6 Ocean Systems

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Executive Summary

Ocean ecosystems have responded and will continue to respond to climate changes of different rates, magnitudes, and durations (*virtually certain*). Human societies depend on marine ecosystem services, which are sensitive to climate change (*high confidence*), in particular the provisioning of food (fisheries and aquaculture) and other natural resources; nutrient recycling; regulation of global climate including production of oxygen (O_2) and removal of atmospheric carbon dioxide (CO_2); protection from extreme weather and climate events; and aesthetic, cultural, and supporting services. {6.3, 6.4, 6.5}

Climate change alters physical, chemical, and biological properties of the ocean (*very high confidence*). Oceanic drivers include salinity, circulation, temperature, carbon dioxide (CO_2), oxygen (O_2), nutrients, and light. These drivers shape the physiological performance of individual cells and organisms and ultimately determine ecosystem composition, spatial structure, and functioning. {6.1.1, 6.3}

The fossil record and present field and laboratory observations confirm links between key environmental drivers and responses of ocean ecosystems to climate change (*high confidence*). For millions of years in Earth history, natural climate change at rates slower than today's anthropogenic change has led to significant ecosystem shifts (*high confidence*), including species emergences and extinctions (*high confidence*). Contemporary multi-decadal natural climate variations associated with regional transient warming periods by 1°C have led to fundamental restructuring of ecosystems and large socioeconomic implications (*high confidence*). {6.1.2, 6.3.1, 6.4}

Vulnerability of most organisms to warming is set by their physiology, which defines their limited temperature ranges and hence their thermal sensitivity (*high confidence*). Temperature defines the geographic distribution of many species and their responses to climate change. Shifting temperature means and extremes alter habitat (e.g., sea ice and coastal), and cause changes in abundance through local extinctions and latitudinal expansions or shifts (*very high confidence*). Vulnerability is greatest in polar animals owing to their narrow temperature ranges (*medium confidence*) and in tropical species living close to upper thermal limits (*medium confidence*). Although genetic adaptation occurs (*medium confidence*), the capacity of present-day fauna and flora to compensate for or keep up with the rate of ongoing thermal change is limited (*low confidence*). {6.3.1, 6.3.5, 6.5.2}

The warming-induced shifts in the abundance, geographic distribution, migration patterns, and timing of seasonal activities of species (*very high confidence*) have been and will be paralleled by a reduction in their maximum body size (*medium confidence*). This has resulted and will further result in changing interactions between species, including competition and predator-prey dynamics (*high confidence*). Numerous observations over the last decades in all ocean basins show global-scale changes including large-scale distribution shifts of species (*very high confidence*) and altered ecosystem composition (*high confidence*) on multi-decadal time scales, tracking climate trends. The distribution and abundance of many fishes and invertebrates have shifted poleward and/or to deeper, cooler waters (*high confidence*). Poleward displacements of phyto- and zooplankton have occurred by hundreds of kilometers per decade (*high confidence*). Some warm-water corals and their reefs have responded with species replacement, bleaching, and a decreased coral cover causing habitat loss (*high confidence*). While marine reptiles such as turtles encounter direct effects of warming, impacts to seabirds and marine mammals are mostly indirect through effects of warming on their prey (*high confidence*). {6.3.1, 6.3.7, 6.5, Boxes CC-CR, CC-MB}

In response to further warming by 1°C or more by the mid-21st century and beyond, ocean-wide changes in ecosystem properties are projected to continue (*high confidence*). Large irreversible shifts in the spatial distribution of species and seasonal timing of their activities (feeding, growth, development, behaviors, and productivity) will have implications for species composition, and ecosystem goods and services. {6.3.1, 6.4, 6.5, 6.6}

By the mid-21st century, the spatial shifts of marine species will cause species richness to increase at mid- and high latitudes (*high confidence*) and to decrease at tropical latitudes (*medium confidence*), resulting in global redistribution of catch potential for fishes and invertebrates, with implications for food security (*medium confidence*). Animal displacements are projected to lead to high-latitude invasions and high local extinction rates in the tropics and semi-enclosed seas. This will cause a 30 to 70% increase in the fisheries yield of some high-latitude regions by 2055 (relative to 2005), a redistribution at mid-latitudes, but a drop of 40–60% in the tropics and the Antarctic, based on 2°C warming above preindustrial values (*medium confidence* in the direction of trends in fisheries yields, *low confidence* in

the magnitude of change). If a decrease in global net primary production (NPP) or a shift toward smaller primary producers occurs, the overall fisheries catch potential may also decrease. {6.3.1-4, 6.4.1, 6.5.1-4}

Open ocean NPP is projected to fall globally depending on RCP scenario (*medium confidence*). The estimated decrease will occur by up to 9% by 2100 under the RCP8.5 business-as-usual climate scenario (relative to 1990, *low confidence*). The oceans currently provide about half of global NPP. Environmental controls on NPP include temperature, CO_2, nutrient supply, and light (through cloud cover, mixed layer depth), all of which will be altered (WGI AR5 Section 6.3). Present observations indicate increasing NPP at high (Arctic) latitudes (*medium confidence*), projected to continue beyond 2100 (*medium confidence*). This increase is offset by a decrease at temperate and tropical latitudes (*medium confidence*). Poor representation of shelf and coastal regions hamper projections in global NPP models for near-shore waters, reducing confidence in global projections. {6.3.4, 6.5.1, Box CC-PP}

Large-scale processes and climatic feedbacks sustained by microbes (bacteria, archaea, unicellular algae, and protozoans) play key roles in marine ecosystems (e.g., carbon and nitrogen (N_2) fixation or nutrient recycling) and will be altered by climate change (*medium confidence*). Identifying which microbial species, groups, and processes are being affected and how these will be altered is difficult, as these organisms and their responses to environmental change are extremely diverse and often modulated by biological interactions or changes in circulation and nutrient supply (*limited evidence*, *low agreement*). Warming will cause species-specific responses, such as enhancing metabolic rates and exceeding thermal tolerances, which will affect abundance, distribution, and community structure. Warmer, CO_2- and nutrient-enriched coastal oceans may stimulate harmful algal blooms (*medium confidence*), and the redistribution of certain microbes causing diseases such as cholera (*medium confidence*). {6.3, 6.4.2}

Rising atmospheric CO_2 over the last century and into the future not only causes ocean warming but also changes carbonate chemistry in a process termed ocean acidification (WGI AR5 Sections 3.8.2, 6.4.4). Impacts of ocean acidification range from changes in organismal physiology and behavior to population dynamics (*medium* to *high confidence*) and will affect marine ecosystems for centuries if emissions continue (*high confidence*). Laboratory and field experiments as well as field observations show a wide range of sensitivities and responses within and across organism phyla (*high confidence*). Most plants and microalgae respond positively to elevated CO_2 levels by increasing photosynthesis and growth (*high confidence*). Within other organism groups, vulnerability decreases with increasing capacity to compensate for elevated internal CO_2 concentration and falling pH (*low* to *medium confidence*). Among vulnerable groups sustaining fisheries, highly calcified corals, mollusks, and echinoderms are more sensitive than crustaceans (*high confidence*) and fishes (*low confidence*). Trans-generational or evolutionary adaptation has been shown in some species, reducing impacts of projected scenarios (*low* to *medium confidence*). Limits to adaptive capacity exist but remain largely unexplored. {6.3.2, Box CC-OA}

Few field observations conducted in the last decade demonstrate biotic responses attributable to anthropogenic ocean acidification, as in many places these responses are not yet outside their natural variability and may be influenced by confounding local or regional factors. Shell thinning in planktonic foraminifera and in Southern Ocean pteropoda has been attributed fully or in part to acidification trends (*medium* to *high confidence*). Coastward shifts in upwelling CO_2-rich waters of the Northeast Pacific cause larval oyster fatalities in aquacultures (*high confidence*) or shifts from mussels to fleshy algae and barnacles (*medium confidence*), providing an early perspective on future effects of ocean acidification. This supports insight from volcanic CO_2 seeps as natural analogs that macrophytes (seaweeds and seagrasses) will outcompete calcifying organisms. During the next decades ecosystems, including cold- and warm-water coral communities, are at increasing risk of being negatively affected by ocean acidification, especially as ocean acidification will be combined with rising temperature extremes (*medium* to *high confidence*, respectively). {6.1.2, 6.3.2, 6.3.5}

The expansion of hypoxic regions termed Oxygen Minimum Zones (OMZs) and anoxic "dead zones," observed over the last 50 years and projected into the future under climate change, especially if combined with nutrient enrichment (eutrophication), will constrain the habitat of O_2-dependent organisms and benefit anaerobic microbes (*medium confidence*). Hypoxia tolerance varies among species and is influenced by temperature, elevated CO_2, food consumption, and O_2 demand (*high confidence*). Warming-induced stratification limits the exchange of gases between water layers. Enhanced oxygen consumption by heterotrophic organisms depletes the oxygen further, causing a community shift toward lower species richness and hypoxia-tolerant specialists. Under extreme hypoxia ecosystems are

dominated by microbes. These OMZs are also characterized by microbial removal of fixed nitrogen (denitrification), which can significantly reduce the low-latitude nutrient inventories with implications for regional productivity. {6.3.3, 6.3.5}

The climate-change-induced intensification of ocean upwelling in some eastern boundary systems, as observed in the last decades, may lead to regional cooling rather than warming of surface waters and cause enhanced productivity (*medium confidence*), but also enhanced hypoxia, acidification, and associated biomass reduction in fish and invertebrate stocks. Owing to contradictory observations there is currently uncertainty about the future trends of major upwelling systems and how their drivers (enhanced productivity, acidification, and hypoxia) will shape ecosystem characteristics (*low confidence*). {6.1.1, 6.3.2, 6.3.3, 6.3.5-6, Box CC-UP}

Environmental drivers acting simultaneously on ocean biota* often lead to interactive effects and complex responses (*high confidence*). Interactions of temperature, ocean acidification, and hypoxia narrow thermal ranges and enhance sensitivity to temperature extremes in organisms such as corals, coralline algae, mollusks, crustaceans, and fishes (*high confidence*). In primary producers, light and individual nutrients can also interact with temperature and acidification. Combined warming and ocean acidification reduce calcification in warm-water corals (*high confidence*). Ocean acidification will alter availability of trace metals (*low confidence*). (*The term biota encompasses the organisms of a region, habitat, or geological period.) {6.3.2.2, 6.3.5, 6.5.2}

The combination and often amplification of global and regional climate change and local anthropogenic drivers result in enhanced vulnerability of natural and human systems (*high confidence*). Major regional and local drivers include fishing, pollution, and eutrophication. {6.3.5, 6.4, 6.5}

The progressive redistribution of species and the reduction in marine biodiversity in sensitive regions and habitats puts the sustained provision of fisheries productivity and other ecosystem services at risk, which will increase due to warming by 1°C or more by 2100 compared to the present (*high confidence*). Human societies respond with limited adaptive capacity. Socioeconomic vulnerability is highest in developing tropical countries involving a risk of reduced supplies, income, and employment from marine fisheries (*high confidence*). This emphasizes disparities in food security between developed and underdeveloped nations. {6.4.1, 6.5}

With continuing climate change, local adaptation measures (such as conservation) or a reduction in human activities (such as fishing) may not sufficiently offset global-scale effects on marine ecosystems (*high confidence*). Effects of climate change will thus complicate management regimes such as of marine protected areas once species undergo distributional shifts. This increases the vulnerabilities of marine ecosystems and fisheries. {6.4.2.1}

Geoengineering approaches involving manipulation of the ocean to ameliorate climate change (such as nutrient fertilization, binding of CO_2 by enhanced alkalinity, or direct CO_2 injection into the deep ocean) have very large environmental and associated socioeconomic consequences (*high confidence*). Some actually require purposeful alteration of ocean ecosystems for implementation. Alternative methods focusing on solar radiation management (SRM) leave ocean acidification largely unabated as they cannot mitigate CO_2 emissions. {6.4.2}

6.1. Introduction: Point of Departure, Observations, and Projections

The oceans cover about 71% of Earth's surface to an average depth of 3700 m. Their importance for life on Earth, including humans, is vast (FAQ 6.1). Marine habitats display natural variability on various spatial and temporal scales but a dearth of long-term observational data from the vast open oceans limits our understanding of the causes and ecological consequences of this variability. The available information indicates that climate controls ocean temperatures, chemistry, circulation, upper ocean stratification, nutrient supply, and sunlight exposure. These drivers affect marine ecosystems through direct effects on organisms, amplified by their changing interactions with other species. Food webs are modified by changes in phytoplankton growth and the availability of live organisms or their decomposing bodies, that is, debris or dissolved organic matter, as food to (chemo-)heterotrophs (organisms gaining energy by feeding on organic matter). Organismal responses lead to changes in biogeochemical processes, such as the carbon cycle, and in biological diversity and the services the oceans provide.

Some impacts of climate change on marine ecosystems and their services were addressed in the IPCC Fourth Assessment Report (AR4): WGII Chapters 4 to 6 (ecosystems, food, coastal areas), and regional chapters, for example, 15 (polar regions) and 16 (small islands). The ecosystem assessment in WGII AR4 Chapter 4 focused on terrestrial, coastal, and marine systems, their properties, goods, and services. It emphasized the difficulty in assessing future ecosystem responses as a result of ecosystem complexity, different vulnerabilities of species, and ecosystem-specific, critical thresholds associated with nonlinear responses to environmental change. Focusing on terrestrial ecosystems, WGII AR4 Chapter 4 concluded that more than 2°C to 3°C warming above preindustrial levels causes high extinction risks to 20 to 30% of present-day species (*medium confidence*), paralleled by substantial changes in ecosystem structure and functioning (*high confidence*). The authors projected that a wide range of planktonic and benthic calcifiers will be impacted by ocean warming (*very high confidence*) and acidification (*medium confidence*), particularly in the Southern Ocean. They characterized sea ice and coral reef biomes as highly vulnerable. Key uncertainties identified in AR4 were the incomplete knowledge of ocean acidification (addressed in present Section 6.3.2), synergistic effects and their mechanisms (Section 6.3.5), biotic feedbacks to the climate system (Section 6.4), and the impacts of interactions between climate change, human uses, and ecosystem management (Section 6.4.2).

Much more than in previous IPCC reports (Figure 1-2), impacts on the oceans are a focus in AR5. This allows for a more comprehensive discussion of phenomena and impacts, as well as the associated uncertainties and the levels of confidence in observed and projected changes. The present chapter focuses on the general principles and processes characterizing climate change impacts on ocean systems and on the uses of these systems by human societies. For projections of responses to climate change, the chapter also assesses our understanding of underlying functional mechanisms causing change across all levels of biological organization, from molecules to organisms to ecosystems. As the ocean is a heterogeneous environment, the comparison of major ocean regions is required to understand variability and differences in key processes and carbon inventories (Box CC-PP, Figure 1). We discuss the changes and variability in the ocean's principal physical and chemical properties and assess knowledge drawn from paleo- and historical to present observations. We develop a conceptual framework for analyzing

Frequently Asked Questions

FAQ 6.1 | Why are climate impacts on oceans and their ecosystems so important?

Oceans create half the oxygen (O_2) we use to breathe and burn fossil fuels. Oceans provide about 17% of the animal protein consumed by the world's human population, or almost 20% of that protein consumed by 3 billion people. Oceans are home to species and ecosystems valued in tourism and for recreation. The rich biodiversity of the oceans offers resources for innovative drugs or biomechanics. Ocean ecosystems such as coral reefs and mangroves protect the coastlines from tsunamis and storms. About 90% of the goods the world uses are shipped across the oceans. All these activities are affected by climate change.

Oceans play a major role in global climate dynamics. Oceans absorb 93% of the heat accumulating in the atmosphere, and the resulting warming of oceans affects most ecosystems. About a quarter of all the carbon dioxide (CO_2) emitted from the burning of fossil fuels is absorbed by oceans. Plankton convert some of that CO_2 into organic matter, part of which is exported into the deeper ocean. The remaining CO_2 causes progressive acidification from chemical reactions between CO_2 and seawater, acidification being exacerbated by nutrient supply and with the spreading loss of O_2 content. These changes all pose risks for marine life and may affect the oceans' ability to perform the wide range of functions that are vitally important for environmental and human health.

The effects of climate change occur in an environment that also experiences natural variability in many of these variables. Other human activities also influence ocean conditions, such as overfishing, pollution, and nutrient runoff via rivers that causes eutrophication, a process that produces large areas of water with low oxygen levels (sometimes called "dead zones"). The wide range of factors that affect ocean conditions and the complex ways these factors interact make it difficult to isolate the role any one factor plays in the context of climate change, or to identify with precision the combined effects of these multiple drivers.

effects on organisms and ecosystems and assess present knowledge derived from experiments, field studies, and numerical model projections mostly using Representative Concentration Pathways (RCPs) of climate change scenarios to provide trajectories of climate change drivers (Moss et al., 2010). Finally, we assess the implications of such changes for ecosystem services, and identify plausible socioeconomic consequences.

Assessing climate change impacts on coastal systems is the topic of Chapter 5. An integrative treatment of regional climate changes and impacts in seven key ocean regions is the focus of regional Chapter 30. Marine issues are also included in regional Chapters 22 to 29, with a focus on polar oceans (Chapter 28) and small islands (Chapter 29). Topics important to several chapters, such as ocean acidification, upwelling systems, primary productivity, changes in biogeography, and coral reefs, are discussed in joint assessments presented in the respective cross-chapter boxes.

6.1.1. Changes in Physical and Chemical Variables

Trends in ocean conditions over the last 60 years reflect significant human impacts beyond natural variability on temperature, salinity, dissolved inorganic carbon and oxygen content, pH, and other properties of the upper ocean (e.g., Pierce et al., 2012; Sen Gupta and McNeil, 2012; WGI AR5 Section 3.8, Table 10.1). With climate change, marine ecosystems are and will be exposed to rising temperature, ocean acidification, expansion of hypoxic zones, and other environmental drivers changing concomitantly.

6.1.1.1. Temperature and Salinity

Over the last 39 years, oceans have warmed at average rates of >0.1°C per decade in the upper 75 m and 0.015°C per decade at 700 m depth (WGI AR5 Section 3.2.2, Figure 3.1). Trends differ regionally, seasonally, and interannually (WGI AR5 Section 2.7; for ocean regions see Section 30.5 in the present volume). Temperature changes are particularly large at El Niño-Southern Oscillation (ENSO) with high (3- to 4-year) and low (5- to 7-year) frequencies, and on multi-decadal scales (>25 years, Figure 6-1). The strongest warming trends are found at high latitudes where most of the inter-decadal variability occurs, while tropical oceans are dominated by interannual frequencies. Global climate models have explored changes in different frequency domains, but their spatial resolution is poor (WGI AR5 Sections 11.3.3, 12.4.7).

Temperature variations are often accompanied by changes in salinity. Increased salinity results from reduced precipitation relative to evaporation, for example, above the thermoclines (layer separating the upper mixed layer from deeper water where temperature and density change rapidly with depth) of subtropical gyres at mid- to low latitudes since 1950 (WGI AR5 Chapter 3). Decreased salinity due to enhanced precipitation relative to evaporation has occurred at some tropical and higher latitudes, exacerbated by sea ice melt (Durack et al., 2012). Both warming and freshening cause enhanced density stratification, a trend projected to continue into the 21st century (WGI AR5 Chapter 3, Section 11.3.3, Figure 12.34; Helm et al., 2010). Mean sea surface temperature in 2090 will be 2.7°C warmer than in 1990 (RCP8.5; WGI AR5 Chapter 12; Bopp et al., 2013).

6.1.1.2. Carbon Dioxide-induced Acidification

Rising carbon dioxide (CO_2) concentrations in air (given as partial pressures, $pCO2$, in µatm) cause increasing upper ocean CO_2 levels (Watson et al., 2009). Starting from a preindustrial value of 280 µatm atmospheric pCO_2 levels will have reached around 500 µatm by 2050 following the Special Report on Emissions Scenarios (SRES; IPCC, 2000) and all RCPs (Moss et al., 2010; Meinshausen et al., 2011). By 2100 values are projected to reach between 420 µatm and 940 µatm depending on the RCP. The rise in pCO_2 causes ocean acidification (OA), measured as a decline in water pH (negative log of proton concentration), accompanied by a fall in both carbonate ion (CO_3^{2-}) concentration and the saturation states (Ω) of various calcium carbonates ($CaCO_3$; Zeebe and Westbroek, 2003; WGI AR5 Section 3.8.2, Box 3.2, Chapter 6, Figure 6.29). Hence, the seawater solubilities of three forms of $CaCO_3$, namely calcite, magnesium-calcite, and aragonite, increase. These minerals are important components of shells and skeletons of many marine organisms (Section 6.3.2).

Ocean acidification occurs on a background of natural temporal and spatial variability of pH, pCO_2, and Ω. In the open ocean, the mean pH (total scale, pH_T) of surface waters presently ranges between 7.8 and 8.4 (WGI AR5 Section 3.8.2). In stratified mid-water layers, largely isolated from gas exchange between surface waters and air, decomposition of organic material leads to lowered oxygen (O_2) and elevated CO_2 levels (Paulmier et al., 2011) associated with lower pH values. The few existing field data of sufficient duration, resolution, and accuracy (WGI AR5 Figure 3.18) show that trends in anthropogenic OA clearly deviate from the envelope of natural variability (Friedrich et al., 2012). OA presently ranges between –0.0013 and –0.0024 pH_T units per year (WGI AR5 Section 3.8.2, Table 3.2, Box 3.2; Dore et al., 2009). Average surface ocean pH has decreased by more than 0.1 units below the preindustrial average of 8.17. By 2100 pH is expected to change by –0.13, –0.22, –0.28, and –0.42 pH_T units, at CO_2 levels of 421, 538, 670, and 936 ppm under RCP2.6, 4.5, 6.0, and 8.5 climate scenarios, respectively (WGI AR5 Figure 6.28). The rate of acidification in surface waters varies regionally and is 50% higher in the northern North Atlantic than in the subtropical Atlantic (Olafsson, 2009). Salinity reduction caused by ice melt or excess precipitation (Jacobs and Giulivi, 2010; Vélez-Belchí et al., 2010) exacerbates OA by diluting the concentrations of substances acting as buffers (Steinacher et al., 2009; Denman et al., 2011). At high sustained CO_2 concentrations the changes in ocean chemistry will take thousands of years to be buffered by the natural dissolution of $CaCO_3$ from sediments and tens to hundreds of thousands of years to be eliminated completely by the weathering of rocks on land (Archer et al., 2009).

6.1.1.3. Hypoxia

The average dissolved oxygen concentration in the ocean is presently 162 µmol kg^{-1} (Sarmiento and Gruber, 2006). Concentrations range from over 500 µmol kg^{-1} in productive Antarctic waters super-saturated with oxygen (Carrillo et al., 2004) to zero in coastal sediments and in permanently anoxic deep layers of isolated water bodies, such as the Black Sea and the Cariaco Basin. Hypoxia results from oxygen depletion in excess of supply as in stratified water bodies (Section 6.1.1.2). Vast Oxygen Minimum Zones (OMZs) exist between less than 100 and more

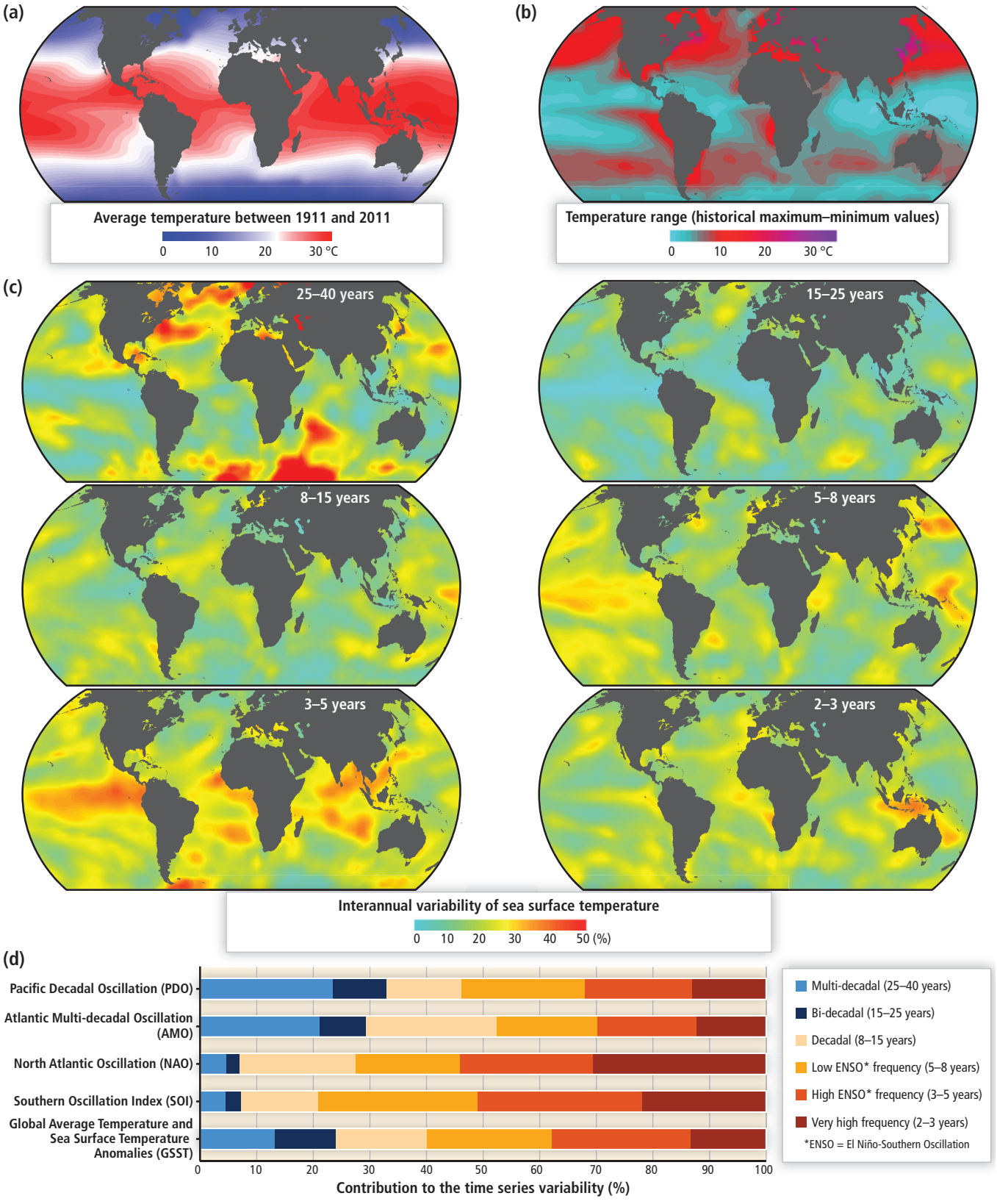


Figure 6-1 | Sea surface temperature variability between 1911 and 2011. (a) The sea surface temperature average for the period. (b) The temperature range calculated as the difference between the maximum and minimum values for each grid component during the century. (c) The spatial distribution of variability by time scales (based on the Extended Reynolds Sea Surface Temperature, NOAA, 2012) corresponds to the multi-decadal (25 to 40 years), bi-decadal (15 to 25 years), decadal (8 to 15 years), low ENSO (El Niño-Southern Oscillation) frequency (5 to 8 years), high ENSO frequency (3 to 5 years), and very high frequency (2 to 3 years) scales. The summed variabilities from the same 2°x2° box in all six maps corresponds to 100% of the time series variability. (d) The spectral density of some of the most widely used climate indices, accumulated in the same frequency windows. The total bar length (100%) corresponds to the cumulative variability of each time series between the 2 and 40 year frequency window. Climate indices were obtained from the NOAA ESRL Physical Sciences Division website.

than 900 m depths in Eastern Atlantic and Pacific tropical oceans. The ecological literature applies the term hypoxia (see Section 6.3.3) to O_2 concentrations below 60 µmol kg^{-1} (estimated at about 5% of global ocean volume; Deutsch et al., 2011). Pacific OMZs regularly reach oxygen levels below 20 µmol kg^{-1} (about 0.8% of global ocean volume; Paulmier and Ruiz-Pino, 2009), lower than Atlantic ones. Suboxic waters at <4.5 µmol O_2 kg^{-1} occupy about 0.03% of the ocean volume, mainly in the northeastern tropical Pacific (Karstensen et al., 2008).

OMZs are naturally present in many habitats including marine sediments, but are also expanding due to anthropogenic influences. Over the past 50 years, open ocean O_2 concentrations have decreased by a mean rate of 0.1 to >0.3 µmol kg^{-1} yr^{-1} (WGI AR5 Section 3.8.3; Stramma et al., 2008). In some OMZs the rate has been much higher due to warming, increased stratification, and rising biological O_2 demand (WGI AR5 Section 3.8.3). Long-term declines in O_2 by about 7 µmol kg^{-1} per decade have been documented at mid-water depths over much of the subarctic North Pacific (Keeling et al., 2010). In coastal regions, extremely hypoxic "dead zones" that exclude animal life, have increased from 42 reported in the 1960s to more than 400 in 2008 and been attributed to high oxygen demand from eutrophication, the local enrichment of nutrients, resulting in organic matter loading and its decay as well as nitrous oxide formation and release (Naqvi et al., 2000; Díaz and Rosenberg, 2008; Zhang et al., 2010).

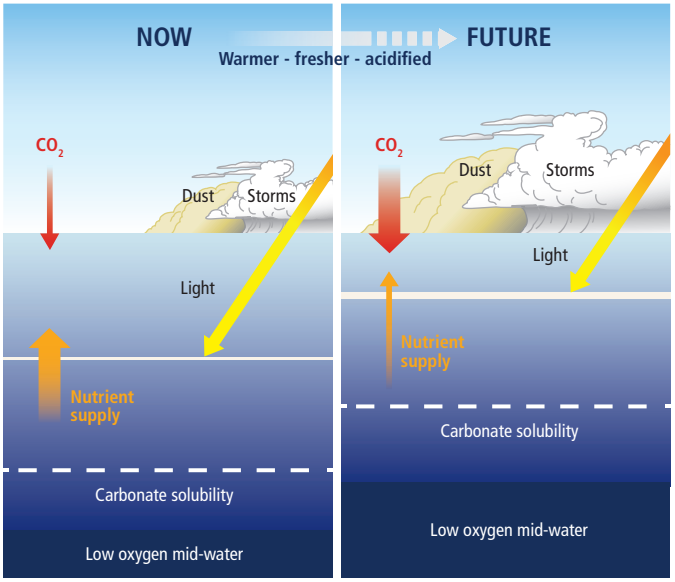


Figure 6-2 | Projected alteration (magnitude and frequency) of oceanic fluxes and atmospheric events due to a changing climate in the coming decades. Ocean properties will be altered from the sunlit surface layer to the mid-water stratum. In the surface ocean, the depth of the mixed layer (solid horizontal line) will shallow resulting in higher mean light levels. Increased density stratification (i.e., a strengthening sea water density gradient represented by the increasing thickness of the solid horizontal line) will reduce the vertical supply of nutrients for photosynthesizing organisms residing in the mixed layer. Anthropogenic CO_2 will acidify, that is, lower the pH of the surface ocean (note this happens in a pH range higher than 7 such that oceans will remain alkaline but less so due to acidification). The penetration of acidified waters to depth will result in a shallower depth (dashed horizontal line) at which $CaCO_3$ structures, such as shells, dissolve. At depth, the location of low-O_2 waters will progressively become shallower. In addition, changes in storm activity and dust deposition will influence ocean physics and chemistry, with consequent effects on ocean biota and hence ecosystems (courtesy of Reusch and Boyd, 2013).

Future warming will *likely* accelerate the spread of hypoxic zones, especially in temperate to sub-polar regions. Most models project decreasing global ocean oxygen contents by 1 to 7% from present-day concentrations in 2100 (Keeling et al., 2010; WGI AR5 Figure 6.30 under RCP8.5), with a mean decline by 3.4% in 2090 compared to the 1990s (Bopp et al., 2013). Warming and freshening of the surface layer will increase stratification and reduce the depth of winter mixing. The evolution of low O_2 zones will be linked to changes in fluvial runoffs (e.g. Milly et al., 2008; see also Section 5.3.4.3), the wind regime (e.g., Vecchi and Soden, 2007), as well as the intensity, duration, and seasonal timing of upwelling events (Snyder et al., 2003; see also Section 30.5.2). The potential contributions of destabilized methane hydrates and bacterial methane oxidation to exacerbate hypoxia and acidification at high latitudes remain to be explored (Westbrook et al., 2009). Currently, there is no consensus on the future volumes of hypoxic and suboxic waters because of large uncertainties in potential biogeochemical effects and in the evolution of tropical ocean dynamics due to both natural and anthropogenic causes (WGI AR5 Section 6.4.5). While volumes with O_2 concentrations <80 µmol kg^{-1} are projected to increase by several percent, suboxic waters <5 µmol O_2 kg^{-1} may undergo a 30% increase by 2100 compared to 2005 (*low confidence*; Bopp et al., 2013).

6.1.1.4. Light and Nutrients

Most models project that the mixed layer at the ocean surface (see Figure 6-2) will become shallower in the coming decades through a strengthening of the vertical density gradient (e.g., Sarmiento et al., 1998; Sallée et al., 2013). Mean light levels encountered by phytoplankton are set by incoming light from solar radiation, the depth of the mixed layer, and the degree to which underwater light is attenuated by living and non-living particles (Kirk, 1994). A shallower mixed layer will *likely* result in the resident phytoplankton receiving higher mean underwater light levels if the organisms are physically mixed through this stratum (Figure 6-2).

Enhanced, seasonally prolonged stratification (Holt et al., 2010), especially in the tropics, the North Atlantic, the Northeast Pacific, and the Arctic (Capotondi et al., 2012), will lead to decreased vertical transport of nutrients to surface waters (Doney, 2010; Figure 6-2). River plumes (Signorini et al., 1999), nutrient accumulation in the pycnocline as reported for North Pacific waters (Whitney, 2011), human-induced eutrophication, enhanced upwelling (Box CC-UP), and tidal mixing and estuarine circulation in coastal oceans could partly compensate for the projected reduction in nutrient supply in the oceans (*limited evidence*, *medium agreement*).

6.1.2. Historical and Paleo-Records

6.1.2.1. Historical Observations

Ocean ecosystems are variable in time and space, and in a non-steady-state, reflected in indices such as the North Atlantic Oscillation (NAO) Index, the Atlantic Multi-decadal Oscillation (AMO), the Arctic Climate Regime Index (ACRI), Pacific Decadal Oscillation (PDO), or the El Niño-Southern Oscillation (ENSO) (WGI AR5 Box 2.5; Figure 6-1; Section 30.5).

The combination of large, global data sets such as Reynolds, National Center for Atmospheric Research (NCAR), International Comprehensive Ocean-Atmosphere Data Set (ICOADS) with multi-decadal time series, for example, near Hawaii (HOT), Bermuda (BATS), the Ligurian Sea (DYFAMED), the Canaries (ESTOC), Kerguelen Island (KERFIX), Hokkaido Island (KNOT), and Taiwan (SEATS) has provided data on the physical and biogeochemical state of the oceans (Karl et al., 2003). These have been augmented by the limited-term, high-resolution programs World Ocean Circulation Experiment (WOCE) and Joint Global Ocean Flux Study (JGOFS).

Historical data sets provide baseline information on ecosystem states and document the responses of biota to both natural variability in the ocean system and surface ocean warming since the 1970s (Figure 6-3; Section 6.3.1). Such data sets are rare and regionally biased. Examples include changes in geographic ranges of plankton and seasonal timing (phenology) of different components of the ecosystem detected by the Continuous Plankton Recorder (CPR: e.g., Edwards et al., 2001; Richardson et al., 2006; Box 6-1) or multi-decadal shifts in pelagic ecosystems (CalCOFI) including higher parts of the food chain such as sardines and anchovies (Brinton and Townsend, 2003; Chavez et al., 2003; Lavaniegos and Ohman, 2003; see also Section 6.3.1) and the skeletal archives of long-lived organisms such as coralline algae (Halfar et al., 2011), bivalves (Schöne et al., 2003), and corals (De'ath et al., 2009).

Systematic, long-term interdisciplinary observations using repeated, highly calibrated measurements at a given field site are required to capture high- and low-frequency events, for example, regime shifts (abrupt changes between contrasting, persistent states of any complex system; deYoung et al., 2008). Direct observations are complemented by satellite remotely sensed data sets. Ocean color data (e.g., Coastal Zone Color Scanner (1978–1986), Sea-Viewing Wide Field-of-View Sensor (SeaWiFS, 1997–2010), and Moderate Resolution Imaging Spectroradiometer (MODIS-AQUA, 2002 to the present); McClain, 2009) provide estimates of chlorophyll concentrations (a proxy for phytoplankton stocks and net primary production (NPP); Sections 6.2.1, 6.3.4; Saba et al., 2011). Total chlorophyll cannot be measured from space; therefore, the near-surface value (approximately one optical depth) is extrapolated to whole water-column chlorophyll based on vertical distribution using region-specific algorithms. Large uncertainties persist, as these estimates reflect both phytoplankton stocks and their physiological status (Dierssen, 2010; Behrenfeld, 2011). The approximately 15-year archived time series of SeaWiFS is too short to reveal trends over time and their causes. It is an example for the general issue that undersampling of ocean phenomena in time and space limits our current ability to assess present states, to distinguish effects of anthropogenic change from natural variability, and to project future changes (Henson et al., 2010; Beaulieu et al., 2013; Box CC-PP).

