atlantic walrus was probably found in the Gulf of St. Lawrence, where they were exterminated by hunting.

Many seabirds feed on ice, in the water, and in the benthos. The High Arctic Ivory gull (*Pagophila eburnea*) and Ross's gull (*Rhodostethia rosea*) feed on pelagic and ice-associated crustaceans, small fish (notably polar cod), and carcasses, feces, and other remnants of marine mammals including polar bear kills. Glaucous gull (*Larus hyperboreus*) is also a generalist predator and scavenger on a wide range of prey including bird eggs and chicks, polar cod, capelin, fish roe, mussels, sea urchins, and other invertebrates in the Arctic. In the Low- and sub-Arctic, black-legged kittiwake (*Rissa tridactyla*) and northern fulmar (*Fulmarus glacialis*) are two abundant feeders on invertebrates and small fish at or close to the sea surface.

Auks – notably dovekie (or little auk, *Alle alle*) and various species of auklet (least auklet, *Aethia pusilla*, crested auklet, *A. cristatella*, and others) – are common plankton feeders and among the most numerous of all seabirds. Their main prey is large calanoid copepods. The larger common and thick-billed murre (*Uria aalga* and *U. lomvia*) are auks that occur in great numbers at large breeding colonies in Low Arctic and sub-Arctic waters, where there is a combination of cliffs and a rich supply of large zooplankton (krill and amphipods) and small fish (e.g., polar cod and capelin). Murres are conspicuous components of Arctic food webs and have several different subspecies (three to four). In sub-Arctic areas the Atlantic puffin (*Fratercula arctica*) and the Pacific horned puffin (*F. corniculata*) are abundant; breeding where there is an abundant supply of small fish such as herring and capelin. Black guillemot (*Cepphus grylle*) is a dispersed generalist species feeding on a variety of small demersal and pelagic fishes and invertebrates, including polar cod, amphipods, sculpins, blennies, and others. In sub-Arctic and Low Arctic coastal environments eiders are abundant and conspicuous. Common eider (*Somateria mollissima*) and king eider (*S. spectabilis*) have circumpolar distributions, with

the latter being more common in the Arctic whereas several subspecies of common eider occur in boreal and sub-Arctic waters. Spectacled eider (*S. fischeri*) and Steller's eider (*Polysticta stelleri*) are found in the Pacific sector (Steller's eider also breeds in western Siberia). Eiders dive in relatively shallow water (to depths of 30–60 m), where they feed on benthic invertebrates, especially mollusks (for common and spectacled eiders), but also crustaceans and echinoderms. In contrast, Steller's eider specializes on feeding in shallow inshore eelgrass (*Zostera*) or algal beds. Perhaps most remarkably, long-tailed duck (*Clangula hyemalis*), another abundant circumpolar species, is considered to be the deepest diving waterfowl feeding on various benthic invertebrates, predominantly crustaceans and mollusks at depths over 60 m. Less important species such as scoters (black, white-winged, and surf scoters – *Melanitta nigra*, *M. fusca* and *M. perspicillata*) and mergansers (common and red-breasted mergansers – *Mergus merganser* and *M. serrator*), forage mainly in shallow nearshore waters, where scoters eat clams, mussels, periwinkles, and other snails, as well as crabs and shrimps. Mergansers eat mainly small fish in freshwater, estuarine, and coastal habitats.

3.4 Taxon-specific responses to ocean acidification

Information about Arctic species or ecosystem processes is limited. Therefore, the material presented in this section is mainly drawn from non-Arctic studies under the broad assumption that many of these processes will be similar in the Arctic. Each section begins with coverage of what is known from non-Arctic species and is followed by an assessment of what this means for Arctic species.

3.4.1 Effects of ocean acidification on viruses

3.4.1.1 Marine viruses (non-Arctic studies)

There are no studies that definitively show direct effects of ocean acidification on marine viruses. However, since the life cycle and persistence of viruses are directly linked to their hosts, viral processes such as lytic events may be indirectly influenced by ocean acidification. Elevated $p\text{CO}_2$ has been reported to have no effect (Rochelle-Newall et al., 2004), a positive effect, and a negative effect on viral abundance (see review by Danovaro et al., 2011). The effects of ocean acidification on viral infection rates are equally unknown, although several studies indicate that elevated $p\text{CO}_2$ can compromise immune systems of marine invertebrates (e.g., Hernroth et al., 2011; Munari et al., 2012).

3.4.1.2 Polar/Arctic marine viruses: Marine viruses associated with sea ice

Very few data are available on marine viruses associated with sea ice (Maranger et al., 1994; Gowing et al., 2002, 2004; Gowing, 2003; Wells and Deming, 2006). Viral concentrations in sea ice can be 10- to 100-fold greater than concentrations in the underlying water column (Maranger et al., 1994; Gowing et al., 2004), however, the phylogenetic diversity of sea-ice viral communities is unknown at present. Two studies have

isolated bacterial viruses from sea ice, both of which would be considered cosmopolitan in their distribution (Borriss et al., 2003; Wells and Deming, 2006), but data on eukaryotic sea-ice-inhabiting microbes are totally lacking as is their response to ocean acidification.

3.4.2 Effects of ocean acidification on bacteria

3.4.2.1 Bacteria and bacterial processes (non-Arctic studies)

In some studies, bacterial communities responded indirectly to ocean acidification *via* direct effects of acidification on phytoplankton abundance, production, and calcification (McDonald et al., 2009; Liu et al., 2010). Consequently, acidification-induced increases in phytoplankton dissolved organic matter (DOM) production (either by extracellular secretion and/or grazing by protozoa) may enhance biogeochemical activities in some bacterial communities (although it should be noted that phytoplankton responses to elevated $p\text{CO}_2$ are not consistent between studies – see Section 3.4.3).

Although the bacterial community does not appear to be strongly affected by $p\text{CO}_2$, elevated $p\text{CO}_2$ generally increases bacterial productivity (Grossart et al., 2006; Allgaier et al., 2008), whereas bacterial abundance does not change with $p\text{CO}_2$ (Allgaier et al., 2008; Paulino et al., 2008). Variable responses to elevated $p\text{CO}_2$ have been reported for extracellular enzyme activity (Grossart et al., 2006; Piontek et al., 2010; Yamada and Suzumura, 2010) and bacterial diversity (reviewed by Liu et al., 2010).

Some special functions of the microbial food web might be affected by ocean acidification, with potential consequences for ocean biogeochemistry. Note also that the activities in the microbial food web have effects on the pH of seawater through processes such as photosynthetic fixation of CO_2 (increasing pH), microbial degradation of organic material to CO_2 (decreasing pH), and calcite formation (reducing alkalinity). Global-change phenomena occurring in the Arctic that may affect photosynthesis (increased water-column stability, nutrient runoff, improved light conditions due to reduced ice cover, etc.), bacterial activity (increased influx of dissolved organic carbon to the Arctic Ocean from Russian and Canadian rivers, increased denitrification in areas with reduced oxygen content, etc.), or calcification (e.g., changes in the pattern of *Emiliania huxleyi* blooms due to changes in temperature and currents) will therefore, through the associated microbial processes, modify the geographical and temporal patterns in pH variation created by atmospheric CO_2 (see Chapter 2).

The two microbial processes that have received particular attention in relation to changes in $p\text{CO}_2$ and pH are (1) ‘C-overconsumption’, whereby more CO_2 is fixed per nitrogen consumed at high $p\text{CO}_2$, i.e., changing the ‘Redfield ratio’ of C-fixation, and (2) calcification, where a reduced pH lowers the saturation level for calcite and aragonite and, therefore, makes seawater corrosive to calcium carbonate (CaCO_3). The latter process is covered in detail in Chapter 2, Section 2.3.5.

Increased $p\text{CO}_2$ may stimulate carbon fixation and thus potentially increase C:N (e.g., Leonardos and Geider, 2005). The C:N-ratio of material exported from the photic zone is crucial to

the efficiency of the biological C-pump, transferring carbon from the atmosphere to the oceanic interior. Even a small increase in C:N may be important since it could constitute a negative bio-feedback where the efficiency of the biological pump increases as atmospheric CO_2 increases. A C:N = 106:16 = 6.6 (molar) stoichiometric coupling in photosynthesis, as implied by the Redfield ratio, is an average value from which large deviations are observed when examining different phytoplankton species and different growth conditions (Geider and La Roche, 2002), implying a rather loose coupling between the acquisition-incorporation processes for carbon and nitrogen. The most convincing data sets indicating C-overconsumption are from the near-natural systems studied in mesocosms. In a study from Raunefjorden in western Norway, Riebesell et al. (2007) quantified the effect to be an increase in C:N from 6 to 8 as manipulated atmospheric CO_2 increased from 350 to 1050 ppm. How this extra organic carbon is partitioned within the system is not well known, but at least parts seem to be directed to the pool of transparent exopolymeric particles (TEP). Models of the C-overconsumption effect have been constructed that combine an increase in particulate organic carbon (POC) with TEP production (Schartau et al., 2007).

