Chapter 6. Ocean Systems

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Executive Summary

Ocean ecosystems and their services will continue to respond to climate change (*high confidence*). Human societies benefit from and depend on 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, climate regulation, protection from natural hazards, and aesthetic, cultural, and supporting services. [6.3.6, 6.4, 6.5]

Climate change is manifesting itself in the alteration of abiotic and biotic properties of the ocean (*high confidence*). Abiotic drivers changing in the ocean include circulation intensity, temperature, oxygen (O_2) and nutrient inventories, carbon dioxide (CO_2), ocean pH, salinity, and light regime. Biotic drivers range from the physiology of individual cells and organisms to ecosystem structure and function. [6.1.1, 6.2.2]

Marine ecosystems were and are being exposed to and affected by climate changes of different rates, magnitude and duration (*very high confidence*). In Earth history, natural climate change at rates slower than today's anthropogenic change has led to significant ecosystem shifts (*high confidence*). The fossil record and present field and laboratory observations confirm key environmental drivers and responses of ocean ecosystems to climate change (*high confidence*), including migration, altered ecosystem composition, changes in abundance, and extinctions (*high confidence*). [6.1.2, 6.3]

The combination and often amplification of climate change drivers acting globally and additional human-induced local drivers such as overfishing, pollution, and eutrophication exacerbating hypoxia, result in enhanced vulnerability of natural and human systems to climate-related forcings presently and into the future (*high confidence*). Key observations and vulnerabilities are reflected in the progressive redistribution of species, changes in species' abundance and the reduction in marine biodiversity in sensitive regions and habitats, putting the sustained provision of ecosystem services and fisheries productivity at risk (*high confidence*). Socio-economic vulnerability is high particularly in tropical developing countries, progressively increasing the risk of reduced food supply, income and employment (*high confidence*). Key uncertainties include the up-scaling of climate change effects from organism to ecosystem level, the adaptive capacity of marine organisms and human societies to these impacts, the interactions with other human drivers, the sustenance of biogeochemical functions and productivity in the global ocean, and the effectiveness of climate mitigation and adaptation measures.

Physical effects of climate change on marine ecosystems may act, under some circumstances, as an additional pressure that cannot be mitigated by local conservation measures or a reduction in human activities like fishing (*high confidence*). Effects of climate change will thus complicate management regimes, e.g. presenting direct challenges to the objectives of spatial management once species undergo large-scale distributional shifts. This increases the vulnerabilities of marine ecosystems and fisheries. [6.4]

Understanding of physiology combined with field observations demonstrates that vulnerability of most organisms is defined by their specialization on specific, limited temperature ranges and accordingly, by their thermal sensitivity (*high confidence*). Temperature defines the geographical distribution of species and their responses to climate change (*medium confidence*). Temperature extremes act through losses in abundance and (e.g. sea ice and coastal) habitat, local extinction and latitudinal shifts (*very high confidence*). Vulnerability is greatest in polar animals due to narrow temperature ranges (*medium confidence*) and in e.g. tropical species living close to their upper thermal limits (*medium confidence*). Some warm water corals and their reefs will continue to respond to warming with species replacement, bleaching from loss of associated algae and a decreased coral cover resulting in habitat loss (*high confidence*). In general, knowledge of the mechanisms of climate effects helps to understand changes in the past, present and future. Genetic adaptation may occur; the capacity to compensate for or keep up with the rate of ongoing thermal change is limited (*low confidence*). [6.2.2-5, 6.3.2, 6.5.2]

Warming is causing shifts in the geographical distribution, abundance, and migration patterns of species, paralleled by a reduction in their body size and a shift in the timing of seasonal activities. This results in altered interactions between species including changes in competition and predator-prey dynamics (*high confidence*). There are many observations of poleward shifts in the distribution and abundance of fishes and invertebrates and/or of their shifts to deeper and cooler waters (*high confidence*). Poleward shifts of plankton have occurred up to 250 km per decade, up to 30 times faster than terrestrial species (*high confidence*). While marine turtles also experience direct effects of warming, birds and mammals are mostly indirectly impacted through sensitivities of their prey to these altered conditions (*high confidence*) [6.2.2, 6.2.5, 6.3., 6.5].