6.1.2.2. Paleontological Records

Paleontological records in marine sediments provide long-term, low-resolution data on the spatial distributions of organisms and their abundances from all ages and latitudes. This information can be readily related to the concurrent shifts in multiple environmental properties that are also recorded in these sediments. The records provide insights into shifts, expansions, and contractions of biogeographic ranges; species extinctions and emergences; and changes in species abundance, as well as the environmental forcings to which organisms respond. Temporal trends reveal influences of temperature, hypoxia, CO_2, and food availability on organisms and ecosystems (Section 6.1.1; Figure 6-3).

Owing to insufficient resolution, the geological record often does not allow the direct attribution of a biological change to a single driver or the identification of various drivers and their relative importance. Support for projections of future changes in present-day ecosystems and their services is thus limited (*low confidence*; Sections 6.4, 6.5). Nonetheless, information gained from the geological record is invaluable, as both paleo and present climatic shifts share the same combination and sign of environmental changes: increasing atmospheric CO_2 causing warming and CO_2 enrichment in the surface ocean, leading to enhanced stratification of the upper ocean and a decrease in dissolved O_2 (WGI AR5 Chapter 3; Section 5.3). A combination of models (WGI AR5 Chapters 3, 6, 12) and geological data can be used to forecast future impacts on ocean biota (*medium confidence*).

The last glacial-interglacial transition is associated with an average increase in atmospheric CO_2 of approximately 1 µatm per century between 18 and 10 thousand years before present (kyr BP) (WGI AR5 Chapter 5), a significantly slower increase than the approximately 90 µatm in the last century (WGI AR5 Chapters 5, 6). Consequently, the average pH change of 0.002 pH units per century during the glacial-interglacial transition is small relative to the ongoing anthropogenic perturbation of >0.1 pH unit per century (WGI AR5 Section 3.8.2). Overall the upper glacial ocean was more O_2-rich than today's ocean (Jaccard and Galbraith, 2012) and between 0.7°C and 2.7°C colder, with strong regional differences of up to 10°C cooling in the North Atlantic and 2 to 6°C in the Southern Ocean (WGI AR5 Chapter 5, Table 5.2). During warming from the glacial into the interglacial marine plankton such as foraminifera, coccolithophores, diatoms, dinoflagellates, and radiolarians showed marked poleward range expansion (*high confidence*; see WGI AR5 Section 5.7; CLIMAP Project Members, 1976; MARGO Project Members, 2009). Under the lower glacial CO_2 concentrations, calcification in planktonic foraminifera was higher (*limited evidence*, *medium agreement*).

The most prominent abrupt climate change periods in the recent geological record, developing within 10 to 100 years, are associated with Dansgaard-Oeschger (DO) and Heinrich events (WGI AR5 Section 5.7), which occurred repetitively during the last 120 kyr. Whereas the atmospheric changes happened within a few decades, the sea surface temperature in the North Atlantic changed by up to 5°C within decades to centuries (WGI AR5 Section 5.7). Southern Ocean temperature changes were slower (hundreds to thousands of years; Barker et al., 2009). The cold phase of a DO event led to the migration of polar foraminiferal species toward the equator, in the North Atlantic as far south as the Iberian Peninsula (Martrat et al., 2004). Abrupt (approximately 100-year) abundance changes in the Southern Ocean were associated with latitudinal shifts in the Antarctic Circumpolar Current and associated species (Barker et al., 2009) akin to modern changes in plankton range due to warming (Box CC-MB, Box 6-1). During the DO warm phases the Monsoon-driven Arabian Sea upwelling records show enhanced primary

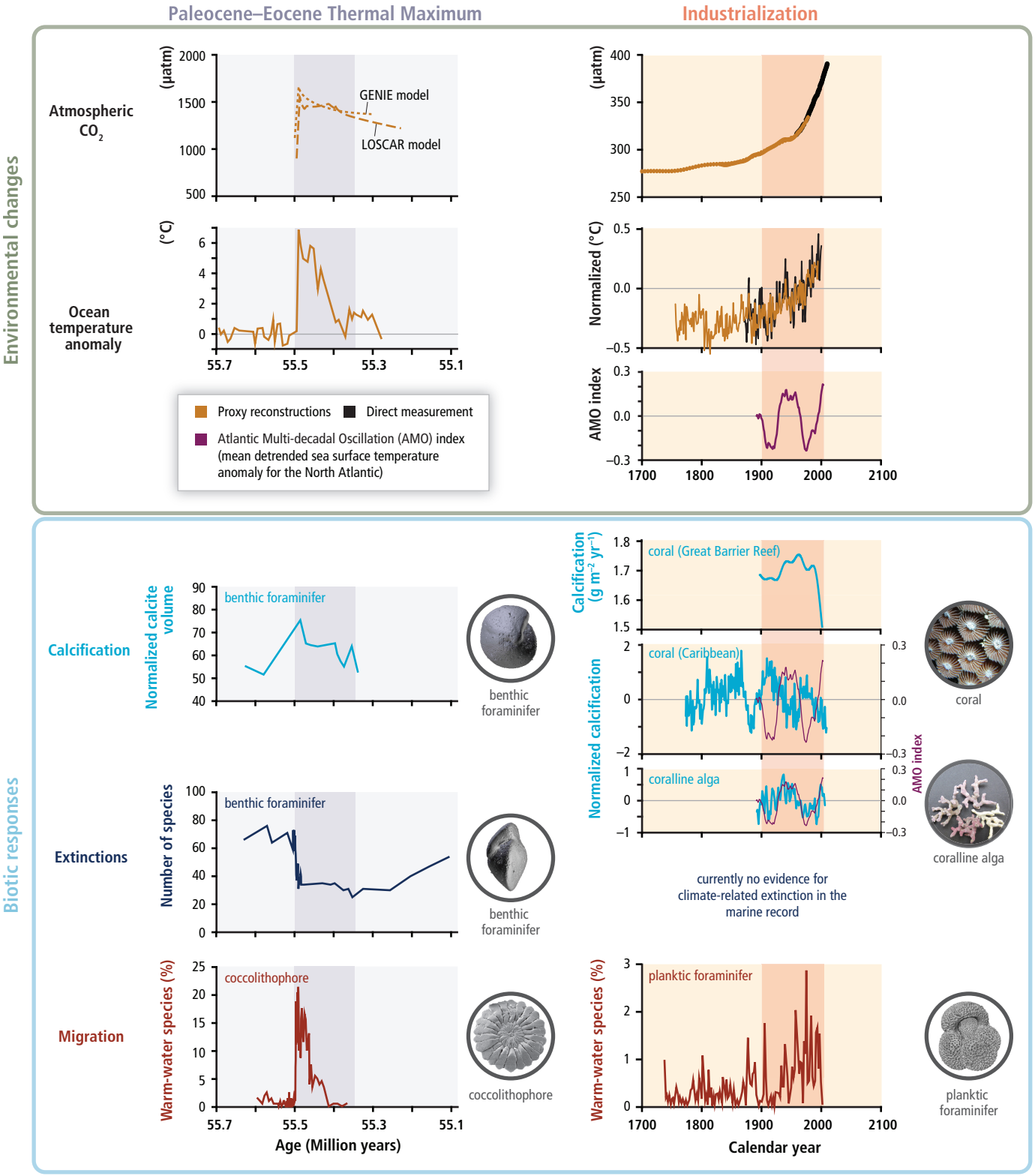


Figure 6-3 | Environmental changes (top) and associated biological responses (bottom) for the Paleocene–Eocene Thermal Maximum (PETM, left) and the industrial era (right). The PETM represents the best geological analog for the future ocean because of its rapid environmental change. Episodes of largest environmental change are indicated with darker bands. Note the different time scale between the two columns. Both time intervals are characterized by rapid warming both on land and in the ocean (modern: Wilson et al., 2006 and PETM: Kennett and Stott, 1991) and increases in CO_2 (modern: Etheridge et al. 1996; Keeling et al., 2005 and PETM: Zeebe et al., 2009 (LOSCAR model); Ridgwell and Schmidt, 2010 (Grid Enabled Integrated Earth System Model (GENIE model))). For the recent industrial era, the Atlantic Multi-decadal Oscillation (AMO; see Figure 6-1 and Section 6.1.2.1) is shown to highlight an example of high-frequency sea surface temperature fluctuations (Enfield et al., 2001) and their influence on marine biota. Note the species-specific calcification responses to climate change with decreases, increases, and high variability (coralline alga: Halfar et al., 2011; coral: Vásquez-Bedoya et al., 2012; De'ath et al., 2013; PETM: Foster et al., 2013). While there was extinction during the PETM (Thomas, 2003), there is currently no evidence for climate-related extinction in the marine record. Warming led to migration of warm-water species into previous cold-water habitats (modern: Field et al., 2006; PETM: Bralower, 2002). Pictures are examples of organisms highlighting the processes in each panel, and are not to scale.

and export production, reduced oxygenation, and denitrification, all within approximately 200 years (Higginson et al., 2004).

The last time the atmospheric CO_2 content approached that of today was during the Pliocene warm period (3.3 to 3.0 million years ago (Ma)), with long periods of atmospheric CO_2 levels between 330 and 400 µatm (Pagani et al., 2010; Seki et al., 2010) and equilibrated temperatures approximately 2°C warmer than today (*medium confidence*; Haywood et al., 2009; WGI AR5 Chapter 5). The Mid-Pliocene Warm Period saw a poleward expansion of tropical planktonic foraminifera (*high confidence*; Dowsett, 2007). Coccolithophores (Bown et al., 2004), corals (Jackson and Johnson, 2000), and mollusks (Vermeij and Petuch, 1986) remained unaffected with respect to rates of species extinction or emergences compared to background rates.

Perhaps the best analog for the future ocean is the Paleocene-Eocene Thermal Maximum (PETM, 55.3 Ma). The PETM was an event of warming (Dunkley Jones et al., 2013), and ocean acidification (Zachos et al., 2005) over millennia (Cui et al., 2011; Stassen et al., 2012) with increased runoff and nutrients into the shelf ecosystems. Model simulations for the PETM show 10 times lower rates of CO_2 input and hence ocean acidification compared to today (*medium confidence*; Ridgwell and Schmidt, 2010). Depending on the assumed rate and magnitude of the CO_2 release, models project pH declined by 0.25 to 0.45 units in PETM surface waters and a reduction in surface ocean aragonite saturation from $\Omega = 3$ to $\Omega = 2$ or even as low as 1.5 (Ridgwell and Schmidt, 2010). Warming caused range expansions of warm-water taxa toward higher latitudes (*high confidence*). The composition of plankton assemblages changed both within and between phytoplankton groups (Gibbs et al., 2006; Sluijs and Brinkhuis, 2009), possibly reflecting the warming trend and/or changes in nutrient availability (Sections 6.2.2-3). There was no bias in extinction toward more heavily calcifying species, possibly as slow CO_2 input led to minor surface water acidification. By contrast, benthic foraminifera, the dominant deep water eukaryote, recorded up to 50% extinction (Thomas, 2007). In contrast to sediment dwellers, more mobile pelagic crustaceans (ostracods) did not show any significant change in species composition (Webb et al., 2009). In shallow coastal waters, calcareous algae and corals were replaced by symbiont-bearing benthic foraminifera (*medium confidence*; Scheibner and Speijer, 2008).

The warm climates of the Mesozoic (251 to 65 Ma) led to a number of anoxic events in the oceans (Jenkyns, 2010). In some cases, OMZs expanded vertically, leading to anoxia in upper water layers (Pancost et al., 2004). Some of the Cretaceous oceanic anoxic events were associated with extinctions or increased species turnover (normalized sum of originations and extinctions) of planktonic foraminifera and radiolarians (30%). Such turnover was very small in other groups of organisms (e.g., a maximum of 7% of coccolithophores; Leckie et al., 2002). The attribution of these evolutionary changes to reduced O_2 is tenuous as warming, changes in nutrient supply, and possibly ocean acidification occurred concomitantly (Hönisch et al., 2012).

Global-scale collapse of marine ecosystems is rare, even in the geological record. Some mass extinctions, in particular the Permian Period extinction 251 Ma, have been associated with large-scale inputs of carbon into the atmosphere and ocean, with associated warming and deep-sea O_2 decline (Knoll et al., 2007; Kiessling and Simpson, 2011). The end-Permian mass extinction preferentially affected reef organisms such as corals and sponges resulting in a 4 Myr period without reef builders (Kiessling and Simpson, 2011), and underscores that vulnerabilities differ among organisms depending on anatomy, physiology, and ecology (Knoll and Fischer, 2011). The rates of environmental change and any potential acidification have not yet been accurately constrained for these events.

Of the last 100 Myr, only the last 2 Myr had CO_2 levels of approximately 190 to 280 ppm, comparable to preindustrial values. Values like those predicted for the mid and end of this century can solely be found in the geological record older than 33 Ma, with large uncertainties in the absolute numbers (WGI AR5 Section 5.3; Hönisch et al., 2012). That marine biota thrived throughout high CO_2 times cannot imply that marine organisms will remain unaffected in a future warm, high-CO_2 world. The key environmental issue of the 21st century is one of an unprecedented rate of change, not simply magnitude, of CO_2 levels (Hönisch et al., 2012). The current rate and magnitude of ocean acidification are at least 10 times faster than any event within the last 65 Ma (*high confidence*; Ridgwell and Schmidt, 2010) or even 300 Ma of Earth history (*medium confidence*; Hönisch et al., 2012). The slower events in geological history provide *robust evidence* (*high agreement*) for environmentally mediated changes in biogeographic ranges of fauna and flora, their compositional changes, extinctions, and, to much lesser degree, emergences (*very high confidence*). No past climate change event perfectly parallels future projections of anthropogenic climate change, which is unprecedented in evolutionary history. Existing similarities indicate, however, that future challenges (Sections 6.1.1, 6.3.1-8) may be outside the adaptive capacity of many organisms living in today's oceans (*low* to *medium confidence*).

6.2. Diversity of Ocean Ecosystems and Their Sensitivities to Climate Change

Global-scale observation and modeling studies provide *robust evidence* of present and future climate-mediated alterations of the ocean environment (*high agreement*; Section 6.1.1; WGI AR5 Chapters 3, 6; Bopp et al., 2013), which in turn impact ocean ecosystems (*high confidence*; Boyd and Doney, 2002; Drinkwater et al., 2010; Hoegh-Guldberg and Bruno, 2010). An assessment of present findings and projections requires knowledge of the characteristics of ocean biota and ecosystems and their climate sensitivity.

Life on Earth is diverse as a result of nearly 4 billion years of evolutionary history. Marine microorganisms are the oldest forms of life and the most functionally diverse; multicellular organisms are constrained to limited functional abilities. Knowledge of overarching similarities across the organism domains Archaea, Bacteria, and Eukarya (Woese et al., 1990) or kingdoms Bacteria, Protozoa, Fungi, Plantae, Animalia, and Chromista (Cavalier-Smith, 2004) would facilitate projections of climate impacts. The phylogenetic and metabolic diversity of microbes (i.e., viruses, archaea, bacteria, protists, and microalgae) sustains key ecosystem processes such as primary production, CO_2 fixation and O_2 production, the conversion of nitrogen into ammonia (N_2 fixation), and the use of nitrate, sulfate, CO_2, and metals (iron and manganese) in metabolism instead of O_2 when it is absent. Microbes enhance the horizontal

transfer of genetic information between unrelated individuals, thereby enhancing biodiversity (McDaniel et al., 2010). Microbes may respond to climate change by exploiting their large diversity, undergoing species replacements (Karl et al., 2001), and thereby sustain their biogeochemical roles. Species replacements also occur among plants and animals, but in most cases research has focused on their resilience, well-being, abundance, survival, and conservation under climate change (FAQ 6.2).

6.2.1. Pelagic Biomes and Ecosystems

Pelagic organisms are key to biogeochemical processes in the ocean. The base of the marine food web is the photosynthetic fixation of CO_2 by phytoplankton, a process termed (net) primary production (NPP; Box CC-PP). Photosynthesis is controlled by light, temperature, inorganic nutrients (CO_2, nitrate, phosphate, silicate, and trace elements including iron), and the density-dependent stability of the surface mixed-layer depth (MLD) (Section 6.1.1; Figure 6-2; Sverdrup, 1953; González-Taboada and Anadón, 2012). Environmental variability and the displacement of organisms by ocean currents cause variability in phytoplankton productivity, competitiveness, and natural selection (Margalef, 1978) and result in changes in carbon sequestration (Box CC-PP; Figure 6-4). Nutrient limitation leads to a decrease in NPP or chlorophyll levels and a reduction in the amount of energy supplied to higher trophic levels, including fish and invertebrates (*high confidence*; Ware and Thomson, 2005; Brander, 2007), affecting fishery yields (Cheung et al., 2008; Friedland et al., 2012). The wide range of trophic structures in marine food webs and the potentially nonlinear changes in energy transfer under different NPP and temperature scenarios (Stock and Dunne, 2010) hamper accurate projections of changes in higher trophic levels.

6.2.2. Benthic Habitats and Ecosystems

The ocean's primary production is inextricably linked with benthic (sea floor) communities via the biological pump (Figure 6-4), the chemical exchange of nutrients and gases, and the existence of organisms with both pelagic and benthic life history stages. Even in abyssal habitats, a continuous rain of organic detritus serves as the primary source of carbon and energy. Therefore climate impacts on surface marine ecosystems will impact even the deepest benthic communities, even if direct changes to their physical habitat do not occur (Smith et al., 2009).

Benthic organisms living in shallow waters or the intertidal zone (where they encounter temporary exposure to air) are exposed to widely fluctuating and progressively changing means and extremes of environmental variables, such as temperature, oxygen, CO_2, salinity, and sea level (WGI AR5 Chapters 3, 13; Sections 6.3.1-3, 6.3.5). Plants and sessile or slow moving animals may be unable to escape from unfavorable changes except by means of advection of fertilized eggs or planktonic larvae. If climate change harms those species engineering benthic habitats, the entire ecosystem may be impacted. This concerns those ecosystem engineers, which form habitat from the structures they produce (e.g., corals forming skeletons; Section 6.3.1) and those forming habitat through their behavior (e.g., worms reworking and irrigating sediment in a process termed bioturbation). Effects on both types of ecosystem engineers (Sections 6.3.1-8) influence the regeneration of nutrients and affect benthic-pelagic coupling.

6.3. Climate Change Impacts from Organism to Ecosystem

Understanding climate-induced alterations in the functioning of individual organisms, species populations, communities (assemblages of various species), and ecosystems builds on studies in the laboratory, in micro- and mesocosms (closed small- to medium-sized experimental systems approximating natural conditions, holding selected biological communities), and of biota or communities in the field as well as modeling. These data inform us which taxonomic groups in what regions are more susceptible to climate change (Boyd et al., 2011). Empirical studies of marine organism and ecosystem sensitivities have begun identifying the mechanisms and processes linking climate to ecosystem changes (Drinkwater et al., 2010; Ottersen et al., 2010). Changes in ecological community composition, species interactions, and food web dynamics often build on organismal effects elicited by climate forcing (e.g., Section 6.3.1.5; Boyd et al., 2010; Ottersen et al., 2010). The underlying mechanisms respond to climate-related factors in a hierarchy from organism (highest), tissue, cell to molecular (lowest)

Table 6-1 | To assess how a changing climate will alter the ocean's biological pump (Figure 6-4) and determine the resulting biogeochemical feedbacks on global climate, changes in a wide range of processes from cells to ocean basins, and from epipelagic to mesopelagic, must be quantified. This table illustrates the complexity of the integrated knowledge platform needed to provide evidence of these biogeochemical ramifications and thus the present limits to clear conclusions about climate-induced effects on the biological pump (NPP = net primary production; C = carbon; TEP = transparent exopolymer particle; DOM = dissolved organic matter; POM = particulate organic matter).

Alteration of physiological rates	Biogeographical changes/ community shifts	Altered foodweb structure: trophodynamics	Changes to particle dynamics	Biogeochemical changes/ climatic feedbacks
• NPP (Bopp et al., 2002, 2013) • Particle solubilization through bacterial ectoenzymes (Christian and Karl, 1995) • TEP production (Engel et al., 2004) • Microzooplankton grazing rates (Rose et al., 2009)	• Microbial community structure (Giovannoni and Vergin, 2012) • Phytoplankton community structure, e.g., biomes (Boyd and Doney, 2002) • Alteration of zooplankton biomes (Beaugrand et al., 2009) • Faunistic shifts at depth (Jackson and Burd, 2001)	• Altered prey-predator linkages (Lewandowska and Sommer, 2010)	• Faecal pellet geometry (Wilson et al., 2008) • C partitioning between DOM vs. POM, e.g., TEP (Riebesell et al., 2007) • Sinking rates/seawater viscosity (Lam and Bishop, 2008) • Ballasting, e.g., calcite versus opal (Klaas and Archer, 2002)	• Particle flux/C sequestration (Bopp et al., 2002) • Shifts in elemental stoichiometry of planktonic communities (Karl et al., 2003) • Remineralization rate; $[O_2]$, hypoxia; nutrient resupply (Gruber, 2011) • Activity of the microbial loop; vertical carbon export (Grossart et al., 2006; Piontek et al., 2010)

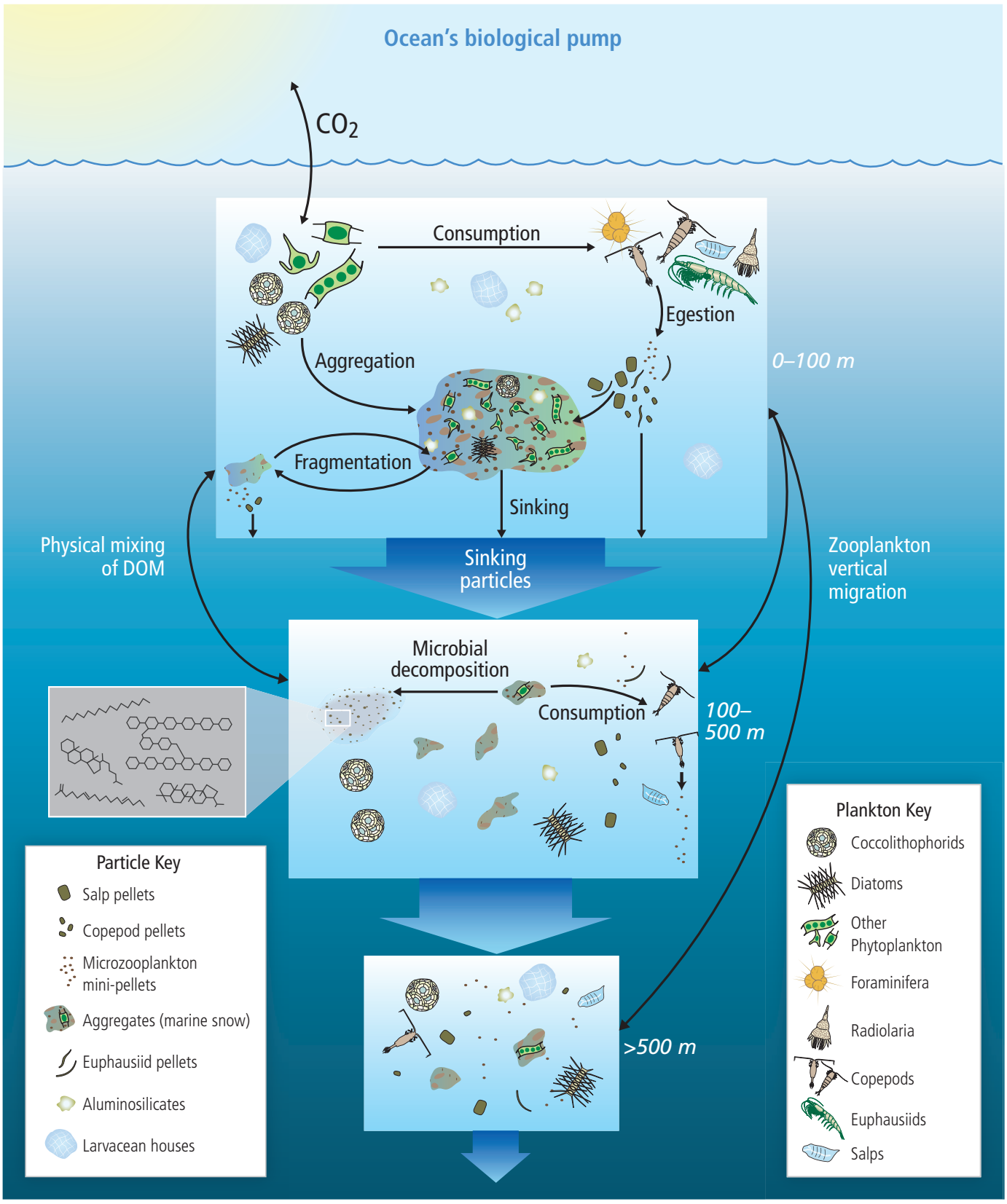


Figure 6-4 | A schematic representation of the ocean's biological pump, which will be influenced by climate change and is a conduit for carbon sequestration. It is difficult to project how the pump might be altered and whether it would represent a positive or negative feedback to climate change through the cumulative effects of affected processes, surface to depth (Table 6-1): shifts in net primary production, floristic and faunistic community composition in the pelagic realm, and in grazing rates; alterations to the ballasting of settling particles and the proportion of net primary production released as dissolved organic matter; modified bacterial enzymatic rates and particle solubilization; faunistic shifts at depth. Note that the relative sizes of the organisms, particles, and particle building blocks are not presented to scale (modified from Buesseler et al. (2008) by J. Cook / WHOI).

Frequently Asked Questions

FAQ 6.2 | What is different about the effects of climate change on the oceans compared to the land, and can we predict the consequences?

The ocean environment is unique in many ways. It offers large-scale aquatic habitats, diverse bottom topography, and a rich diversity of species and ecosystems in water in various climate zones that are found nowhere else.

One of the major differences in terms of the effect of climate change on the oceans compared to land is ocean acidification. Anthropogenic CO_2 enters the ocean and chemical reactions turn some of it to carbonic acid, which acidifies the water. This mirrors what is also happening inside organisms once they take up the additional CO_2. Marine species that are dependent on calcium carbonate ($CaCO_3$), such as shellfish, seastars, and corals, may find it difficult to build their shells and skeletons under ocean acidification. In general, animals living and breathing in water like fish, squid, and mussels have between five and 20 times less CO_2 in their blood than terrestrial animals, so CO_2-enriched water will affect them in different and potentially more dramatic ways than species that breathe in air.

Consider also the unique impacts of climate change on ocean dynamics. The ocean has layers of warmer and colder water, saltier or less saline water, and hence less or more dense water. Warming of the ocean and the addition of more freshwater at the surface through ice melt and higher precipitation increases the formation of more stable layers stratified by density, which leads to less mixing of the deeper, denser, and colder nutrient-rich layers with the less dense nutrient-limited layers near the surface. With less mixing, respiration by organisms in the mid-water layers of stratified oceans will produce oxygen-poor waters, so-called oxygen minimum zones (OMZs). Large, more active fish can't live in these oxygen poor waters, while more simple specialized organisms with a lower need for oxygen will remain, and even thrive in the absence of predation from larger species. Therefore, the community of species living in hypoxic areas will shift.

State-of-the-art ecosystem models build on empirical observations of past climate changes and enable development of estimates of how ocean life may react in the future. One such projection is a large shift in the distribution of commercially important fish species to higher latitudes and reduced harvesting potential in their original areas. But producing detailed projections, for example, what species and how far they will shift, is challenging because of the number and complexity of interactive feedbacks that are involved. At the moment, the uncertainties in modeling and complexities of the ocean system even prevent any quantification of how much of the present changes in the oceans are being caused by anthropogenic climate change or natural climate variability, and how much by other human activities such as fishing, pollution, etc.

It is known, however, that the resilience of marine ecosystems to adjust to climate change impacts is *likely* to be reduced by both the range of factors and their rate of change. The current rate of environmental change is much faster than most climate changes in the Earth's history, so predictions from longer term geological records may not be applicable if the changes occur within a few generations of a species. A species that had more time to adapt in the past may simply not have time to adapt under future climate change.

levels of biological organization (Pörtner, 2002a; Pörtner and Knust, 2007; Raven et al., 2012). Such knowledge aids the interpretation and attribution to climate change of observed effects and is a major asset for projections of future impacts.

The genetic and physiological underpinning of climate sensitivity of organisms sets the boundaries for ecosystem response and provides crucial information on sensitivities, resilience, and the direction and scope of future change. As anthropogenic climate change accelerates, a key issue is whether and how quickly organisms can compensate for effects of individual or multiple drivers, by short-term acclimatization or long-term evolutionary adaptation across generations. Evolutionary adaptation depends on the genetic variation within a population, from which the environment selects the fittest genotypes (Rando and Verstrepen, 2007; Reusch and Wood, 2007). Genetic variation depends on mutation rates, generation time, and population size (Bowler et al., 2010). However, epigenetic mechanisms, such as modifications of the genome by DNA methylation, can also influence fitness and adaptation (Richards, 2006) and can be remarkably rapid as seen in terrestrial ecosystems (Bossdorf et al., 2008). In plants and animals the rate of evolutionary adaptation is constrained by long generation times, but enhanced by high phenotypic variability and high mortality rates among early life stages as a selection pool (e.g., Sunday et al., 2011). The limits to acclimatization or adaptation capacity are presently unknown.

However, mass extinctions occurring during much slower rates of climate change in Earth history (Section 6.1.2) suggest that evolutionary rates in some organisms may not be fast enough to cope.

Comprehensive understanding of climate change effects on ecosystems requires addressing the effects of individual drivers across organism taxa (Sections 6.3.1-4), the integrated action of multiple drivers (Section 6.3.5), the consequences for food webs (Section 6.3.6), and the specific effects on animals breathing in air (Section 6.3.7) and operating at the highest trophic levels.

6.3.1. Temperature Effects

The effects of temperature on ecosystems largely result from organismal responses. This requires that information on organisms' thermal sensitivities, limits, and functional properties is used to assess how temperature changes have affected and will continue to affect species distributions, abundances, diversity, trophic interactions, community assemblages, risks of species extinctions, and ecosystem functioning. Organisms also respond to temperature-driven changes in the physical environment such as stratification, reduced sea ice cover, and freshening. Ambient temperature interacts with other drivers such as ocean acidification and hypoxia (Section 6.3.5). Ambient temperature plays a more limited role for marine mammals and seabirds (Section 6.3.7).

6.3.1.1. Principles

All organisms including marine ones have limited temperature ranges within which they live and function. Organismal performance is related to temperature by curves called thermal reaction norms (Figure 6-5), which *likely* apply across all organisms (Chevin et al., 2010), from viruses (Knies et al., 2006), bacteria (Ratkowsky et al., 1983), and phytoplankton (Eppley, 1972; Thomas et al., 2012) to macroalgae and plants (Bolton and Lüning, 1982; Müller et al., 2009; Vitasse et al., 2010) and animals (Huey and Kingsolver, 1989; Angilletta, 2009). Heat tolerance thresholds differ greatly between organisms and are hypothesized to be lowered by rising organizational complexity and body size (Pörtner, 2002a,b). Maximum heat limits of animals and plants are close to the maximum

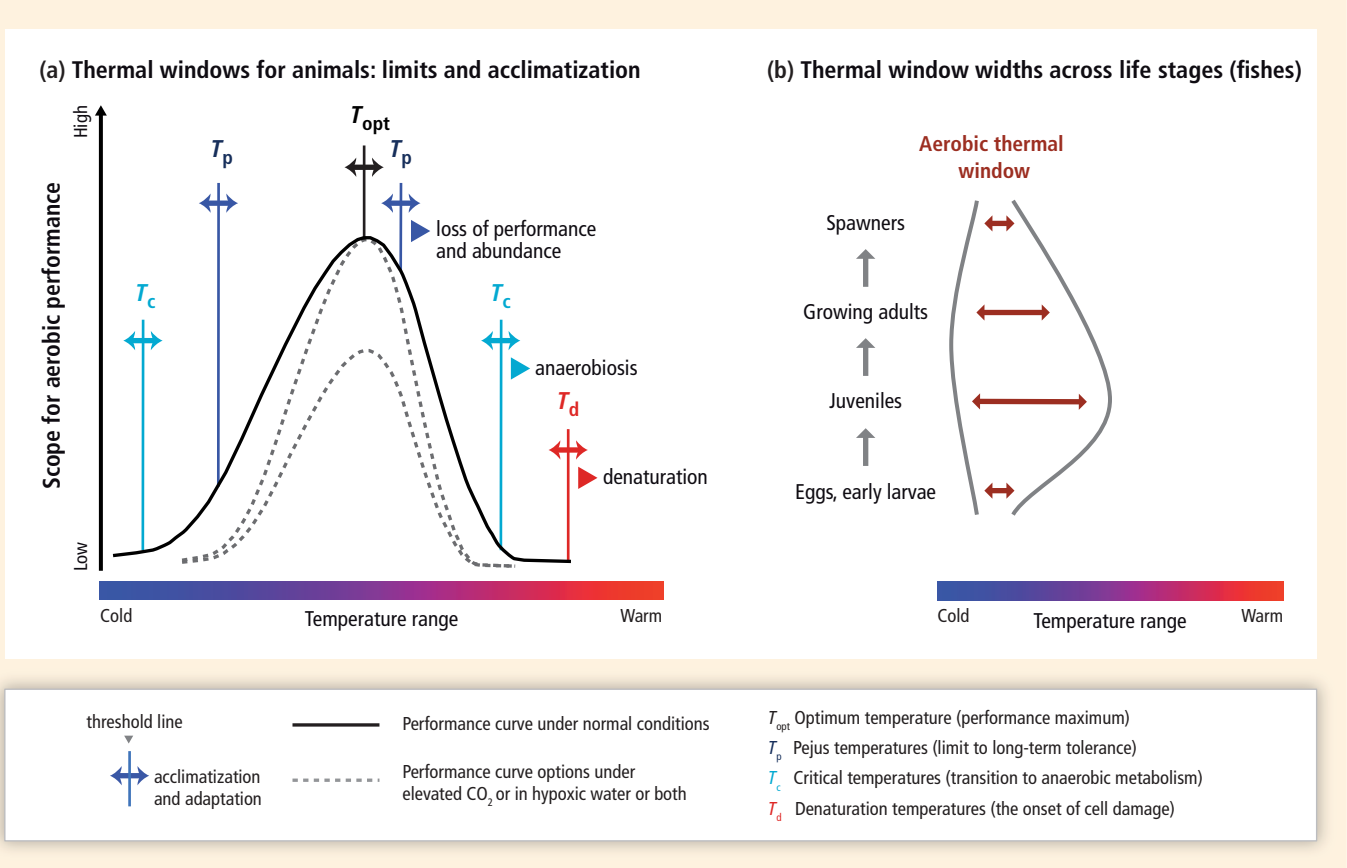


Figure 6-5 | Thermal specialization of an organism explains the why, how, when, and where of climate sensitivity. (a) The thermal tolerance range and performance levels of an organism are described by its performance curve (exemplified for an animal). Each performance (e.g., exercise, growth, reproduction) is maximal at its optimum temperature (T_{opt}), and becomes progressively constrained during cooling or warming. Surpassing the first low- and high-temperature thresholds (T_p; p, pejus: getting worse) means going into time-limited tolerance. Once further cooling or warming surpasses the next low or high thresholds (T_c; c, critical), oxygen availability becomes insufficient and an anaerobic metabolism begins. Denaturation temperatures (T_d) are even more extreme and characterized by the onset of damage to cells and proteins. Horizontal arrows indicate that T_p, T_c, and T_d thresholds of an individual can shift, within limits, between summer and winter (seasonal acclimatization) or when the species adapts to a cooler or warmer climate over generations (evolutionary adaptation). Under elevated CO_2 levels (ocean acidification) and in hypoxic waters performance levels can decrease and thermal windows narrow (dashed gray curves). (b) The width of the thermal range (horizontal arrows) also changes over time when an individual develops from egg to larva to adult and gains weight and size. Blue to red color gradients illustrate the range between cold and warm temperatures (after Pörtner, 2002a, 2012; Pörtner and Farrell, 2008).