Production of TEP has often been associated with diatom growth, but the primary phytoplankton response to an experimental increase in CO_2 seems to be in the picoplanktonic size fraction with very small cells (< 2 μm) and is consistent with what was observed in a mesocosm experiment in Kongsfjorden, Svalbard, in which the first of a succession of three consecutive blooms exhibited a stimulation of the picoplankton size fraction (Meakin and Wyman, 2011). A phytoplankton-bacteria relationship that has received a lot of attention is the phytoplankton production of the osmolyte DMSP (dimethylsulfoniopropionate) apparently sensitive to acidification, but in a manner variable between species (Spielmeyer and Pohnert, 2012). Mesocosm studies have only revealed small, although statistically significant effects of ocean acidification on DMS (dimethylsulfide) concentration (Vogt et al., 2008). Since bacteria subsequently consume DMS, probably including the numerically often-dominant SAR11 clade (Reisch et al., 2011), interactions leading to changes in species composition could be possible.

Mesocosm studies in Spitsbergen found few or no substantive effects of elevated $p\text{CO}_2$ on bacterial community composition (Roy et al., 2013).

3.4.2.2 Polar/Arctic bacteria: Bacteria and sea ice

Polar sea ice supports high bacterial productivity and diversity, making this one of the most significant ecosystems in the Arctic and Antarctic (Garrison et al., 1986; Grossmann and Dieckmann, 1994; Amon et al., 2001). Although significant differences in the physics and chemistry of Arctic and Antarctic sea ice cause differences in DOM, particulate organic material (POM), and nutrients, bacterial diversities in Arctic and Antarctic sea ice are similar (Brown and Bowman, 2001; Brinkmeyer et al., 2003; Junge et al., 2004). Bacterial community diversity within sea ice is highly correlated with the diversity in the underlying seawater (Bowman et al., 2012). The response of sea ice bacteria to ocean acidification is unknown.

3.4.3 Effects of ocean acidification on phytoplankton

3.4.3.1 Phytoplankton (non-Arctic studies)

No consistent response to elevated $p\text{CO}_2$ has been observed for marine phytoplankton cell-division rates (Riebesell and Tortell, 2011). For example, ocean acidification has positive effects on division rates in diatoms (e.g., Gervais and Riebesell, 2001), dinoflagellates (Burkhardt et al., 1999), some coccolithophores (Shi et al., 2009; Rickaby et al., 2010), and some cyanobacteria (Barcelos e Ramos et al., 2007; Hutchins et al., 2007); negative (Iglesias-Rodriguez et al., 2008; Langer et al., 2009; Muller et al., 2010) or neutral (Buitenhuis et al., 1999; Zondervan et al., 2002) effects in some coccolithophores; and negative effects in some cyanobacteria (Czerny et al., 2009). Similar variability in response to ocean acidification has been noted in photosynthetic and carbon-fixation rates of marine phytoplankton (Riebesell and Tortell, 2011). Some recent papers concluded that a number of marine phytoplankton are resilient to lowered pH and altered carbonate chemistry (see Hansen et al., 2007; Nielsen et al., 2010, 2011; Riebesell and Tortell, 2011; Renaud et al., 2012). These species would, therefore, be at a competitive advantage over those that are impacted by ocean acidification.

Increasing $p\text{CO}_2$ promotes nitrogen fixation in some cyanobacteria (Barcelos e Ramos et al., 2007; Hutchins et al., 2007; Levitan et al., 2007) and causes a decline in iron availability to phytoplankton (Shi et al., 2010). Ocean acidification can directly influence phytoplankton population community composition (Tortell et al., 2008), and indirectly affect community structure, nutrient utilization, and productivity through nutrient stoichiometry (Blackford, 2010).

Varying responses in calcification in phytoplankton have been a centre of debate in ocean acidification research. Most calcifying phytoplankton show decreased calcification in response to elevated CO_2 / reduced pH. However, some coccolithophores increase their calcification at higher CO_2 whereas others show no response or a non-uniform trend (e.g., Riebesell et al., 2000; Engel et al., 2005; Iglesias-Rodriguez et al., 2008; Barcelos e Ramos et al., 2007; Muller et al., 2010; Fiorini et al., 2011; Raven, 2011).

3.4.3.2 Arctic phytoplankton

Increased $p\text{CO}_2$ has mild negative effects on growth rate in some sea-ice diatoms (Torstensson et al., 2012), however data on other species are lacking. Coccolithophore populations are at risk, although significant gaps exist regarding the contribution of species other than its most abundant and best studied representative, *Emiliania huxleyi*, to polar populations. Non-bloom coccolithophore populations are known to play a major role in carbon export in the subtropics (Sarmiento et al., 2002), but controls on non-bloom populations in polar regions and their contribution to the carbon cycle remain unknown.

More generally, satellite data show that peak phytoplankton blooms now arrive up to 50 days earlier than in 1997 (Kahru et al., 2011). The community composition of these blooms

has also shown measurable trends, with recent shifts toward dominance by smaller phytoplankton. Similar trends toward more picophytoplankton and fewer nanophytoplankton have also been associated with ocean acidification (Newbold et al., 2012), and with a freshening of the Arctic Ocean and reduction in nutrient supply (Li et al., 2009). These shifts may not cause substantial changes in total production but are likely to have broader effects on the food web. For example, the smaller size of primary producers may reduce transfers of carbon up the food chain.

3.4.4 Effects of ocean acidification on foraminifera

3.4.4.1 Foraminifera (non-Arctic studies)

Planktonic foraminifera can contribute up to 50% of the total carbonate in the ocean sediment, playing an important role in the carbonate pump (Schiebel, 2002).

Like most actively calcifying taxa, calcareous foraminifera construct their tests internally (Lowenstam and Weiner, 1989). Increasing $p\text{CO}_2$ generally results in less massive tests for calcareous species (Spero et al., 1997; Kuroyanagi et al., 2009; Dias et al., 2010). Survival of foraminifera around seafloor CO_2 -injection cylinders is generally unaffected by moderate (<0.2 pH units) acidification, but extreme reductions (2.0 pH units) cause calcareous forms to disappear entirely while thecate (organic) and agglutinated forms remain unaffected (Dias et al., 2010). These patterns mirror survivorship changes seen at the Triassic-Jurassic boundary, although why that is so is unclear (Hautmann et al., 2008) and at the Paleocene-Eocene Thermal Maximum (Zachos et al., 2005).

3.4.4.2 Arctic foraminifera

Carbonate sedimentation in the Arctic is highly dependent on the presence of planktonic foraminifera, and they are responsible for the majority of calcite production (Hendry et al., 2009). In particular, a large portion of recent carbonate in the Norwegian–Greenland Sea sediments is produced by *Neogloboquadrina pachyderma* and *Globigerina quinqueloba* the dominant planktonic species (Carstens and Wefer, 1992; Carstens et al., 1997; Pflaumann et al., 1996). Arctic sedimentation rates vary greatly. On the shelves, sedimentation rates over 30 cm/ky (Polyak et al., 2009; Farmer et al., 2010) have been calculated, whereas rates in basins are less than 1 cm/ky. The planktonic:benthic ratios of foraminifera (Stehli and Creath, 1964) in Arctic shelf seas are generally low, but below 200 m can be ≤ 32 (Murray, 1991; Bergsten, 1994). However, Scott et al. (1989) found that the planktonic to benthic ratio was 1:1 in the deep Arctic where there is no organic influx.

Planktonic and benthic foraminifera typically construct tests of calcium carbonate or of agglutinated sediments, although organic- and siliceous-walled forms are found (Sen Gupta, 2002). Planktonic foraminiferal species diversity is extremely low in the Arctic; assemblages are typically dominated by the polar species *Neogloboquadrina pachyderma*, with the subpolar species *Globigerina quinqueloba*, which is also common (Carstens and Wefer, 1992; Carstens et al., 1997). A few other

Globigerinita species are found in small (<2%) proportions (Carstens and Wefer, 1992; Arnold and Parker, 1999). Although *N. pachyderma* and *G. quinqueloba* can be found as deep as 200 m, the highest abundances of these species are in the upper 50 m of the water column in northernmost regions (above 83° N), whereas in southern areas they are found primarily below the pycnocline (Carstens and Wefer, 1992).

Benthic foraminiferal species diversity in the Arctic is low, in part because of its oceanographic isolation. Very small forms (mean test size 79 µm) dominate (Tomanek et al., 2011) in ice-covered regions as well as in some other areas (Michaelidis et al., 2005). Agglutinated foraminifera dominate deeper waters below the calcium carbonate compensation depth (Scott and Vilks, 1991), whereas calcareous species are typically found at shallower depths in cold water. Some calcareous forms, predominately hyaline rotalid foraminiferan tests, can also be found below 1000 m (Lagoe, 1976).

There is currently no evidence that calcite undersaturation impacts recent foraminiferal faunas in eastern and central Arctic bottom waters (Bergsten, 1994) or bathyal Holocene sediments in the Sea of Okhotsk (Barash et al., 2008). However, Gregory et al. (2010) attributed dissolution of near-surface foraminifera to changes in water-column saturation. Moy et al. (2009) also suggested that a 30–35% reduction in shell weight of present-day Southern Ocean *Globigerina bulloides* (relative to pre-industrial Holocene samples) was due to increased $p\text{CO}_2$. Manno et al. (2012a) found no effect of $p\text{CO}_2$ (0.3 pH unit reduction) on survival of *Neogloboquadrina pachyderma*, but shell diameters were significantly smaller under acidification.

Limited evidence indicates that a ~0.2 pH unit decline will have few if any effects on survival of foraminifera, but may influence growth rates. Larger declines in pH are likely to reduce the diversity and survival of calcifying species, and hence, decrease sedimentation of inorganic carbon. The broader ecosystem consequences of increased dominance by non-calcifying species are unknown.

3.4.5 Effects of ocean acidification on macroalgae

3.4.5.1 Macroalgae (non-Arctic studies)

Temperate and tropical non-calcifying macroalgae typically show increases in growth and photosynthesis with high $p\text{CO}_2$ (Borowitzka and Larkum, 1976; Hall-Spencer et al., 2008; Connell and Russell, 2010). Calcifying macroalgae, in contrast, show significant reductions in recruitment and growth under elevated $p\text{CO}_2$ (Hall-Spencer et al., 2008; Kuffner et al., 2008; Martin et al., 2008; Gao and Zheng, 2010) and reductions (Martin and Gattuso, 2009; Ries et al., 2009; Robbins et al., 2009) or non-linear responses (Borowitzka and Larkum, 1976; Anderson et al., 2011a; Price et al., 2011) of net calcification. At the same time, photosynthetic rate of calcifiers typically increases as a function of increasing $p\text{CO}_2$ (Borowitzka and Larkum, 1976; Anderson et al., 2011a; Price et al., 2011). Magnesium content of high-Mg calcite secreted by coralline red algae declined with increasing $p\text{CO}_2$ (Ries, 2010), indicating that coralline red algae may secrete a range

of high-Mg calcites, and that higher-Mg phases preferentially dissolve away under more acidic conditions. The very scant available data indicate growth of calcifying macroalgae may be compromised under future ocean acidification, whereas most non-calcifiers will probably benefit – directly from increased $p\text{CO}_2$ and perhaps indirectly from reduced competition from encrusting calcifying species.

3.4.5.2 Polar/Arctic macroalgae

Studies of polar macroalgae are lacking. Of the few Arctic species that have been studied, non-calcifying red algae (which typically come from habitats with lower natural pH oscillations than green and brown algae) respond positively to higher seawater $p\text{CO}_2$ (Kubler et al., 1999; Gattuso and Hansson, 2011).

Calcified macroalgae may be vulnerable to extreme changes in pH because many polar species are typically weakly calcified. However, data for living Arctic species are lacking. A recent study of temperate and tropical brown macroalgae indicate that in at least in one genus, *Padina*, lower pH conditions may still allow calcification due to increased photosynthesis (Johnson et al., 2012). Studies of post-mortem dissolution rates of the thallus of encrusting Antarctic coralline algae showed that rates were greater under acidification than non-acidification conditions (McClintock et al., 2011).

3.4.6 Effects of ocean acidification on corals

3.4.6.1 Tropical corals

Globally, corals are important calcifiers, and their aragonite skeletons and reefs provide shelter and habitat for a great diversity of other species. Calcification rates of tropical corals are linearly related to Ω_{Ar} of the surrounding seawater (Langdon and Atkinson, 2005). Consequently, CO_2 -induced reductions in Ω_{Ar} are projected to have strong negative effects on corals and coral reefs (Hoegh-Guldberg et al., 2007). Corals calcify internally, and pH within the calcifying polyp varies diurnally by up to 1.8 units (Al-Horani et al., 2003). Nonetheless, acidification to pHs well above daily minima observed within the polyp causes a $\leq 50\%$ reduction in calcification and growth rates (Schneider and Erez, 2006; Kroeker et al., 2010, 2013; Hofmann et al., 2011). Effects of elevated $p\text{CO}_2$ on earlier life stages of corals are less well investigated, but available data indicate negative effects on fertilization, larval metamorphosis, and juvenile growth (Albright et al., 2010; Nakamura et al., 2011). The generally negative responses outlined are not universal, and a few studies show adult corals can calcify at very low Ω_{Ar} levels (reviewed by Hofmann et al., 2010; Form and Riebesell, 2012). This ability may be related to high nutritional status.

3.4.6.2 Polar/Arctic corals

Cold-water coral reef-like structures or mounds (formed by scleractinian corals) and coral gardens (mostly gorgonians) provide important habitats for many organisms including commercially important fish (Kutti and Fosså, 2009). Model

projections suggest that about 70% of cold-water corals, and especially those at higher latitudes, will be in undersaturated ($\Omega_{Ar} < 1$) waters by the year 2100 (e.g., Turley et al., 2007; Chapter 2, Section 2.6.3). Although Dullo et al. (2008) suggested that *Lophelia* may occur in a temperature-salinity niche, very little is known about the distribution of corals in the Arctic, or about possible effects of acidification on cold-water corals. Some data are available for *Lophelia pertusa*, a common reef builder in the sub-Arctic; acidification of ≤ 0.1 pH units reduced calcification rate of *L. pertusa* by $\leq 29\%$ (Maier et al., 2009; Form and Riebesell, 2012). However, longer-term experiments using gradual declines to lower pHs showed calcification was slightly enhanced over initial values, and net growth was sustained even at $\Omega_{Ar} < 1$ (approx. pH ≤ 7.7 ; Form and Riebesell, 2012). This highlights the need for long-term experiments. Importantly, older skeletons of *L. pertusa* and the dead reef mounds themselves are exposed to seawater and are, therefore, likely to experience dissolution at $\Omega_{Ar} < 1$. The ecological consequences of this are not yet known.

Available data indicate that ocean acidification may have limited impacts on live cold-water corals (*Lophelia*), especially if adequate food is available. However, there is currently a complete lack of knowledge about the dispersive early life stages and newly settled juveniles. Effects on dead coral structures – and hence reefs – as well as on non-*Lophelia* species, are unknown. The important role of cold-water corals as habitat for other species means this is a critical gap in knowledge.

3.4.7 Effects of ocean acidification on mollusks

3.4.7.1 Mollusks (non-Arctic studies)

Mollusks are highly diverse with over 20 000 marine species (Chapman, 2009). As calcifiers of tremendous ecological and economic importance, they are one of the key groups studied in ocean acidification research. Data are available for three classes of mollusk: bivalves (especially oysters and mussels), gastropods (notably pteropods), and cephalopods. Mollusks have highly diverse body plans, physiology, calcification mechanisms, and ecology. It is therefore not surprising that a wide range of biological responses to ocean acidification has been described, from an apparent positive effect on fitness-related parameters in a few species (e.g., reduced mortality in a bivalve; Range et al., 2011) to no effects ($\sim 50\%$ of all tested species) or negative effects ($\sim 50\%$ of all tested species). Ocean acidification may impact survival and growth (e.g., Talmage and Gobler, 2009, 2010), calcification (e.g., Ries et al., 2009), physiology (e.g., Melzner et al., 2011), immunology (e.g., Bibby et al., 2008), proteomics (e.g., Tomanek et al., 2011), evolutionary processes (e.g., Sunday et al., 2011), and acclimation (e.g., Parker et al., 2012). In particular, the planktonic pteropods have been relatively well studied due to their ecological importance as a food source, and due to the sensitivity of calcification of a key species, *Limacina helicina*, to elevated $p\text{CO}_2$ (Comeau et al., 2009, 2010; Lischka et al., 2011).

Acute experiments with bivalves show strong reductions in adult calcification under ocean acidification (Gazeau et al., 2007). However, longer-term incubations demonstrate that adults can calcify at $\Omega_{Ar} < 1$ if sufficient food is available

(Michaelidis et al., 2005; Tunnicliffe et al., 2009; Thomsen et al., 2010; Melzner et al., 2011). Clearly, biological control over calcification is possible even where Ω_{Ar} approaches zero, as long as the shell is protected by the organic periostracum and there is sufficient energy to fuel calcification. Early life-history stages tend to be more susceptible (Talmage and Gobler, 2009, 2010; Gazeau et al., 2010; and many others), although successful settlement and dominance of mytilid mussels and other calcifying invertebrates have been observed at seawater $p\text{CO}_2$ values of 700–1000 μatm (Thomsen et al., 2010). Again, this indicates that either local adaptation and/or adequate energy supplies can also allow early life stages to overcome negative impacts of ocean acidification (see Kelly and Hofmann, 2013). Reductions in growth and calcification have typically been observed at much higher $p\text{CO}_2$, and may be related to elevated metabolic rates and subsequent energy budget re-allocation (Thomsen and Melzner, 2010; Melzner et al., 2011).