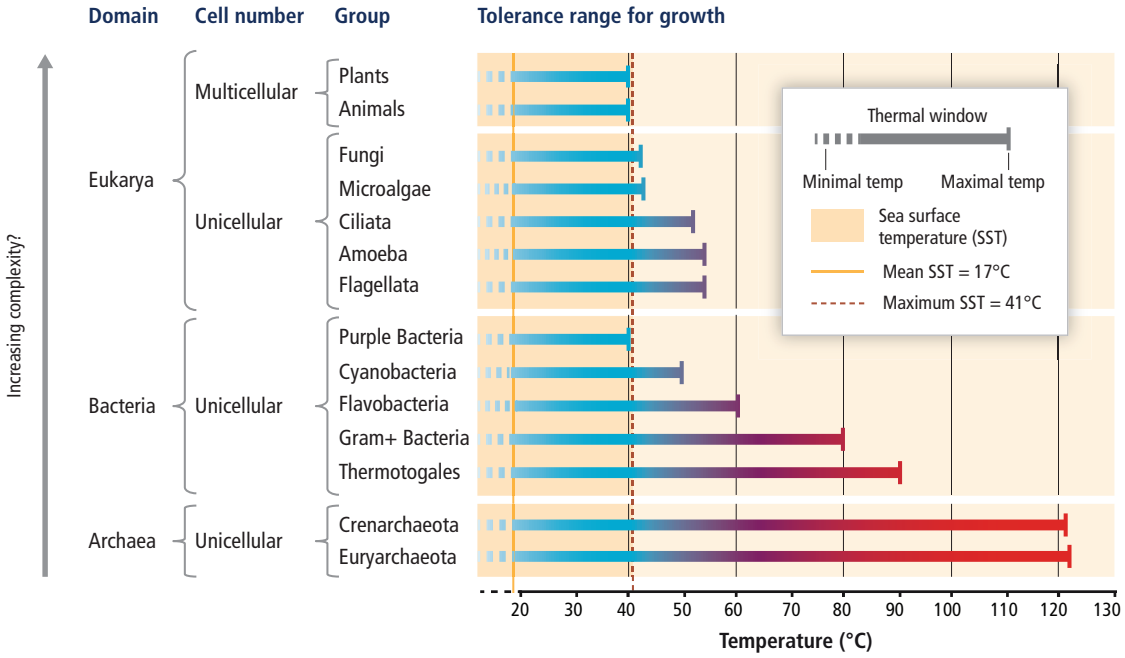


Figure 6-6 | Maximal values of temperature covered by various domains and groups of free-living marine organisms (bacteria to animals; domains and groups modified after Woese et al., 1990). High organizational complexity is hypothesized to be associated with decreasing tolerance to heat and to enable an increase in body size which in turn, decreases heat tolerance further (Sorokin and Kraus, 1962; Chevaldonné et al., 2000; Alker et al., 2001; Baumgartner et al., 2002; Pörtner, 2002a,b; Campbell et al., 2006; De Jonckheere et al., 2009, 2011). In the domain Bacteria, the Thermotogales are less complex and most tolerant to high temperatures (Huber et al., 1986; Tenreiro et al., 1997; Takai et al., 1999; Ventura et al., 2000; Abed et al., 2002). The highest temperature at which growth can occur is 122°C for hydrothermal vent archaea, seen under elevated hydrostatic pressure in laboratory experiments (Kashefi and Lovley, 2003; Takai et al., 2008).

temperature found in the warmest oceans (Figure 6-6). Knowledge of reaction norms, thermal limits, and underlying mechanisms is most advanced in animals (Pörtner et al., 2012; see also Section 6.3.1.4). Their role in underpinning biogeography has not been explored systematically in other organisms (e.g., Green et al., 2008), reducing the confidence level in assessments of thermal impacts. In animals, changes in physiological performances influence growth, body size, behavior, immune defense, feeding, reproductive success, biogeography, phenology, and therefore ecosystem structure and functioning. Shape and width of the curves can shift through acclimatization and evolutionary adaptation (Figure 6-5a) and during life history (Figure 6-5b), with implications for the distribution boundaries of species or populations (Section 6.3.1.5).

For any species, tracking the climate-induced displacement of tolerated ambient temperatures by undergoing shifts in biogeographical ranges to, e.g., higher latitudes during warming (Section 6.3.1.5; Figure 6-7) can be understood as a simple mode of adaptation, implemented through dispersal (e.g., of pelagic life stages), active movements (e.g., of migrating adult fishes), or passive displacement (e.g., of early life stages or plankton with drifting water masses). Conversely, fully completed acclimatization or evolutionary adaptation (Figure 6-5) would involve shifting thermal tolerance ranges and allow species to resist the temperature trend (e.g., warming) and to sustain fitness in their previous habitat.

6.3.1.2. Microbes

Temperature effects on growth, abundance, distribution, phenology, and community structure of highly diverse microbes have large implications for ecosystem functioning (Section 6.3; Box CC-PP). A warming ocean may initially enhance the metabolic rates of microbes (Banse, 1991) and stimulate their overall growth (Bissinger et al., 2008). Data from the Continuous Plankton Recorder (Section 6.1.2) in the Northeast Atlantic confirm that warming from 1960 to 1995 enhanced phytoplankton growth (Edwards et al., 2001). Eventually, with warming, the thermal tolerance of some groups will be challenged (Chevin et al., 2010), leading to the replacement of species. This is reflected in increasing fractions of smaller phytoplankton in warmer relative to colder waters (Morán et al., 2010; Flombaum et al., 2013).

In response to transient warming, phytoplankton distribution in the North Atlantic shifted poleward by hundreds of kilometers per decade since the 1950s. Phenology of plankton in the North Atlantic was also affected, with differences in sensitivity between groups (*high confidence*; Section 6.3.1.5; Box 6-1). Coccolithophore blooms (*Emiliania huxleyi*) in the Bering Sea were reported for the first time during the period 1997–2000, probably in response to a 4°C warming, combined with a shallower mixed layer depth, higher light levels and low zooplankton grazing (Merico et al., 2004). Loss of multi-year Arctic sea ice has had a profound effect on the diversity, structure, and function of the epipelagic microbial assemblage (i.e., found in the layer into which enough light penetrates for photosynthesis) (Comeau et al., 2011), and further warming is likely to have even greater impacts on the food web and on ecosystem services (*medium confidence*). Warming may also have caused the southward range extension of coccolithophores in the Southern Ocean in the 2000s (Cubillos et al., 2007). However, further experimental and field observations (Giovannoni and Vergin, 2012) are required to validate model projections (Taucher

and Oschlies, 2011) of differential responses to warming by different microorganisms.

6.3.1.3. Macroalgae and Seagrasses

Macrophytes in coastal waters (Chapter 5) cover 0.6% of the world's marine areas and supply about 2 to 5% of total oceanic production (Smith, 1981; Charpy-Roubaud and Sournia, 1990; Field et al., 1998). They have limited temperature ranges and are sensitive to temperature extremes (*high confidence*), resulting in changes of photosynthesis, growth, reproduction, and survival (following the principles of Figures 6-5, 6-6; and Harley et al., 2012), with consequences for their abundance, distribution, and productivity. Ice retreat in polar areas leads to an expansion of macroalgal distribution, for example, in the Antarctic (Quartino et al., 2013).

Warm- versus cold-water-adapted species may have different sensitivities to warming and show a range of responses in distribution shifts (Lima et al., 2007). Temperate macroalgae with wide windows of thermal tolerance acclimatize by shifting these windows following seasonal temperature changes (Kübler and Davison, 1995). Antarctic and tropical macroalgae are exposed to permanently low or high temperatures, respectively, and have consequently specialized in a limited temperature range, paralleled by a low acclimatization potential (Pakker et al., 1995; Eggert et al., 2006; Gómez et al., 2011). Thus, Antarctic and tropical macroalgae appear to be most vulnerable to warming (*high confidence*; Short and Neckles, 1999). While observations in the tropics indicate that seagrasses tolerate higher temperatures than seaweeds (Campbell et al., 2006), an increase in maximum temperature by >1°C from 1988–1999 to 2002–2006 (Section 30.5.3.1.5) led to increased seagrass shoot mortality in the Mediterranean Sea (Marbà and Duarte, 2010). The molecular basis of acclimatization and evolutionary adaptation, as well as their limitation in relation to the climate regime, require further study in the macrophytes.

6.3.1.4. Animals

The mechanisms shaping the thermal performance curve and, thereby, an animal's thermal niche have been explained by the concept of "oxygen and capacity limited thermal tolerance" (OCLTT), applicable to marine invertebrates and fishes (Pörtner et al., 2010; see also Figure 6-5a, FAQ 6.2). The temperature range at which animals can function best results from optimal oxygen supply at minimal oxygen usage. At temperature extremes, oxygen supply capacity becomes constrained in relation to demand, and metabolism becomes thermally limited. Beyond upper and lower temperature thresholds (T_p, Figure 6-5a), growth, reproduction, and other key functions decrease. These thresholds change during the individual life cycle, and with body size. At large body size, limitations in oxygen supply are exacerbated and heat tolerance limits shift to lower temperatures.

Surpassing species-specific heat tolerance limits (Figure 6-5, T_p) during warming causes a reduction of abundance (Pörtner and Knust, 2007; Katsikatsou et al., 2012), coral losses (Donner et al., 2005), shifts in the seasonal timing of (zooplankton) biomass formation (Mackas et al., 1998; Schlüter et al., 2010), and changes in growth (Lloret and Rätz, 2000; Brunel and Dickey-Collas, 2010). During early life, owing to incomplete development, or as adult spawners, owing to large body size, animals may become more sensitive to warming because of narrower thermal windows (Pörtner et al., 2008). This may cause high vulnerability of winter-spawning Atlantic cod to warming winter to spring temperatures (Table 6-2). In contrast, adult bigeye, bluefin, and skipjack tuna spawn at high temperatures. They need to prevent overheating by moving to cooler (deeper) waters (Lehodey et al., 2011).

Although temperature means are still most commonly used when attributing responses of marine organisms to climate effects, temperature extremes rather than means are most often mediators of effects (e.g., Easterling et al., 2000; Wethey et al., 2011; Wernberg et al., 2013; Figure 6-5). During heat exposure near the borders of the distribution range (including the high intertidal or warming surface waters), reductions in growth, activity, and abundance accompany even small (<0.5°C) shifts in ambient temperature extremes (e.g., Takasuka and Aoki, 2006; Pörtner and Knust, 2007; Nilsson et al., 2009; Neuheimer et al., 2011). Local extinction events follow as a result of mortality or behavioral avoidance of unfavorable thermal environments (Breau et al., 2011). Shifted species distribution ranges follow temperature clines from high to low, usually along latitudes, a lateral gradient at basin scale (Perry et al., 2005; Poloczanska et al., 2013), or a vertical temperature gradient to deeper waters (*high confidence*; Dulvy et al., 2008; Section 6.5.3; see also Figure 6-5b, Box CC-MB).

Adopting OCLTT principles has enabled modeling studies to project climate effects (Section 6.5), and paleo-studies to explain climate-induced mass extinction events and evolutionary patterns in Earth history (Pörtner et al., 2005; Knoll et al., 2007). For example, long-term observations show that warming affects the body size of marine fishes (*medium confidence*). Assessing effects of warming on body size may be complicated by effects on the animal's energy budget, the changing availability and body size of prey species, community structure, species interactions, or effects of fishing (Genner et al., 2010; Cheung et al., 2013a). Below the thermal optimum, warming causes growth and weight-at-age of some juvenile or younger fish populations to increase (e.g., Brunel and Dickey-Collas, 2010; Neuheimer and Grønkjær, 2012). However, OCLTT predicts that small individuals are more heat tolerant than large ones, in line with observations of falling animal body sizes in warming oceans (Box 6-1; e.g., Daufresne et al., 2009). This trend is projected to continue into the 21st century (*medium* to *high confidence*; Cheung et al., 2013a).

Thermal windows of fishes and invertebrates roughly match ambient temperature variability (Figure 6-1) according to climate regime and seasonality (Pörtner and Peck, 2010; Sunday et al., 2012). Sub-Arctic, small, or highly mobile species are eurytherms. They function across a wide temperature range, that is, they have wide thermal windows and distribution ranges, at the expense of higher energetic costs and associated lifestyles (Pörtner, 2002a, 2006). Conversely, high polar species are stenotherms, that is, they have narrow thermal windows and low energy demand lifestyles, making them sensitive to temperature change. In a warming world, polar stenotherms will be marginalized, with no possibility to escape to colder regions (*high confidence*). However, extinction of polar species has not yet been reported. As marine fishes and invertebrates in the Southern Hemisphere are

Table 6-2 | Selected examples of species responses and underlying mechanisms to changing temperature, oxygen level and ocean acidification (OA). References are indicated by superscript numbers and in the footnote.

	Phenomenon	Key drivers	Mechanism/Sensitivity
Biogeography	Northward shift in the distribution of North Sea cod (*Gadus morhua*) stocks between 1977 and 2001. [1,2]	Temperature	Bottlenecks of high sensitivity during early life stages as well as adult spawning stage in winter/early spring.
	Shift from sardines (*Sardinops melanostictus*) to anchovies (*Engraulis japonicus*) in the western North Pacific observed between 1993 and 2003. [3,4]	Temperature	Thermal windows of growth and reproductive output are found at higher temperatures for anchovies than sardines, food preferences of the competing species being similar.
	Variable sensitivity of Pacific tuna species to the availability of dissolved O_2. Bigeye tuna routinely reach depths where ambient O_2 content is below 1.5 ml L^{-1} (≈ 60 µmoles kg^{-1}). [5, 6]	Oxygen	Oxygen transport via hemoglobin is adapted to be highly efficient supporting high metabolic rates as needed during feeding in the OMZ.
	Northward movement of species and the conversion of polar into more temperate and temperate into more subtropical system characteristics in the European Large Marine Ecosystems between 1958–2005. [7, 8]	Warming and current advection	Effects are attributed to climate change but may be influenced by nutrient enrichment and overfishing.
Abundance	Increase in abundance of arctic boreal plankton species, notably the copepods *Calanus hyperboreus*, *Calanus glacialis* and the dinoflagellate *Ceratium arcticum* between 1960 and 2000 in the Newfoundland Shelf, Northwest Atlantic. [9,10]	Temperature	Temperature sensitivity of phyto- and zooplankter resulting from cooling due to increased influx of Arctic water.
	A benthic fish species, the eelpout (*Zoarces viviparus*) at its southern distribution limit, the German Wadden Sea, displayed abundance losses during warming periods and rising summer extreme temperatures between 1993 and 2005, with early disappearance of the largest individuals. [11]	Temperature	Temperature extremes exceed organism's thermal windows, with largest individuals being relatively less tolerant to high temperature than smaller individuals.
	Variable sensitivities to OA within and across animal phyla (Figure 6-10b). [12–21]	Anthropogenic OA, sea water acidification by elevated pCO_2 in OMZs, upwelling areas, involving anthropogenic ocean acidification.	Lowered extracellular (blood plasma) pH causing a lowering of the rates of ion exchange and metabolism in muscle or liver (hepatocytes) of vertebrates and invertebrates. High sensitivity at reduced energy turnover in tissues and/or whole organism by reduced ion exchange, use of more energy efficient transport mechanisms, reduced protein synthesis, enhanced nitrogen release from amino acid catabolism and protein degradation, slower growth.
Phenology	Migration time of pink salmon (*Oncorhynchus gorbuscha*) in Alaska is almost two weeks earlier in 2010s relative to 40 years ago. [22]	Warming	Rapid microevolution for earlier migration timing.
	In the waters around the UK, during a period of warming between 1976 and 2005, the seasonal timing of biological events of all major marine taxonomic groups (plant/phytoplankton, invertebrate and vertebrates) advanced, on average, by 0.31 to 0.43 days $year^{-1}$. [23]	Warming	Sensitivity to seasonal temperature changes as a result of specific thermal windows of different organisms.
Body size and growth	Asymptotic body sizes of different populations of Atlantic cod (*Gadus morhua*) and Atlantic Herring (*Clupea harengus*) are negatively related to temperature. [24, 25]	Warming	At large body size, oxygen supply limitations are exacerbated and the organism reaches its long-term heat tolerance limits at lower temperatures, thus limiting the maximum body size that can be reached.

1. Perry et al. (2005); 2. Pörtner et al. (2008); 3. Takasuka et al. (2007); 4. Takasuka et al. (2008); 5. Lehodey et al. (2011); 6. Seibel (2011); 7. Beaugrand et al. (2009); 8. Philippart et al. (2011); 9. Johns et al. (2001);10. Greene and Pershing (2003); 11. Pörtner and Knust (2007); 12. Reipschläger and Pörtner (1996); 13. Pörtner et al. (2000); 14. Vezzoli et al. (2004); 15. Langenbuch and Pörtner (2003); 16. Fernández-Reiriz et al. (2011); 17. Langenbuch and Pörtner (2002);18. Langenbuch et al. (2006); 19. Michaelidis et al. (2005); 20. Pörtner et al. (1998); 21. Stumpp et al. (2012); 22. Kovach et al. (2012); 23. Thackeray et al. (2010); 24. Taylor (1958); 25. Brunel and Dickey-Collas (2010).

adapted to less variable ocean temperatures than those in the Northern Hemisphere (Jones et al., 1999; Figure 6-1), they may generally be more vulnerable to warming extremes than Northern ones. Tropical species (with thermal windows of intermediate width) live close to the highest temperatures tolerated by marine animals (Figure 6-6). Vulnerability is, therefore, highest for polar stenotherms, similar or lower for tropical, and lowest for temperate species (*high confidence*).

Short-term shifts in thermal thresholds of an individual organism may happen over days and weeks, such as during seasonal acclimatization. Long-term shifts occur over many generations during evolutionary adaptation of a population to cooler or warmer climates (Figure 6-5a; Pörtner, 2006; Pörtner et al., 2008; Eliason et al., 2011). Both acclimatization and adaptation involve adjustments in biochemical characters (membranes, enzymes); however, the capacity to shift those boundaries is limited and depends on the species and the prevailing climate regime (Pörtner et al., 2008, 2012). Ocean acidification, hypoxia, food availability, and stress affect those limits (Section 6.3.5; Figure 6-5a).

Local adaptation may reduce climate vulnerability at the species level, by causing functional and genetic differentiation between populations, thereby enabling the species to cover wider temperature ranges and live in heterogeneous environments. Local adaptation on small spatial scales is particularly strong in intertidal organisms (Kelly et al., 2012). On larger scales, the widening biogeographic and roaming ranges of

Northern Hemisphere eurytherms into Arctic waters (Pörtner et al., 2008) are supported by the differentiation into populations with diverse thermal ranges, combined with high acclimatization capacity. By contrast, such capacity is small in high polar, for example, Antarctic species (Peck et al., 2010). Tropical reef fishes undergo rapid warm acclimation across generations (Donelson et al., 2012) but some may approach animal heat limits. The rates, mechanisms, and limits of thermal acclimatization and evolutionary adaptation are poorly understood (*low confidence*).

6.3.1.4.1. Warm- and cold-water coral communities

Tropical corals live in shallow water and differ from most other animals by hosting dinoflagellates (*Symbiodinium* sp.) in their tissues, which provide the host with organic carbon from photosynthesis and with nitrogen and enable the corals to build and sustain carbonate reefs (Box CC-CR). High light, rapid salinity changes, and small increases in temperature can trigger "coral bleaching", the loss of symbionts and tissue color. In case of warming, early steps involve shifts in the photosynthetic processing of light, generating Reactive O_2 Species (ROS) that may in turn damage the symbionts (Hoegh-Guldberg and Smith, 1989; Glynn and D'Croz, 1990; Jones et al., 1998; Hoegh-Guldberg, 1999). Mass bleaching correlates with small temperature anomalies (+1°C to 2°C of the long-term summer maximum, satellite observations), causing mortalities (Goreau and Hayes, 1994; Strong et al., 2011) and decreasing coral abundance, on average by 1 to 2% per year (*high confidence*; Bruno and Selig, 2007; see also Box CC-CR; Section 30.5.6).

The degree of impact will depend on the coral reefs' adaptability to thermal stress and the interaction of multiple drivers (Meissner et al., 2012; Teneva et al., 2012; see also Box CC-CR). Such capacity is suggested by different heat tolerances among coral genera (Hoegh-Guldberg and Salvat, 1995; Loya et al., 2001), the exchange of genetic clades of *Symbiodinium* with more tolerant varieties (Baker, 2001; Jones et al., 2008), as well as acclimatization phenomena (Howells et al., 2012).

Studies of the thermal sensitivity of deeper-living cold-water corals (without endosymbionts) are scarce. One species, *Lophelia pertusa*, responds to about 3°C warming with a threefold increase in metabolic rate (Dodds et al., 2007), indicating a narrow thermal window in the cold (cf. Pörtner, 2006).

6.3.1.5. Ecosystems

Heat exposure of ecosystem engineers may threaten the existence of a whole ecosystem. During the last warm interglacial period equatorial coral reefs deteriorated and retreated (Kiessling et al., 2012), a finding emphasizing their thermal sensitivity (Veron et al., 2009) and showing that warming oceans can reach temperatures well beyond the upper heat limits of distinct animal groups and marine animals overall (Figure 6-6). In the present-day Great Barrier Reef, a large-scale survey found diverse coral types along a climatic gradient, with no consistent response to climatic drivers (Hughes et al., 2012). However, warm-induced bleaching has contributed to the progressive decrease in live coral cover observed over the last decades (De'ath et al., 2012; see also Box CC-CR; Section 30.5.6).

Within ecosystems, shifting competitive or trophic interactions, differential risks for species extinctions and, thereby, scenarios of community-level responses to temperature change (Urban et al., 2012; Milazzo et al., 2013) can be traced back to changing differences in the performance of participating animal species (Figure 6-7; e.g., Cairns et al., 2008; Harley, 2011; Pörtner, 2012). Knowledge is insufficient to assess interactions of species from different domains, impeding a deeper understanding of shifting distributions, abundances, community assemblages, and food webs in space and time (*low confidence* in current understanding; Parmesan and Matthews, 2005).

For example, in a coastal microcosm (small-scale, simplified experimental ecosystem) resident heterotrophic bacteria were stimulated by warming more than a laboratory-reared phytoplankter (Wohlers-Zöllner et al., 2011). Also, high- to low-latitude transects in both the North and South Atlantic revealed a shift between cold and warm waters, from photo-autotrophs (gaining energy from photosynthesis) to chemo-heterotrophs (Hoppe et al., 2002). Thermal stimulation of bacteria over phytoplankton has biogeochemical implications, for example, microbially mediated CO_2 flow to the atmosphere might increase (Sarmento et al., 2010). The principles and wider applicability of these findings require further investigation (*limited evidence*, *low agreement*; Kirchman et al., 2009).

Observations of shifting distributions and phenologies, reproduction, and range shifts of phytoplankton, zooplankton, other invertebrates, fishes, and seabirds in pelagic and coastal marine ecosystems have at least partly been attributed to temperature-mediated biological responses (*high confidence*; see also Figure 6-8; Box 6-1; Box CC-MB). In the North Atlantic as a key example, many biological events have been occurring earlier in the year (*robust evidence*, *high agreement*; Box 6-1; Section 30.5.1.1.1). Species richness has increased as a result of shifts in ranges and abundances. In the Norwegian and Barents Seas, a time series (1959–2006) of four commercial fish species and their zooplankton prey showed that climate shapes population growth rates through complex influences early in life, including direct temperature effects on growth, indirect effects via the biomass of zooplankton prey, and delayed feedback effects through predators (Stige et al., 2010). Differential species responses to temperature and trophic amplification were demonstrated to modify species interactions at five trophic levels: primary producers (phytoplankton); primary, secondary, and tertiary consumers (zooplankton, fishes, and jellyfishes); and benthic detritivores (echinoderms and bivalves) (Kirby and Beaugrand, 2009). Also, the responses of various plankton functional groups, such as diatoms, dinoflagellates, and copepods, to warming are not synchronous, resulting in predator-prey mismatches that carry over to higher trophic levels (*high confidence*; Edwards and Richardson, 2004; Costello et al., 2006; see also Figure 6-7a; Section 6.3.6). In the intertidal, warming-induced changes in relative species ranges lead to shifts in dominance through competitive interactions and to modifications in predator pressure (Poloczanska et al., 2008; Harley, 2011). Trans-Arctic interchange of species between Atlantic and Pacific has happened repeatedly in warm periods of the Pleistocene (Dodson et al., 2007) and may occur again, now facilitated by ballast transport by enhanced trans-Arctic shipping (*low* to *medium confidence*).

Warming may increase the risk of disease outbreaks or parasite infections, in marine organisms and ecosystems, and ultimately, humans (*medium*

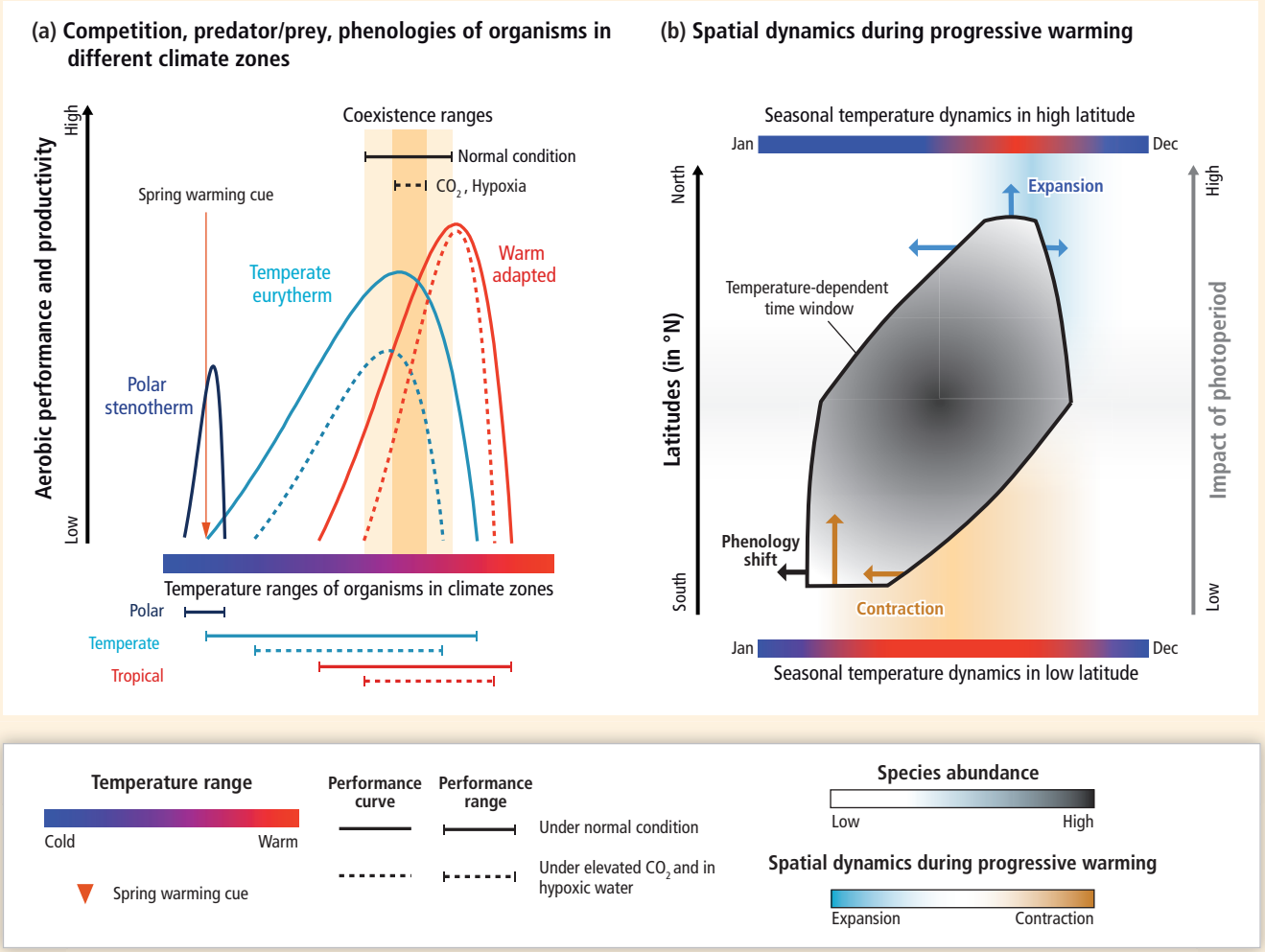


Figure 6-7 | Role of thermal tolerance and performance of organisms at ecosystem level. (a) Thermal tolerance ranges (Figure 6-5) differ between species across polar, temperate, and tropical climate zones, then overlap between coexisting species. Shifting temperatures and specific effects of additional drivers on the respective performance curves (dashed lines) change the fitness of coexisting species relative to each other as well as their temperature range of coexistence (after Pörtner and Farrell, 2008). Warming alters the timing of seasonal activities (e.g., elicited by spring warming cues) to earlier, or can benefit only one of two interacting species (e.g., in predator–prey dynamics or competition), causing shifts in predominance. (b) During climate warming a largely unchanged thermal range of a species causes it to follow its normal temperatures as it moves or is displaced, typically resulting in a poleward shift of the biogeographic range (exemplified for the Northern Hemisphere; modified after Beaugrand, 2009). The polygon delineates the distribution range in space and seasonal time; the level of gray denotes abundance. The Southern time window of tolerated temperatures shifts to earlier and contracts, while the Northern one dilates (indicated by arrows). Species display maximum productivity in low latitude spring, wide seasonal coverage in the center, and a later productivity maximum in the North. The impact of photoperiod (length of daily exposure to light) increases with latitude (gray arrow). Water column characteristics or photoperiod may overrule temperature control in some organisms (e.g., diatoms), limiting northward displacement.

confidence; Altizer et al., 2013; Burge et al., 2014). Some marine pathogens and protist diseases are shifting their distribution poleward as oceans warm (e.g., Baker-Austin et al., 2013; Burge et al., 2014). Climate change may weaken the immune response of hosts, particularly fishes and invertebrates, and increase their susceptibility to disease, as observed during warming in coral reefs of the Pacific and Caribbean (Harvell et al., 2009). Global outbreak frequencies of jellyfish aggregations may follow rising sea surface temperatures (SSTs) (*low confidence*; Mills, 2001; Purcell and Decker, 2005), but evidence is inconclusive. Some studies report an increasing trend (Brotz et al., 2012) and others do not support this view (Condon et al., 2013).

In conclusion, organisms live in limited temperature ranges and are sensitive to temperature extremes (*very high confidence*). Temperature governs the biogeography, diversity, development, reproduction, behavior, and phenology of marine species as well as the composition of communities in both pelagic and benthic systems and the seasonal timing of relevant processes (phenology) (*very high confidence*). Ecosystems functioning at the coldest temperatures and warm adapted ones existing at their upper thermal limits are more sensitive (*medium confidence*).

6.3.2. Carbon Dioxide Effects

Evidence for biological effects of ocean acidification stems from paleo-observations (Section 6.1.2), few observations in the field (Section 6.3.2.5), studies at volcanic CO_2 seeps as natural analogs, and mostly from short- to medium-term (hours to months) experiments in the

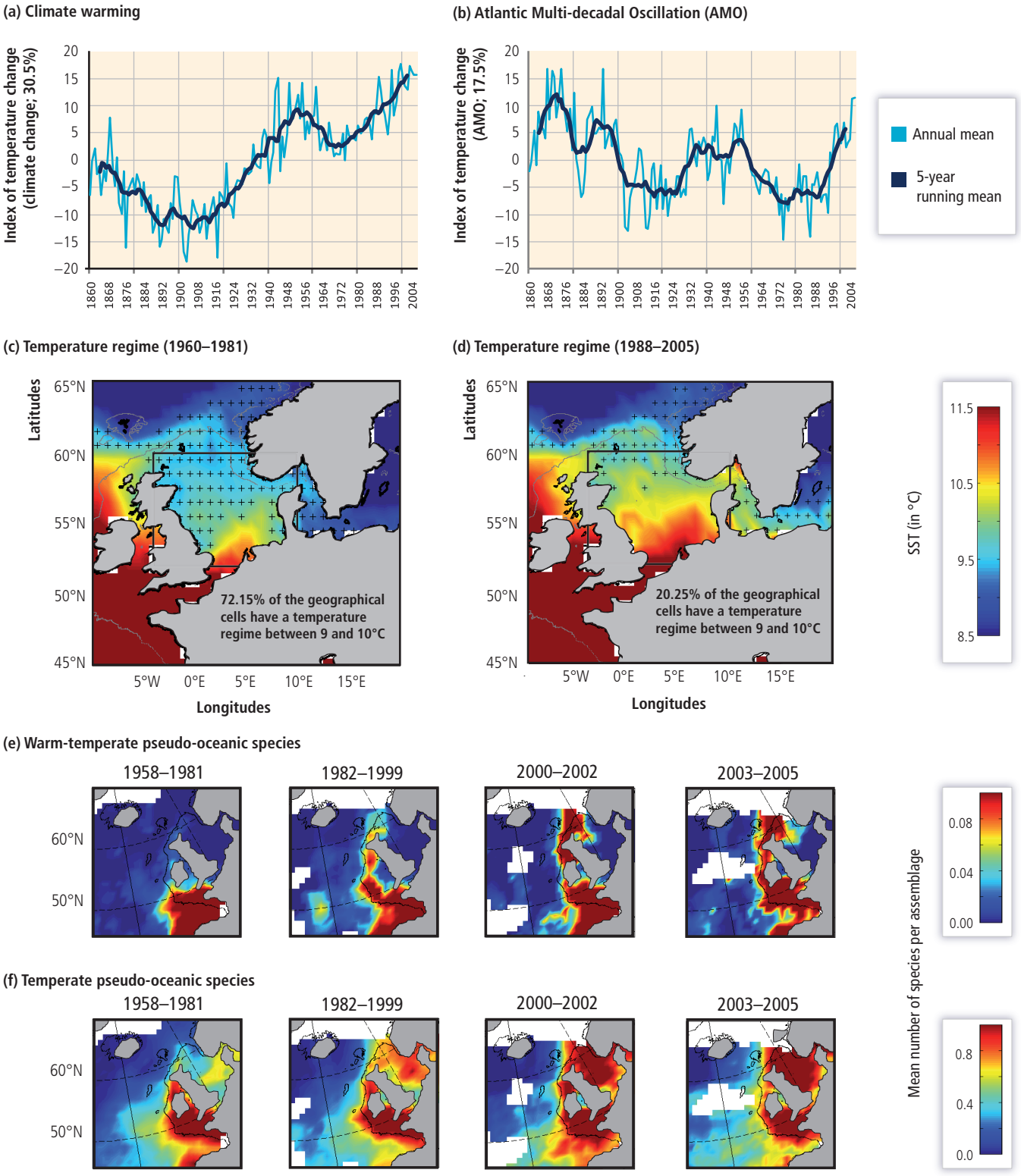
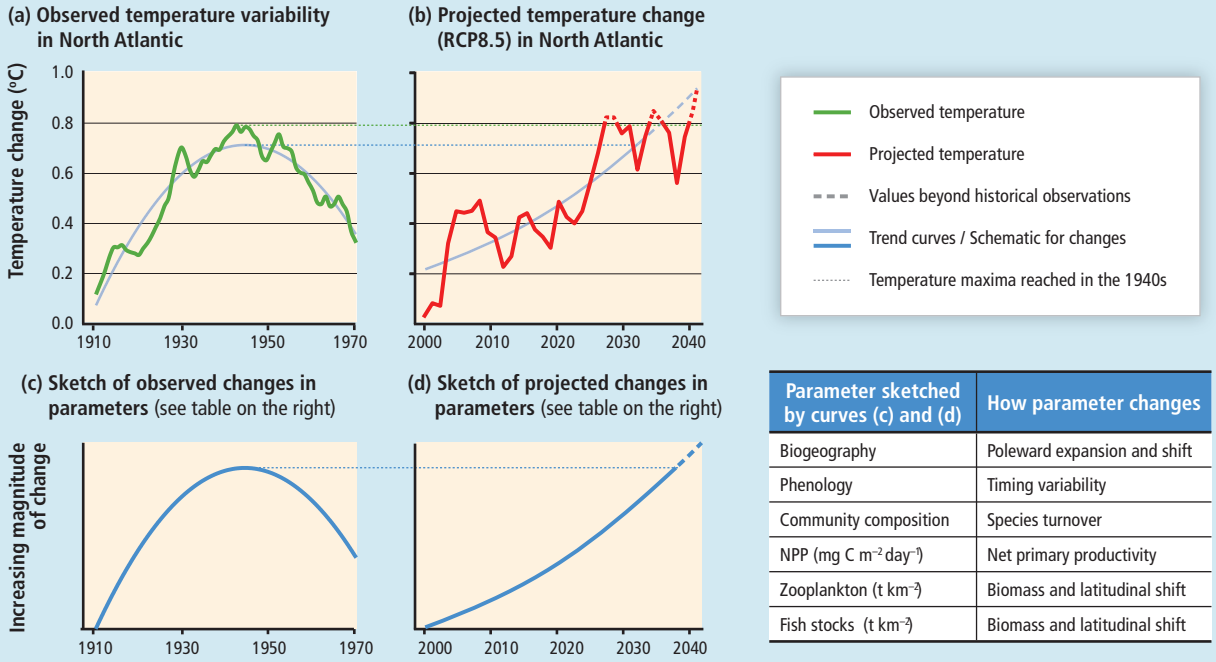


Figure 6-8 | Multi-decadal changes in ecosystem structure in the Northeast Atlantic driven by warming from both anthropogenic climate change and natural climate variability. (a) Index of temperature change over the North Atlantic (31°N to 65°N and 99°W to 11°E) reflecting climate change. This index is the first principal component (i.e., explaining 30.5% of observed variability) based on a principal component analysis (PCA) performed on sea surface temperature. (b) Index of temperature change (17.5% of observed variability) reflecting the Atlantic Multi-decadal Oscillation (AMO). The index is the second principal component. (c, d) Observed mean annual sea surface temperature in the North Sea during 1960–1981 (c) and 1988–2005 (d). The location of the critical thermal boundary (9°C to 10°C) is indicated by "+." (e) Long-term changes in the mean number of warm-temperate pseudo-oceanic species from 1958 to 2005. (f) Long-term changes in the mean number of temperate pseudo-oceanic species from 1958 to 2005. The period 1958–1981 was a period of relative stability and the period 1982–1999 was a period of rapid northward shifts, indicating that the abrupt ecosystem shift observed in the North Sea was part of a large-scale response of the zooplankton biodiversity to warming temperatures (see a–d). Average values are below 1 because they are annual averages. Note that the color bar is 10-fold smaller for warm-temperate pseudo-oceanic species because these species are less frequently observed than their temperate counterparts. Panels (a) and (b) from Edwards et al. (2013), and (c)–(f) from Beaugrand et al. (2008, 2009).

Box 6-1 | An Atlantic Ocean Example: Long-Term Responses of Pelagic Organisms and Communities to Temperature

Long-term observations (Sections 6.1.2, 30.5.1.1.1) encompassing the pelagic Northeast Atlantic over a 50-year period and longer (Figures 6-8, 6-9) show changes in the seasonal abundance of phytoplankton, rapid northerly displacements of temperate and subtropical zooplankton (e.g., calanoid copepods) and phytoplankton (e.g., dinoflagellates and diatoms), and the resulting changes in the ecosystem functioning and productivity (*high confidence*; Edwards et al., 2001; Beaugrand et al., 2002; Edwards and Richardson, 2004). The range limit of warm water copepods shifted by 10° north since 1960 (Beaugrand et al., 2009), with attendant mismatch in the seasonal timing of trophic levels (predators and prey) and functional groups (Edwards and Richardson, 2004). Modes of climate variability reflected in climate indices like the Northern Hemisphere Temperature (NHT) and the North Atlantic Oscillation (NAO) over multi-decadal periods accompanied these changes (Figure 6-1). In cooler regions, increased phytoplankton activity caused by warming favored growth, resulting in the observed increase in phytoplankton biomass, whereas a decrease in nutrient supply would have prevented growth in warmer regions and caused a decrease in biomass (Richardson and Schoeman, 2004; see also Section 6.3.4). Hinder et al. (2012) attributed a recent decline in North Sea dinoflagellates relative to diatoms to warming, increased summer windiness, and thus water column turbulence. The ecosystem response to natural climate variability in the past provides a glimpse into the climate-induced changes of the near future (Figure 6-9).



Parameter sketched by curves (c) and (d)	How parameter changes
Biogeography	Poleward expansion and shift
Phenology	Timing variability
Community composition	Species turnover
NPP (mg C m^{-2} day^{-1})	Net primary productivity
Zooplankton (t km^{-2})	Biomass and latitudinal shift
Fish stocks (t km^{-2})	Biomass and latitudinal shift

Figure 6-9 | Schematic depiction of observed effects of approximately 1°C ocean warming in the northern North Atlantic driven by climate variability (a,c) versus effects expected from anthropogenic climate change (b,d). (a) Transient warming and cooling associated with Atlantic Multi-decadal Oscillation (AMO) variability (Drinkwater, 2006), based on the Kola Section temperatures (0 to 200 m; Stations 3 to 7, 71.5° to 72.5°N, 33.5°E) in the Barents Sea obtained from http://www.pinro.ru and filtered using a 20-year running mean. Similar trends occurred across most of the northern North Atlantic although the amplitude and timing of the peaks and troughs varied spatially. (b) Warming driven by climate change for the same region (Representative Concentration Pathway 8.5 (RCP8.5) simulations averaged from Coupled Model Intercomparison Project Phase 5 (CMIP5) models, computed as the mean over the upper 200 m in the grid box (2.5° × 2.5°) centered at 71.25°N and 33.75°E). (c) Warming and subsequent cooling in the northern North Atlantic during the period shown in (a) resulted in complex multi-faceted changes (shown schematically) in net primary production (NPP), zooplankton biomass, and fish stock abundances. There was a general poleward shift and range expansion of many commercial (e.g., Atlantic herring, Atlantic cod, haddock) and non-commercial species, reversed during the subsequent cooling period. Poleward shifts in spawning areas (e.g., Atlantic cod) were also reversed as the waters cooled. Shifts in seasonal timing (phenology) and community composition were influenced by earlier arrivals and later retreat of migratory fish (not shown). For more details see Drinkwater (2006). (d) Projected effects of climate mediated warming on northern sub-polar and polar biota based on model projections of altered NPP (Bopp et al., 2013), and of the range shift of exploited fishes and invertebrates (Cheung et al., 2009, 2013a). The projected trends in (d) will differ with latitude, for example, decreased NPP at lower latitudes and no significant change to NPP in temperate waters (Bopp et al., 2013). Higher NPP supported and is projected to support higher trophic levels at high latitudes (c,d; Section 6.3.4). Note that climate variability will be superimposed on anthropogenic warming (b; see Figures 6-1, 6-8a,b). Dashed lines indicate projected changes to continue beyond the range of historical observations.

Continued next page →

Box 6-1 (continued)

In regions of high vulnerability to climate, mild warming can trigger rapid and substantial ecosystem shifts, offering a way to anticipate future changes (Figure 6-9). In line with the increased understanding of physiology (Section 6.3.1.1), warming in the temperate to polar North Atlantic was paralleled by a reduction in the average body lengths of about 100 copepod species, from 3 to 4 mm to 2 to 3 mm (Beaugrand et al., 2010). Warming also correlated with an increase in species richness among copepods and within the dinoflagellate genus *Ceratium*. In diatoms, which are major contributors to carbon export (Armbrust, 2009), warming and decreasing annual variability in SST resulted in lower diversity, smaller size, and reduced abundance (Beaugrand et al., 2010). Morán et al. (2010) found that temperature alone explained 73% of the variance in the contribution of small cells (picophytoplankton) to total phytoplankton biomass in the eastern and western temperate North Atlantic from –0.6 to 22°C. More recently, Marañón et al. (2012) analyzed data from polar, sub-polar, and tropical regions and suggested that nutrient availability may influence cell size more than temperature.

The ecosystem regime shift observed in North Sea plankton in the late 1980s involved an increase in phytoplankton stocks and changes in species composition and abundance among holozooplankton (animals that are planktonic for their entire lifecycle) (Reid et al., 2001; Kirby and Beaugrand, 2009; Kirby et al., 2009; Lindley et al., 2010). This shift was paralleled by the northward propagation of a critical thermal boundary (CTB, i.e., the boundary of the sub-polar gyre) between the temperate and the polar biomes (Beaugrand et al., 2008; see also Box CC-PP, Figure 1). Warming to above the CTB coincided with pronounced and large-scale variations in phytoplankton productivity, an increase in calanoid copepod diversity (Beaugrand et al., 2008) and herring abundance (Schlüter et al., 2008), a reduction in the mean size of calanoids, and a decrease in the abundance of southern Atlantic cod populations in the North Atlantic Ocean (e.g., the North Sea; Pörtner et al., 2008; Beaugrand et al., 2010). These patterns also extend to the southern North Sea, where elevated salinities and average warming by 1.6°C, both in summer and winter between 1962 and 2007, expanded the time window for growth of microalgae and possibly supported the invasion and increase in numbers of warm-adapted silicified diatoms (Wiltshire et al., 2010). Recent findings indicate a regime shift in the Bay of Biscay and the Celtic and the North Seas in the mid to end 1990s (Luczak et al., 2011). Changing plankton composition and changing abundances of both sardine and anchovies (Raab et al., 2013) paralleled stepwise warming.

Northward range extensions or redistributions in fishes were largest along the European Continental shelf and attributed to regional warming, for example, by 1.0°C from 1977 to 2001 in the North Sea, with winter warming being closely correlated with the shift of Atlantic cod (Perry et al., 2005; see also Section 6.3.1). Similar trends were observed due to warming by 1°C to 2°C in the waters south and west of Iceland during the past 15 years (Valdimarsson et al., 2012). In the Northwest Atlantic Arctic and sub-Arctic, winter and spring warming caused expansion of the area matching the thermal optimum of Atlantic salmon at 4°C to 8°C and caused greater growth (Friedland and Todd, 2012). Pelagic sardines and anchovies entered the North Sea in the early to mid-1990s, after about 40 years of absence, in response to intensified NAO and AMO (Alheit et al., 2012). Red mullet and bass extended into western Norway; Mediterranean and northwest African species extended to the south coast of Portugal (Brander et al., 2003; Beare et al., 2004; Genner et al., 2004; see also Section 30.5.1.1.4).

In the Northwest Atlantic cooling and freshening occurred during the late 1980s to early 1990s and seemed to have the opposite effect, as capelin and their predator, Atlantic cod, shifted farther south (Rose and O'Driscoll, 2002). Between the early 1990s and mid-2000s in the Northwest Atlantic sub-polar gyre, phytoplankton biomass increased, due to warming. At the same time, Arctic copepod species became more abundant, due to increased influx of Arctic water (Head and Pepin, 2010). Although temperatures have risen on the Newfoundland Shelf (Colbourne et al., 2011), capelin and cod remain scarce for reasons probably unrelated to climate (DFO, 2011a,b). Farther south, Arctic freshwater inflows caused freshening and increased stratification of the area around the Gulf of Maine throughout the 1990s, resulting in enhanced phytoplankton abundance, a larger and later fall bloom, increased abundance of small copepods, and a decrease in the large copepod *Calanus finmarchicus* (deYoung et al., 2004; Pershing et al., 2005, 2010). Various fish species showed poleward shifts in distribution (Table 6-2) that were associated with reduced survival of larval cod (Mountain and Kane, 2010) and fewer right whale calves (Greene et al., 2003), but increased herring abundance (Greene and Pershing, 2007).

Frequently Asked Questions

FAQ 6.3 | Why are some marine organisms affected by ocean acidification?

Many marine species, from microscopic plankton to shellfish and coral reef builders, are referred to as calcifiers, species that use solid calcium carbonate ($CaCO_3$) to construct their skeletons or shells. Seawater contains ample calcium but, to use it and turn it into $CaCO_3$, species have to bring it to specific sites in their bodies and raise the alkalinity (lower the acidity) at these sites to values higher than in other parts of the body or in ambient seawater. That takes energy. If high CO_2 levels from outside penetrate the organism and alter internal acidity levels, keeping the alkalinity high takes even more energy. The more energy is needed for calcification, the less is available for other biological processes such as growth or reproduction, reducing the organisms' weight and overall competitiveness and viability.

Exposure of external shells to more acidic water can affect their stability by weakening or actually dissolving carbonate structures. Some of these shells are shielded from direct contact with seawater by a special coating that the animal makes (as is the case in mussels). The increased energy needed for making the shells to begin with impairs the ability of organisms to protect and repair their dissolving shells. Presently, more acidic waters brought up from the deeper ocean to the surface by wind and currents off the Northwest coast of the USA are having this effect on oysters grown in aquaculture.

Ocean acidification affects not only species producing calcified exoskeletons. It affects many more organisms either directly or indirectly and has the potential to disturb food webs and fisheries. Most organisms that have been investigated display greater sensitivity at extreme temperatures so, as ocean temperatures change, those species that are forced to exist at the edges of their thermal ranges will experience stronger effects of acidification.

laboratory or field, exposing organisms to projected future CO_2 levels (Sections 6.3.2.1-4). A surging number of studies is providing evidence that rising CO_2 levels will increasingly affect marine biota and interfere with ecological and biogeochemical processes in the oceans (*high confidence*; FAQs 6.2, 6.3).

6.3.2.1. Principles

The absorption of rising atmospheric CO_2 by oceans and organisms changes carbonate system variables in the water and in organism internal fluids, that is, the relative proportions of CO_2, carbonate, bicarbonate, and hydrogen ions (pH). Internal pH must be tightly controlled, as some processes, such as calcification, release protons thereby affecting pH and as other biochemical processes are pH sensitive. Accumulation of CO_2 and the resulting acidification can also affect a wide range of organismal functions, such as membrane transport, calcification, photosynthesis in plants, neuronal processes in animals, growth, reproductive success, and survival. Effects translate from organism to ecosystem.

The capacity of organisms to resist and compensate for the CO_2-induced acidification of internal fluids depends on acid-base regulation, that is, the capacity of ion exchange to accumulate bicarbonate internally, an aspect unexplored in many phyla (*low* to *medium confidence*; Figure 6-10a; e.g., animals: Heisler, 1986; Claiborne et al., 2002; Pörtner, 2008; phytoplankton: Taylor et al., 2011; see also FAQ 6.3).

In unicellular microbes the regulation of intracellular pH may play a key role in modulating CO_2 responses (Taylor et al., 2011). Findings in invertebrates and fish indicate an additional role for extracellular pH (Figure 6-10a); effective pH values may vary between species. Organisms pre-adapted to elevated CO_2 may minimize the decrease in pH (acidosis). They may also modify their sensitivity such that they respond less or not at all to the acidosis. Recent evidence, however, emphasizes a role for acid-base regulation in a natural low-pH setting. Between two urchin species, only the one successful in maintaining its setpoints of extracellular pH is able to settle close to volcanic CO_2 seeps (Calosi et al., 2013). Compensating for the acidosis may cause increased energy demand and respiration rates. In general, such capacity rises with metabolic energy turnover, for example, it is higher in more active marine animals, such as fishes, cephalopods, and pelagic copepods, and in mobile coastal crabs compared to sessile species (Pörtner et al., 2005, 2011; Ishimatsu et al., 2008; Melzner et al., 2009; Ishimatsu and Dissanayake, 2010; see also Table 6-3). This matches the sensitivity distribution seen among animals at the phylum level (*medium confidence*; Figure 6-9b).

Some species have lower metabolic rates in response to acidosis (Pörtner et al., 1998; Michaelidis et al., 2005; Pörtner, 2008; Liu and He, 2012; Navarro et al., 2013); others display increased energy turnover and food ingestion rates, possibly indicating a capacity to resist acidification effects (Parker et al., 2011; Saba et al., 2012). The effects of the acidosis on various processes relevant to fitness may explain changes in whole-organism energy demand, probably paralleled by modified ion exchange, protein synthesis, and growth and feeding rates. The magnitude of effect depends on the CO_2 concentrations reached (Figure 6-10b).

The internal formation of carbonate from bicarbonate is essential to calcification, which is the formation of solid $CaCO_3$ in internal or external

calcified structures, used for defense and structural support. Calcification usually occurs in separate body or cell compartments, where pH and thus CO_3^{2-} concentration and saturation Ω (Section 6.1.1) are maintained at values higher than in other body fluids or ambient water (Taylor et al., 2011; Trotter et al., 2011; McCullough et al., 2012; Venn et al., 2013). CO_2 impedes the formation of carbonate such that calcification rate decreases. It may be maintained by enhanced transport of ions, incurring elevated energetic costs (Figure 6-10).

External carbonate structures like shells rely on ambient seawater being supersaturated with carbonates. Decreasing oceanic carbonate levels reduce the saturation levels (Ω) of calcite or aragonite in the water. Reduction to below unity may lead to the corrosion of carbonate shells (FAQ 6.3). However, many species protect their shells from direct contact with seawater by various types of organic coating (e.g., a periostracum in mollusks and brachiopods, an epicuticle covering the carapace of crustaceans, an epidermis covering the tests of urchins, epithelial tissue covering aragonite in corals, and coralline algae precipitating $CaCO_3$ (mostly Mg-calcite) within their cell wall). A meta-analysis of the effects of ocean acidification on biological processes indicates that reductions in the rate of net calcification (calcification minus dissolution) and survival are the most uniform responses across organisms studied, relative to other, more variable impacts such as reduced growth, development, and abundance (Kroeker et al., 2013; see also Box CC-OA).

Some organisms benefit from elevated CO_2 partial pressures (pCO_2). Photosynthesis and/or nitrogen fixation in selected microorganisms are impacted by OA, but effects are species or taxon specific, possibly depending on how they acquire carbon, that is, the presence and in particular the type, capacity, and energetic costs of carbon-concentrating mechanisms (CCMs; Giordano et al., 2005; Kranz et al., 2011).

A comprehensive picture of responses to CO_2 requires consideration of variable sensitivities between species and life stages and taxon-specific sensitivity distributions, as shown by a meta-analysis of animal data (Wittmann and Pörtner, 2013; see also Figure 6-10b). Echinoderms, bivalves, gastropods, and corals begin to respond negatively at lower CO_2 levels than crustaceans or cephalopods (Figure 6-10b). This sensitivity

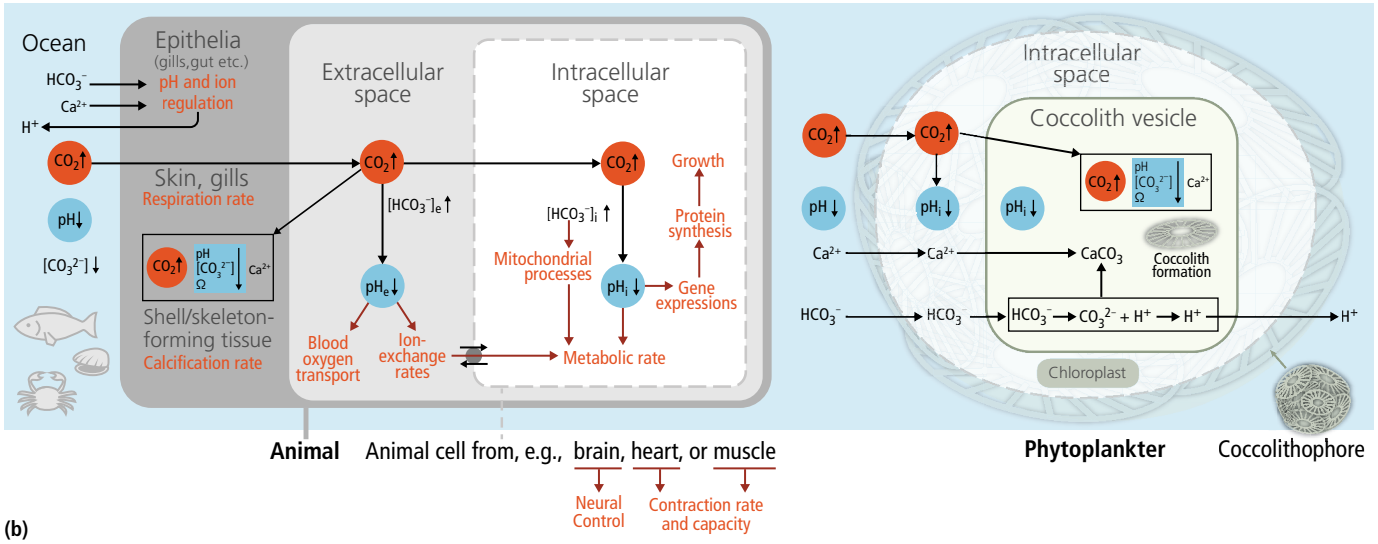
Table 6-3 | Tolerances to ocean acidification in marine taxa, assessed from laboratory and field studies of species in the CO_2 partial pressure (pCO_2) range from <650 to >10000 µatm, compared to present day atmospheric levels of 400 µatm. (It should be noted that anthropogenic CO_2 emissions add to the natural variability of CO_2 concentrations in marine environments, which can reach much higher than atmospheric levels.) Variables studied include growth, survival, calcification, metabolic rate, immune response, development, abundance, behavior, and others. Neither all life stages, nor all variables, including the entire range of CO_2 concentrations, were studied in all species. *Confidence* is based on the number of studies, the number of species studied, and the agreement of results within one group. + denotes that possibly more species or strains (genetically distinct populations of the same species) were studied, as only genus or family were specified; beneficial: most species were positively affected; vulnerable: more than 5% of species in a group will be negatively affected by 2100; tolerant: more than 95% of species will not be affected by 2100. RCP 6.0: Representative Concentration Pathway (RCP) with projected atmospheric pCO_2 = 670 µatm; RCP 8.5: pCO_2 = 936 µatm in 2100 (Meinshausen et al., 2011). *Confidence* is limited by the short- to medium-term nature of various studies and the lack of sensitivity estimates on evolutionary time scales, that is, across generations (see separate reference list, Online Supplementary Material). Note that the assessment of variability between species from the same animal phylum has revealed an increase in the fraction of sensitive species with rising CO_2 levels; see Figure 6-10.

Taxon	No. of studies	No. of parameters studied	Total no. of species studied	pCO_2 where the most vulnerable species is negatively affected or investigated pCO_2 range[a] (µatm)	Assessment of tolerance to RCP 6.0 (*confidence*)	Assessment of tolerance to RCP 8.5 (*confidence*)
Cyanobacteria	17	5	9+	180–1250[a]	Beneficial (*low*)	Beneficial (*low*)
Coccolithophores	35	6	7+	740	Tolerant (*low*)	Vulnerable (*medium*)
Diatoms	22	5	28+	150–1500[a]	Tolerant (*low*)	Tolerant (*low*)
Dinoflagellates	12	4	11+	150–1500[a]	Beneficial (*low*)	Tolerant (*low*)
Foraminifers	11	4	22	588	Vulnerable (*low*)	Vulnerable (*medium*)
Seagrasses	6	6	5	300–21000[a]	Beneficial (*medium*)	Beneficial (*low*)
Macroalgae (non-calcifying)	21	5	21+	280–20812[a]	Beneficial (*medium*)	Beneficial (*low*)
Macroalgae (calcifying)	38	10	36+	365	Vulnerable (*medium*)	Vulnerable (*high*)
Warm-water corals	45	13	31	467	Vulnerable (*medium*)	Vulnerable (*high*)
Cold-water corals	10	13	6	445	Vulnerable (*low*)	Vulnerable (*medium*)
Annelids	10	6	17+	1200	Tolerant (*medium*)	Tolerant (*medium*)
Echinoderms	54	14	35	510	Vulnerable (*medium*)	Vulnerable (*high*)
Mollusks (benthic)	72	20	38+	508	Vulnerable (*medium*)	Vulnerable (*high*)
Mollusks (pelagic)	7	8	8	550	Vulnerable (*low*)	Vulnerable (*medium*)
Mollusks (cephalopods)	10	8	5	2200 (850 for trace elements)	Tolerant (*medium*)	Tolerant (*medium*)
Bryozoans	7	3	8+	549	Tolerant (*low*)	Vulnerable (*low*)
Crustaceans	47	27	44+	700	Tolerant (*medium*)	Tolerant (*low*)
Fish[b]	51	16	40	700	Vulnerable (*low*)	Vulnerable (*low*)

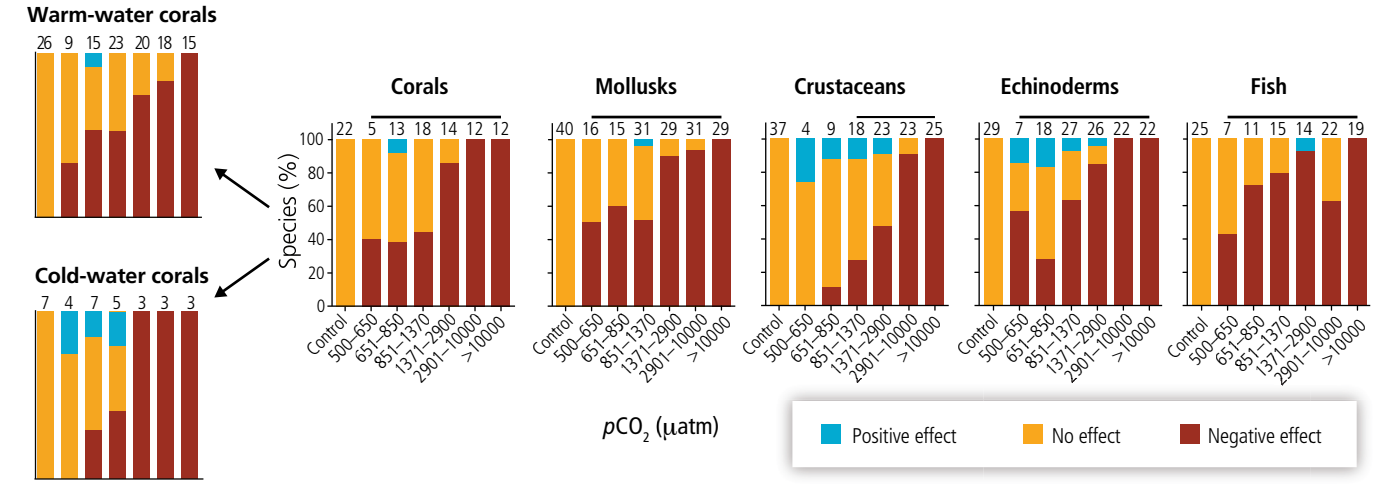
[a]Rather than a sensitivity threshold the entire range of investigated pCO_2 values is given for groups of photosynthetic organisms. In all studies photosynthetic rates are stimulated to different, species-specific degrees by elevated pCO_2, indicating low vulnerability. Coccolithophores and calcifying algae are assessed as being more sensitive than other photosynthetic organisms due to reduced calcification and shell dissolution.

[b]Confidence levels for fishes were converted from medium to low, in light of uncertainty on the long-term persistence of behavioral disturbances.

(a)


Ocean
Epithelia
(gills,gut etc.)
pH and ion regulation
Extracellular space
Intracellular space
Skin, gills
Respiration rate
Shell/skeleton-forming tissue
Calcification rate
Growth
Protein synthesis
Mitochondrial processes
Gene expressions
Blood oxygen transport
Ion-exchange rates
Metabolic rate
Intracellular space
Coccolith vesicle
Coccolith formation
Chloroplast
Animal
Animal cell from, e.g., brain, heart, or muscle
Neural Control
Contraction rate and capacity
Phytoplankter
Coccolithophore

(b)


Warm-water corals
26 9 15 23 20 18 15
Cold-water corals
7 4 7 5 3 3 3
Corals
Mollusks
Crustaceans
Echinoderms
Fish
Species (%)
Control
500–650
651–850
851–1370
1371–2900
2901–10000
>10000
pCO2 (µatm)
Positive effect
No effect
Negative effect

(c)

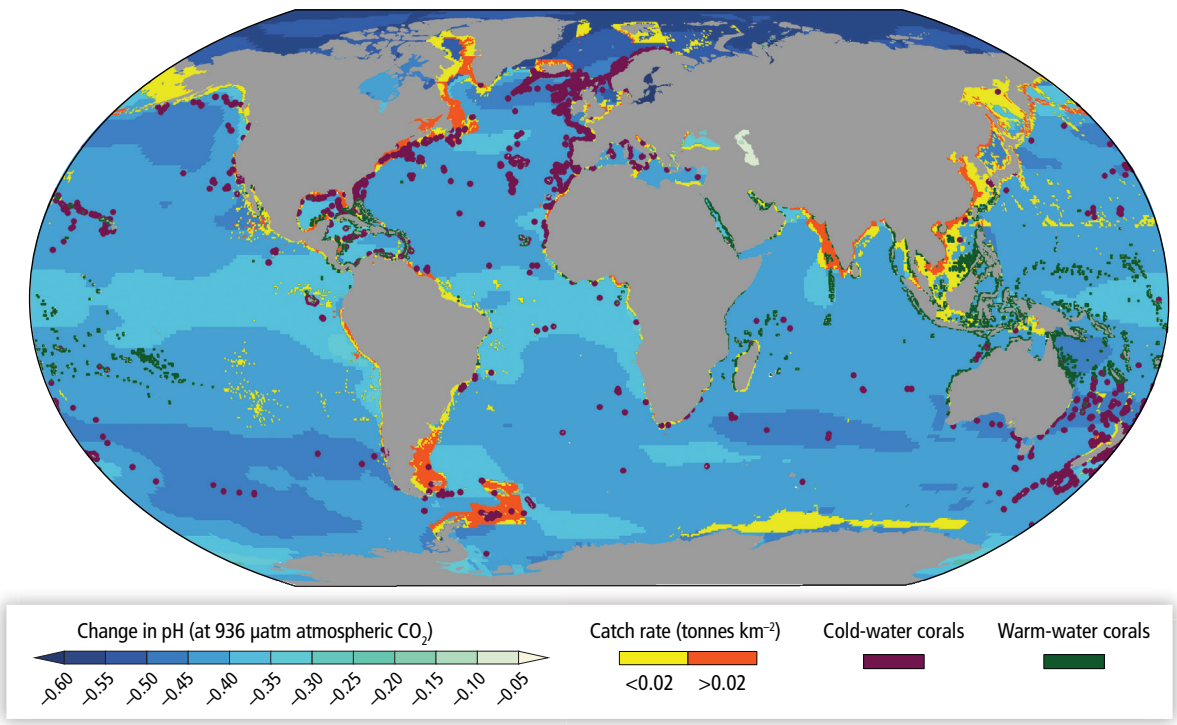

Change in pH (at 936 µatm atmospheric CO2)
-0.60 -0.55 -0.50 -0.45 -0.40 -0.35 -0.30 -0.25 -0.20 -0.15 -0.10 -0.05
Catch rate (tonnes km-2)
<0.02 >0.02
Cold-water corals
Warm-water corals

Figure 6-10 | (a) Responses of a schematized marine animal (left) and a phytoplankter (right) to ocean acidification. Effects are mediated via diffusive CO_2 entry (black arrows) into body and cell compartments, resulting in a rise in pCO_2 (highlighted in red), a drop in compartmental pH (highlighted in blue), and their effects (red arrows) on various processes (red text) in tissues and cellular compartments, as well as on calcium carbonate saturation state (Ω) at calcification sites (after Pörtner, 2008; Taylor et al., 2011). Variable sensitivity relates to the degree of pH decline and compensation, depending on the capacity of pH and ion regulation. (b) Distribution of sensitivities across species within animal phyla, under progressively rising water CO_2 levels, as percent of studied cold- and warm-water coral (mostly scleractinia), echinoderm, molluskan, crustacean, and fish species affected negatively, positively, or not at all (for effects considered, see text). As not all life stages, variables, and pCO_2 ranges were covered in all species, two assumptions partially compensate for missing data: 1) Negative effects at low pCO_2 will remain negative at high pCO_2. 2) A positive or neutral outcome at both low and high pCO_2 will be the same at intermediate pCO_2. As responses reported for each species vary for each pCO_2 range, variable species numbers result (on top of columns). The total number of species studied in a group is shown as the number above the control column. The control category corresponds to 380 μatm. For 2100, RCP scenarios falling within each CO_2 partial pressure (pCO_2) category are as follows: RCP4.5 for 500–650 μatm (approximately equivalent to ppm in the atmosphere), RCP6.0 for 651–850 μatm, and RCP8.5 for 851–1370 μatm. By 2150, RCP8.5 falls within the 1371–2900 μatm category. Horizontal lines above columns represent frequency distributions significantly different from controls (Wittmann and Pörtner, 2013). Data for warm- and cold-water corals as in Table 6-3. (c) Areas with reported annual catches of marine calcifiers (crustaceans and mollusks) ≥ 0.005 tonnes km^{-2} depicted on a global map (weighted mean of the orange color area =0.07 tonnes km^{-2}) showing the distribution of ocean acidification in 2100 according to RCP8.5 (WGI AR5 SPM; pH change from 1986–2005 to 2081–2100) as well as the distribution of warm-water (green dots) and cold-water coral communities (purple dots).

pattern resembles the one seen in the Permian mass extinction (Knoll et al., 2007; Knoll and Fischer, 2011). The picture for fishes is less clear, as the present findings of high vulnerability are not met by similar observations in the fossil record. Evolutionary adaptation may thus eliminate or minimize reported effects.

The capacity for pH and ion regulation and other relevant processes can be upregulated by gene expression, as seen in acclimation studies in echinoderm larvae (O'Donnell et al., 2010; Martin et al., 2011) and fishes (Deigweiher et al., 2008; Tseng et al., 2013), in warm-water coral branches (Kaniewska et al., 2012), but not in a study of warm-water coral larvae (Moya et al., 2012). Few studies address whether and to what extent species undergo evolutionary adaptation to high pCO_2, as seen in the coccolithophore *Emiliania huxleyi* over 500 asexual generations (Lohbeck et al., 2012). In organisms with longer generation times, perturbation studies in the laboratory measure tolerance and acclimation, but not adaptation or natural selection. Animal adaptation is accelerated by high functional variability among larvae, enabling selection of resistant genotypes (*low* to *medium confidence*; Sunday et al., 2011; Parker et al., 2012; Pespeni et al., 2013). This may explain the selective mortality seen in Atlantic cod larvae under elevated CO_2 (Frommel et al., 2012). Both acclimatization and adaptation will shift sensitivity thresholds but the capacity and limits of species to acclimatize or adapt remain largely unknown and hence impacts of acute exposures cannot easily be scaled up to effects on the longer, evolutionary time scales of ocean acidification (Wittmann and Pörtner, 2013). Observations in ecosystems characterized by permanently elevated or fluctuating CO_2 levels, such as upwelling areas, OMZs (Section 6.1.1), or seeps, reflect the existence of sensitivity thresholds (*high confidence*; Section 6.3.2.5) but organisms may have evolved a higher resistance to increased CO_2 levels than elsewhere (*low confidence*).

Table 6-3 compiles effects of ocean acidification observed across taxa in laboratory and field experiments. The latter include studies in mesocosms and at natural analogs, submarine CO_2 venting areas at locales such as Ischia, Italy (Hall-Spencer et al., 2008), Papua New Guinea (Fabricius et al., 2011), and Puerto Morelos, Mexico (Crook et al., 2012). It should be noted that anthropogenic CO_2 accumulation according to RCPs adds to the natural variability of CO_2 concentrations in marine environments. Many groups, especially sessile or non-photosynthetic calcifiers, have sensitive species with vulnerability thresholds surpassed under RCP6.0 by 2100 (*low* to *medium confidence*).

Recent meta-analyses also summarize OA effects, two for biogeochemical processes and relative effect sizes (Harvey et al., 2013; Kroeker et al., 2013), one for the distribution of sensitivity between species within major animal phyla and its change depending on ambient pCO_2 (Figure 6-10; Wittmann and Pörtner, 2013). All of these analyses consider the interaction of warming and CO_2 accumulation (Section 6.3.5). Present limitations in understanding the mechanisms of effect and their long-term persistence compounds accurate projections of the long-term effects of OA (*medium confidence*; Wittmann and Pörtner, 2013).

6.3.2.2. Microbes

The physiology of both calcifying (coccolithophores) and non-calcifying phytoplankton can be influenced by changes in carbonate system variables caused by ocean acidification (Figure 6-10a). Growth and photosynthetic rates of diatoms in laboratory cultures are considered relatively insensitive to elevated CO_2 (Rost et al., 2003; Trimborn et al., 2008). Dinoflagellate sensitivity to elevated CO_2 is poorly studied (Hansen et al., 2007), but in one species carbon fixation rates were enhanced at 750 µatm CO_2 while growth remained unaffected (Fu et al., 2008). Indirect effects of ocean acidification on phytoplankton physiology include altered availability of trace metals needed for many biochemical cycles (Hoffmann et al., 2012).

Harmful algal blooms are a growing problem in coastal waters worldwide (Section 6.4.2.3), and many of the various phytoplankton species that produce bio-accumulated toxins are sensitive to changes in the seawater carbonate buffer system (Hallegraeff, 2010; Fu et al., 2012). For example, the dominance and community structure of harmful bloom dinoflagellates can be profoundly altered by changing pCO_2 (Tatters et al., 2013), and both toxic dinoflagellates and diatoms have been shown to produce higher toxin levels under near-future levels of ocean acidification (Fu et al., 2010; Sun et al., 2011).

Some planktonic N_2-fixing cyanobacteria (diazotrophs), for example, strains (genetically distinct populations of the same species) of offshore cyanobacteria of the genera *Trichodesmium* and *Crocosphaera*, respond to rising CO_2 with increased rates of both carbon and N_2 fixation (Fu et al., 2008; Lomas et al., 2012). In contrast, laboratory studies using the bloom-forming cyanobacteria *Nodularia* (an organism largely found in coastal stratified, eutrophic waters) revealed decreased growth and N_2

fixation under elevated CO_2 conditions (Czerny et al., 2009). The wide range of responses in N_2 fixation (e.g., Hutchins et al., 2007; Levitan et al., 2007; Kranz et al., 2010) may be explained by different CO_2 affinities (i.e., dependences of growth rates on CO_2 concentration) of a range of N_2-fixing cyanobacteria (*Trichodesmium* and *Crocosphaera*) from different oceanic biomes. Some species/strains operate at close to maximum growth rates at present-day oceanic CO_2 levels, whereas others had sub-optimal growth rates under these conditions (Hutchins et al., 2013). To date, the physiological mechanisms underlying these responses remain unknown, especially in open-ocean nitrogen fixers. Cyanobacteria may reallocate energy from their energetically expensive CCMs toward N_2 fixation and the acquisition of growth limiting nutrients (Kranz et al., 2010; Levitan et al., 2010), but evidence for such diversion of energy is lacking. Whether nitrogen fixation will increase with progressive ocean acidification remains to be explored (*low confidence*, *limited* in situ *evidence*, *medium agreement*).

The responses of coccolithophore calcification to OA are species specific and highly variable. The function(s) of calcification are not well understood, making it difficult to evaluate the consequences of lowered calcification (e.g., Rost et al., 2008). Reductions, increases, and unchanged calcification rates (and shell structure) have all been found in different coccolithophore species for RCP8.5 CO_2 conditions projected around 2100 (Riebesell et al., 2000; Zondervan et al., 2001; Langer et al., 2006; Iglesias-Rodriguez et al., 2008). Calcification in coccolithophores is species (Langer et al., 2006) and in *Emiliania huxleyi* even strain specific (Langer et al., 2009, 2011; Hoppe et al., 2011). It thus remains unclear whether OA will result in exoskeletons that are insufficiently calcified for sustained structural support and protection in coccolithophores (*medium evidence*, *low agreement*).