The coastal cuttlefish, *Sepia officinalis*, is physiologically robust to 6-week exposure to very high $p\text{CO}_2$ (6000 μatm), although calcification of the cuttlebone increased (Gutowska et al., 2008), which may negatively impact buoyancy regulation. Embryonic *S. officinalis* are more sensitive, showing developmental delay at elevated $p\text{CO}_2$ (>3500 μatm ; Hu et al., 2011). Open-water species, such as the squid *Dosidicus gigas*, live in less variable $p\text{CO}_2$ environments and are expected to be more sensitive. *D. gigas* shows mild metabolic depression at $p\text{CO}_2 = 1000$ μatm (Rosa and Seibel, 2008). No other data for responses of cephalopods to ocean acidification are available.

3.4.7.2 Polar/Arctic mollusks

Bivalves, pteropod gastropods and cephalopods are important components of the Arctic food web (see Section 3.3.2), and consequently impacts of ocean acidification on these species may have broader emergent effects on Arctic ecosystems. The few available studies of polar/Arctic species have reported negative impacts; however, elevated $p\text{CO}_2$ had no impact on survivorship of the Antarctic bivalve *Laternula elliptica* over a longer exposure period of 120 days. Physiological and gene-expression patterns indicated that individuals may not be able to withstand elevated $p\text{CO}_2$ over longer periods (Cummings et al., 2011).

Pteropods can represent as much as 93% of the total zooplankton biomass in high-latitude regions (Hunt et al., 2008) and play a significant role in contributing to carbonate and organic carbon flux and sequestration (Falk-Petersen et al., 2002; Karnovsky et al., 2008; Manno et al., 2010). They play an important role in the food web, and are food resource for many predators such as herring, salmon, whales, and seabirds (e.g., Doney et al., 2009). Models indicate that a 10% reduction of the pteropod population would cause a 20% reduction in mature body weight of pink salmon (*Oncorhynchus gorbuscha*; Feely et al., 2010). Ocean acidification decreases calcification in pteropods (Comeau et al., 2009, 2010; Lischka et al., 2011), increases respiration rates (especially in combination with increased temperature; Comeau et al., 2010) and increases mortality of pre-winter juveniles (Lischka et al., 2011) and adults (Bednarsek et al., 2012; but see Comeau et al., 2012a). Although pteropods can calcify in undersaturated waters, it is possible the extra energy cost necessary to counteract shell

dissolution could seriously affect their energy budget (Lischka et al., 2011; Manno et al., 2012b). Recently, model projections of ocean acidification indicated that in much of the Arctic pteropods would be unable to precipitate calcium carbonate by the end of the 21st century (Comeau et al., 2012b).

Available data indicate that calcifying Arctic mollusks are likely to be negatively impacted by ocean acidification, and especially so at sensitive early life-history stages and/or for thin-shelled planktonic species such as thecosomatous pteropods. The effects of ocean acidification on ecologically important non- (or poorly) calcifying species such as squid are unknown, and data on these species are urgently required.

3.4.8 Effects of ocean acidification on echinoderms

3.4.8.1 Echinoderms (non-Arctic studies)

Most echinoderms calcify as adults and larvae, and consequently echinoderms are one of the primary targets for ocean acidification research (Figure 3.2). The many available studies show that echinoderm responses are generally highly species-, population- and individual-specific, ranging from likely species extinction (9% of studied species; such as the brittlestar *Ophiothrix fragilis*; Dupont et al., 2008), through direct or indirect negative effects (such as delay in development) (52% of studies), to positive effects (6% of studies; e.g., Dupont et al., 2010). It is important, however, to note that most published studies are short term (60% less than two weeks) and focus only on one life stage.

3.4.8.2 Polar/Arctic echinoderms

It has been hypothesized that echinoderms – and especially taxa with high Mg-calcite skeletons – will play the role of the ‘canary in the coal mine’ in polar regions (e.g., McClintock et al., 2011; Sewell and Hofmann, 2011). Available experimental data generally show negative impacts of ocean acidification on a range of processes such as growth. However, these effects do not (as yet) appear to be greater than equivalent responses in temperate and tropical species. For example, some aspects of larval development of the Antarctic sea urchin *Sterechinus neumayeri* are negatively affected by ocean acidification but to a lesser extent than for temperate and tropical species (Clark et al., 2009). Other reported effects of ocean acidification include: increased metabolic rates in the Arctic brittlestar *Ophiocten sericeum* (Wood et al., 2011); reduced ingestion and altered metabolism and immune-system responses in the boreo-Arctic urchin *Strongylocentrotus dreobachiensis* (Dupont and Thorndyke, 2012; Stumpp et al., 2012); developmental delay in the sub-Antarctic urchin *Arbacia dufresni* (Catarino et al., 2012), and reduced fertilization success in the Antarctic urchin *Sterechinus neumayeri* (Sewell and Hofmann, 2011).

While some reports from polar echinoderm species show neutral responses to ocean acidification, the majority of responses reported are negative. Echinoderms are key components of benthic carbon cycling in the Arctic (Renaud et al., 2007) and therefore ocean acidification-induced changes in abundances and performance of Arctic echinoderms are likely to have broader impacts on Arctic benthic ecosystems.

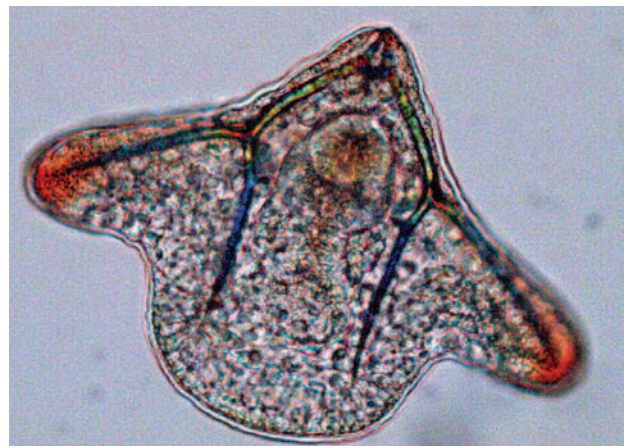
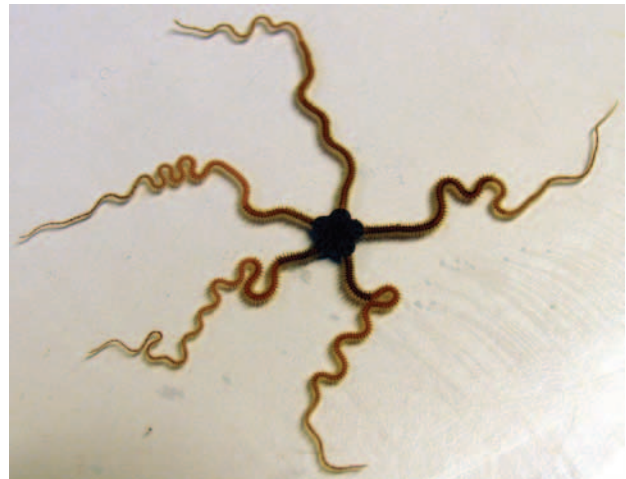


Figure 3.2. Brittlestars (e.g. *Amphiura filiformis*, adult (upper) and larvae (middle)) are particularly sensitive to ocean acidification, while some seastars appear to benefit from ocean acidification (e.g. *Crossaster papposus*, larvae (lower)).

3.4.9 Effects of ocean acidification on crustaceans

3.4.9.1 Crustaceans (non-Arctic studies)

Crustaceans are a highly diverse group of organisms, many of which are highly calcified, and many of which also play key roles in Arctic ecosystems. Perhaps the most ecologically important of these are the pelagic copepods, and yet few studies have investigated effects of ocean acidification on copepods.



Figure 3.3. The effects of ocean acidification have been investigated in several polar/Arctic crustaceans. For example, barnacles such as *Semibalanus balanoides* (upper), copepods such as *Calanus finmarchicus* (middle) and the shore crab, *Carcinus maenas* (lower). Photos: Fredrik Pleijel.

Most work has focused on effects on processes other than calcification (the exoskeleton of pelagic copepods has little, or no, calcium carbonate), and most studies have found no, or only small, responses to ocean acidification. Even exposure to very high $p\text{CO}_2$ levels (pH 7.4) only reduced survival in one species (of four studied), slightly reduced ($\leq 20\%$) egg-hatching success in one species (of three studied), and had no statistically significant effect on egg-production rate (four species) (Kurihara et al., 2004a,b; Kurihara and Ishimatsu, 2008; Mayor et al., 2007). Negative effects on larval (nauplius) survival have been reported but only at extreme levels of $p\text{CO}_2$ (Kurihara et al., 2004a,b). These results indicate that planktonic copepods may not be sensitive to ocean acidification at levels expected to occur within the 21st century. However, an Arctic perspective is lacking.

A number of studies have investigated responses of decapod crustaceans to ocean acidification. The balance of evidence indicates that acidification to levels projected for the year 2100 will influence decapod crustaceans substantially (Whiteley, 2011; Flores et al., 2012). Reported impacts include diverse effects on calcification; negative effects on embryonic development (e.g., Egilsdottir et al., 2009); positive, neutral, and negative effects on larvae (e.g., Arnold and Parker, 1999; Walther et al., 2010, 2011; Flores et al., 2012); and negative effects on growth rates and molting frequencies (Whiteley, 2011). Ocean acidification also affects behavioral patterns in hermit crabs (de la Haye et al., 2011) and penaeid prawns (Dissanayake and Ishimatsu, 2011). At an ecosystem level, abundance and diversity of marine benthic communities decline under ocean acidification, but only at $\text{pH} \leq 7.3$ (Hale et al., 2011).

The effects of ocean acidification on barnacles have been investigated in several species. Results vary, with some species showing reduced shell growth (*Eliminius modestus*) and calcification (*Semibalanus balanoides*), while others showed increased shell growth (*Balanus amphitrite*, *B. improvisus*) and calcification (*B. amphitrite*) (Findlay et al., 2009, 2010a,b; McDonald et al., 2009). Effects on barnacle embryos and larvae also vary: larval condition, cyprid size, larval settlement, and metamorphic success in *B. amphitrite* were all unaffected by very high $p\text{CO}_2$ levels (pH 7.4; McDonald et al., 2009), whereas less extreme levels of ocean acidification had negative effects on *S. balanoides* (Findlay et al., 2009). *Balanus amphitrite* shows changes in gene expression, with negative consequences for energy metabolism and respiration (Wong et al., 2011). Work on multiple stressors produced complex effects, for example, the effects of increasing temperature override those of acidification above a critical threshold (13°C , *S. balanoides*, Findlay et al., 2010b).

3.4.9.2 Polar/Arctic crustaceans

The boreal/Arctic copepod, *Calanus finmarchicus*, is a key species in the sub-Arctic (see Figure 3.3), and although egg-production rates were unaffected by extreme $p\text{CO}_2$ (8000 ppm = pH 6.95), substantial reductions in egg-hatching success were observed (Mayor et al., 2007). The effects of warming-driven northward-range extension of *C. finmarchicus* (Reygondeau and Beaugrand, 2011) in combination with ocean acidification are unknown. Barnacle species in the Arctic are few and are

limited by the extent of sea ice (which scrapes them from the rocks). *Semibalanus balanoides* is common in boreal and ice-free Arctic waters (the larvae tolerate several weeks of freezing in sea ice; Pineda et al., 2005), and the invasive *Balanus improvisus* has also been reported from the Arctic. The responses of these species to elevated $p\text{CO}_2$ (typically ~ 1000 μatm , $\text{pH} \approx 7.7$) are mixed, but generally negative, showing small reductions in shell calcification, or compensatory calcification, which incurs increased metabolic costs (Findlay et al., 2011). Data for boreo-Arctic decapod species include the shore crab *Carcinus maenas*, the spider crab *Hyas araneus*, and the lobster *Homarus gammarus*. High levels of $p\text{CO}_2$ ($\text{pH} 7.3$) changed gene expression in the gills of the shore crab, although this did not translate into measurable physiological responses (Fehsenfeld et al., 2011). Similar pH drops caused reduced Ca^{2+} uptake by spider crab larvae, especially in populations from Svalbard (the northern margin of the species range; Walther et al., 2011), reduced larval development rate, reduced larval growth and reduced larval condition (Walther et al., 2010), and narrowed the thermal-tolerance window of spider crab adults (Walther et al., 2009). Decreasing pH by 0.3 units had no significant effects on survival, growth (carapace length), and development rates of larvae of the lobster *Homarus gammarus*, but did cause reductions in $\text{Ca}^{2+}/\text{Mg}^{2+}$ content of the larval carapace (Arnold et al., 2009). Interestingly, recent work showed that exposure to pH 7.7 for five months caused reductions in closure strength of the crusher chela (used in feeding and defense against predators) in *C. maenas* (Landes and Zimmer, 2012).

The available data indicate that although crustaceans in general are relatively robust to ocean acidification, polar and Arctic species show significant reductions in function, especially during the larval stages, which is likely to be translated into lower survivorship and reduced population viability.

3.4.10 Effects of ocean acidification on other invertebrates

3.4.10.1 Other invertebrates (non-Arctic studies)

Beyond the cnidarians (corals), mollusks, echinoderms, and crustaceans (see e.g., Doney et al., 2009), there is only direct evidence on the impact of near-future ocean acidification on five other invertebrate phyla: Acoela (positive effect; Dupont and Thorndyke, 2012), Annelida (negative or no effect; Widdicombe and Needham, 2007), Bryozoa (negative or no effect; e.g., Rodolfo-Metalpa et al., 2010), Nematoda (negative effect; Barry et al., 2004), and Nemertea (no effect; Ericson et al., 2010). This illustrates that little research focus (<5% of literature on invertebrates) is currently placed on those taxa that might be less vulnerable to the anticipated changes in ocean chemistry (Melzner et al., 2009a).

3.4.10.2 Polar/Arctic other invertebrates

Only one published paper considers the impact of ocean acidification on a polar (Antarctic) species. Near-future ocean acidification conditions had no significant effect on fertilization and early embryogenesis of the Nemertean *Parborlasia corrugates* (Ericson et al., 2010).

3.4.11 Effects of ocean acidification on fishes

3.4.11.1 Fishes (non-Arctic studies)

Juvenile and adult fishes have sufficient capacity and flexibility in their acid-base regulation systems to cope with the projected changes in environmental CO_2 levels over the 21st century (Pörtner, 2008; Melzner et al., 2009a,b). However, due to their high surface-to-volume ratios and less developed acid-base regulation systems, eggs and early larval stages might be more sensitive to changes in environmental CO_2 levels (Kikkawa et al., 2003; Ishimatsu et al., 2004). Recent experimental work has demonstrated direct, negative effects of high CO_2 on larval growth and survival of some marine fishes (Baumann et al., 2012; Frommel et al., 2012), but not others (Munday et al., 2009a, 2011a). In addition to growth and survival, laboratory experiments have documented effects of elevated CO_2 on other physiological processes. Rearing at elevated CO_2 concentrations (>1000 μatm CO_2) resulted in hyper-calcification of the otoliths in larval sea bass *Atractoscion nobilis* (pelagic spawner) (Checkley et al., 2009) and in clownfish (*Amphiprion percula*; benthic spawning species) reared at ~ 1700 μatm CO_2 but not at lower CO_2 concentrations more likely to be observed in the ocean within the next 50–100 years (Munday et al., 2011b).

Little is known about the effects that chronic exposure to high $p\text{CO}_2$ might have on fish reproduction. The few preliminary studies available indicate that impacts are small. Sperm motility of some flatfish species is arrested by mild increases in $p\text{CO}_2$ (Inaba et al., 2003), but similar effects were not observed in the Baltic cod, *Gadus morhua* (Frommel et al., 2010), or 11 other species from a range of families (Inaba et al., 2003). Sensitivity of fish eggs to elevated CO_2 varies markedly between species, but species tested to date typically have 24h LC50 (lethal concentration resulting in 50% mortality) values well above 10 000 μatm CO_2 (Ishimatsu et al., 2008). Rearing eggs of Atlantic herring in acidified water had no detectable effect on fertilization success, embryonic development, hatch rate, length and weight at hatching, and yolk size (Franke and Clemmesen, 2011). Furthermore, Munday et al. (2009b) did not detect any effect of exposure to ~ 1000 μatm CO_2 on the embryonic duration or survival of clownfish eggs. Consequently, the evidence currently indicates that embryos of marine fish are tolerant of increases in oceanic $p\text{CO}_2$ up to the stage of hatching.

Larval stages are predicted to be more sensitive to elevated $p\text{CO}_2$ than adults because they have a larger surface-area-to-volume ratio, and are, therefore, more susceptible to changes in ambient conditions, but also because they might have less developed mechanisms for acid-base balance compensation (Ishimatsu et al., 2008; Melzner et al., 2009a). Although very little is known about the mechanisms and pathways of acid-base regulation in larval fishes, it is clear that they must be capable of acid-base homeostasis, at least in later ontogenetic stages (Brauner, 2008). Larval mortality of the estuarine species *Menidia beryllina* increased when exposed to near-future CO_2 levels (Baumann et al., 2012), and tissue development was disrupted in Atlantic cod reared at high CO_2 (1800 and 4200 μatm CO_2) (Frommel et al., 2012). These studies indicate that larval stages of some marine fishes may be sensitive to rising CO_2 levels in the ocean.

However, Miller et al. (2012) found that reduced growth and survival observed in juvenile anemonefishes *Amphiprion melanopus* reared at high CO₂ levels were reversed when the parents experienced the same CO₂ conditions as the juveniles. This indicates that it is premature to conclude that near-future CO₂ levels will have negative effects on the growth, development, or survival of marine fishes until more studies include exposure to high CO₂ during both the parental and offspring generations, as well as for multiple generations.