Foraminifera display decreasing calcification and shell weight under elevated CO_2 (Lombard et al., 2010). Changes in historical specimens (Moy et al., 2009; see Section 6.3.2.5.1) and during glacial-interglacial cycles (Barker and Elderfield, 2002) support projections of future reductions in net calcification by foraminifera (*medium* to *high confidence*).

6.3.2.3. Macroalgae and Seagrasses

Primary production, shoot density, reproductive output, and below-ground biomass of seagrasses generally respond positively to elevated pCO_2, indicating CO_2 limitation of their productivity. Such effects were identified in both laboratory and field above 720 to 1800 µatm (*high confidence*; e.g., Palacios and Zimmerman, 2007; Hall-Spencer et al., 2008; Andersson et al., 2011; cf. Section 5.4.2.3). Production, growth, and recruitment of most but not all non-calcifying seaweeds also increased at CO_2 levels from 700 to 900 µatm (RCP8.5; Porzio et al., 2011; Kroeker et al., 2013). Some non-calcifying seaweeds and seagrasses will thus benefit from future ocean acidification (*high confidence*) but OA exposes them to higher than usual grazing as a consequence of losing deterrent phenolic substances (*low confidence*; Arnold et al., 2012).

Calcifying algae (corallines) show complex and species-specific responses of photosynthesis to elevated CO_2, but calcification is impacted once species-specific pCO_2 thresholds are surpassed (*medium confidence*; Anthony et al., 2008; Martin and Gattuso, 2009). At habitat temperature calcification by temperate coralline red and calcareous green algae increased at CO_2 levels up to 900 µatm and decreased only at the highest concentration applied (2850 µatm), but did not fall below rates found at present-day pCO_2 (Ries et al., 2009). During 3 months of exposure, growth of *Lithothamnion glaciale*, a cold-water calcareous red alga, decreased progressively with rising CO_2 levels, and its structural integrity was weakened beyond 590 µatm (Ragazzola et al., 2012), potentially influencing ecosystem function. Some calcifying algae may thus be impacted by future ocean acidification (*medium confidence*).

6.3.2.4. Animals

Studies of marine animals and their life stages show a high diversity and variability of processes affected by ocean acidification. Many variables studied reflect physiological performance (O_2 consumption, exercise, behavior, calcification, growth, immune response, acid-base balance, gene expression, fertilization, sperm motility, developmental time, production of viable offspring, and morphology; Table 6-3; Figure 6-10). In some species growth may be stimulated by OA, in others depressed or unaffected (cf. Gooding et al., 2009; Munday et al., 2009a, 2011a; Dupont et al., 2010). The degree of CO_2-induced acidosis and its compensation by ion exchange may shape sensitivity (Section 6.3.2.1). Full exploitation of the ability to resist pCO_2 increases depends on the availability and high quality of food and the strengthening of fitness (Gooding et al., 2009; Melzner et al., 2011). However, food quality of prey organisms may decrease under elevated pCO_2. For example, slower reproduction and growth of the copepod *Acartia tonsa* under 760 µatm pCO_2 was related to the decreasing quality of its diatom food (Rossoll et al., 2012).

Changes in calcification rates reported from CO_2 manipulation experiments vary widely. Reduced calcification and weakened calcified structures were seen under elevated pCO_2 in corals (see Section 6.3.2.4.2), echinoderms (Kurihara and Shirayama, 2004), mollusks (Gazeau et al., 2013), and larval crustaceans (Arnold et al., 2009; Walther et al., 2011). Some adult limpets and urchins increased calcification rates at pCO_2 from 600 to 900 µatm, before it fell at even higher pCO_2. In some adult crabs, lobsters, and shrimps calcification rates increased further with rising pCO_2 (Ries et al., 2009). Stronger internal structures such as cuttlebones and otoliths resulted from enhanced calcification under elevated pCO_2 in juvenile cuttlefish (cephalopods: Gutowska et al., 2008) and fishes (Checkley, Jr. et al., 2009; Munday et al., 2011b), with unclear impacts on fitness. Energy costs in epithelia or calcification compartments may be enhanced by elevated pCO_2 causing a stimulation of metabolism (Section 6.3.2.1). In some cases, this may indicate imbalances in energy budget rather than increased CO_2 resistance, for example, if costs are down-regulated in muscle or liver. Enhanced calcification can then occur at the expense of growth (*medium confidence*; Wood et al., 2008; Beniash et al., 2010; Thomsen and Melzner, 2010; Parker et al., 2011).

Studies on calcifying zooplankton focused on pteropods (planktonic mollusks with aragonite shells). These form an integral part of the food web, both as grazers and prey, for example, for pink salmon (Armstrong et al., 2005; Hunt et al., 2008). In the Sub-Arctic, the Arctic, and the Southern Ocean, pteropods will reduce calcification in response to OA

until at least the end of the century (*medium confidence*; Orr et al., 2005; Comeau et al., 2009; Lischka et al., 2011).

Elevated CO_2 causes behavioral disturbances in fishes (studied mostly in larvae and juveniles; Munday et al., 2010; Ferrari et al., 2011; Domenici et al., 2012; Jutfeld et al., 2013) through neural mechanisms (Nilsson et al., 2012). The long-term persistence and evolutionary relevance of these behavioral effects need further study before general conclusions can be drawn (*low confidence*; Wittmann and Pörtner, 2013; see also Table 6-3).

6.3.2.4.1. Animal life cycles

It is generally held that organisms at early life stages are always more sensitive to environmental stress than adults. In the context of ocean acidification this statement is supported by findings like larval oyster fatalities in aquaculture caused by upwelled CO_2-rich waters (*high confidence*; Barton et al., 2012). A key aspect may also be that larvae growing or developing more slowly under elevated CO_2 as in various groups including fishes (Baumann et al., 2012; see also Section 6.3.2.1) may encounter enhanced mortalities due to prolonged predator exposure. Comparative studies of animal sensitivities to OA over a complete life cycle or during critical transition phases (e.g., fertilization, egg development and hatching, metamorphosis, molting) are scarce and do not support generalized conclusions (*low confidence*).

Effects of elevated CO_2 on one life stage or transition phase may affect or carry over to the next one. Molting success into the final larval stage was reduced in a crab species (Walther et al., 2010). In a sea urchin species, negative impact was found to accumulate during 4 months acclimation of adults reducing reproductive success. This impact was, however, compensated for during extended acclimation of female urchins for 16 months (Dupont et al., 2013). Negative impact was still transferred from urchin larvae to juveniles under elevated pCO_2. Conversely, adult oysters acclimated to high CO_2 acquired resistance which was carried over to their offspring (Parker et al., 2012). More long-term acclimation studies to realistic emission scenarios are needed for generalized conclusions. Furthermore, the preposition that juvenile life stages are always more sensitive than adults needs thorough re-investigation in the context of ocean acidification, especially in the context of the notion that larvae may provide a selection pool for survival of the most suitable phenotypes (*low confidence*; Section 6.3.2.1).

6.3.2.4.2. Warm- and cold-water coral communities

In warm-water reef-building corals, OA causes genus-specific reductions in calcification (Leclercq et al., 2002; Langdon and Atkinson, 2005; Kleypas and Langdon, 2006). Nutrient availability to symbionts may sustain calcification. Heterotrophic feeding by the corals also supports energy-dependent calcification and acid-base regulation, and thus resilience (Edmunds, 2011; Figure 6-10). Females may sacrifice calcification more than males due to energetic trade-offs with reproduction (Holcomb et al., 2012). Warm-water corals are thus sensitive to future OA (*high confidence*; Table 6-3).

The cold-water coral *Lophelia pertusa* shows resilience to ocean acidification. In short-term ship-board incubations pH reductions between 0.15 and 0.3 units (540 and 790 µatm) led to calcification rates reduced by 30 to 56% (Maier et al., 2009), especially in young, fast growing polyps. However, net calcification was maintained at seawater aragonite saturation <1. Exposure to a pCO_2-induced pH reduction by 0.1 units or even to the projected end of century pCO_2 of 930 µatm led to calcification rates being maintained over 6 to 9 months (Form and Riebesell, 2012; Maier et al., 2013). This ability is probably due to a regulated upward shift of pH and carbonate saturation at organismal calcification sites (McCulloch et al., 2012; see also Figure 6-10). Natural distribution of other cold-water species covers wide natural pH gradients in Chilean fjords (*Desmophyllum dianthus*; Jantzen et al., 2013) and ranges into waters with undersaturated carbonates as in Australian waters (four scleractinian corals; Thresher et al., 2011). Pre-adaption to elevated pCO_2 apparently exists; however, species vulnerabilities to further increases in pCO_2 have not been investigated. Again, vulnerability is species specific, colonial scleractinians may be limited to water saturated or near-saturated with aragonite, whereas others are not (Thresher et al., 2011). Conclusions on the relative vulnerability of the group appear premature (Table 6-3). To what extent a further lowering of carbonate saturation values will influence the future distribution of various calcite or aragonite forming cold-water corals is not clear (*low confidence*; Guinotte et al., 2006).

6.3.2.5. Ecosystems

For insight into ecosystem level processes, laboratory studies have been supplemented with experimental studies in large volume mesocosms (i.e., >1000 L) and in the field, and with long-term field observations. Together they inform the debate over the attribution of field observations to ocean acidification.

6.3.2.5.1. Evidence from field observations

Contributions of anthropogenic ocean acidification to climate-induced alterations in the field have rarely been established and are limited to observations in individual species (see also Section 30.5.1.1.3). Shell thinning in modern planktonic foraminifera (collected 1997–2004) in the Southern Ocean compared to those from the Holocene and before was attributed to anthropogenic ocean acidification (Moy et al., 2009). Both anthropogenic OA and the upwelling of CO_2-rich deep waters (Section 30.5.4.1.4) were held responsible for shell thinning in planktonic foraminifera in the Arabian Sea over the last century (de Moel et al., 2009) or in live pteropods collected in 2008 in the Southern Ocean (*medium evidence*, *medium agreement*; Bednaršek et al., 2012). However, no changes were observed in a 57-year record of the composition and abundance of calcifying zooplankton in the increasingly acidified California Current System (Ohman et al., 2009). Possible explanations for the absence of significant responses in some studies include insufficient lengths of time series (Section 6.1.2), organisms being pre-adapted to naturally high CO_2 in upwelling or other systems, linked to a low signal-to-noise ratio, or the difficulty of detecting small OA effects in comparison with larger ecosystem effects of other drivers such as temperature, for example, in calcifying plankton (Beaugrand et

al., 2013). Similarly, declines in coral calcification and performance in the field (De'ath et al., 2009) were attributed to thermal extremes, but may also include an as-yet unclear contribution from OA.

6.3.2.5.2. Microbial communities and nutrient cycles

Laboratory experiments, coastal mesocosm studies (Weinbauer et al., 2011), and field experiments (Beman et al., 2011; Law et al., 2012) have yielded various, sometimes conflicting, results on the effects of CO_2 on microbial processes. From a meta-analysis of available data, Liu et al. (2010) conclude that the rates of several microbial processes will be affected by OA, some positively, others negatively. The potential of the microbial community to adapt to ocean acidification and maintain functionality, either by genetic change at the species level or through the replacement of sensitive species or groups at the community level, remains to be explored further. At the present time there is insufficient field-based evidence to conclude that elevated CO_2 will affect natural assemblages of microorganisms (*limited evidence*, *low agreement*) with the possible exception of the negative impact on calcification (Joint et al., 2011).

Experimental studies on OA effects (through reduced pH or increased CO_2) on autotrophic and heterotrophic microbial production have provided inconsistent results. Microbes are characterized by large diversity and broad environmental adaptation, and hence may respond to environmental challenges by exploiting such diversity via species replacements (Krause et al., 2012). This makes it difficult to project the findings of laboratory experiments investigating the response of microbes to OA to the ecosystem level. Relevant variables include cellular elemental stoichiometry (C:N:P ratios; Riebesell, 2004; Fu et al., 2007), rates of CO_2 and N_2 fixation (Riebesell, 2004; Hutchins et al., 2007, 2009), rates of nitrification (Beman et al., 2011), changes in the proportion of dissolved organic carbon (i.e., DOC) to particulate photosynthate produced during carbon fixation (Kim et al., 2011), and the response of viruses (Danovaro et al., 2011).

Field experiments led to the projection that nitrification rates (ammonia oxidation to nitrite and nitrite oxidation to nitrate) of bacteria and archaea will be reduced by 3 to 44% when pH is reduced by 0.05 to 0.14 (Beman et al., 2011), corresponding to a mean rise in CO_2 by approximately 100 µatm. The reported decrease in nitrification occurred regardless of natural pH variability, providing no evidence for acclimation of the nitrifiers to reduced pH, for example, in upwelling areas. Potential changes in microbial cell abundance, possibly as a result of lower cellular nitrification rates, could further decrease the total rate of nitrification.

It remains unclear whether OA has contributed to the systematic changes in phytoplankton abundance and community structure observed over recent decades, which have largely been attributed to warming (Chavez et al., 2011). In natural assemblages from coastal and polar waters, NPP is stimulated by increased CO_2 (*medium confidence*; Riebesell et al., 2008; Tortell et al., 2008). Small differences in CO_2 sensitivity may lead to pronounced shifts in the dominance of species (Tortell et al., 2008; Beaufort et al., 2011). Quantification of the calcite mass of the coccolithophore community in the present ocean and over the last 40 kyr were in large part attributed to shifts between differently calcified species and morphotypes according to carbonate chemistry (Beaufort et al., 2011). The same study, however, also observed heavily calcified *Emiliania huxleyi* morphotypes in upwelling systems characterized by low pH, a finding which highlights the complexity of assemblage-level responses and may indicate pre-adaptation to elevated pCO_2. Owing to the complex response patterns, it is not possible to project ecosystem-level effects from effects on coccolithophore calcification in monospecific culture experiments (*low confidence*). Projections of OA impacts on phytoplankton become even more complicated by synergistic interactions with other drivers (Boyd, 2011; see also Section 6.3.5).

6.3.2.5.3. Macrophytes and macrofauna

Macrofauna and macrophyte communities have been studied in mesocosms and in ecosystems exposed to shifted upwelling regimes or at natural volcanic CO_2 vents (Fabricius et al., 2011; Kroeker et al., 2011). The latter are considered as natural analogs of future ocean acidification. An 8-year trend of (variable) pH decline in upwelled waters along the Northeast Pacific coast was paralleled by shifts in community composition, where shelled species like mussels were replaced by fleshy algae and barnacles (Wootton et al., 2008). Macrofaunal calcifiers at CO_2 vents (Hall-Spencer et al., 2008; Fabricius et al., 2011) and in mesocoms (Christen et al., 2013) display a lowering of species richness. These findings suggest that non-calcifiers increasingly outcompete calcifiers once pH_T decreases to a mean of 7.8 to 7.7 (*medium confidence*). Finally, a loss of calcifiers from mesocosms occurred around 0.5 units below the pH values expected from OA under RCP8.5 by 2100 (*medium confidence*; Christen et al., 2013). At CO_2 seeps, calcitic bryozoans replace coralline algae, which have more soluble high-calcite skeletons (Martin et al., 2008). Seagrasses and non-calcifying algae gain a competitive advantage (Fabricius et al., 2011). Coral communities exposed to high pCO_2 waters (from upwelling or seeps) have lower growth, calcification, and biodiversity (Manzello et al., 2008; Fabricius et al., 2011), resulting in a shift from net accretion to erosion (Box CC-CR). The use of seeps as analogs of future OA is limited as pH variability is high at these sites, such that effective values may be lower than indicated by the average change (Hall-Spencer et al., 2008; Porzio et al., 2011). During periods of high pH at the seeps, they are recolonized by invertebrates and fishes from neighboring areas with normal pH, compromising assessments of long-term sensitivity thresholds. Overall, findings available from mesocosms and natural analogs indicate losses in diversity, biomass, and trophic complexity of benthic marine communities due to elevated CO_2 (*high confidence*) and support the projection of similar shifts in other systems with continued OA (*medium confidence*).

Enhanced freshwater input by poorly buffered rivers or by precipitation, into estuaries, brackish oceans like the Baltic (Section 30.5.3.1.4), and into freshening polar oceans, reduces salinity and alkalinity at rising atmospheric pCO_2 and thereby, alters the carbonate system and enhances OA (Section 6.1.1). Estuaries usually have OMZs, where background pCO_2 is elevated. Its reduction by dilution causes the acidification effect to be somewhat less. Enhanced pH reduction and variability in hyposaline waters may constrain the distribution of sensitive species further (*low confidence*; Miller et al., 2009; Denman et al., 2011).

6.3.2.5.4. Conclusions

Natural analogs and laboratory and mesocosm experiments provide evidence for differential effects of ocean acidification on species and communities. Sensitivity to OA is species specific (*high confidence*); differential sensitivities and associated shifts in performance and distribution will change predator-prey relationships and competitive interactions (*low* to *medium confidence*). OA may stimulate global net primary production (*low confidence*) and nitrogen fixation (*medium confidence*). OA will increase the abundance and primary production of non-calcifying macrophytes, but will be harmful to calcifying algae and many heterotrophs (*medium confidence*). Ecosystems relying on calcified structures and at risk of dissolution under OA include warm-water coral reefs (*high confidence*) and their cold-water equivalent (*medium confidence*). Further studies need to explore how OA may change the composition of communities, impact food webs, and affect higher trophic levels.

6.3.3. Life in Hypoxia and Anoxia

6.3.3.1. Principles

Hypoxia constrains organisms which rely on aerobic metabolism (Section 6.1.1; FAQ 6.2). Below O_2 concentrations of 60 µmol kg^{-1}, commonly termed hypoxic (Section 6.1.1.3), communities undergo species losses and replacements and are transformed into communities with species showing characteristic hypoxia adaptations. However, O_2 can limit animal life at even higher levels, just below air saturation (Gilly et al., 2013). Organisms' tolerance thresholds have been defined by either the critical O_2 partial pressure (P_c) or concentration (O_2crit). Thresholds vary across domains and are highest for large multicellular organisms. Among these, the P_c at rest varies depending on species, body size, and life stage. In animals below the P_c aerobic metabolic rate fails to be maintained and anaerobic metabolism contributes to energy production (Pörtner and Grieshaber, 1993). The critical oxygen threshold is set by the capacity of ventilatory and circulatory systems to supply O_2 and cover demand. The threshold increases once metabolism is stimulated by muscular activity, temperature, or food uptake (Pörtner, 2002a; Ekau et al., 2010; Seibel, 2011; see also Figure 6-11). At extreme temperatures, O_2crit approaches the oxygen content of air-saturated water (Pörtner, 2010; McBryan et al., 2013), indicating high sensitivity to hypoxia in the warmth. Most animals can only sustain anaerobic metabolism temporarily, even if they are energy efficient and survive long periods of anoxia (Grieshaber et al., 1994). Such time-limited tolerance is higher in large than in small individuals or larvae, related to the higher capacity of anaerobic metabolism in large specimens (Gray et al., 2002; Jessen et al., 2009).

6.3.3.2. Microbes

Bacteria and protists consume ambient oxygen down to very low levels in oxygen minimum zones and sustain OMZs by their metabolic diversity (Figure 6-11; WGI AR5 Section 3.8.3). OMZs form habitat for both anaerobic and aerobic microbes that can utilize very low (<1 µmol kg^{-1}) O_2 concentrations (Stolper et al., 2010). Hypoxia is paralleled by elevated pCO_2 and enhanced acidification. Expanding OMZs will select for the proliferation of spezialized microbes (*high confidence*).

6.3.3.3. Animals and Plants

In mesopelagic OMZs, zooplankton also contribute to the development of hypoxia (Robinson et al., 2010; see also FAQ 6.2). During daytime zooplankton congregate at the upper margin of OMZs, where the degradation of organic material causes intensified respiration and oxygen depletion (Bianchi et al., 2013). Animals living permanently in the OMZ still cover virtually all energy demand by aerobic metabolism. This requires special adaptations leading to a reduction in O_2 and energy demand, and the improved ability to use available O_2 efficiently. Enhanced hypoxia tolerance reflected in low O_2crit values is supported by small body size and by cold temperature (Vetter et al., 1994; Pörtner, 2002b; Levin et al., 2009). Accordingly, low O_2 levels support abundant meiofauna (very small fauna, <1 mm) that benefit from abundant food and reduced predation by larger organisms (Levin, 2003). Under suboxia only specialists can survive (Vaquer-Sunyer and Duarte, 2008). Expansion of suboxic and anoxic centres of pelagic OMZs and benthic dead zones will lead to loss of habitat for animal life (*high confidence*).

Large, more active animals such as fishes, crustaceans, and muscular (as opposed to ammoniacal) squids tend to have high O_2 demands associated with high O_2crit thresholds, and are therefore excluded from permanently hypoxic water bodies. However, even in high-activity animal groups some specialists such as Humboldt squid or bigeye tuna have adapted to enter hypoxic environments though only temporarily (Richards et al., 2009; Seibel, 2011). The time-limited tolerance of animals to hypoxia below the O_2crit is maximized by the depression of energy demand, for example, during periods of metabolic arrest (e.g., developmental arrest or diapause of copepods; Auel et al., 2005). Hypoxia-adapted lifeforms will benefit from expanding OMZs (*high confidence*).

There is little information on the hypoxia sensitivity of macrophytes or their O_2crit values. In eelgrass (*Zostera marina*), warming causes the hypoxia threshold to rise due to a strong increase in tissue respiration. Concomitant water or sediment hypoxia can elicit tissue anoxia and sudden die-offs (Raun and Borum, 2013). By contrast, macroalgae attached to rocks rarely encounter anoxia (Raven and Scrimgeour, 1997). Expanding benthic OMZs will constrain the distribution of macrophytes (*medium confidence*).

6.3.3.4. Ecosystems

OMZs, shoaling, and expanding vertically and laterally (Gilly et al., 2013) will cause habitat and abundance losses for intolerant taxa such as mesopelagic (Koslow et al., 2011) and epipelagic fishes with a high O_2 demand (*medium confidence*; Prince et al., 2010; Stramma et al., 2012; see also FAQ 6.2). In line with the distribution of hypoxia sensitivities (Figure 6-11; Sections 6.3.3.1, 6.3.3.3), expanding OMZs will further constrain the distribution of key zooplankton and nekton species and influence their diurnal and ontogenetic vertical migrations (*medium confidence*; Ekau et al., 2010). The composition of microbial and faunal pelagic communities will shift from diverse mid-water assemblages to

migrant biota that return to oxygenated surface waters at night (Seibel, 2011). Dissolved O_2, among other factors, plays an important role in shaping large alternating fluctuations of sardine and anchovy abundances, particularly off Peru. Anchovies are not strongly affected by a shallow oxycline (<10 m), while sardines actively avoid such conditions (Bertrand et al., 2010). Where OMZs intersect the continential shelves, groundfishes (McClatchie et al., 2010) and large benthic invertebrates such as crabs display high mortalities (Chan et al., 2008). Susceptibility of early life stages to hypoxia in both pelagic and benthic ecosystems (Ekau et al., 2010) threatens population survival. Effects of hypoxia propagate along the food chain, constraining fish stocks and top predators (*high confidence*; Stramma et al., 2010). Hypoxia reduces biodiversity (Levin et al., 2009; Gooday et al., 2010) and causes the marginalization of calcifiers, due to low metabolic rates and high pCO_2 (*high confidence*; Levin, 2003; Levin et al., 2009).

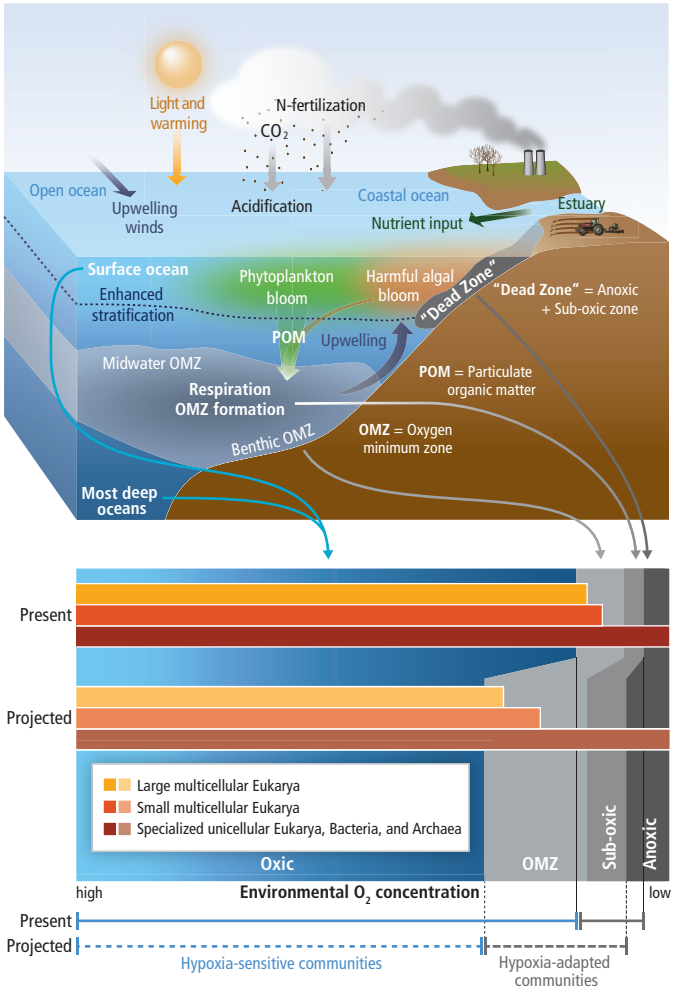


Figure 6-11 | (a) Principal mechanisms underlying the formation of hypoxic conditions and their biological background (modified from Levin et al., 2009; Levin and Sibuet, 2012). The buoyancy flux from fluvial discharges produces sharp density stratification at the base of the freshened layer (also valid for ice melt and high precipitation) near the surface and, hence, vertical mixing is greatly reduced. In consequence, the nutrient inputs from the river and the atmosphere accumulate in a narrow upper layer, leading to blooms of phytoplankton, possibly including harmful algae. The enhancement of oxygen consumption due to aerobic decomposition of sinking particulate organic matter (POM) results in hypoxic conditions of benthic and mid-water oxygen minimum zones (OMZs). Enrichment of nutrients (eutrophication) results in coastal dead zones. In the open oceans, heating of the upper layer increases stratification, while the wind-driven upwelling of hypoxic, nutrient-rich water from deeper layers adds to the formation of the OMZs (Box CC-UP). (b) Distribution of free-living marine organisms (microbes such as archaea, bacteria, protists, small and large multicellular animals, and plants) across the ranges of O_2 concentrations in various water layers. Hypoxia tolerance is enhanced in small compared to large organisms, allowing unicellular species and small animals to thrive in extremely hypoxic habitats. Species richness and body size of animals decrease with falling O_2 levels.

The expansion and enhanced variability of OMZs increases dissimilatory nitrate reduction and anaerobic ammonium oxidation (anammox), both releasing N_2 into the atmosphere, reducing the availability of fixed nitrogen, and limiting oceanic primary productivity (*medium confidence*). Water column denitrification and N_2 fixation are spatially and temporally variable (*limited evidence*, *low confidence*), suggesting that climate effects on these processes are unlikely to operate uniformly (Brandes et al., 2007; Fernandez et al., 2011; Franz et al., 2012).

If O_2 levels decline and OMZs expand, tolerant taxa, such as anaerobic bacteria (Ulloa et al., 2012), gelatinous zooplankton (medusae, ctenophores), selected fishes (gobies, hake), and possibly selected cephalopods (Gilly et al., 2006; Bazzino et al., 2010) will respond with range expansions or population growth. Similar phenomena are expected with intensified upwelling causing extensive mortalities of coastal fishes and invertebrates (Box CC-UP). A community change toward hypoxia-tolerant fauna will occur in mid-water (*high confidence*). The diversity of macroorganisms will decrease and, finally, higher marine organisms will disappear and heterotrophic microorganisms will dominate (*high confidence*). In isolated water bodies such as the Black Sea, warming will lead to the expansion of anoxia and hydrogen sulphide (H_2S) poisoning, reduce pelagic and bottom faunal distributions, and shape trophic relations, energy flows, and productivity (Daskalov, 2003; Fashchuk, 2011).

6.3.4. Mixed Layer Depth and Light Shaping Net Primary Production

The upper ocean is characterized by physical and chemical gradients in the surface mixed layer that influence the magnitude of photosynthetic carbon fixation, often termed net primary production (NPP). The availability of light and nutrients to photoautotrophs sets daily rates of NPP and may be altered directly or indirectly, through changing mixed layer depths, shifts in the circulation regime at different spatial scales, and the physical displacement of organisms (Section 6.1.1.4; Box CC-PP; Figure 6-2). A changing climate will affect mixed layer depth, cloudiness, and/or sea ice areal extent and thickness and thereby modulate NPP (*high confidence*). A stronger vertical density gradient will reduce the communication between the sunlit upper ocean where photosynthesis takes place and the underlying nutrient-rich waters (Figure 6-2). The supplies of plant nutrients (macro-nutrients) such as nitrate, and of micro-nutrients such as iron (Pitchford and Brindley, 1999) vary seasonally (Boyd, 2002) and regionally (Moore et al., 2002), such that NPP may be simultaneously limited (co-limited) by more than one resource (Saito et al., 2008; see also Section 6.3.5).

The changing range and intensity of underwater light will lead to changes in NPP as well as in phytoplankton community composition (Doney, 2006; Boyd et al., 2010). The response of phytoplankton to

changing sunlight involves photo-physiological acclimation via changes in cellular chlorophyll, but such acclimation is constrained by unidentified limits (Falkowski and Raven, 1997). A longer growing season, with more sea ice-free days between 1998 and 2009, may have increased NPP in open Arctic waters (Arrigo and van Dijken, 2011; see also Box CC-PP), complemented by massive under-ice blooms as seen in 2011, favored by light that penetrates surface melt ponds and thinner, for example, first-year ice (Arrigo et al., 2012). There are also reports of increased incidences of high phytoplankton stocks, and hence of greater NPP, deeper in the water column (i.e., where it cannot be detected by satellite) during summer in the Arctic, which have implications to assessing changes in NPP from space (Hill et al., 2013). Little is known about shifts from sea ice algae to free-drifting phytoplankton expected with a decrease in sea ice cover and effects of increased light in polar waters in the coming decades (*low confidence*). In the Arctic, summer ice melt led to a rapid export of sea-ice algae to the deep ocean (Boetius et al., 2013). As some krill feed primarily on sea ice algae, it is unclear (*low confidence*) whether they will adapt to feeding mainly on free-drifting phytoplankton (Smetacek and Nichol, 2005).

A range of time series observations, from *in situ* phytoplankton abundances to satellite remote sensing, have been used to assess whether phytoplankton stocks and hence rates of NPP have altered over recent decades. Increases in phytoplankton stocks were found in regions where colder waters had warmed in the Northeast Atlantic, whereas the opposite trend was observed for warm-water regions from a phytoplankton abundance time series (Richardson and Schoeman, 2004). Lower chlorophyll concentrations at warmer SSTs in nutrient-poor low-latitude waters, based on satellite ocean color data, have been interpreted as an effect of increased stratification on phytoplankton stocks. It has thus been suggested that expanding, permanently stratified, low-chlorophyll, tropical regions (WGI AR5 Chapter 3) indicate declining phytoplankton stocks in the warming oligotrophic waters of the North and South Pacific and North and South Atlantic (*limited evidence*, *low agreement* due to methodological uncertainties; Box CC-PP; Polovina et al., 2008; Signorini and McClain, 2012; see also Section 30.5.1.1.2). Furthermore, a transition to conditions favoring increased frequency or even permanence of El Niño in a warmer future (Wara et al., 2005) and further expansion of subtropical ocean gyres (Polovina et al., 2008; see also Section 30.5.6) may lead to lower global ocean NPP (*low* to *medium confidence*).

However, these long-term "blended" projections (i.e., constructing a biomass time series using multiple proxies such as ocean transparency) of a global decrease in phytoplankton biomass (Boyce et al., 2010) have been refuted (Mackas, 2011; McQuatters-Gollop et al., 2011; Rykaczewski and Dunne, 2011). Time series shorter than 20 years do not resolve impacts of bi-decadal variation such as the Pacific Decadal Oscillation or the lunar nodal cycle (e.g., Watanabe et al., 2008; Henson et al., 2010). Analysis of continental shelf ecosystems, including field data in the most productive upwelling areas covering the last 20 years (e.g., Chavez et al., 2011), revealed a large variety of trends at scales of several decades but a general increase in NPP on most shelves (Sherman and Hempel, 2009; Bode et al., 2011), possibly caused by natural climate variability, anthropogenic climate change, and/or anthropogenic eutrophication. Recent field measurements document increasing quantities of both anthropogenic fixed N (Duce et al., 2008) and biologically fixed atmospheric nitrogen (Mouriño-Carballido et al., 2011) entering the open ocean, which could lead to increased NPP especially in warm, stratified tropical and subtropical oceans provided sufficient phosphate and other growth requirements are present (*low confidence*; e.g., Sohm et al., 2011).

For heterotrophs, from bacteria to fish, mammals, and birds, the uptake of organic material as food, ultimately provided by NPP, is central not only to productivity but also for fueling energy-consuming functions including the resistance of organisms to environmental change and pathogens (Sections 6.3.1-2). Any direct influence of climate on the abundance and quality of feed organisms will thus translate to indirect effects on the productivity and well-being of foraging animals (*high confidence*; Figures 6-5a, 6-7a, 6-12).

Overall, pelagic systems respond to climate change by region-specific changes in productivity with the projection of a small net reduction in global ocean NPP by 2100 (*medium confidence*; Box CC-PP). The spatial reorganization of NPP between latitudes affects higher trophic levels by alteration of the composition and functioning of pelagic communities (*medium confidence*).

6.3.5. Concurrent Responses to Multiple Drivers

Climate change alters oceanic properties globally, with concurrent changes in temperature, dissolved CO_2 and O_2, light, and nutrient concentrations (e.g., Sarmiento et al., 1998; Matear and Hirst, 1999; Boyd and Doney, 2002; Ekau et al., 2010; see also Figure 6-2). Additional direct human interventions at regional scale comprise the introduction of non-native species, overfishing, pollution, long-range atmospheric transport of nitrogen, point-source eutrophication, and habitat destruction (Carlton, 2000; Boyd and Hutchins, 2012). Worldwide alterations in marine ecosystems (Pauly et al., 1998; Österblom et al., 2007) have been linked to direct human activities, especially fishing (Frank et al., 2005; deYoung et al., 2008; Casini et al., 2009), but may also be caused to some extent by climate variability and change (Cheung et al., 2013a).

Alteration of each individual property has pronounced effects on organisms from microbes to animals, and hence on ecosystems (Sections 6.3.1-4). The cumulative effects of these factors will result in complex patterns of change, from organismal physiology to the areal extent and boundaries of biogeographic regions (Table 6-4). In many organisms, effects of ocean acidification interact with those of other key drivers such as temperature and hypoxia (Boyd, 2011; Gruber, 2011; Pörtner, 2012) and translate from molecular to ecosystem level impacts. In phytoplankton, low light (Zondervan et al., 2002) or nitrogen limitation (Sciandra et al., 2003) limit beneficial OA effects on photosynthesis and have a strong negative effect on plankton calcification (Rokitta and Rost, 2012). Nutrients and light support functional adjustments to OA through gene expression changes (Dyhrman et al., 2006; Richier et al., 2009).

Similar to today, paleo-events such as the Palaeocene-Eocene Boundary demonstrate concurrent warming, enhanced stratification of the oceans, deoxygenation of deeper waters, and OA, albeit at a rate more than 10 times slower than today's rate (Section 6.1.2). Both the complexity of paleo-ecosystem changes and the complexity of present effects confound

the clear attribution of biological trends to individual drivers (Parmesan et al., 2011). For warming and hypoxia, changes are accelerated by effects of shifting seasonal or even diurnal extremes and their frequency on organisms and ecosystems (*medium evidence*, *medium agreement*) (e.g., Pörtner and Knust, 2007; Díaz and Rosenberg, 2008). This may also apply to effects of anthropogenic OA (*limited evidence*, *low agreement*).

6.3.5.1. Principles

Effects of various climate drivers on ocean ecosystems are intertwined and effects may be exacerbated by responses of biota. For example, warming reduces O_2 solubility and enhances biotic O_2 demand, which exacerbates hypoxia, produces CO_2, and causes acidification (Millero, 1995; Brewer and Peltzer, 2009). Drivers act with either additive, synergistic (i.e., amplification of) or antagonistic (i.e., diminution of) effects. A meta-analysis of 171 experimental studies that exposed marine systems to two or more drivers identified cumulative effects that were additive (26%), synergistic (36%), or antagonistic (38%) (Crain et al., 2008). Effects range from direct impacts of ocean warming on organismal physiology (Pörtner and Knust, 2007) to ocean acidification acting together with warming, for example, on coccolithophore calcite production and abundances (Feng et al., 2009), or with hypoxia and/or salinity changes (Table 6-4). Interactions of predominantly temperature, ocean acidification, and hypoxia have *likely* been involved in climate-driven evolutionary crises during Earth history (Pörtner et al., 2005; see also Section 6.1.2).