Concentrations of CO₂ reported to cause mortality in adult fish are generally an order of magnitude or more higher (>10 000 µatm) than the CO₂ levels projected for the atmosphere and shallow ocean by the end of the 21st century (up to ~1000 ppm under a business-as-usual scenario of CO₂ emissions) (Ishimatsu et al., 2008). Therefore, direct effects of rising CO₂ levels on mortality are unlikely for adults. Very high concentrations of CO₂ (>10 000 µatm) are known to affect respiration, circulation, and metabolism of some fishes (Ishimatsu et al., 2005); however, the effects of CO₂ concentrations projected to occur in the shallow ocean this century are largely unknown. One concern is that increased energetic costs of acid-base balance and/or reduced respiratory capacity may limit the scope for aerobic performance as CO₂ levels rise (Pörtner and Farrell, 2008). In one of the few studies conducted to date, aerobic scope in two tropical cardinal fishes (*Ostorhinchus doederleini* and *O. cyanosoma*) declined by >30% when they were exposed to ~1000 µatm CO₂ at the average summer temperature (29 °C) for the study population and at temperatures up to 3 °C above average (Munday et al., 2009a). In contrast, Atlantic cod maintained their standard and active metabolic rates, critical swimming speeds, and aerobic scope after prolonged exposure (four and 12 months) to 3080 and 5800 µatm CO₂ (Melzner et al., 2009b). These contrasting results indicate that sensitivity to elevated CO₂ varies greatly among species and possibly that aerobic performance of cool-water fishes will be more tolerant of rising pCO₂ than in warm-water fishes. Pörtner and Knust (2007) demonstrated that oxygen limitation due to rising water temperature was likely to be responsible for range contractions and population declines of North Sea eel pout (*Zoarces viviparous*), and rising CO₂ levels may compound this problem, although this has not yet been tested. In general, the metabolic performance of species and life stages with high-oxygen demand, such as pelagic species and pelagic larvae, are predicted to be most sensitive to elevated oceanic CO₂ levels.

A potentially serious consequence of rising pCO₂ is that it can affect sensory systems and behavior of some marine fishes (Munday et al., 2009c, 2010; Simpson et al., 2011; Domenici et al., 2012). Larval reef fish exposed to elevated CO₂ lose their ability to discriminate between ecologically important chemical cues, such as odors from different habitat types, kin and non-kin, and the smell of predators (Munday et al., 2009c; Dixon et al., 2010). Recent experiments report that the response to auditory cues is also affected (Simpson et al., 2011) and a range of behavioral problems has been detected, including the loss of behavioral lateralization (Domenici et al., 2012). Whether elevated CO₂ causes similar behavioral impairment in larvae of polar fishes is unknown, but should be a priority area for further research.

Recent experiments have demonstrated that adult reef fish also suffer impaired olfactory ability and altered behavior when

exposed to elevated pCO₂, with potential effects on predator-prey interactions (Cripps et al., 2011; Ferrari et al., 2011) and homing to resting sites (Devine et al., 2012). Given that adult reef fish experience significant daily fluctuation in pH and pCO₂ in coral reef habitat (Ohde and van Woesik, 1999; Kuffner et al., 2008), and thus might be expected to have some tolerance to higher CO₂ levels, it should be expected that behavior of adult fish in other habitats, including polar regions, will also be affected. New research shows that elevated pCO₂ alters fish behavior by interfering with brain neurotransmitter function, specifically GABA-A receptors (Nilsson et al., 2012). Given the ubiquity of GABA-A receptors in the vertebrate brain, there is good reason to expect that polar fishes might be susceptible. The ecosystem effects of impaired sensory behavior, altered predator-prey interactions, and changes in behavioral attributes are unknown, but have the potential to be significant.

Striking differences in the responses to elevated CO₂ have been detected, both within and between species. If this variation has a genetic basis, rapid selection of tolerant individuals might be expected (see Munday et al., 2013). Therefore, an understanding of how individuals respond to elevated CO₂, and the variation in performance within local populations, is needed to make predictions about how species from all habitats and ecosystems will respond to future ocean conditions.

3.4.11.2 Polar/Arctic fishes

The effect of ocean acidification on Arctic fishes is unknown. The most applicable work to date on the direct effects of ocean acidification has focused on two commercially important (and closely related) gadoids, Atlantic cod and walleye pollock (*Theragra chalcogramma*). Consistent with expectations for larger-bodied fishes, experiments on juveniles of these species found that long-term exposure to elevated CO₂ (>2500 µatm) did not significantly impact growth or swimming capacity (Melzner et al., 2009b; Hurst et al., 2013). Conversely, a study rearing larval cod in mesocosms found increased incidence of developmental anomalies at high-CO₂ levels (1800 and 4200 µatm; Frommel et al., 2012). However, the physiological damage incurred by larval Atlantic cod due to high pCO₂ rapidly disappeared with the development of pH regulatory mechanisms (Frommel et al., 2012). Further, fish reared at those high-CO₂ levels (much higher than would be expected under most scenarios) did not exhibit slower overall growth or behavioral changes (Frommel et al., 2012; Maneja et al., 2013). An important caveat is that these experiments have been conducted with animals from more southerly populations at warmer temperatures, reflecting conditions in the more southerly portions of each species range. It is possible that adaptations of Arctic populations to other climate and habitat features increases sensitivity to ocean acidification or that the physiological ability of these fishes to adapt to elevated CO₂ may be compromised at lower temperatures when metabolic rates are constrained. This concern extends to other benthic fishes adapted to the persistently low temperatures of the Arctic (Pane and Barry, 2007). Further, whether the sensory and cognitive disruption at elevated CO₂ levels in coral reef fishes occurs in Arctic species is unknown (but see Maneja et al., 2013), as are the ecological consequences of these effects (but see Ferrari et al., 2011).

Polar cod (*Boreogadus saida*), a circumpolar species, channels up to 75% of the energy from zooplankton to vertebrate predators including seabirds, seals, whales, and polar bears (Bradstreet et al., 1986; Welch et al., 1992). This species typically represents the bulk ($\geq 50\%$) of ichthyoplankton occurring in Arctic seas, including the Beaufort and Chukchi Seas (Chiperzak et al., 2003a,b; Parker-Stetter et al., 2011; Rand and Logerwell, 2011; Paulic and Papst, 2013; K. Suzuki, University of Laval, unpublished data). Like most marine fishes, the larvae of polar cod feed almost exclusively on copepod nauplii (Drolet et al., 1991; Michaud et al., 1996) while juveniles feed on copepodites (Renaud et al., 2012). The calanoid species *Calanus* spp. and *Pseudocalanus* spp. comprise the bulk of prey ingested by polar cod at all life-history stages (Dominique Robert and colleagues, Memorial University of Newfoundland, unpublished data). Potential impacts of increasing $p\text{CO}_2$ on copepods have been examined using the temperate and boreal species *Acartia* spp. and *Calanus finmarchicus* (Kurihara, 2008; Whiteley, 2011). While detrimental effects were observed on *C. finmarchicus* at $p\text{CO}_2$ levels much higher than those predicted in nature in the foreseeable future, no study has reported acidification impact on copepods under CO_2 levels projected for the next two centuries. For instance, even exposure to a high- CO_2 concentration of 2380 ppm did not affect the survival, growth, and development of *Acartia tsuensis* at all life stages through two successive generations (Kurihara and Ishimatsu, 2008). Therefore, ocean acidification is unlikely to impact polar cod through decreased prey availability.

3.4.12 Effects of ocean acidification on seabirds and marine mammals

The effect of ocean acidification on seabirds and marine mammals will be through the food chain. For example, those seabirds or mammals that feed upon calcifying forms (e.g., pteropods, bivalves – see Section 3.3) may have to switch to other food sources if these species disappear as a result of ocean acidification.

3.5 Ecosystem-level responses to ocean acidification

The effects of ocean acidification on ecosystems are far more complex than the sum of the individual parts outlined in single-species or single-factor studies. Controlled mesocosm studies (e.g., Riebesell, 2004; Hale et al., 2011; Eklof et al., 2012) provide an approach that has shown that complex emergent results can arise from inter-specific differences in scaling of responses to ocean acidification, often in combination with other stressors. Kordas et al. (2011) gave an excellent example of how climate change effects on a simple predator-prey system (seastars and mussels) can lead to non-intuitive outcomes: increased predation rates by the seastar at higher temperatures outweighed the benefits of increased growth rates of the mussels, so that the overall effect of temperature on the mussel was negative. Equivalent investigations of the effects of ocean acidification on the shore crab *Carcinus maenas* and its prey, the snail *Littorina littorea*, showed that negative effects of acidification on both species (decreased chela strength in the crab, and decreased shell strength in the snail), resulted

in no net change in predation pressure (Landes and Zimmer, 2012; see also Hoegh-Guldberg and Bruno, 2010; Potera, 2010; Griffith et al., 2011, for effects on food webs). Rossoll et al. (2012) also demonstrated that $p\text{CO}_2$ can impact food quality with negative consequences for the next trophic levels (copepods, fish larvae).

Emergent ecosystem responses to ocean acidification will be a result of biotic and abiotic factors operating independently and in combination. At the biotic level, responses will be determined by the relative scaling of responses to ocean acidification in different species that interact. This principle is exemplified by the predator-prey examples above (Kordas et al., 2011; Landes and Zimmer, 2012), but also includes the influence of nutritional status on tolerance to ocean acidification (e.g., Thomsen et al., 2010), as well as how ocean acidification affects relative competitive ability (for which no relevant examples could be found). Abiotic stressors such as temperature, salinity, and pollutants not only affect species directly, but will also mediate the ecological interactions between them by moderating the relative scalings of their responses to ocean acidification. For example, including the effects of ocean warming in investigations of the effects of ocean acidification on the crab *C. maenas* preying on the snail *L. littorea* did not alter the relative scalings. Responses were the same at both temperatures (Landes and Zimmer, 2012), although the capacity for interactions between these variables is clear. To date, there are very few studies that have investigated the combined effects of biotic and abiotic factors on ocean acidification responses in marine waters, including the Arctic (but see Findlay et al., 2010b; Wood et al., 2011, and Eklof et al., 2012). Such studies are urgently needed.

With respect to Arctic food webs, there are as yet no data available. Therefore, there is a pressing need for studies on ecosystem-level responses to ocean acidification, from simple predator-prey interactions to higher-level emergent ecosystem responses.

3.6 Observations in naturally occurring low pH and/or high- CO_2 regions

Observations in areas that have natural gradients of pH, such as CO_2 vents (Hall-Spencer et al., 2008; Fabricius et al., 2011), estuaries, areas with acid soil runoff (Amaral et al., 2011; Mucci et al., 2011), and upwelling areas, provide opportunities to study the effects of a gradient of low pH on ecosystem-level responses in a variety of coastal ecosystems, as well as the adaptation of individual organisms (Wootton et al., 2008; Thomsen et al., 2010; Barry et al., 2011). The acidified waters near tropical and temperate CO_2 vents affect calcification, recruitment, growth, survival, and species interactions (Hall-Spencer et al., 2008; Fabricius et al., 2011). Many species of microalgae, macroalgae, seagrass, foraminifera, corals, polychaetes, crustaceans, mollusks and bryozoans are remarkably tolerant of long-term exposures to high and variable CO_2 levels at the vents (Kroeker et al., 2010, 2013; Johnson et al., 2011). However, a fall in mean pH from 8.1 to 7.8 can have detrimental effects on the recruitment of benthic organisms from the plankton (Cigliano et al., 2010) and many adult communities show dramatic reductions in biodiversity along the gradients of

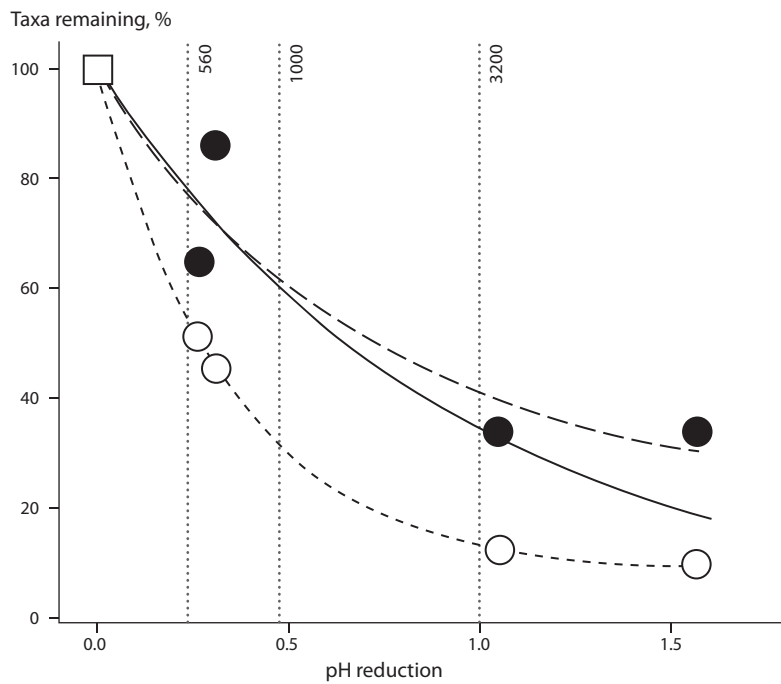


Figure 3.4. Change in Mediterranean coastal biodiversity as a function of declining pH. The biodiversity remaining (percentage of taxa that occurs in areas with no pH reduction [open square]) is shown for calcifying taxa (51 taxa total, white circles) and non-calcifying taxa (71 taxa total, black circles). Atmospheric $p\text{CO}_2$ levels (ppm CO_2) that would be required to cause pH changes in ocean surface waters equivalent to those observed at three locations along a pH gradient are indicated by dotted vertical lines. For calcifiers (short dashed curve), non-calcifiers (long dashes), and all taxa combined (solid), exponential regressions explained 99%, 90%, and 88% of the variance. Fitted regressions indicate a loss of biodiversity of about 40% for non-calcifiers and all taxa, and about 70% for calcifiers, for a pH reduction corresponding to the atmospheric $p\text{CO}_2$ level projected by climate models for 2100. Source: Jason Hall-Spencer, University of Plymouth.

increasing CO_2 in both temperate and tropical coral systems with around 30% fewer species in adult communities at mean pH 7.8 than in adjacent areas at mean pH 8.1 (Hall-Spencer et al., 2008; Fabricius et al., 2011). Important groups, such as coralline algae, calcified foraminifera, and sea urchins are common outside the vent systems but are absent from areas with mean pH ≤ 7.8 (Figure 3.4). However, these studies also show many more subtle effects such as changes in the architecture and community composition of corals in response to differential tolerances to ocean acidification (Fabricius et al., 2011) that had not been predicted. These natural analogs have the disadvantage of being constrained to a limited area: mobile species and/or life-stages may choose to move away or be advected to non-acidified environments. Similarly, ocean acidification-sensitive early life stages generated in distant, non-acidified, habitats may be able to recruit into acidified areas once they have grown beyond a size- or tolerance-threshold (e.g., Ferrari et al., 2011). Consequently, although natural ocean acidification analogs provide a valuable picture of some ecosystem-level effects this picture is inevitably incomplete.

A key question is how results from acidified areas in temperate and tropical systems might translate to polar waters. For example, the effects of naturally high CO_2 on mussels vary dramatically depending on food availability; populations in the Baltic Sea are able to settle and grow well but are unable to do so in the oligotrophic conditions of the Tyrrhenian Sea (Thomsen et al., 2010; Melzner et al., 2011; Rodolfo-Metalpa et al., 2011). To better understand the effects of low pH / saturation state on Arctic ecosystems, ecological shifts that occur along natural pH / carbonate-saturation gradients such as in upwelling areas or in fjords and in areas affected by tundra soil runoff are important to investigate. Areas of naturally lower pH in Arctic waters may be an important focus of future studies to reveal which types of organisms are resistant to ocean acidification and so provide a glimpse of the future diversity and functioning of marine ecosystems as anthropogenic CO_2 emissions rise.

3.7 Caveats

3.7.1 Time-scales of experiments in the context of acclimation and adaptation

The literature on the impact of ocean acidification is mostly based on short-term perturbation experiments. For example, 66% of all studies exploring the impact of ocean acidification on echinoderms consider exposure times of less than two weeks (data updated from Dupont et al., 2010). However, longer acclimation times (more than ten weeks) to high $p\text{CO}_2$ trigger negative effects on survival on such long-lived adult invertebrates (Pörtner et al., 2004; Shirayama and Thornton, 2005; Kurihara et al., 2008). Moreover, short exposure times are not sufficient to allow (or take into account) potential acclimation to a new environment. For example, the sea urchin *Strongylocentrotus purpuratus* is able to reshape its skeleton and change its behavior in a matter of eight to 20 weeks when exposed to a different habitat structure (Hernández and Russell, 2010). As a consequence, short-term exposure may both over- (no acclimation, no selection, no positive carry-over effects) and underestimate (not enough time to induce lethal effects, no negative carry-over effects) the real impacts of a chronic exposure to high $p\text{CO}_2$. The roles of natural variability and rate of change are other neglected parameters that may lead to over- and underestimation of the real impact of ocean acidification on marine species. For practical reasons, most perturbation experiments published to date used abrupt changes in pH. However, abrupt changes can lead to an overestimate of the real impact on fitness (e.g., $p\text{CO}_2$ changes on terrestrial ecosystems; Klironomos et al., 2005).