Effects on individual organisms may also reflect intertwined impacts of ocean warming, acidification, and hypoxia, which may operate through interrelated functional principles (Pörtner, 2012). Such knowledge helps to reconcile apparently contrasting findings. For example, warming toward the thermal optimum (Figure 6-5a) stimulates resistance to OA; CO_2-induced disturbances of growth and calcification were reversed by concomitant warming (Findlay et al., 2010; Sheppard-Brennand et al., 2010; Walther et al., 2011). Warming to above optimum temperatures, however, constrains performance and exacerbates sensitivity to hypoxia and/or elevated CO_2 (Figure 6-5, e.g., via decreased calcification; Rodolfo-Metalpa et al., 2011). Both hypoxia and/or elevated CO_2 in turn enhance heat sensitivity, as seen for CO_2 in crustaceans (via decreased heat limits: Walther et al., 2009; Findlay et al., 2010), coral reef fishes (via reduced performance: Munday et al., 2009b), and corals (via decreased calcification and CO_2-enhanced bleaching: Reynaud et al., 2003; Anthony et al., 2008). This translates into a narrowing of the thermal niche (Walther et al., 2009; see also Figure 6-5), which will shrink biogeographic ranges, affect species interactions, and shift phenologies (Figure 6-7a). Hence, extreme warming and hypoxia exacerbate CO_2 effects and vice versa (*medium confidence*). Such principles need to be reconfirmed across organism taxa (Pörtner, 2012).

Differences in organism adaptation to a climate zone's characteristic temperatures, temperature variability, oxygen content, and ocean chemistry may shape vulnerability to climate change. In high polar species evolutionary cold adaptation enhances vulnerability to warming

Table 6-4 | Potential interactions between modes of anthropogenic forcing (environmental; foodwebs; harvesting) on different levels of biological organisation. These interactions, from simple to complex, are illustrated with examples from the published literature. Unknown denotes no published information is available for each of these categories. NA denotes not applicable for this category.

Biological organization studied at ecosystem level	Anthropogenic forcing			
	Single environmental driver	Multiple environmental drivers	Fishing/foodwebs	Fishing/climate change
Individuals	Lab experiments and field observations show that warming alters organismal physiology and thereby growth (Pörtner and Knust, 2007).	Shipboard manipulation experiment addressing interactive effects of temperature and CO_2 on coccolithophore calcification (Feng et al., 2009).	NA	Unknown
Population	Physiological effects of warming change population abundance *in situ* (Pörtner and Knust, 2007). Lab cultures show how altered pH elicits different responses of coccolithophore species (Langer et al., 2006).	Lab cultures show differential responses of cyanobacterial groups to temperature and CO_2 (Fu et al., 2007).	Altered maturation age and growth rate of populations due to fishing (Fairweather et al., 2006; Hseih et al., 2006).	Interactive effects on cod populations of fishing and alteration of salinity (Lindegren et al., 2010).
Ecosystem	Mesocosm experiments simulating the effect of individual drivers (e.g., ocean acidification effects on benthos: Christen et al., 2013; and on pelagic communities: Riebesell et al., 2013).	Mesocosm experiments studying differential effects of light and temperature, on copepods versus diatoms (Lewandowska and Sommer, 2010).	Effects of fishing on ecosystem structure — trophic cascades (Frank et al., 2005).	Interplay of fishing and climate pressures on ecosystems promotes lower trophic levels (Kirby et al., 2009); enhances diversity loss in benthic communities (Griffith et al., 2011).
Biome	Time series observations on warming and geographical shifts of zooplankton biomes (Beaugrand et al., 2009).	Unknown	Unknown	Unknown

Approaches: = Experiments (lab or field) = Observations = Modeling = Not applied

(*medium confidence*). In OMZs, marine sediments, and in polar waters (due to high solubility in the cold), CO_2 levels are elevated and adaptation may reduce sensitivity and reliance on calcified structures (Clark et al., 2009; Walther et al., 2011; Maas et al., 2012). The observed shift from "overcalcified" to "weakly calcified" coccolithophores *Emiliania huxleyi* in cold waters may reflect a related shift in ecotype dominance (*limited evidence*, *medium agreement*; Cubillos et al., 2007).

Despite such potential adaptation, polar calcifiers exposed to higher CO_2 and lower carbonate saturation levels have been hypothesized to be highly sensitive to further CO_2 accumulation (*limited evidence*, *high agreement*; Orr et al., 2005). Here it appears relevant that cold temperature reduces energy demand and thereby lowers resistance to ocean acidification. Both energy demand and resistance are higher in eurytherms than in high polar and deep sea stenotherms (*limited evidence*, *medium agreement*; Pörtner, 2006; e.g., crustaceans: Pane and Barry, 2007: cf. Whiteley, 2011). In turn, tropical species may be more sensitive than temperate zone species (Pörtner et al., 2011). This rough differentiation of sensitivity is complicated by the local adaptation of populations from within-species genetic variability (*low confidence*).

Temperature influences hypoxia sensitivity (Section 6.3.3). Warming causes the minimum tolerated O_2 level to rise, enhancing vulnerability (*high confidence*). Conversely, hypoxia enhances vulnerability to warming in animals. This may occur fastest in warm oceans, where metabolic rates are higher and animals live closer to upper thermal limits (*medium confidence*; Pörtner, 2010). However, evolutionary adaptation has led to high hypoxia tolerance (low P_c or O_2crit values) in some warm-adapted coral reef fishes. Further warming then causes a rise in P_c which cannot be compensated for (Nilsson et al., 2010). Limits to hypoxia adaptation coincide with upper thermal limits (*medium confidence*).

Complexity in responses rises with the number of drivers involved. Enhanced river runoff and increased precipitation cause a shift from marine to more brackish and even freshwater communities, with unclear consequences for effects of other drivers. Falling primary production reduces resilience of higher trophic levels (Kirby and Beaugrand, 2009; Stock et al., 2011). The introduction of non-indigenous species, when supported by climate-induced shifts in interactions, may promote the displacement of ecotypes and shifts in ecosystem functioning, for example, in the Mediterranean Sea (Occhipinti-Ambrogi, 2007; Coll et al., 2010).

6.3.5.2. Microbes

Both synergistic and antagonistic effects of multiple drivers on microbial biota in the surface ocean have been observed in manipulation or modeling experiments (Folt et al., 1999; Boyd et al., 2010; Gruber, 2011). The productivity of many microbes was simultaneously limited by, for example, availability of nitrate and phosphate, cobalt and iron (Saito et al., 2002; Bertrand et al., 2007), or iron and light (Boyd et al., 2010; see also Section 6.2.2). Warming and high CO_2 synergistically enhanced photo-physiological rates of the cyanobacterium *Synechococcus*, whereas the cyanobacterial group *Prochlorococcus* showed no change (Fu et al., 2007). The magnitude of CO_2 effects on growth, fixation rates, or elemental ratios within single species is often strongly modulated by nutrient availability and light conditions (e.g., Sciandra et al., 2003; Zondervan et al., 2002; Kranz et al., 2010). Such differences cause floristic shifts in phytoplankton with the potential to restructure predator-prey interactions (Table 6-4).

Co-limiting factors vary by group, such as nitrogen fixers (e.g., Hutchins et al., 2007; Kranz et al., 2010), diatoms (Boyd et al., 2010), and coccolithophores (e.g., Feng et al., 2009; Rokitta and Rost, 2012). This limits the ability to project climate change effects (Boyd et al., 2010). The most reliable projections at ocean basin scale come from modeling, which mainly points to synergistic effects, such as those of elevated CO_2, hypoxia, and warming. For example, OA is projected to alter sinking particles (C:N ratio and/or reduced calcite content and slower sinking) with a consequent knock-on effect on water column O_2 demand already stimulated by warming, thereby causing expansion of OMZs (Gruber, 2011).

6.3.5.3. Animals and Plants

High oxygen availability alleviates thermal stress as seen in fish and mollusks (Mark et al., 2002; Pörtner et al., 2006). Conversely, hypoxia reduces heat tolerance (Section 6.3.5.1), but acclimation to hypoxia compensates for this and increases thermal tolerance (Burleson and Silva, 2011), for example, by enhancing blood pigment content or reducing energy demand. Tolerances to hypoxia and to high temperature may positively correlate in some fishes, indicating potential for adaptive evolution under climate change (*low confidence*; McBryan et al., 2013).

As a consequence of hypoxia narrowing thermal ranges (Section 6.3.5.1), combined warming and expanding hypoxia may cause mid-water mesopelagic and demersal fish stocks to decline at rates much quicker than anticipated in the California Current Ecosystem (McClatchie et al., 2010; Koslow et al., 2011). In benthic fauna, warming will also increase vulnerability to hypoxia. Experiments showed a rise in lethal oxygen concentrations by 25% and thereby reducing survival by 36% at 4°C warmer temperatures (Vaquer-Sunyer and Duarte, 2011). Hence, warming is expected to expand the area of ecosystems affected by hypoxia even if oxygen concentrations remain unchanged (*high confidence*). Under combined hypoxia and warming, CO_2 can extend short-term passive tolerance (despite constraining long-term tolerance). It facilitates a reduction in energy demand (Reipschläger et al., 1997; Pörtner et al., 2000), thereby extending survival of transient extremes of temperatures or hypoxia (*medium confidence*).

In macroalgae (non-calcifying) light availability modulates the response to elevated pCO_2 and temperature levels (Russell et al., 2011; Sarker et al., 2013). In warm-water corals, warming acting synergistically with CO_2 reduces calcification and increases sensitivity to bleaching (*high confidence*; Anthony et al., 2008). Combined warming and OA following SRES B1 (≈RCP4.5, reduced emission) and A1FI (≈RCP8.5, business-as-usual) scenarios in mesocosms caused losses of symbionts and corals, and a nocturnal decalcification of the reef community in summer. Present-day conditions already imply reduced resilience to episodic extreme events such as cyclones (Dove et al., 2013; see also Box CC-CR).

6.3.5.4. Ecosystems

The cumulative impacts of climate change drivers underlie alterations of species interactions and ecosystem structure and functioning, including changes in trophodynamics and the physical and chemical characteristics of habitats (*high confidence*). These effects combine with more indirect effects, such as shifts in stratification and productivity, expanding oxygen minimum zones, and the changing composition and biomass of food (partly resulting from direct effects on prey organisms) (*high confidence*). These complexities reduce the precision and reliability of quantitative projections (Section 6.5), including uncertainties concerning shifts in upwelling and their future role in global primary production and the development of fish stocks (Box CC-UP).

At the level of animal communities, effects of various drivers remain largely unexplored, some are highly complex. For example, the net eastward shift of Pacific skipjack tuna between 1980 and 2009 was linked to the shifting aggregation of macrozooplankton and micronekton, involving complex interactions of climate variability (due to ENSO; Section 30.5.2), warming ocean surface, shallowing mixed layer depth relative to the position of the warm pool, and the convergence of the pool with the Pacific Equatorial Divergence Province (Lehodey et al., 2011; see also Section 30.5.6.1.1). Interactive drivers will affect the relative performance of interacting species, thereby shifting species ranges, interactions, and food webs (*medium confidence*; Figure 6-7a). Adaptation to various climate zones modifies the roles of light and temperature in seasonalities and species interactions (Bradshaw and Holzapfel, 2010). Moderate hypoxia expansion in warming seas, for example, as the stratified central North Sea (Queste et al., 2013) may well influence the degree of temperature-induced species displacements (Figure 6-7b).

Impacts of climate change on benthic ecosystem engineers can also profoundly alter ecosystems. Tropical corals respond to ocean warming and acidification by increased bleaching, impeded calcification rates, and increased incidence of disease (*high confidence*; Veron et al., 2009; Veron, 2011; see also Sections 6.3.1-2, 30.5.6; Box CC-CR). In coral reefs under multiple stressors, differentiation of these large-scale phenomena into species-specific sensitivities is highly uncertain as trend data are virtually nonexistent (Brainard et al., 2011). Little is known about impacts on deep-water or cold-water corals and sponges, tropical calcified algae, bryozoans, sponges, and tube-forming serpulid worms (Wood, 1999). The reliance of all of these on surface productivity makes them vulnerable to any alteration in food supply. Projected severe stress from increased temperature, hypoxia, and ocean acidification will cause reduced performance and increasing mortality in ecosystem engineers (*high confidence*), and a deterioration of habitat characteristics for other organisms (*medium* to *low confidence*).

As a corollary, shifts in the geographical distributions of marine species (e.g., to higher latitudes or deeper waters; Figure 6-7b; Section 6.5.2) cause changes in community composition and interactions (Harley, 2011; Simpson et al., 2011; Hazen et al., 2013). Some species may gain predominance and abundance from fitness benefits (Figure 6-7) while others become less competitive or easier prey (Occhipinti-Ambrogi, 2007). Thereby, climate change will reassemble communities and affect biodiversity, with differences over time and between biomes and latitudes (*high confidence*; Parmesan and Matthews, 2005; Sala and Knowlton, 2006; Cheung et al., 2009; Parmesan et al., 2011; see also Box CC-PP; Section 6.5).

6.3.6. Food Web Consequences

Community reassembly under climate change involves a change in species composition and strongly alters food web structure, for example, causing shifts in trophic pathways (Kirby and Beaugrand, 2009; Moloney et al., 2011; see also Figure 6-12), some of which are irreversible (Jarre and Shannon, 2010). Through trophic cascades (Cury et al., 2003; Luczak et al., 2011), climate affects predation, competition, and food availability (e.g., via changes in NPP; Figure 6-12; Utne-Palm et al., 2010), including fish stocks (Parsons and Lear, 2001; Brown et al., 2010). Trophic amplification then drives an ecosystem towards a new stable structure or regime, which may be difficult to reverse (Folke et al., 2004). Warming may result in consumer control of food web structure because respiration of heterotrophic zooplankton and bacteria increases more strongly with warming than does photosynthesis of autotrophic phytoplankton (*medium confidence*; O'Connor et al., 2009).

Many impacts of climate change on food webs resemble those caused by fishing, pollution, eutrophication, and associated hypoxia (Section 6.3.3), and habitat change (Brander, 2007); unambiguous attribution to climate remains difficult (*low* to *medium confidence*; Parmesan et al., 2011). Some of these factors also affect food web responses to climate change. Fishing truncates the age and size structure of populations, making them more dependent on annual recruitment and reducing their ability to buffer environmental fluctuations (Genner et al., 2010; Planque et al., 2010; Botsford et al., 2011; see also Figure 6-12). Both adult and larval fishes show greater variability in abundance in exploited compared to unexploited populations (Hsieh et al., 2008). Warming, acidification, and removal of top or competing predators may all contribute to large fluctuations in gelatinous plankton (e.g., jellyfish) populations (*low confidence*; Molinero et al., 2005; Richardson and Gibbons, 2008; Richardson et al., 2009; Condon et al., 2012).

Analyzing impacts on key species provides insight into how individual components of a food web will respond to perturbations. However, projections of future states must include the complex food web interactions that influence the species and system-level responses, which affect stability and resilience of the overall ecosystem (Neutel et al., 2007; Dunne and Williams, 2009; Romanuk et al., 2009). There is no single approach currently available that includes the complex links within and among ecosystems, biogeochemistry, and climate as needed for projections of future states of marine food webs (Fulton, 2011; Moloney et al., 2011). In conclusion, there is *low confidence* in the quantitative projections of such changes (for further discussion see Section 6.5).

6.3.7. Marine Reptiles, Mammals, and Birds

6.3.7.1. Principles

Marine reptiles (turtles, snakes, crocodiles), mammals, and seabirds breathe air but live mostly in water; some shift or expand their ranges

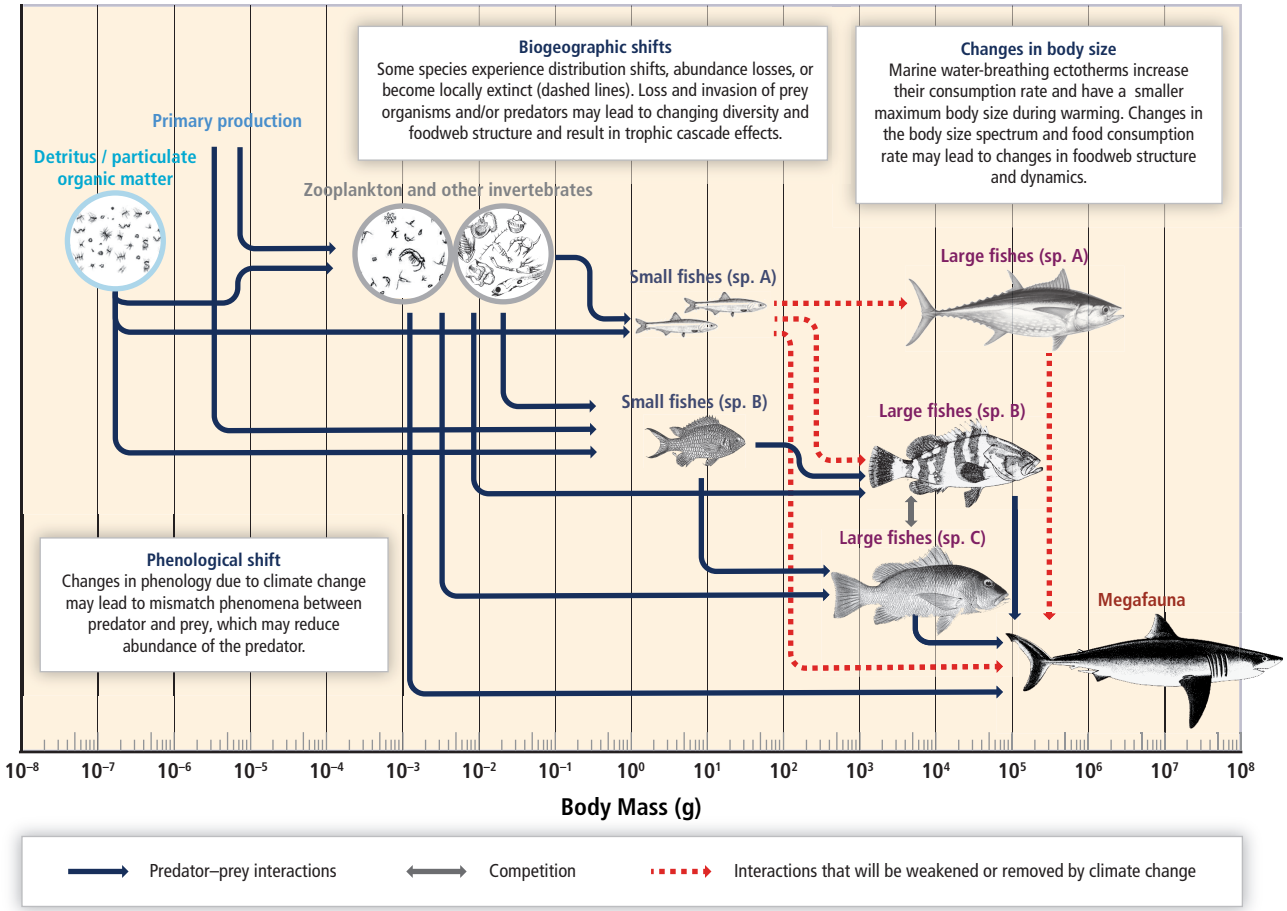


Figure 6-12 | Schematic diagram of expected responses to climate change in a marine food web. A coupled pelagic and benthic food web is structured by the body size spectrum of species. Combined warming, hypoxia, and ocean acidification reduce body size, shift biogeographies, change species composition and abundance, and reconfigure trophic linkages and interaction dynamics. Fishing generally removes large-bodied species and truncates the body-size spectrum of the community. This confounds the detection and attribution of food web responses to climate change. Arrows represent species interactions (e.g., between predator and prey or competitors for food or space). Broken lines reflect the potential loss of populations and trophic linkages due to climate change.

as a result of climate warming. The body temperature of ectothermic reptiles is set by ambient conditions; only at large body size may their body store heat and its temperature be higher than ambient. Reptiles are thus more responsive to temperature than homeothermic seabirds and marine mammals (McMahon and Hays, 2006), which regulate their body temperature by adjusting metabolic heat production and insulation from the environment, a trait beneficial especially in the cold. Various degrees of body core insulation in mammals and birds constrain their distribution to either warmer or colder waters (by poor or high insulation, respectively). However, large body sizes enable some aquatic air breathers to travel across the widest temperature ranges possible in some of the largest migrations on Earth.

Changes in water chemistry and hypoxia have minimal direct influences on the air-breathing vertebrates, reflecting their large independence from physical and chemical drivers in the oceans. There is evidence for increased sound propagation in a CO_2-enriched ocean, but no evidence yet for any effect on biota (Ilyina et al., 2010). If habitat structures offering retreat or ambush disappear, this will increase the energetic costs of life. Warming waters increase the cost of pursuit-diving as prey fishes increase swimming velocity. The predation success of such mammals (e.g., sea lions) and seabirds (e.g., penguins, cormorants) is thus constrained to waters ≤20°C (Cairns et al., 2008), a trend that extrapolates into the future (*low* to *medium confidence*). As prey distributions shift, foragers tied to land between trips may be constrained by the physiological costs of finding prey (Péron et al., 2012; Hazen et al., 2013). If food items are only found in thermally restricted areas or move to greater depths, mammals and birds may become constrained to certain distribution ranges or to the physiological limits of their diving ability (McIntyre et al., 2011). Conversely, hypoxic habitat compression for fishes may facilitate foraging opportunities for their air-breathing predators (Hazen et al., 2009). Accordingly, many air-breathers encounter changing habitat and food availability with climate change (*high confidence*).

6.3.7.2. Field Observations

Some species of seabirds, marine mammals, and sea turtles have responded to the anomalous ocean climate of the 20th century (*high confidence*; Hughes, 2000). There is insufficient information to assess effects on sea snakes or crocodiles. Poleward distribution shifts of turtles consistent with recent warming have been recorded in almost all marine groups. Decadal-scale climate fluctuations affect their recruitment

success and nesting abundance (Van Houtan and Halley, 2011), with an inverse correlation between warming and abundance in various species and regions (Balazs and Chaloupka, 2004; Chaloupka et al., 2008; Mazaris et al., 2009). Extreme weather causes nest flooding, considerably reducing hatching success (Van Houtan and Bass, 2007); projected sea level rise (WGI AR5 Chapter 13) will exacerbate such impact. Those with high fidelity to nesting and foraging sites (Cuevas et al., 2008) are impacted more than those capable of changing those sites (Fish et al., 2009; Hawkes et al., 2009). Continued warming, modulated by changing rainfall (Santidrián Tomillo et al., 2012), may skew turtle sex ratios toward females, increase egg and hatchling mortality (Fuentes et al., 2009), cause earlier onset of nesting (Pike et al., 2006; Mazaris et al., 2008), decrease nesting populations (Chaloupka et al., 2008), and shift dietary breadths (Hawkes et al., 2009), leading to projected recruitment declines (e.g., leatherback turtles; Saba et al., 2012). Vulnerability due to shifting sex ratio alone remains unclear, as nesting beaches have persisted with low production of male hatchlings over decades or longer (*low confidence*; Godfrey et al., 1999; Broderick et al., 2000; Hays et al., 2003). The absence of sea turtles in certain regions may be best explained by the temporal unavailability of food resources or strong thermoclines restricting their bottom foraging abilities (Braun-McNeill et al., 2008; Gardner et al., 2008).

Seabird range modifications probably caused by climate change were recorded in polar areas and the temperate zone of the North Atlantic (Grémillet and Boulinier, 2009). Temperate species have shifted their ranges to higher latitudes in both hemispheres (Bunce et al., 2002; Robinson et al., 2005; La Sorte and Jetz, 2010). Some species, like the king penguin, follow shifting foraging zones (Péron et al., 2012); others, such as the emperor penguin, are affected by changing habitat structure (sea ice; Jenouvrier et al., 2012). Warming causes many bird species to breed earlier (Sydeman and Bograd, 2009). High-latitude, cool-water species undergo extended breeding seasons (Chambers et al., 2011). There is often no agreement, whether changes reflect solely ocean warming, or a combination of factors, such as fishing pressure on seabirds' prey species, sea level rise, and pollution (Galbraith et al., 2005; Votier et al., 2005; Heath et al., 2009). Most shifts in range and seasonal activity involve shifts in trophic relationships (*medium confidence*). Seabirds with narrow geographic domains are expected to be more susceptible to climate change (Chambers et al., 2005; Grémillet and Boulinier, 2009), even leading to local extinctions (e.g., the Galápagos penguin: Vargas et al., 2007; or the marbled murrelet: Becker et al., 2007).

The distribution, phenology, and migratory timing of marine mammals are also shaped by predator-prey dynamics and climate impacts on specific habitats (Calambokidis et al., 2009; Salvadeo et al., 2011). Some marine mammals, that is, dolphin, porpoise, and whale species, shift their distribution poleward to follow the movement of their prey (*medium confidence*; Springer et al., 1999; MacLeod et al., 2005; Simmonds and Isaac, 2007; Salvadeo et al., 2010). As in birds, vulnerability to climate change is high for marine mammals with narrow geographic ranges and high habitat dependence. For example, the critically endangered vaquita, endemic to the Northern Gulf of California, cannot move north because of the land barrier (MacLeod, 2009). The polar bear (Laidre et al., 2008; Rode et al., 2012) and the walrus depend on sea ice as a platform for hunting, resting, and giving birth. For polar bears, access to prey such as ringed seals has been disrupted by the later formation and earlier breakup of sea ice in the eastern Canadian Arctic. Seasonal migrants into the Arctic (fin, minke, gray, killer, humpback whales) may increasingly compete with species adapted to operate in habitat with sea ice (some seals, narwhal, bowhead whale, beluga). Both may benefit from the net loss of sea ice, which will offer them better access to foraging in a pelagic-dominated ecosystem (Moore and Huntington, 2008).

6.3.8. Summary and Conclusions

An organism's capacity to perform, but also its access to food energy fueling that performance, shape its sensitivity to climate change (*high confidence*). Extreme temperatures surpassing the fringes of the thermal envelope cause local abundance losses, extinction, and shifts in temperature-dependent distribution ranges (*high confidence*; Section 6.3.1).

Some climate change effects detected in the field can be attributed to temperature, but few allow clear attribution to other drivers (Sections 6.3.1-5, 6.6). In fishes and invertebrates, specialization in regional climate regimes co-defines sensitivity to warming, acidification, and hypoxia (*high confidence*; Section 6.3.5). In marine mammals, birds, and ectothermic reptiles, changes in life history and population dynamics have often not been directly attributed to climate drivers (*low confidence*), but rather to the availability of habitat and food (*high confidence*; Section 6.3.7).

Natural climatic variability (Figure 6-1) and anthropogenic change, with a strong role of warming, cause large-scale changes in biogeography, abundance, diversity, community composition, and structure of marine species (*very high confidence*; Section 6.3.1). Warming reduces body size (*medium confidence*; Section 6.3.1). Differential species responses modify their interactions across trophic levels through trophic amplification (*medium* to *high confidence*; Section 6.3.6).

Some tropical species and ecosystems exist close to upper thermal limits placing them among the marine ecosystems most affected by climate change (*high confidence*; Section 6.3.1). Corals and coral reefs are primary examples. However, other factors change concomitantly, such that quantifying ecosystem changes attributable to warming or other drivers has not always been possible (Section 6.3.5).

Under future climate change ocean acidification will affect marine organisms and ecosystems for centuries (*high confidence*; Sections 6.3.2, 6.3.5). To date, very few ecosystem-level changes in the field have been attributed to anthropogenic or local ocean acidification (*medium confidence*; Section 6.3.2). Concomitant trends of warming, O_2 depletion, OA, and other drivers prevent clear attribution to OA (Section 6.3.5).

Elevated CO_2 levels stimulate primary production of some macroalgae and seagrass species (*high confidence*), causing them to be more competitive than calcifying organisms (*medium confidence*; Section 6.3.2). High sensitivities to OA are associated with low capacities to maintain pH in internal fluids (*high confidence*). Calcification rates in sensitive invertebrates, including corals, echinoderms, and mollusks, decrease under OA, especially if combined with temperature extremes

Frequently Asked Questions

FAQ 6.4 | What changes in marine ecosystems are likely because of climate change?

There is general consensus among scientists that climate change significantly affects marine ecosystems and may have profound impacts on future ocean biodiversity. Recent changes in the distribution of species as well as species richness within some marine communities and the structure of those communities have been attributed to ocean warming. Projected changes in physical and biogeochemical drivers such as temperature, CO_2 content and acidification, oxygen levels, the availability of nutrients, and the amount of ocean covered by ice will affect marine life.

Overall, climate change will lead to large-scale shifts in the patterns of marine productivity, biodiversity, community composition, and ecosystem structure. Regional extinction of species that are sensitive to climate change will lead to a decrease in species richness. In particular, the impacts of climate change on vulnerable organisms such as warm-water corals are expected to affect associated ecosystems, such as coral reef communities.

Ocean primary production of the phytoplankton at the base of the marine food chain is expected to change but the global patterns of these changes are difficult to project. Existing projections suggest an increase in primary production at high latitudes such as the Arctic and Southern Oceans (because the amount of sunlight available for photosynthesis of phytoplankton goes up as the amount of water covered by ice decreases). Decreases are projected for ocean primary production in the tropics and at mid-latitudes because of reduced nutrient supply. Alteration of the biology, distribution, and seasonal activity of marine organisms will disturb food web interactions such as the grazing of copepods (tiny crustaceans) on planktonic algae, another important foundational level of the marine food chain. Increasing temperature, nutrient fluctuations, and human-induced eutrophication may support the development of harmful algal blooms in coastal areas. Similar effects are expected in upwelling areas where wind and currents bring colder and nutrient-rich water to the surface. Climate change may also cause shifts in the distribution and abundance of pathogens such as those that cause cholera.

Most climate change scenarios foresee a shift or expansion of the ranges of many species of plankton, fish, and invertebrates toward higher latitudes, by tens of kilometers per decade, contributing to changes in species richness and altered community composition. Organisms less likely to shift to higher latitudes because they are more tolerant of the direct effects of climate change or less mobile may also be affected because climate change will alter the existing food webs on which they depend.

In polar areas, populations of species of invertebrates and fish adapted to colder waters may decline as they have no place to go. Some of those species may face local extinction. Some species in semi-enclosed seas such as the Wadden Sea and the Mediterranean Sea also face higher risk of local extinction because land boundaries around those bodies of water will make it difficult for those species to move laterally to escape waters that may be too warm.

(*high confidence*; Section 6.3.5). Thresholds beyond which effects occur can be quantified only with *low confidence*; there are differential sensitivities and thresholds between taxa and species (*high confidence*; Section 6.3.2).

Expansion of oxygen minimum zones leads to community shifts clearly attributable to extreme hypoxia (*high confidence*; Section 6.3.3). Gradual effects of a progressive decline in ocean O_2 levels on communities have not been sufficiently explored.

In general, community reassembly with new species coming in will occur in the transition to future climates (*medium confidence*) and lead to new ecosystem states (*low confidence*; Section 6.3.6). Climate change interacts with top-down human interferences, such as fisheries or other forms of harvesting, which accelerate impacts (*medium confidence*). Nonlinearities challenge the projection of marine ecosystem trajectories (FAQ 6.4).

In microbes, a conceptual foundation suitable to support an integrated understanding of climate impacts on individual species and communities is lacking. Specific physiological responses, such as in primary production, N_2 fixation, or calcification, can be attributed to multiple environmental drivers associated with climate change (*high confidence*; Sections 6.3.1-5).

6.4. Human Activities in Marine Ecosystems: Adaptation Benefits and Threats

Human societies benefit from resources and processes supplied by marine ecosystems, so-called ecosystem services. Attributing and projecting

ecosystem changes and their effects on human communities caused by climate change including ocean acidification is challenging. Insufficient observations compound an understanding of long-term changes and the definition of baseline conditions. Some of the challenges are related to the difficulty of projecting how human communities will adapt to changing marine ecosystem benefits.

6.4.1. Ecosystem Services

Marine ecosystem services (e.g., Chapter 5) include products (food, fuel, biochemical resources), climate regulation and biogeochemical processes (CO_2 uptake, carbon storage, microbial water purification), coastal protection, provision of space and waterways for maritime transport, cultural services (recreational and spiritual opportunities, aesthetic enjoyment), and functions supporting all other ecosystem services (nutrient cycling, photosynthesis, habitat creation). Most components of the marine environment contribute to more than one major category of ecosystem service: for example, ocean primary productivity is classified as a supporting service, but it affects provisioning services via changes in fisheries, generation of fossil fuel resources, regulating services via the global carbon cycle and climate regulation, and cultural services via the enjoyment of a healthy ecosystem. Rarely has economic damage of climate change to a whole ecosystem been evaluated and projected. The projected loss of tropical reef cover due to ocean acidification under SRES A1 and B2 scenarios will cause damages of US$870 and 528 billion (year 2000 value) by 2100, respectively (cost rising with parallel economic growth; Brander et al., 2012; see also Box CC-OA). Such loss is felt most strongly in the respective regions.

6.4.1.1. Food from the Sea

Fisheries provide 3 billion people with almost 20% of their average per capita intake of animal protein (FAO, 2012a), 400 million depend critically on fish for their food (Garcia and Rosenberg, 2010). Total world marine capture fisheries catches stabilized in the mid-1990s at about 90 million tons per year. Marine aquaculture of primarily mollusks and crustaceans contributes more than 63 million tons annually to seafood production, mostly concentrated in coastal areas (FAO, 2012b). The growth of aquaculture has decelerated, but is still considered a development opportunity and a strong need in regions such as Africa and Latin America (Section 7.4.2.2).

Climate-induced shifts in ecosystems and fisheries production will create significant challenges to sustainability and management (Section 7.5.1.1.3), particularly for countries with fewer resources and lower adaptive capacity, including many low-latitude and small island nations (*high confidence*; Allison et al., 2009; Worm et al., 2009; Cooley et al., 2012; see also Sections 7.2.1.2, 7.4.2.1, 30.6.2; WGIII AR5 Section 2.1). Vulnerability will be exacerbated by increases in the frequency and severity of extreme events (e.g., floods or storms) damaging infrastructure, homes, health, livelihoods, or non-marine food security (Kovats et al., 2003; Rosegrant and Cline, 2003; Adger et al., 2005; Haines et al., 2006).

The projected trends in fish stocks will widen the disparity in food security between developing and developed nations. Fish migrations due to warming (Section 6.3.1) have already shifted the composition of fisheries catches (Pinsky and Fogarty, 2012; Cheung et al., 2013a) and altered stock distributions (Sabatés et al., 2006). Further warming may be beneficial for fisheries productivity in some regions such as the North Atlantic, because of the poleward shift of exploited species and changes in primary productivity (Arnason, 2007; Stenevik and Sundby, 2007; Cheung et al., 2010; see also Box 6-1; Section 30.5.1.1.1), or for some Pacific Islands due to the eastward redistribution of tuna stocks (Lehodey, 2000; Lehodey et al., 2011). Resulting changes in accessibility and fishing operations costs are projected to straddle economic zones, perturb international fishery agreements, and cause excessive exploitation (Hannesson, 2007; Sumaila et al., 2011; see also Sections 7.3.2.4, 7.4.2; WGIII AR5 Section 4.3.7).

Invertebrate fisheries and aquaculture appear very vulnerable to the impacts of ocean acidification (Barton et al., 2012; see also Box CC-OA; Figure 6-10). This concerns especially shelled mollusks, with a substantial decline in their global production projected between 2020 and 2060 under the SRES A2 business-as-usual scenario (Cooley and Doney, 2009; Cooley et al., 2012). Effects on calcifying plankton will propagate through the food web, making estimates of economic impact on fish catch by OA difficult, also due to complex interactions with other stressors like warming and fisheries management (Griffith et al., 2012; Branch et al., 2013). Model projections suggest a potential loss of up to 13% (SRES A1FI scenario) to annual total fishery value in the USA, or globally more than US$100 billion annually by 2100 (Cooley and Doney, 2009; Narita et al., 2012). Vulnerability differs highly between nations according to the contribution of such fisheries to their economy (Cooley et al., 2012; see also Sections 7.3.2.4, 7.4.2). These projections are sensitive to the projected vulnerabilities of the organisms to ocean acidification (*medium confidence*; Section 6.3.2).

Fishing reduces abundances at high trophic levels, but increases abundances at mid-trophic levels. It reduces species numbers, simplifies ecosystem structure, and increases ecosystem sensitivity to climate change (Perry et al., 2010). Exploitation of fish stocks and the alteration of their demography, population dynamics, and life history traits (Petitgas et al., 2006; Perry et al., 2010; Planque et al., 2010) can reduce the capacity of fish populations to buffer changes in climate variability (Ottersen et al., 2006; Genner et al., 2010), and increase variability in population size. Interactions between warming, OA, and human activities such as fishing may thus exacerbate climate impacts on a wide range of ocean processes and services, including marine fisheries (*medium confidence*; Tables 6-4, 6-6; Section 30.6.2).