One of the critical gaps in knowledge is the lack of information on long-term exposure taking into account phenotypic plasticity and natural selection during multi-generation exposures. In other words: is there enough genetic variability and plasticity for populations to cope with near-

future ocean acidification? Phenotypic plasticity occurs when individual genotypes produce different phenotypes in different environmental conditions. This is an adaptive strategy, but is complicated by the fact that plasticity is itself genetically determined and can be under strong selective pressure. Thus, species and populations experiencing high environmental variability may have higher acclimation potential to additional stressors. Natural selection occurs when some genotypes have higher fitness and, therefore, are selected within a population during environmental changes. These parameters are critical and yet have only been considered in relatively few studies (Dupont and Thorndyke, 2008; Kurihara et al., 2008; Parker et al., 2012; but see Garrard et al., 2013). Evolutionary perspectives are only now starting to be considered. Using different clones of bryozoans, Pistevos et al. (2011) demonstrated the existence of genotype variation, which may sustain populations by natural selection during falling pH. Sunday et al. (2011) showed that the sea urchin *S. franciscanus* has vastly greater levels of phenotypic and genetic variation for larval size in future CO₂ conditions compared to the mussel *Mytilus trossulus*. Further, selectively bred fast-growing oysters were more resilient to ocean acidification (Parker et al., 2012).

In a recent paper, Parker et al. (2012) pre-exposed adult oysters to high pCO₂ (856 µatm) for five weeks during reproductive conditioning and showed a positive carry-over effect on larval growth. On the other hand, exposure to an environmental stressor also can induce negative carry-over effects that persist into later stages. For example, exposure to an environmental stressor during the pelagic phase can reduce juvenile performance and be exacerbated if stressful conditions persist (Emler and Sadro, 2006). Adult sea urchin pre-exposure to elevated pCO₂ had a direct negative impact on subsequent larval settlement success. Five to nine times fewer offspring reached the juvenile stage in cultures using gametes collected from adults previously acclimated to high pCO₂ for four months (Dupont and Thorndyke, 2012). In conclusion, considering impacts on a single life-history stage can also lead to misinterpretation of the impact of high pCO₂ on a given species.

3.7.2 Multiple stressors

In the Arctic Ocean, the main drivers of change in the near-future will be warming and multi-year ice melt, which will drive shifts in geographic range – and hence species composition of ecosystems (e.g., Beaugrand et al., 2008) – as well as changes in physiology. Some cold-water adapted high polar species may be marginalized and lost as their physical niche contracts (as in montane streams, e.g., Sauer et al., 2011), or suffer reduced productivity (e.g., Torstensson et al., 2012). At the same time temperature may favor an increase in general productivity that could benefit other species (e.g., Miller et al., 2012). The combination of temperature changes with ocean acidification has the potential to further constrain benefits (Pörtner and Knust, 2007), although available evidence is as yet limited. In addition to increased pCO₂ (i.e., ocean acidification), the additional influence of ice melt to freshen the water column may also have an effect on organisms, although again, data are lacking. A large meta-analysis of multiple stressors in climate change from non-polar regions showed that effects of a wide range of stressors were additive (26% of cases), synergistic (36% of cases) or antagonistic (38% of cases; Crain et al., 2008). The distributions of additive, synergistic and antagonistic effects were also reflected in studies involving ocean acidification, although the number of studies involved was very low (Crain et al., 2008).

3.8 Research priorities

There is an almost complete lack of information on the effects of ocean acidification (in isolation or in combination with other environmental stressors) on keystone species and processes in the Arctic. Accordingly, there is an urgent need for focused research on the likely impacts of ocean acidification on a range of taxa and processes. Some of these are listed below. Note that these points are not mutually exclusive and should, whenever possible, be combined. Further, notwithstanding logistical difficulties, experiments should be conducted *in situ* whenever possible and/or using pelagic and benthic mesocosms (Figure 3.5).

- In field studies, locate pH and CO₂ sensors in the same places that assessments of biological and ecological responses are being conducted.

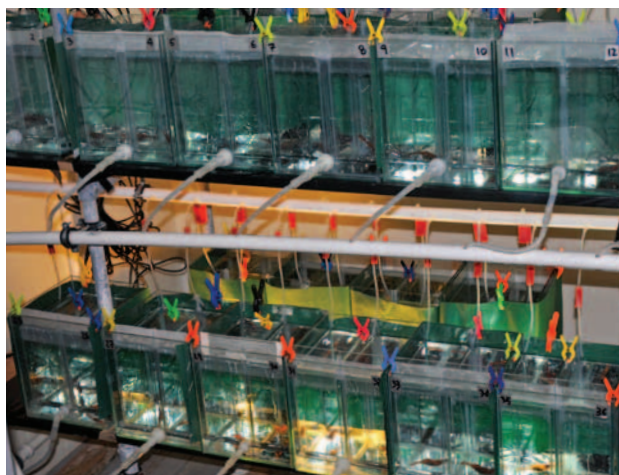


Figure 3.5. Two experimental approaches to investigate the impact of ocean acidification on marine species: laboratory-based perturbation experiments (left, Maj Arnborg) and large-scale field-based mesocosms (right, Maike Nicolai).

- Assess responses of key components of Arctic and sub-Arctic food webs to ocean acidification and determine whether their responses are in any way different from those observed in other geographic regions, for example: viral and microbial communities; heterotrophic and mixotrophic protists; planktonic and under-ice microalgae and how seasonal changes in sea-ice coverage influences primary production and carbon transfer through the food web; clarify the relative effects of the acidification-induced changes in proportion of carbon species used in calcification (CO_2 , HCO_3^- , and CO_3^{2-}); foraminiferans (e.g., determine the respective functional roles of calcifying and non-calcifying foraminifera in order to assess the ecosystem consequences of diversity shifts under ocean acidification); corals (e.g., determine the effects of ocean acidification on *Lophelia* and non-*Lophelia* Arctic coral species and the effects of acidification-mediated loss of unprotected coral structure on coral-associated biodiversity); crustaceans, especially the copepods *Calanus finmarchicus*, *C. hyperboreus* and *C. glacialis*, amphipods (*Themisto libellula*), pteropods (mostly *Limacina helicina*) and commercially important crabs; fish, especially Arctic cod (*Arctogadus glacialis*), polar cod (*Boreogadus saida*), and capelin; seabirds and marine mammals (e.g., assess the dietary flexibility of seabirds and marine mammals to, for example, switch to food sources not affected by ocean acidification).
- Adaptive capacity and environmental plasticity of all stages of the life cycle, including possible local adaptations. This could include (but need not be limited to): long-term transgenerational and selective-breeding experiments; long-term studies investigating adaptations and acclimation capacity; long-term studies investigating the potential for effects to ‘carry-over’ to subsequent life stages and/or generations; address the issue of whether the increased generation time of many Arctic species confers reduced adaptive capacity to near-future climate change (in comparison to temperate and tropical species); multi-population studies to quantify genetic and phenotypic intra-specific variation of key traits influencing fitness; effects of multiple stressors (ocean acidification, carbonate saturation state, temperature, salinity, oxygen, toxins, etc.) on species-level and ecosystem-level processes (including trophic interactions); assess the effects of food limitation / nutritional status on species-level and ecosystem-level processes (e.g., do Arctic species show the same amelioration of ocean acidification impacts under high food / nutrient levels?).

3.9 Conclusions and recommendations

- Based on studies from other oceans, it is highly likely that a significant change will occur in Arctic marine ecosystems due to ocean acidification.
- Presently, too few data are available to determine how vulnerable Arctic ecosystems are to ocean acidification.
- It is likely that some organisms will benefit (e.g., seagrasses, some phytoplankton) from a high- CO_2 world, while others will be disadvantaged (e.g., calcifiers), possibly to the point of local extinction.
- Early life stages and life-stage transitions (e.g., molting) are, in general, more susceptible to ocean acidification.
- There are major knowledge gaps on ecological interactions and on individual species response through acclimation and adaptation.
- Ocean acidification impacts must be assessed in the context of other ecosystem drivers associated with change in the Arctic (e.g., warming, loss of ice cover, freshening of surface waters).

Ocean acidification may cause changes to Arctic marine systems at the organism and ecosystem levels. At the organism level, there will be both direct effects on physiology and behavior and indirect effects *via*, for example, trophic interactions (e.g., food availability and quality). Ocean acidification will affect energy flux through food webs and material flux through changes in the vertical movement of organic and inorganic matter. Pelagic and benthic calcifiers are at greatest risk to ocean acidification. The early life stages of both invertebrates and vertebrates, particularly larval forms with limited autoregulatory capacity, will generally be more susceptible. Sessile benthic organisms will in general be more susceptible to ocean acidification and are likely to be excluded from some regions in which they were previously present. On the other hand, productivity of autotrophs (e.g., dinoflagellates) are likely to increase as may primary productivity (as a result of higher CO_2 and temperature). Organisms inhabiting regions that have always exhibited marked fluctuations in pH and CO_2 may prove highly resilient to ocean acidification. Northward movement of some organisms – driven by warming of the oceans – may be limited by direct or indirect effects of ocean acidification. These potential impacts of ocean acidification on the Arctic are considered in the modeling scenarios presented in Chapter 4.