A 2°C global temperature increase by 2050 is estimated to cause global losses in landed value of US$17 to 41 billion annually (in 2005 value), with an estimated cost of adaptation for the fisheries of US$7 to 30 billion annually over a 40-year time frame between 2010 and 2050. The largest loss in landed value is projected to occur in East Asia and the Pacific (*low confidence*; Sumaila and Cheung, 2010). Overall impacts and the regional manifestations will partially depend on the flexibility and response capacities of food production systems (Elmqvist et al., 2003; Planque et al., 2011a).

Specific implications for the fishing industry are still poorly known, as future projections of shifts in primary production and knock-on effects

through food webs and into fisheries remain uncertain (*low confidence* in effects of changing NPP; Planque et al., 2011b; Stock et al., 2011).

6.4.1.2. Other Provisioning Services

Reductions in marine biodiversity due to climate change and other anthropogenic stressors (Tittensor et al., 2010), such as OA (CBD, 2009) and pollution, might reduce the discovery of genetic resources from marine species useful in pharmaceutical, aquaculture, agriculture, and other industries (Arrieta et al., 2010), leading to a loss of option value from marine ecosystems. Climate change increases the demand for marine renewable energy such as wind and wave power, though with potential ecosystem impacts of their infrastructure (Section 6.4.2).

6.4.1.3. Climate Regulation and Extreme Events

The effect of climate change on marine biota will alter their contribution to climate regulation, that is, the maintenance of the chemical composition and physical processes in the atmosphere and oceans (*high confidence*; Beaumont et al., 2007). Regulatory mechanisms in which organisms (especially phytoplankton) play a key role, include control of the level of atmospheric CO_2 through the balance between photosynthesis and respiration (Johnson et al., 2010), and through the biological and alkalinity pump (Falkowski, 1997; Feely et al., 2008). They also include the modulation of further greenhouse gases such as nitrous oxide (N_2O; Jin and Gruber, 2003; Law, 2008; see also Section 6.1.1.3), and the modulation of other climatically reactive gases such as dimethylsulfide (DMS; Vogt et al., 2008). A projected decrease in global ocean NPP (Section 6.5.1) may result in decreased export of biogenic carbon to the deep ocean (Bopp et al., 2002; Boyd and Doney, 2002; Hashioka and Yamanaka, 2007). A positive feedback on climate change may result; however, many of the factors controlling the pump are poorly understood (Figure 6-4; WGI AR5 Chapter 6).

Coastal marine ecosystems reduce the effects of floods and storm surges which account for most of the natural disasters affecting people in coastal regions (IPCC, 2012a). Empirical and modeling studies show that coral reefs contribute to buffering the impact of tsunamis (Fernando et al., 2005; Gravelle and Mimura, 2008; see also Sections 5.4.2.4, 30.5; Box CC-CR). Experiments and models indicate that warming and OA slow coral growth by nearly 50% by 2050 (Box CC-CR; Section 5.4.2.4), making some islands and coastal areas more vulnerable to tsunamis, storm surges, wave energy, and coastal erosion (*high confidence*). Wetlands and mangroves provide biologically diverse buffer zones (Section 5.4.2.3). The combined impacts of climate change, pollution, deoxygenation, and other overlapping stressors, on mangroves and wetlands have not been determined (Cooley et al., 2009; Cooley, 2012). Some of these stressors enhance each other's effects in coastal systems (Feely et al., 2010; Cai et al., 2011; Howarth et al., 2011).

6.4.1.4. Cultural Services

Cultural services encompass a wide array of services with marine biodiversity as a core component supporting recreation and tourism as the economically most relevant. Tropical coral reefs and their enormous biodiversity sustain substantial tourist industries, presently with global annual net benefits of about US$9.6 billion (Cesar et al., 2003; see also Box CC-CR; Section 30.6.2.2). If reef services degrade, coastal visitors might choose alternative attractions (UNWTO, 2008). Increased travel to see disappearing ecosystem types (e.g., Antarctica: Liggett et al., 2011) or in previously inhospitable areas or seasons (Amelung et al., 2007; Moore, 2010) create new pressures and are unsustainable as the locations of key attractors shift (e.g., cetaceans: Lambert et al., 2010; Salvadeo et al., 2013).

Climate change may endanger harvests of marine species with spiritual and aesthetic importance to indigenous cultures, raising ethical questions about cultural preservation (e.g., Nuttall, 1998). In coastal communities, losing the aesthetic values of marine ecosystems may harm local economies: better water quality and fewer harmful algal blooms are related to higher shellfish landings and real estate prices (Jin et al., 2008).

Some heritage benefits of preserving marine ecosystems consist of the economic value of a healthy, diverse ecosystem to future generations. Any climate-related biodiversity loss or pollution of marine ecosystems would decrease the bank of resources for future opportunities. For example, the research and conservation value of coral reef biodiversity and its non-use value are estimated together at US$5.5 billion annually (Cesar et al., 2003). As with spiritual and aesthetic benefits, maintaining heritage benefits under climate change poses challenges for managers concerning equity and ethics as well as multigenerational (and possibly multi-cultural) ethical questions.

6.4.1.5. Supporting Services

Fully identifying the services supporting other ecosystem benefits is virtually impossible, as they are diverse in nature and scale. Ecosystem engineers play an important role in these services. Damage to calcifying algae and corals will reduce habitat for other species (Section 6.3.5), biodiversity, cultural and leisure values, and their climate regulation capacity.

Waterways for shipping are expected to change in the next several decades (*very high confidence*; Chapter 28; Section 30.6.2.3). Reductions in Arctic sea ice allow new trade routes such as the Northwest Passage (Wilson et al., 2004; Granier et al., 2006), enabling economically viable trans-Arctic shipping, and access to regional resources for exploitation and tourism. This development would increase emission of greenhouse gases and other pollutants (Lauer et al., 2009; Corbett et al., 2010), and facilitate the invasion of non-indigenous species carried on hulls and in ballast waters (Lewis et al., 2004).

6.4.2. Management-Related Adaptations and Risks

6.4.2.1. Ecosystem Management

A changing climate will have both positive and negative consequences for managing ocean resources (*high confidence*) (Eide and Heen, 2002;

Eide, 2007; see also Section 6.4.1). Ecosystem-based management (EBM, an approach recognizing all, including human interactions, within an ecosystem) or the ecosystem approach (EA, a strategy for the integrated management of living resources promoting both conservation and sustainable use) are increasingly adopted globally (FAO, 2003) to deal with the multitude of human pressures on marine ecosystems (Sherman et al., 2005; Hoel, 2009). Extended EBM addresses changes driven by climate and human activities, considering that diverse drivers will interact and confound each other (Planque et al., 2010; Eero et al., 2011; see also Section 6.3.5). Human activities will undermine resilience to other, including climate, impacts or undermine the effectiveness of mitigation and adaptation measures, by increasing variability (thereby reducing predictability), and limiting scope for adaptation (*high confidence*; e.g., Hughes, 2004; Sissener and Bjørndal, 2005; Eero et al., 2011). Thus, managing ecosystems under climate change increases the resilience of ecosystems and adaptive capacity of management systems through reducing other human perturbations (e.g., overfishing) (Brander, 2008; see also Section 7.5.1.1.3). Managing ecosystems also reduces the consequences of ocean acidification until CO_2 emission reduction becomes effective (Rau et al., 2012; Billé et al., 2013; McLeod et al., 2013; see also Box CC-OA). Ecosystem resilience is enhanced by reducing regional eutrophication (Falkenberg et al., 2013), or in aquaculture by avoiding acidified water (Barton et al., 2012) and by selecting and cultivating pre-adapted strains (Parker et al., 2012).

However, effects of climate change cannot be reversed by reducing the impacts of non-climatic drivers, emphasizing the need for adaptive management. Increased variability of ecosystem responses to climate change and the low predictability of some biological responses undermine the effectiveness of management and conservation measures. A particular risk is that climate change may contribute to large-scale ecosystem regime shifts (Section 6.3.1.5; Box 6-1). Detecting and forecasting such shifts from time series of environmental and biological data (Carpenter and Brock, 2006; deYoung et al., 2008), is constrained by an insufficient number of observations and limited quantitative understanding (Section 6.1.2). Biogeographic shifts challenge spatial management (Box CC-MB; Sections 6.3.1, 6.5), which is a fundamental part of EBM (Douvere, 2008), and demand that "fixed in law forever" site-attached zoning to protect specific species may need to become more flexible to maintain the original objectives as species move or community structures shift (*high confidence*; Soto, 2001; Hawkins, 2012).

6.4.2.2. Geoengineering Approaches

Geoengineering approaches to mitigate climate change and its effects, include Solar Radiation Management (SRM) and Carbon Dioxide Removal (CDR; see Table 6-5; IPCC, 2012b). SRM aims to reduce warming by increasing albedo, for example, via stratospheric injection of sulfate aerosol (Crutzen, 2006). SRM may affect marine ecosystems through changes in precipitation. With continued CO_2 emissions it leaves ocean acidification largely unabated as it cannot mitigate rising atmospheric CO_2 concentrations (Vaughan and Lenton, 2011; Williamson and Turley, 2012). Termination of SRM after its implementation involves the risk of rapid climate change and more severe effects on ecosystems (Russell et al., 2012).

Proposed CDR techniques include both ocean- and land-based approaches (Vaughan and Lenton, 2011; see also Section 30.6.4). CO_2 storage in geological reservoirs may occur beneath the seafloor, for example, in porous marine aquifers, and includes the risk of CO_2 leakage to the marine environment. Proposals to directly or indirectly sequester CO_2 into the ocean (Caldeira et al., 2005; Boyd, 2008; Shepherd et al., 2009; see also Table 6-5; WGIII AR5 Section 7.5.5) include, among others, the use of ocean fertilization techniques by nutrient addition, the direct storage of biomass in the deep ocean, the addition of alkalinity for build-up of dissolved inorganic carbon (DIC; i.e., carbonate), and the direct CO_2 injection into the deep ocean (Williamson et al., 2012). All of these approaches have potentially negative consequences for marine ecosystems.

Ocean fertilization by adding iron to high-nutrient low-chlorophyll (HNLC) oceanic waters could increase productivity and the net export of organic material to the deep ocean and its consecutive decomposition, causing deep-water accumulation of CO_2. Fertilization would affect all major marine biogeochemical cycles of the ocean with unclear side effects that could include the formation of methane (CH_4) and N_2O (Law, 2008) or the stimulation of harmful algal blooms (Trick et al., 2010). The enhanced NPP would add more carbon to the base of food webs (de Baar et al., 2005) and stimulate growth, for example, of deep-sea benthos (Wolff et al., 2011). Any regional increase in organic material (through fertilization or intentional storage of biomass) would cause enhanced O_2 demand and deep-water O_2 depletion (Sarmiento et al., 2010; Table 6-5), increasing the level and extent of hypoxia and associated impacts on marine ecosystems (Sections 6.3.3, 6.3.5, 30.5.7). The synergistic effects of CO_2-induced acidification will exacerbate the biological impacts (*high confidence*).

Neutralizing the acidifying water by the addition of alkalinity, for example, calcium oxide, would require large-scale terrestrial mining with associated consequences (Caldeira et al., 2005). The biological effects of increased concentrations of Ca^{2+} ions and dissolved inorganic carbon remain insufficiently explored. Direct injection of CO_2 or its localized disposal in the ocean (e.g., as a lake in a deep-sea valley) causes locally highly increased CO_2 and acidification effects on deep-sea organisms (*high confidence*; Caldeira et al., 2005; see also Section 6.3.3.4). In contrast to long-term ocean fertilization or storage of biomass, this technique leaves the oxygen inventory of the deep ocean untouched (*limited evidence*, *medium agreement*; Pörtner et al., 2005).

The knowledge base on the implementation of SRM and CDR techniques and associated risks is presently insufficient. Comparative assessments suggest that the main ocean-related geoengineering approaches are very costly and have large environmental footprints (*high confidence*; Boyd, 2008; Vaughan and Lenton, 2011; Russell et al., 2012).

6.4.2.3. Health Issues

Human health and near-shore ecosystems may be directly impacted by climate change effects on harmful algal blooms (HABs; Edwards et al., 2006; see also Section 30.6.3) or disease vectors. Planktonic time-series archives and nearshore sediment cores containing HAB cysts have revealed few examples of strong linkages between altered HABs and

Table 6-5 | Challenges for the oceans that will arise from the employment of a range of geoengineering methods (SRM = solar radiation management; CDR = carbon dioxide removal).

Topic	Brief description	Challenge and impact	References
Solar radiation management techniques	Deflection of approximately 1.8% of sunlight, by various techniques, is able to offset the global mean temperature effects of a doubling of atmospheric CO_2 content from pre-industrial values.	Will leave ocean acidification unabated (*high confidence*). Response of primary production to light reduction unclear.	Crutzen (2006); Caldeira and Wood (2008)
Ocean storage by direct injection	Capture of CO_2 post-combustion from mainly coastal power plants, followed by injection of liquid CO_2 by pipeline or from a ship into the deep ocean.	Will add to ocean acidification and create localized harm to marine life (*high confidence*). Quantities will be small relative to the atmospheric invasion signal. CO_2 injected will dissolve and be transported by ocean circulation with eventual surface exposure.	Caldeira et al. (2005)
Sub-sea geologic storage	Capture of CO_2 from extracted gas or from post-combustion followed by well injection into a porous submarine aquifer beneath impermeable geologic strata.	Extensive experience in place from the Norwegian Sleipner field activity in the North Sea. No evidence of ocean impact from leakage to date.	Benson et al. (2005)
Ocean fertilization	Spreading of trace amounts of reduced iron over very large areas of the surface ocean where excess nutrients occur. Overcoming the local iron deficiency creates extensive phytoplankton blooms drawing down sea surface pCO_2. Fertilization can also be carried out by using direct or indirect (ocean pipes) addition of macronutrients to oceanic regions where they are depleted.	Much of the exported organic matter is remineralized at shallow depths, creating local oxygen stress and shallow CO_2 enrichment and methane and N_2O production. These effects are temporary and the effective retention time is short. If sustained, reduced surface ocean and increased deep ocean acidification. O_2 loss in ocean interior (*medium confidence*).	de Baar et al. (1995); de Baar et al. (2005); Pörtner et al. (2005); Boyd et al. (2007); Buesseler et al. (2008); Law (2008); Cao and Caldeira (2010)
Artificial upwelling or downwelling	Ocean fertilization by bringing nutrient rich deep water (from 200 to 1000 m) to the surface. Downwelling occurs in parallel, transporting physically dissolved CO_2 into the deep ocean.	Deep water contains high levels of CO_2, which if released counteracts the binding of CO_2 by fertilization. No evidence available.	Lovelock and Rapley (2007); Oschlies et al. (2010)
Sequestration of organic carbon	Storage of terrestrial biomass in the coastal or deep ocean.	Physical impact, regional loss of oxygen, CO_2 accumulation and acidification during degradation; increases in methane, N_2O, and H_2S. No evidence available.	Metzger and Benford (2001); Strand and Benford (2009)
Carbonate neutralization	Dissolution of power plant flue gas into sea water yielding an acidic solution that is neutralized by addition of crushed limestone. The resulting bicarbonate-rich fluid is discharged to the ocean.	Involves the transport and crushing to fine scale of large quantities of limestone and the processing of very large quantities of sea water. Environmental impact issues not yet explored.	Rau (2011)
Accelerated olivine weathering	Uses wind powered electrochemical processes to remove HCl from the ocean and neutralizes the acid with silicate minerals such as olivine for disposal. The net result is to add alkalinity to the ocean akin to natural silicate weathering processes.	Complex system as yet untested in pilot processes. Involves mining and crushing large quantities of silicate minerals. Very long time scale consequences uncertain.	House et al. (2007); Köhler et al. (2010)

climate fluctuations (Dale et al., 2006; see also Section 30.5.3.1.2). HABs can be stimulated by warming, nutrient fluctuations in upwelling areas, eutrophication in coastal areas, and enhanced surface stratification (*medium confidence*). Species-specific responses involve shifts in seasonal cycles and blooms (Johns et al., 2003). Ocean acidification may exacerbate the toxicity of species in coastal oceans under nutrient-limited conditions (Tatters et al., 2012; Sun et al., 2011). Suitable adaptation measures include appropriate monitoring of biotoxin problems (Hallegraeff, 2010).

Continued warming of tropical and temperate coastal habitats, excessive nutrient loading leading to phytoplankton and zooplankton blooms, and sea water inundation due to sea level rise are all projected to exacerbate the expansion and threat of cholera (*medium confidence*; see also Sections 11.5.2.1, 30.6.3), although attribution to climate change is confounded by climate variability and non-climate drivers (Lafferty, 2009; Dobson, 2009).

Cholera and its pathogen, the marine bacterium, *Vibrio cholera*, have been widely studied. The pathogen associates with marine organisms, especially chitinized zooplankton (Vezzulli et al., 2010). Where cholera is endemic (e.g., India, Bangladesh, Latin America), outbreaks correlate with warming and high zooplankton abundance (Lobitz et al., 2000; Lipp et al., 2002). Based on an 18-year climate record for Bangladesh, Pascual et al. (2000) reported cholera outbreaks at ENSO events, and the recent reappearance of cholera in Peru has also been linked to the intense 1991–1992 ENSO (Lipp et al., 2002). An increase in sustained maximum temperatures of the Baltic Sea (Section 30.5.3.1.4) has been related to an increase in reported *Vibrio* infections; highest human mortality rates were associated with *V. vulnificus* infections (Baker-Austin et al., 2013). Continued warming of tropical and temperate coastal habitats, excessive nutrient loading leading to phytoplankton and zooplankton blooms, and seawater inundation due to sea level rise are all projected to exacerbate the expansion and threat of cholera (*medium confidence*).

Ciguatera poisoning may occur when people consume fish, mainly from tropical reefs, that have ciguatoxins from the epiphytic dinoflagellate *Gambierdiscus* sp. Historical records show significant correlations between ciguatera poisoning and sea surface temperature in South Pacific nations (Hales et al., 1999). However, the relationship is nonlinear and dependent on the thermal window of the specific dinoflagellate (Llewellyn, 2010). This casts doubt on the accuracy of projected increases in ciguatera poisoning using linear extrapolations from observations (*low confidence*).

6.4.3. Conclusions

Human societies benefit from and depend on marine ecosystem services, including the provisioning of food and other goods, regulation of climate and extreme events, and cultural and supporting services (Section 6.4.1). Attributing and projecting climate-change-mediated shifts in these services remains a challenge, due to the intrinsic difficulty of assessments, lack of baseline and long time series data, and confounding human impacts. However, empirical and modeling studies indicate that climate change impacts on marine ecosystems lead to changes in provisioning, regulating, and supporting services (*high confidence*), as well as cultural services (*limited evidence*, *medium agreement*).

Food production from the sea is facing diverse stressors (Section 6.4.1.1), such as overfishing and habitat degradation, which interact with climate change phenomena, including warming (Section 6.3.1), ocean acidification (Section 6.3.2), and hypoxia (Section 6.3.3). Projections of impacts on capture fisheries are constrained by uncertainties in marine primary production (*medium evidence*, *medium agreement*; Section 6.5.1). Negative effects are projected to be most significant in developing nations in tropical regions (*high confidence*). Nations at higher latitudes may even benefit from climate change effects on ocean ecosystems, at least initially (Section 6.5.3).

Climate change effects on biota will alter their climate regulation through mechanisms such as carbonate production, the biological pump, the balance between photosynthesis and respiration, and the modulation of greenhouse gases (*high confidence*; Section 6.4.1.3). However, projections of the direction and magnitudes of feedbacks are at an early stage (*low confidence*).

Future management of ecosystems and fisheries might have to aim for increasing ecosystem resilience to climate change, for example, through reductions of other human perturbations (Section 6.4.2.1). Active ocean geoengineering strategies to ameliorate climate change may prove detrimental to the functioning of ecosystems, which highlights the need for further research and careful governance (Section 6.4.2.2). There is limited understanding of how harmful algal blooms and pathogens affecting human health will respond to climate change (Section 6.4.2.3; *medium* to *low confidence*).

6.5. Projections of Future Climate Change Impacts through Modeling Approaches

A range of models explore climate change effects on marine biota, from primary producers to higher trophic levels, and test hypotheses about responses of marine species, food webs, and ecosystems (Rose et al., 2010; Fulton et al., 2011; Stock et al., 2011; see also FAQ 6.2). Both empirical and mechanistic approaches are used over a range of temporal and spatial scales (Barange et al., 2010; Stock et al., 2011). There is an increasing need for upscaling from molecular and physiological to ecosystem level (e.g., Le Quesne and Pinnegar, 2012). Uncertainty in projections of changes in marine ecosystems is partly contingent on the level of confidence in climatic and oceanographic projections (Section 6.1.1; WGI AR5 Section 9.8). Models are currently useful for developing scenarios of directional changes in net primary productivity, species distributions, community structure, and trophic dynamics of marine ecosystems, as well as their implications for ecosystem goods and services under climate change. However, specific quantitative projections by these models remain imprecise (*low confidence*; Hannah et al., 2010; Rose et al., 2010; Stock et al., 2011; FAQ 6.4).

Earth System Models couple atmosphere, cryosphere, and hydrosphere (including the oceans), as well as climate and carbon cycles, and project changes in ocean biogeochemistry under a range of CO_2 emission scenarios (WGI AR5 Chapter 6). Models focusing on population and species level responses comprise models of population dynamics, models of species distribution, and models which explicitly link effects of changes in ocean physics and chemistry to changes in interactions between species at different trophic levels, or human activities such as fishing and aquaculture (Rose et al., 2010).

6.5.1. Oceanic Primary Production

Climate-induced effects on global ocean NPP comprise changes in its long-term average, seasonal timing, and peak amplitude (Henson et al., 2013). The magnitude, direction, and pattern of projected changes vary with differences in model structure and parameterization (Box CC-PP; Figure 6-13). Unknown accuracy of current NPP observations further increases the uncertainty of projections, as does the incomplete understanding of effects of multiple drivers on NPP (Sections 6.3.1-5, 6.4). Global coupled climate-ocean biogeochemical Earth System Models (WGI AR5 Chapter 6) project an increase in NPP at high latitudes but a decrease in permanently stratified oceans at mid-latitudes, in the tropics (west tropical Pacific, tropical Indian Ocean, tropical Atlantic), and in the North Atlantic (*medium confidence*; Steinacher et al., 2010; Bopp et al., 2013) (Figure 6-13). The overall result is a reduction in global mean NPP under all RCP scenarios (*medium confidence* in the direction of projected trends, *low confidence* in the magnitude of change).

6.5.2. Higher Trophic Levels

Projected future changes in temperature and other physical and chemical oceanographic factors are expected to affect the distribution and abundance of marine fishes and invertebrates, as elaborated by species distribution models. Limits of distribution ranges of 1066 exploited species are projected to undergo shifts by a median of around 50 km per decade to higher latitudes by 2050 relative to 2000 under the SRES A1B (≈RCP6.0) scenario (Cheung et al., 2009). Some species shift toward the equator following a regional temperature gradient (Burrows et al., 2011; Cheung et al., 2013b; Pinsky et al., 2013). The rate of range shifts is projected to be three times higher for pelagic than for demersal fishes (Cheung et al., 2009), the latter shifting at a rate of around 27 to 36 km per decade (Cheung et al., 2013b). However, the expansion of hypoxic waters may have a greater impact than warming on demersal fishes (Koslow et al., 2011). As a result of distribution shifts, high-latitude regions (the Arctic, Southern Ocean) are projected to have high rates of species invasions. Intermediate latitudes are expected to undergo both invasions and local extinctions. High rates of local extinction are projected for the tropics and semi-enclosed seas (e.g., Mediterranean Sea, Persian Gulf). In addition, the future productivity and distribution

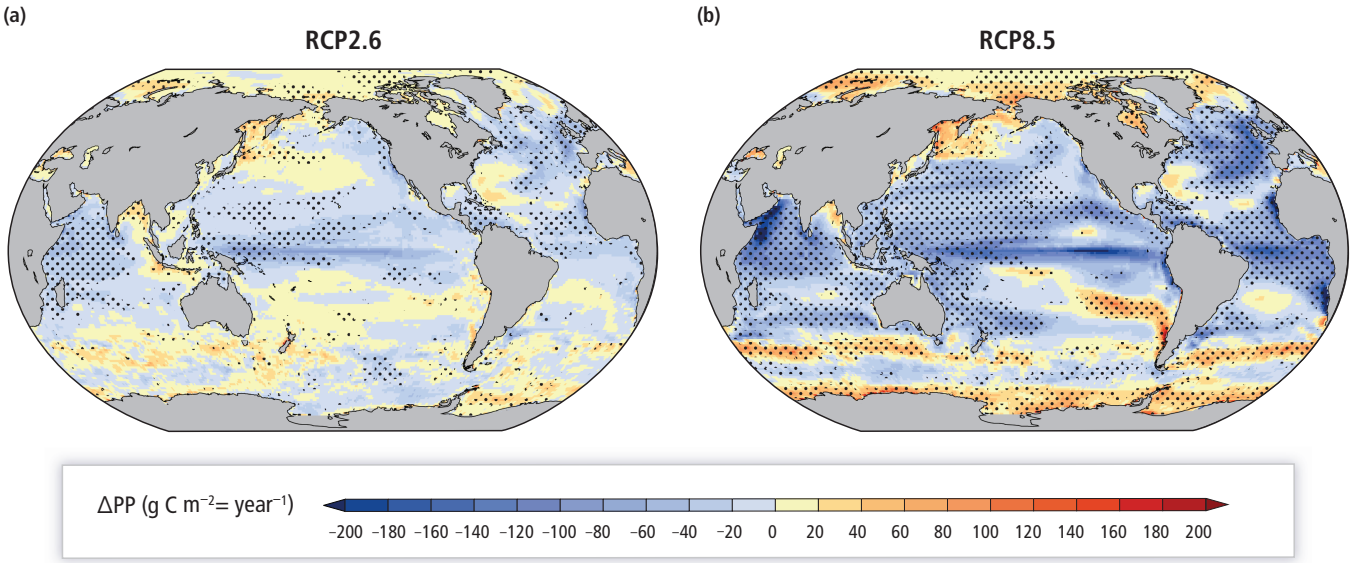


Figure 6-13 | Multi-model annual mean changes of projected vertically integrated net primary production (small and large phytoplankton) under the low-emission scenario Representative Concentration Pathway 2.6 (RCP2.6) (a) and the high-emission scenario RCP8.5 (b) for the period 2090 to 2099 relative to 1990 to 1999 (after Bopp et al., 2013). To indicate consistency in the sign of change, regions are stippled where 80% of the 10 models from the Coupled Model Intercomparison Project Phase 5 (Bopp et al. 2013) agree on the sign of change.

of higher trophic level organisms are projected to change due to changes in primary productivity (Section 6.3.6). For example, the migration route of Pacific sardine is projected to shift because of changes in primary productivity and food availability (Ito et al., 2010). The global pattern of distribution shifts is generally consistent with regional-scale projections and past observations (e.g., Lenoir et al., 2011; Cheung et al., 2013a). However, detailed quantitative projections are sensitive to model structure and assumptions (Hare et al., 2012; Jones et al., 2013) and responses of specific populations may differ from average species responses (Hazen et al., 2013).

Coral reefs are projected to undergo long-term degradation by 2020 to 2100 relative to the 2000s under RCP2.6, 4.5, and 8.5 or their equivalents (Section 30.5.6). Reefs projected to be threatened most by bleaching under the SRES A1B scenario by 2100 include the Central and Western Equatorial Pacific, Coral Triangle, and parts of Micronesia and Melanesia (Teneva et al., 2012). These projections assume that coral bleaching occurs when SST exceeds a certain threshold, and that there is limited potential to shift such threshold by adaptation. Reef degradation will impact ecosystem services (Hoegh-Guldberg, 2011; see also Section 6.4; Box CC-CR).

Some groups of marine air-breathing fauna are projected to shift in distribution and abundance (Section 6.3.7). Cetacean richness will increase above 40° latitude in both hemispheres, while at lower latitudes both pinniped and cetacean richness are projected to decrease by 2040–2049 relative to 1990–1999 under the SRES A1B scenario (Kaschner et al., 2011). Using SST as a predictor, the distribution of loggerhead turtles is projected to expand poleward in the Atlantic Ocean and to gain habitat in the Mediterranean Sea by 2070–2089 relative to 1970–1989 (Witt et al., 2010). Leatherback turtle may decrease in abundance at a rate of 7% per decade because of reduced hatching success with warming following the SRES A2 scenario (Saba et al., 2012). Abundances of some seabirds such as European breeding seabirds (Huntley et al., 2007), Cassin's auklet in the California Current Ecosystem, or emperor penguin in Antarctica are projected to decline because of climate-induced changes in oceanographic conditions, such as temperature and upwelling intensity (Wolf et al., 2010; see also Box CC-UP), or summer sea ice conditions (Jenouvrier et al., 2012). The diversity of megafaunal responses to climate change will have cascading ecosystem impacts, and will affect ecosystem services such as tourism (*high confidence*; Sections 6.3.7, 6.4.1).

6.5.3. Ecosystems and Fisheries

One of the most direct impacts of climate change on marine ecosystem services is through fisheries (Sections 6.4.1, 7.2.1.2, 7.3.2.4, 7.4.2). Projected climate impacts on fisheries are based on recruitment, growth, mortality, abundance, and distribution of fish stocks as well as changes in ocean NPP (Cheung et al., 2008), evaluated from chlorophyll concentration and other variables such as sea surface temperature (Campbell et al., 2002). Friedland et al. (2012) suggested that chlorophyll concentration, indicating both phytoplankton production and biomass, is a better predictor of the fishery yield in large marine ecosystems than NPP. While the principle holds that catch potential is dependent on energy from primary production, quantitative projections of catch potential are limited by residual uncertainty on the best possible indicators of primary production and biomass.

Assuming that the potential fish catch is proportional to NPP, the fish catch in the North Pacific Ocean subtropical biome is projected to increase by 26% through expansion of the biome, while catches in the temperate and equatorial biomes may decrease by 38 and 15%, respectively, through contraction of the biomes by 2100 relative to 2000 under the SRES A2 (RCP6.0 to 8.5) scenario (Polovina et al., 2011). Changes in phytoplankton size structure are projected to affect fisheries catch potential (Cheung et al., 2011), resulting in a 0 up to 75.8% decrease in the potential catch of large fishes in the central North Pacific

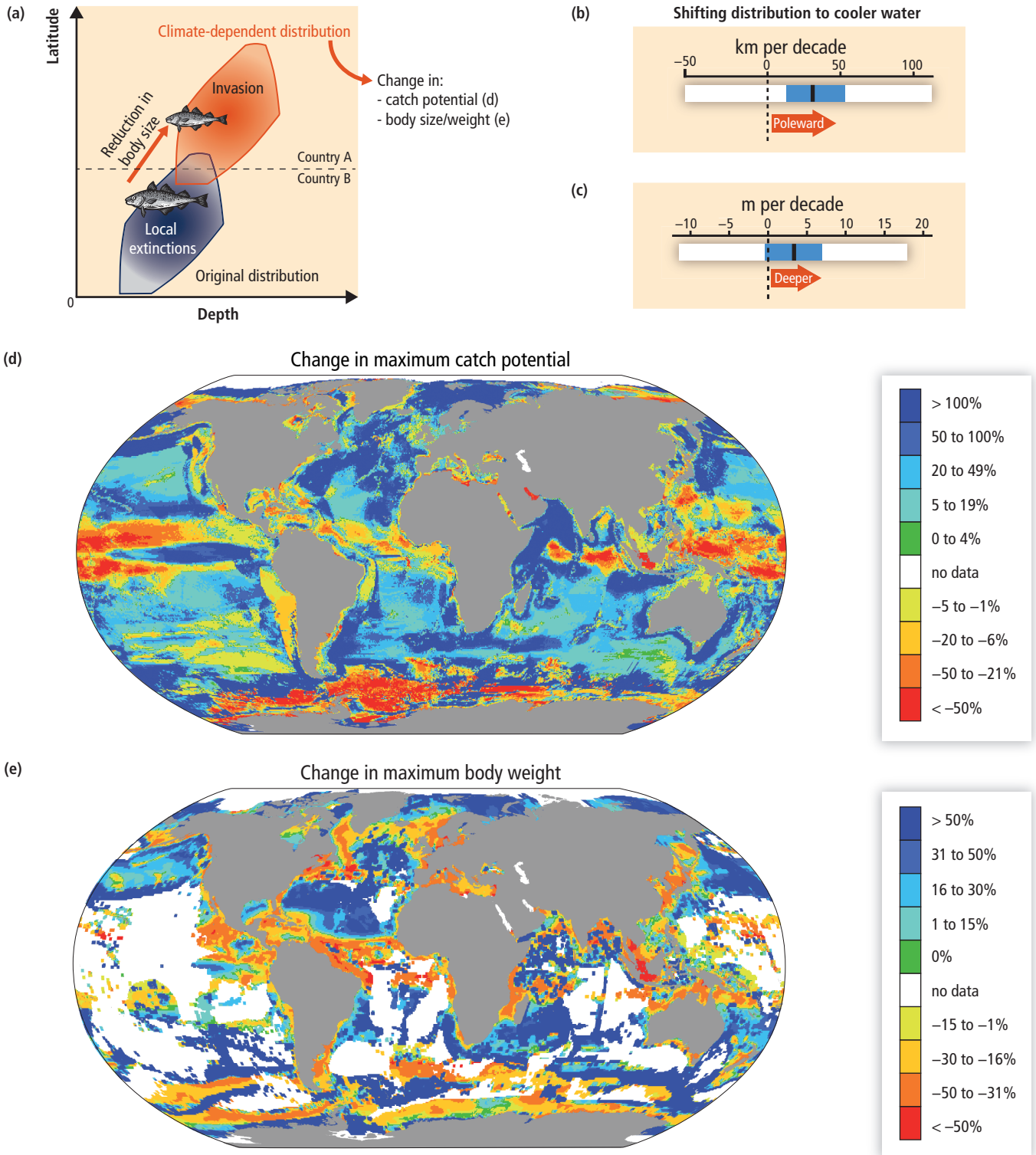


Figure 6-14 | Climate change effects on the biogeography, body size, and fisheries' catch potential of marine fishes and invertebrates. (a) Shifts in distribution range and reduction in body size of exploited fish driven by projected warming, oxygen depletion, and sea ice retreat (cf. Figure 6-7). Whenever the shift in distribution does not fully compensate for warming and hypoxia, the result will be a decrease in body size. Shifts in (b) latitudinal and (c) depth distribution of 610 exploited demersal fishes are projected to have a median (central line of the box) of 31 km per decade and 3.3 m per decade, respectively, with variation between species (box boundary: 25th and 75th percentiles) from 1991–2010 to 2041–2060 under the SRES A2 (between RCP6.0 and 8.5) scenario (Cheung et al., 2011, 2013b). (d) Combining species' range shifts with projected changes in net primary production leads to a projected global redistribution of maximum catch potential. (Analysis includes approximately 1000 species of exploited fishes and invertebrates, under warming by 2°C according to SRES A1B (≈RCP6.0), comparing the 10-year averages 2001–2010 and 2051–2060; redrawn from Cheung et al., 2010.). (e) Changes in species distribution and individual growth are projected to lead to reduced maximum body size of fish communities at a certain site. The analysis includes 610 species of marine fishes, from 1991–2010 to 2041–2060 under SRES A2 (approximately RCP6.0 to 8.5; Cheung et al., 2013b), without analysis of potential impacts of overfishing or ocean acidification. Key assumptions of the projections are that current distribution ranges reflect the preferences and tolerances of species for temperature and other environmental conditions and that these preferences and tolerances do not change over time. Catch potential is determined by species range and net primary production. Growth and maximum body size of fishes are a function of temperature and ambient oxygen level.

and increases of up to 43% in the California Current region over the 21st century under the SRES A2 scenario (Woodworth-Jefcoats et al., 2013). Globally, climate change is projected to cause a large-scale redistribution of global catch potential, with an average 30 to 70% increase in yield at high latitudes and up to 89% in some regions, after 2°C warming from preindustrial periods following SRES A1B (≈RCP6.0) (Cheung et al., 2010; Blanchard et al., 2012; see also Figure 6-14). Redistribution between areas, with average catch potential remaining unchanged, will occur at mid latitudes. A 40 to 60% drop will occur in the tropics and in Antarctica by the 2050s relative to the 2000s (*medium confidence* for direction of trends in fisheries yields, *low confidence* for the magnitude of change). This highlights high vulnerabilities in the economies of tropical coastal countries (Allison et al., 2009; see also Section 6.4).

Fisheries targeting specific species may show more complex responses to climate change. For example, driven by changes in temperature and primary production, catches of skipjack and bigeye tuna in the south Pacific are projected to increase by 2035 relative to 1980–2000 under the SRES B1 and A2 scenario, but for 2100, skipjack tuna catch is projected to decrease under the A2 scenario, while bigyeye tuna catch decreases under both A2 and B1 scenarios (Lehodey et al., 2011). Regionally, tuna catches in the Western Pacific are projected to decrease, while those in the Eastern Pacific will increase (Lehodey et al., 2011). Mollusk fisheries under ocean acidification is discussed under Section 6.4.1.

Identifying responses to climate change is complicated by species interactions and multiple stressors. Major marine habitats and biodiversity hotspots are projected to encounter cumulative impact from changes in temperature, pH, oxygen, and primary productivity by the end of the 21st century (RCP4.5 and 8.5) (Mora et al., 2013). Acidification and hypoxia will reduce maximum catch potential over 50 years from about 2000 onward in both the North Atlantic and Northeast Pacific (Ainsworth et al., 2011; Cheung et al., 2011). Changes in O_2 content as well as warming will drive a global decrease of community-averaged maximum body size of 14 to 24% of exploited demersal marine fishes by 2050 relative to the 2000s under the SRES A2 (RCP6.0 to 8.5) scenario (Cheung et al., 2013b; see also Figure 6-14). The decrease in maximum body size may affect natural mortality rates and trophic interactions, and reduce yield-per-recruit and thus potential catch. Responses of exploited marine species and their fisheries may interact with other human stressors such as overfishing, exacerbating their impacts (e.g., Lindegren et al., 2010; Ainsworth et al., 2011). Through species shifts climate change may also cause overlap of habitats of species targeted by fishing with habitat of threatened species, potentially increasing the chances of the latter of being caught as bycatch (Jones et al., 2013). Moreover, differences in vulnerability and adaptive capacity of species to changing environmental and ecosystem conditions will affect the responses of fisheries to climate change (e.g., Le Borgne et al., 2011; Griffith et al., 2011).

The complex and nonlinear interactions and responses of both biophysical and socioeconomic systems to climate change may lead to changes that have a low probability of occurrence based on empirical data (Doak et al., 2008). The risk of such low-probability but potentially high-impact events may be underestimated in existing model projections (Williams and Jackson, 2007; Lindenmayer et al., 2010). Projected changes in the distribution and production potential of fisheries resources are expected to affect economics, human livelihood, and food security (Allison et al., 2009; Sumaila and Cheung, 2010; *low confidence* in the magnitude and direction of the projected socioeconomic impacts).

6.5.4. Conclusions

Modeling projects that the distribution of invertebrates, fishes, and some marine mammals, birds, and reptiles will shift further under most emission scenarios, with rates and directions of shifts consistent with those observed in the last century (*high confidence*; Sections 6.3.1-7). These projections are valid for those species that adapt not at all or incompletely to warmer temperatures and the associated ecosystem changes, as indicated by present trends (Section 6.3.1; Box CC-MB). For non-adapting species rates of shift will thus increase with increasing rates of warming and higher emission scenarios (*high confidence*), unless the shift is blocked by geographic or other barriers (e.g., light regime; Figure 6-7). The average shift in distribution will continue to be poleward at large spatial scales (*high confidence*; Section 6.5.2; Box CC-MB). Species richness and the abundance of warm-water species will increase at high latitudes (*high confidence*) and decrease in the tropics (*medium confidence*; Section 6.5.2). Projections for individual species and populations are more variable and sensitive to model parameters.

Maximum fisheries catch potential is projected to increase at high and decrease at low latitudes by 2050 under SRES B1 (≈RCP4.5) and A1B (≈RCP6.0) climate scenarios (*medium confidence*; Section 6.5.3). Quantifying such projections is constrained by uncertainties in projected primary production rates (Sections 6.3.4, 6.5.1), biological responses such as species interactions (Section 6.3.6), and in projected effects of multiple climate drivers and human activities (*low confidence*; Section 6.3.5).

Models that integrate climate and ocean changes with biological responses and interactions, and with current human activities, have led to agreement on species and food web responses to climate change (Section 6.5.3). However, most of these models do not include trophic interactions. They insufficiently consider physiological principles and none include evolutionary adaptations that affect responses of biota to physical and chemical changes.

Projections of ocean biogeochemistry represent the open oceans rather well, but coastal and shelf regions only poorly. From a global perspective, open ocean NPP will decrease moderately by 2100 under both medium (SRES B1 or RCP4.5) and high emission scenarios (*medium confidence*; A2 or RCP6.0 to 8.5; Sections 6.3.4, 6.5.1), paralleled by an increase in NPP at high latitudes and a decrease in the tropics (*medium confidence*; Sections 6.3.4, 6.5.1; Box CC-PP).

Overall, the projected responses of marine organisms and ecosystems to climate change include changes in primary productivity (*medium confidence*), species' life history (*medium confidence*), distribution, abundance, and diversity across marine food webs (*high confidence*) in a time frame of 20 to 80 years from 2010, with substantially larger

long-term (end of 21st century) responses under high emission scenarios (*high confidence*). These changes will be largest under business-as-usual scenarios (RCP8.5) and increase the vulnerability of human societies, by affecting income, employment, and food security through their effects on fisheries, tourism, and regulatory services such as coastal protection (*medium confidence*; Section 6.4.1.3; Box CC-CR).

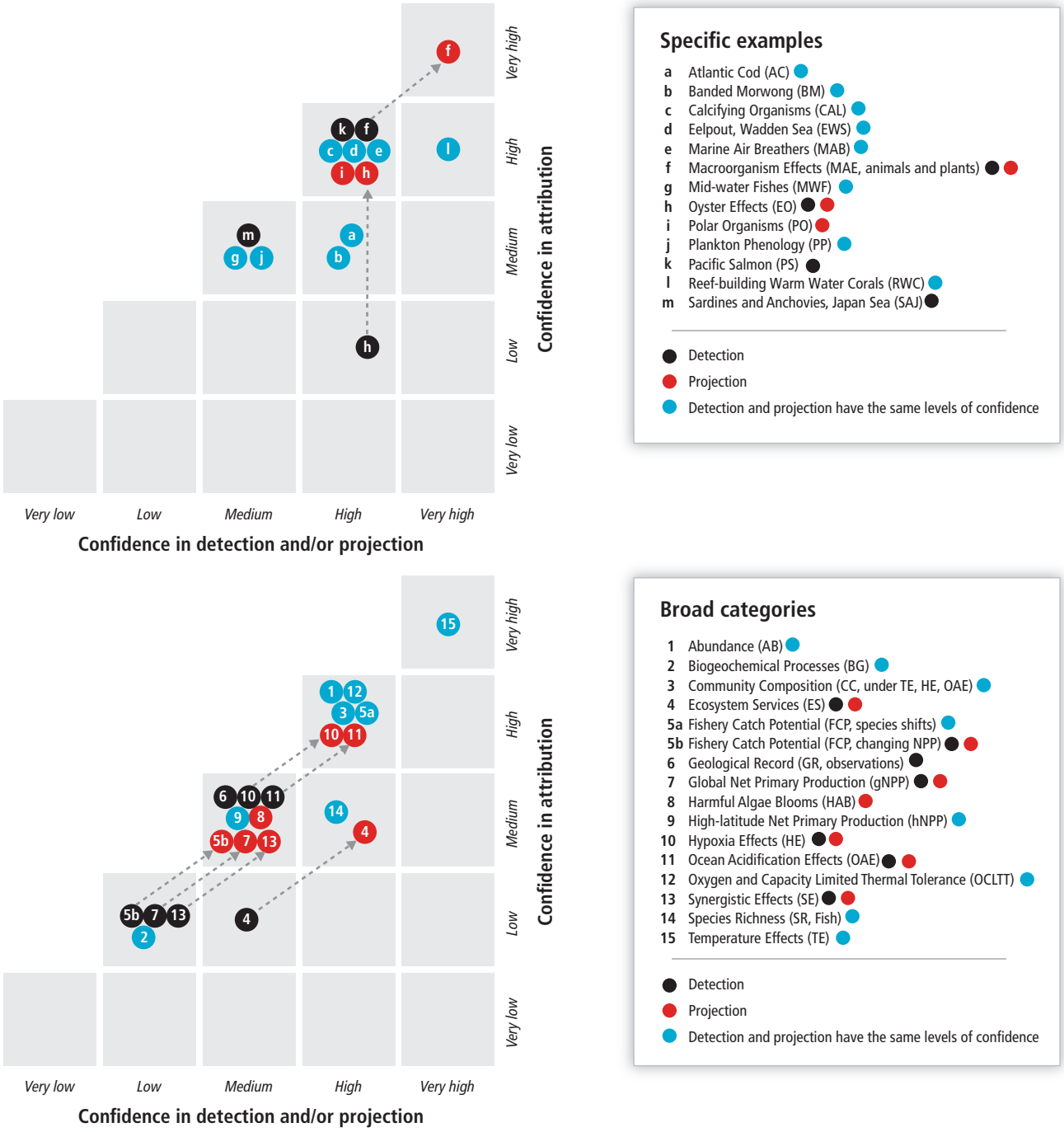


Figure 6-15 | Overview of the levels of confidence in detection, as well as in projection, of climate change effects on ocean systems, in relation to the levels of confidence in attributing these effects to the respective climate forcings. Case studies, processes, and concepts relevant in assessing the effects of climate change are represented by their acronyms in both text and figure. While confidence in the presence of effects is often high, the direct attribution to one driver in field experiments is difficult, as drivers are often highly correlated with each other (e.g., warming with changes in stratification, hence reduced nutrient supply). Some climate change impacts have been condensed into broad categories to avoid overpopulating the figures (e.g., Bio-Geochemical processes, BG). Note that the term "attribution" is used for both present-day detections in the field and future projections, the latter including qualitative and quantitative extrapolations and simulations of future conditions from fundamental principles, experiments, and models. Firm knowledge from experiments (field, laboratory, and modeling) simulating future conditions enhances the respective confidence levels to those for detection or projection. The empirical observations resulting from those experiments are directly attributable to the respective drivers. Confidence in attribution is enhanced if these experiments identify the underlying mechanisms and their responses. See text for the discussion of depicted examples and categories. Confidence assignments focus on the nature and size of effects, not on model capacity to quantify their magnitude reliably.

6.6. Chapter Conclusions and Key Uncertainties

This section provides an overview of confidence levels in the detection and projection of climate change effects on ocean systems, and of confidence levels in their attribution to different forcings. It distinguishes between effects previously observed and those projected, and considers confidence in the knowledge of underlying principles as discussed in this chapter. While the anthropogenic signal is conspicuous in the oceans (Section 6.1.1), clear attribution to anthropogenic influences on climate is not always possible in individual case studies, owing to the inherent variability of the system (Figure 6-15; acronyms of relevant processes, capitalized, link between text and figure).

Present-day observations and those from the Geological Record (GR; Figure 6-15) show similar signs of response to environmental changes, for example, warming at high CO_2 levels, and similar ecological consequences in the ocean (*robust evidence*, *medium agreement*; *medium confidence*). However, the ongoing rate of anthropogenic CO_2 release and hence ocean acidification is unprecedented in the last 65 Ma (*high confidence*) and probably the last 300 Ma (Section 6.1.2).

6.6.1. Key Risks Related to Climate Change: Constraints on Ecosystem Services

Empirical studies provide evidence that climate change has impacted marine ecosystems (*high confidence*; FAQ 6.4; Table 6-6) and has caused changes in provisioning, regulating, and supportive Ecosystem Services (ES; *medium confidence*). Climate change may also have affected cultural services (*limited evidence*, *medium agreement*) but attribution of impacts to these services remains a challenge (*low confidence*), owing to the intrinsic difficulties of assessing these services, the lack of long time-series data, and confounding human impacts. In light of available understanding of cause and effect of climate change impacts on marine ecosystems (*high confidence*), future climate change will affect some ecosystem services (*high confidence* in projection, *medium confidence* in attribution). Projected changes in the availability of marine resources and ecosystem services are expected to affect economics, human livelihood, and food security. Vulnerability is highest for the national economies of tropical coastal countries (*high confidence*).

6.6.1.1. Redistribution and Constraints on Microbial Functions and Primary Productivity

Laboratory and mesocosm studies have identified various microbially mediated processes responding to climate-induced changes in light, nutrient supply, temperature, CO_2, and hypoxia (*high confidence*). Such processes include nitrogen fixation and the nitrogen cycle, carbon sequestration and export production, calcification, respiration, O_2 production, climate-feedback by dimethylsulfide (DMS) production, and nutrient recycling. However, changes in these Bio-Geochemical processes (BG) in the field are difficult to detect, project, and attribute to climate change (*low confidence*; Sections 6.3.1-5).

The trends in net primary production recently reported for much of the low-latitude ocean using satellite observations differ considerably from those few long-term direct estimates of NPP at oceanic time series sites (Sections 6.1.2, 6.3.4). Increased NPP at high latitudes (hNPP, detected and attributable to climate change with *medium confidence*; Section 6.3.4; Box CC-PP) are indicated by satellite images (*medium confidence*) and due to reduction and thinning of sea ice. Trends in NPP will be strengthened with further warming (*medium confidence*). Modeling projects that global NPP (gNPP) will decrease by 2100 under RCP scenarios (*medium confidence*; Section 6.5.1; Box CC-PP).

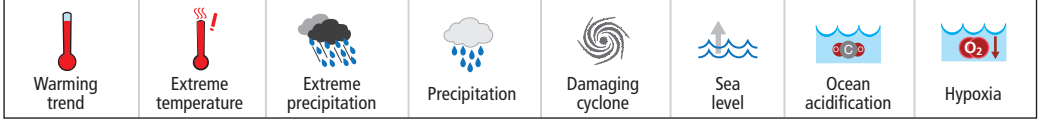
6.6.1.2. Warming-Induced Species Redistribution, Loss of Biodiversity, and Fisheries Catch Potential

Long-term observations show variability in oceanographic conditions with a key role of temperature and changing oceanographic regimes causing observed changes in ecosystem structure and fish stocks (*very high confidence*; cf. Section 30.7.1.1). Temperature Effects (TE) reflect the differential specialization of all life forms in limited ambient temperature ranges (*very high confidence*). Temperature exerts strong MAcroorganism Effects (MAE), that is, on animals and plants. Warming is presently causing and will cause species displacements and largely poleward shifts in biogeographic distribution of zooplankton and fishes, paralleled by altered seasonal activity, species abundance, migration, and body size (*high* to *very high confidence*; Section 6.3.1), and leading to shifts in Community Composition (CC; *high confidence*; Box 6-1). Causes and effects are understood for fishes and most invertebrates via their Oxygen and Capacity Limited Thermal Tolerance (OCLTT; *robust evidence*, *medium agreement*; *high confidence*; Section 6.3.1). Such knowledge supports projections into the future (*high confidence*; Section 6.5), which are influenced by the limited potential of organisms to adapt. Alterations in species ABundance (AB) result when organisms encounter shifting mean and extreme temperatures (*high confidence* in detection and attribution). Such trends will be exacerbated during future warming (*high confidence*; Section 6.5.1).

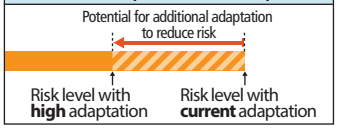
Among prominent examples, warming has caused and will cause northward shift and expansion of the geographic distribution of North Atlantic Cod (AC; *high confidence* in detection or projection, *medium confidence* in detection or projection and attribution; Section 6.3.1) and shifting growth patterns in relation to the distribution of Banded Morwong around New Zealand (BM; *high confidence* in detection or projection, *medium confidence* in detection or projection and attribution). Warming has shifted dominant species from Sardines to Anchovies in the Sea of Japan (SAJ; *medium confidence* in detection, *medium confidence* in detection and attribution; Sections 6.3.1, 6.3.6). Warming extremes have reduced and will further reduce the abundance of Eelpout in the Wadden Sea (EWS; *high confidence* in detection or projection, *high confidence* in detection or projection and attribution; Section 6.3.1). Extreme warming events increase mortalities of Pacific Salmon during spawning migrations (PS; *high confidence* in detection, *high confidence* in detection and attribution; Section 6.3.1) in Fraser River, Canada. At temperate and high latitudes, communities display increasing fish Species Richness (SR) resulting from latitudinal shifts of species and attributed to warming and loss of sea ice, although the relative contributions of regional climate variation and long-term global trends have not been quantified (*high confidence* in detection, *medium confidence* in detection and attribution; Sections 6.3.1, 6.5.2). Latitudinal species shifts are

Table 6-6 | Coastal and oceanic key risks from climate change and the potential for risk reduction through mitigation and adaptation. Key risks are identified based on assessment of the literature and expert judgments made by authors of the various WGII AR5 chapters, with supporting evaluation of evidence and agreement in the referenced chapter sections. Each key risk is characterized as *very low*, *low*, *medium*, *high*, or *very high*. Risk levels are presented for the near-term era of committed climate change (here, for 2030–2040), in which projected levels of global mean temperature increase do not diverge substantially across emissions scenarios. Risk levels are also presented for the longer-term era of climate options (here, for 2080–2100), for global mean temperature increase of 2°C and 4°C above pre-industrial levels. For each time frame, risk levels are estimated for the current state of adaptation and for a hypothetical highly adapted state. As the assessment considers potential impacts on different physical, biological, and human systems, risk levels should not necessarily be used to evaluate relative risk across key risks. Relevant climate variables are indicated by symbols. Acronyms for oceans sub-regions are as follows: HLSBS = High-Latitude Spring Bloom Systems; EUS = Equatorial Upwelling Systems; SES = Semi-Enclosed Seas; CBS = Coastal Boundary Systems; EBUE = Eastern Boundary Upwelling Ecosystems; STG = Sub-Tropical Gyres, DS = Deep Sea (>1000 m).

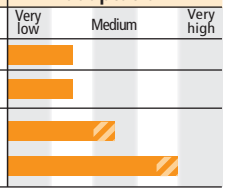
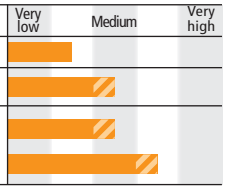
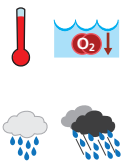
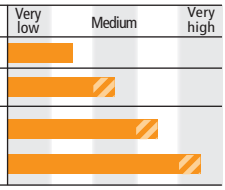
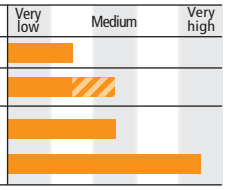
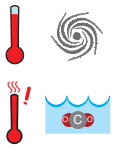
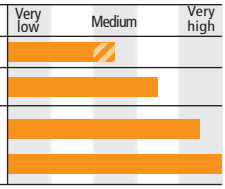
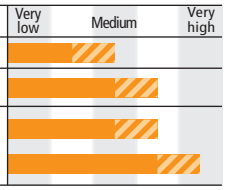
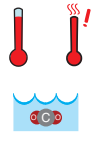
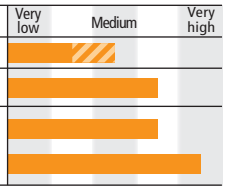
Climate-related drivers of impacts



Level of risk & potential for adaptation

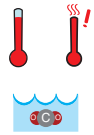
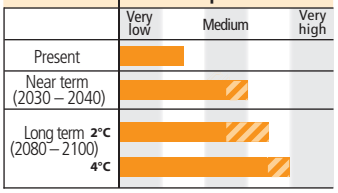
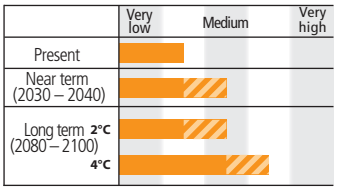
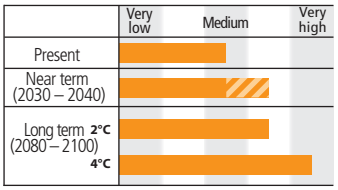
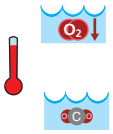
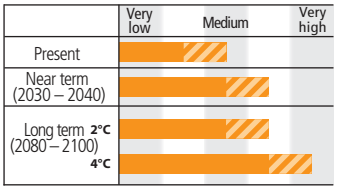
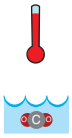
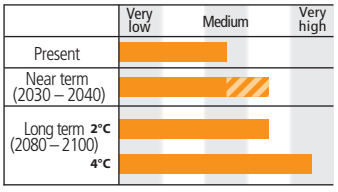
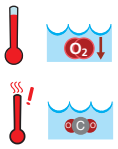
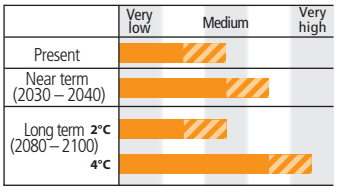


Risks to ecosystems and adaptation options

Key risk	Adaptation issues & prospects	Climatic drivers	Timeframe	Risk & potential for adaptation
Changes in ecosystem productivity associated with the redistribution and loss of net primary productivity in open oceans. (*medium confidence*) [6.5.1, 6.3.4, 30.5.1-2, Box CC-PP]	Adaptation options are limited to the translocation of industrial fishing activities due to regional decreases (low latitude) versus increases (high latitude) in productivity, or to the expansion of aquaculture.		Present Near term (2030 – 2040) Long term (2080 – 2100) 2°C 4°C	
Distributional shift in fish and invertebrate species, fall in fisheries catch potential at low latitudes, e.g., in EUS, CBS, and STG regions. (*high confidence*) [6.3.1, 6.5.2-3, 30.5.1-4, 30.6.2, Box CC-MB]	Evolutionary adaptation potential of fish and invertebrate species to warming is limited as indicated by their changes in distribution to maintain temperatures. Human adaptation options involve the large-scale translocation of industrial fishing activities following the regional decreases (low latitude) versus (possibly transient) increases (high latitude) in catch potential as well as deploying flexible management that can react to variability and change. Further options include improving fish resilience to thermal stress by reducing other stressors such as pollution and eutrophication, the expansion of sustainable aquaculture and development of alternative livelihoods in some regions.		Present Near term (2030 – 2040) Long term (2080 – 2100) 2°C 4°C	
High mortalities and loss of habitat to larger fauna including commercial species due to hypoxia expansion and effects. (*high confidence*) [6.3.3, 30.5.3-5]	Human adaptation options involve the large-scale translocation of industrial fishing activities as a consequence of the hypoxia-induced decreases in biodiversity and fisheries catch of pelagic fish and squid. Special fisheries may benefit (Humboldt squid). Reducing the amount of organic carbon running off coastlines by controlling nutrients and pollution running off agricultural areas can reduce microbial activity and consequently limit the extent of the oxygen drawdown and the formation of coastal dead zones.		Present Near term (2030 – 2040) Long term (2080 – 2100) 2°C 4°C	
Ocean acidification: Reduced growth and survival of commercially valuable shellfish and other calcifiers, e.g., reef building corals, calcareous red algae. (*high confidence*) [5.3.3.5, 6.1.1, 6.3.2, 6.4.1.1, 30.3.2.2, Box CC-OA]	Evidence for differential resistance and evolutionary adaptation of some species exists but is likely limited by the CO_2 concentrations and high temperatures reached; adaptation options include the shift to exploiting more resilient species or the protection of habitats with low natural CO_2 levels, as well as the reduction of other stresses, mainly pollution and limiting pressures from tourism and fishing.		Present Near term (2030 – 2040) Long term (2080 – 2100) 2°C 4°C	
Reduced biodiversity, fisheries abundance and coastal protection by coral reefs due to heat-induced mass coral bleaching and mortality increases, exacerbated by ocean acidification, e.g., in CBS, SES, and STG regions. (*high confidence*) [5.4.2.4, 6.3.1, 6.4.2, 30.3.1.1, 30.3.2.2, 30.5.3-6, Box CC-CR]	Evidence of rapid evolution by corals is very limited or nonexistent. Some corals may migrate to higher latitudes. However, the movement of entire reef systems is unlikely given estimates that they need to move at the speed of 10 – 20 km yr^{-1}. Human adaptation options are limited to reducing other stresses, mainly enhancing water quality and limiting pressures from tourism and fishing. This option will delay the impacts of climate change by a few decades but is likely to disappear as thermal stress increases.		Present Near term (2030 – 2040) Long term (2080 – 2100) 2°C 4°C	
Coastal inundation and habitat loss due to sea level rise, extreme events, changes in precipitation, and reduced ecological resilience, e.g., in CBS and STG subregions. (*medium to high confidence*) [5.4.2.3-7, 5.5.2, 5.5.4, 30.5.6, Box CC-CR]	Options to maintain ecosystem integrity are limited to the reduction of other stresses, mainly pollution and limiting pressures from tourism, fishing, physical destruction, and unsustainable aquaculture; reducing deforestation and increasing reforestation of river catchments and coastal areas to retain sediments and nutrients; increased mangrove, coral reef, and seagrass protection and restoration to protect numerous ecosystem goods and services such as coastal protection, tourist value, and fish habitat.		Present Near term (2030 – 2040) Long term (2080 – 2100) 2°C 4°C	
Marine biodiversity loss with high rate of climate change. (*medium confidence*) [6.3.1-3, 6.4.1.2-3, Table 30.4, Box CC-MB]	Adaptation options are limited to the reduction of other stresses, mainly to reducing pollution and to limiting pressures from tourism and fishing.		Present Near term (2030 – 2040) Long term (2080 – 2100) 2°C 4°C	

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Table 6-6 (continued)

Risks to fisheries				
Key risk	**Adaptation issues & prospects**	**Climatic drivers**	**Timeframe**	**Risk & potential for adaptation**
Decreased production of global shellfish fisheries. (*high confidence*) [6.3.2, 6.3.5, 6.4.1.1, 30.5.5, 30.6.2.1, Box CC-OA]	Effective shift to alternative livelihoods, changes in food consumption patterns, and adjustment of (global) markets.			
Global redistribution and decrease of low-latitude fisheries yields are paralleled by a global trend to catches having smaller fishes. (*medium confidence*) [6.3.1, 6.4.1, 6.5.3, 30.5.4, 30.5.6, 30.6.2]	Increasing coastal poverty at low latitudes as fisheries becomes smaller – partially compensated by the growth of aquaculture and marine spatial planning, as well as enhanced industrialized fishing efforts.			
Redistribution of catch potential of large pelagic-highly migratory fish resources, such as tropical Pacific tuna fisheries. (*high confidence*) [6.3.1, 6.4.3, Table 30.4]	International fisheries agreements and instruments, such as the tuna commissions, may have limited success in establishing sustainable fisheries yields.			
Variability of small pelagic fishes in Eastern Boundary Upwelling systems is becoming more extreme at interannual to multi-decadal scales, making industry and management decisions more uncertain. (*medium confidence*) [6.3.2, 6.3.3, 30.5.5, Box CC-UP]	Development of new and specific management tools and models may have limited success to sustain yields. Reduction in fishing intensity increases resilience of the fisheries.			
Decrease in catch and species diversity of fisheries in tropical coral reefs, exacerbated by interactions with other human drivers such as eutrophication and habitat destruction. (*high confidence*) [6.4.1, 30.5.3-4, 30.5.6, Table 30-4, Box CC-CR]	Restoration of overexploited fisheries and reduction of other stressors on coral reefs delay ecosystem changes. Human adaptation includes the usage of alternative livelihoods and food sources (e.g., coastal aquaculture).			
Current spatial management units, especially the MPAs, may fail in the future due to shifts in species distribution and community structure. (*high confidence*) [6.3.1, 6.4.2.1, 30.5.1, Box CC-MB]	Continuous revision and shifts of MPA borders, and of MPA goals and performance.			

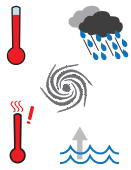
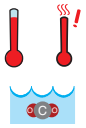
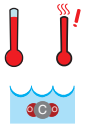
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projected to continue in the 21st century under all IPCC emission scenarios (*high confidence*; Sections 6.3.1, 6.3.5, 6.3.7, 6.4.1, 6.5.2).

Climate-induced regime shifts and regional changes in Plankton Phenology (PP; *medium confidence*) have caused and will cause changes in food composition and availability to animals. Species shifts and changing species composition lead to changes in Fishery Catch Potential (FCP; *high confidence*; 5a in Figure 6-15), partly attributable to climate change (*high confidence*) and to sustained fishing pressure (Section 6.5.3). Fisheries Catch Potentials (FCP) will be redistributed, decrease at low latitudes, and increase at high latitudes (*high confidence*; 5a in Figure 6-15). These trends will possibly be strengthened by the projected decrease in NPP at low latitudes and increase in NPP at high latitudes (*medium confidence*; Sections 6.5.2-3; 5b in Figure 6-15). Polar Organisms (PO) that are unable to migrate to cooler waters, and to acclimatize or to adapt to warming, will become marginalized, contributing to the projected high species turnover in polar areas (*high confidence*; Sections 6.3.1, 6.5.2).

Detected effects on Marine Air Breathers (MAB: mammals, seabirds, and reptiles) include changing abundances and phenology, shifts in species distribution, and in sea turtle sex ratios (*high confidence*), all of which are partly attributed to climate change (*high confidence*). However, few effects are directly linked to climate drivers (e.g., temperature-driven turtle sex ratio); most effects are due to shifts in habitat structure (e.g., loss of sea ice), changing availability of prey organisms, or changes in

Table 6-6 (continued)

Risks to humans and infrastructure				
Key risk	**Adaptation issues & prospects**	**Climatic drivers**	**Timeframe**	**Risk & potential for adaptation**
Coastal socioeconomic security. (*high confidence*) [5.5.2, 5.5.4, 30.6.5, 30.7.1, Table 30-4]	Human adaptation options involve (1) protection using coastal defences (e.g. seawalls) and soft measures (e.g., mangrove replanting and enhancing coral growth); (2) accommodation to allow continued occupation of coastal areas by making changes to human activities and infrastructure; and (3) managed retreat as a last viable option. Options vary from large-scale engineering works to smaller scale community projects. Options are available under the more traditional CZM (coastal zone management) framework but increasingly under DRR (disaster risk reduction) and CCA (climate change adaptation) frameworks.		Present Near term (2030 – 2040) Long term 2°C (2080 – 2100) 4°C	Very low / Medium / Very high * Present * Near term * Long term 2°C * 4°C
	**High confidence* in existence of adaptation measures, *Low confidence* in magnitude of risk reduction			
Reduced livelihoods and increased poverty. (*medium confidence*) [6.4.1-2, 30.6.2, 30.6.5]	Human adaptation options involve the large-scale translocation of industrial fishing activities following the regional decreases (low latitude) versus increases (high latitude) in catch potential and shifts in biodiversity. Artisanal local fisheries are extremely limited in their adaptation options by available financial resources and technical capacities, except for their potential shift to other species of interest.		Present Near term (2030 – 2040) Long term 2°C (2080 – 2100) 4°C	Very low / Medium / Very high
Impacts due to increased frequency of harmful algal blooms (*medium confidence*) [6.4.2.3, 30.6.3]	Adaptation options include improved monitoring and early warning system, reduction of stresses favoring harmful algal blooms, mainly pollution and eutrophication, as well as the avoidance of contaminated areas and fisheries products.		Present Near term (2030 – 2040) Long term 2°C (2080 – 2100) 4°C	Very low / Medium / Very high
Impacts on marine resources threatening regional security as territorial disputes and food security challenges increase (*limited evidence, medium agreement*) [AR5 SREX, 30.6.5, 30.7.2, 12.4-6, 29.3]	Decrease in marine resources, movements of fish stocks and opening of new seaways , and impacts of extreme events coupled with increasing populations will increase the potential for conflict in some regions, drive potential migration of people, and increase humanitarian crises.		Present Near term (2030 – 2040) Long term 2°C (2080 – 2100) 4°C	Very low / Medium / Very high
Impacts on shipping and infrastructure for energy and mineral extraction increases as storm intensity and wave height increase in some regions (e.g., high latitudes) (*high confidence*) [AR5 SREX, 30.6.2.3-4, 30.6.5, 29.3]	Adaptation options are to limit activities to particular times of the year and/or develop strategies to decrease the vulnerability of structures and operations.		Present Near term (2030 – 2040) Long term 2°C (2080 – 2100) 4°C	Very low / Medium / Very high

foraging efficiency, in both mammals (polar bears, walruses) and birds (penguins, albatrosses). Such trends will be exacerbated by future warming (*high confidence*; Sections 6.3.7, 6.5.2).

6.6.1.3. Expanding Hypoxia Affecting Marine Resources

Hypoxic zones in marine sediments and pelagic OMZs will continue to expand in the future, owing to climate-induced warming trends (Section 6.1.1). Local and regional Hypoxia Effects (HE) have been observed (*medium confidence*) and will be exacerbated in the future (*high confidence*; Section 6.3.3) causing habitat loss for groundfishes and pelagic predators and affecting the distribution of key zooplankton and nekton species (*medium confidence*). Progressive hypoxia is causing shifts in community composition toward hypoxia-tolerant species, excluding calcifiers due to elevated pCO_2 (*high confidence*), benefiting specialized microbes, and leading to reduced biodiversity and the loss of higher life forms (*high confidence*; Section 6.3.3). Loss of deep habitat and biomass of Mid-Water Fishes (MWF; Section 6.3.3; *medium confidence* in detection) off California is also attributed to hypoxia (*medium confidence*). These trends will continue into the future (*medium confidence*).

6.6.1.4. Constraints on Marine Calcifiers and Associated Fisheries and Aquaculture due to Ocean Acidification

Ocean acidification will exert negative effects on species and whole ecosystems and their services, especially those relying on carbonate structures such as warm-water coral reefs (*high confidence*; cf. Section 30.7.1.2). Presently, only a small number of field observations have detected Ocean Acidification Effects (OAE; *medium confidence*), but experiments and natural analogs support reliable but qualitative projections and attribution (*high confidence*). A specific glimpse into the future of anthropogenic OA is provided by negative Effects of upwelled CO_2-rich waters on Pacific Oysters (EO) introduced to aquaculture along the North American west coast (*high confidence* in detection, *low confidence* in attribution to anthropogenic causes). Findings in experimental laboratory and field studies as well as at natural analogs support attribution of projected effects to future CO_2

concentrations (*medium confidence*), with species-specific sensitivities across phyla (*high confidence*). Projected effects are most harmful to strong CALcifiers (CAL; *high confidence*), for example, some echinoderms, bivalves, gastropods, warm-water corals, and crustose algae, and less harmful to some crustaceans and, possibly, fishes. Projections from experimental studies and observations at natural analogs indicate shifts in Community Composition (CC) to more active animals and from calcifiers (CAL) to non-calcifiers in all organism groups (*high confidence* in both projection and attribution to increased CO_2; Section 6.3.2; Table 6-3).

6.6.1.5. Interactions of Climate-Related Drivers Exacerbating Impacts on Organisms, Ecosystems, and Their Services

Climate change involves interactions of temperature with other climate-related drivers and their effects (ocean acidification, hypoxia, freshening, nutrient supply, organism shifts resulting in changing interactions between species, changes in habitat structure, e.g., loss of sea ice). Strong interactions with other human impacts like eutrophication, fishing, and other forms of harvesting accelerate and amplify climate-induced changes (*high confidence*; Section 6.3.5, 30.7.1.1). Harmful algal blooms (HAB) will be stimulated by warming, nutrient fluctuations in upwelling areas, eutrophication in coastal areas (Table 6-6), ocean acidification, and enhanced surface stratification (*medium confidence*). Synergistic Effects (SE) will be exacerbated in the future (*medium confidence*), but have not yet been clearly detected and attributed in the field (*low confidence*). For projected future effects, attribution of observed impacts to such synergisms is supported by experimental evidence, especially in animals and plants (*medium confidence*).

Increased bleaching and decreased calcification displayed by several Reef-building Warm-water Corals (RWC; *very high confidence*) over the last 3 decades are attributed to the ongoing warming trend, and the associated rise in extreme temperature events and amplitudes (*high confidence*; Sections 6.3.1, 30.5.6; Box CC-CR). Such trends will be exacerbated by future warming and synergistic effects (*high confidence*; cf. Section 30.5.4.2), with some amelioration by latitudinal shifts and evolutionary adaptation (Section 6.3.1; *low confidence*). Ocean acidification will have an increasing influence on reefs (*high confidence*), as indicated by similar phenomena during mass extinctions in Earth history.

6.6.2. Key Uncertainties

Key uncertainties result from insufficient knowledge of ocean systems. International organizations (both inter- and non-governmental) have the opportunity to play a key role in coordinating research concepts and approaches, working toward a coherent picture of climate change effects on the global ocean. Countries around the world have limited capacity and infrastructure to study the ocean's response to climate change. Long-term observational time series are especially lacking, in both quantity and quality. Research has provided valuable insights, but a unifying approach addressing principles across organism domains and ecosystems is still missing. Processes investigated so far differ largely by study organisms (plants, animals, phytoplankton, and bacteria) and by level of organization (ecosystem, whole organism, tissue, cell, molecular). Especially for microbes, available data are patchy and reported trends are often in different directions, partly due to different experimental protocols and/or over-reliance on species or strains of microbes that are readily culturable, and hence have been used for decades in laboratory research. The knowledge base of climate impacts on species, strains, or communities in the field is insufficient. Scaling from physiological studies on individual species to ecosystem changes has been successful in individual cases but has not been widely implemented, for example, to shifts in species interactions or food webs. An integrated framework of climate sensitivity at the ecosystem level that considers multiple drivers and their interactive effects needs to be developed further. This includes an in depth understanding of ecosystem structure (physical and biological) and functioning, of ecosystem complexity and species interactions, and of the resulting implications for biogeochemical processes. For all climate drivers, especially ocean warming, acidification, and hypoxia, studies integrating mechanistic knowledge and evolutionary adaptation over generations are needed. Research should also cover various climate zones and biomes. Laboratory and modeling experiments are needed to test hypotheses building on long-term field observations and observations at natural or paleo-analogs. Models should better integrate observations and mechanism-based understanding, and better project future interactions between human and natural systems in a changing climate.

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