Modeling projects that, through species gains and losses correlated with warming, the diversity of animals and plants will increase at mid and high latitudes (*high confidence*) and fall at tropical latitudes (*low confidence*) [6.3.2, 6.5.2] leading to a large-scale redistribution of global catch potential for fishes and invertebrates (*medium confidence*). If a decrease in global ocean net primary production or a shift downwards in the size spectrum of primary producers occur, the overall fisheries catch potential will decrease, in ways influenced by other human impacts on ecosystem structure. Animal displacements are projected to lead to a 30–70% increase in the fisheries yield of high-latitude regions but a drop of 40%- 60% in the tropics by 2055 relative to 2005 under the SRES A1B scenario (*medium confidence* for the general trend of shifting fisheries yields, *low confidence* for the magnitude of change). [6.2.5, 6.3.2, 6.4, 6.5]

The oceans currently provide about half of global net primary production (NPP). Environmental controls on NPP include temperature, CO_2, nutrient supply and irradiance all of which are projected to be altered (WGI). The direction, magnitude and regional differences of a change of NPP in the open ocean as well as in coastal waters have *limited evidence* and *low agreement* for a global decrease projected by 2100. At high (polar) latitude an increase in NPP is also projected with *low confidence*. [6.3.1, 6.5.1]

Microbes (Bacteria, Archaea, unicellular algae and protozoans) serve key roles in marine ecosystems and sustain large scale processes and climatic feedbacks which will be altered by climate change (*medium confidence*). Identifying which microbial species or groups and processes are being affected by climate change and how these will be altered is presently based on *limited evidence* and *low agreement* as these organisms and their responses to environmental change are extremely diverse and often modulated by non-linear biological interactions or uncertain changes in circulation and nutrient supply. A warming ocean may enhance the metabolic rates of microbes, but also cause species specific phenotypic and genotypic responses, e.g. challenge their thermal tolerance and thereby, their abundance, distribution and community structure. Warming, more nutrient-rich coastal oceans may enhance the development of harmful algal blooms (*low confidence*) or pathogen distribution like cholera (*low confidence*). [6.2, 6.3, 6.4.2, 6.5]

Rising atmospheric CO_2 not only causes ocean warming but also changes in carbonate chemistry termed ocean acidification. Laboratory, mesocosm and field data show that ocean acidification has ramifications for processes ranging from physiology and behavior to population dynamics (*medium* to *high confidence*). Across organisms, sensitivity decreases with increasing capacity to compensate for the elevated internal CO_2 concentration or falling pH (*medium confidence*). Most plants including algae, respond positively to elevated CO_2 levels by increasing photosynthesis and growth (*high confidence*). A wide range of sensitivities to projected acidification exists within and across organism phyla (*high confidence*). Laboratory work demonstrated a capacity to undergo trans-generational or evolutionary adaptation in some species, thereby reducing the impact of the projected change (*low* to *medium confidence*). Limits to adaptational capacity remain unexplored (*low confidence*). [6.2.2-6, 6.3.4]

Field observations attributed to anthropogenic ocean acidification are few due to limited changes in water chemistry between pre-industrial times and today. Shell thinning in planktonic foraminifera from various regions and Southern Ocean pteropoda has been attributed fully or in part to acidification trends (*medium confidence*). Coastward shifts in upwelling regimes of the Northeast-Pacific and upwelled CO_2-rich waters presently causing larval oyster fatalities in aquacultures (*high confidence*) or shifts from mussels to fleshy algae and barnacles (*medium confidence*) provide an early perspective on future effects of ocean acidification. Ecosystems at risk of ocean acidification are warm and cold water coral reefs (*high* or *medium confidence*). However, sensitivity is species specific; e.g. cold water corals display significant capacity to compensate for exposure to acidified seawater (*medium confidence*) in long-term laboratory cultures. [6.1.2, 6.2.2, 6.2.5, 6.3.4]

Several environmental drivers act simultaneously on ocean biota, often leading to interactive effects and complex responses (*high confidence*). For example, physiological knowledge projects that ocean acidification and hypoxia narrow thermal ranges and enhance sensitivity to temperature extremes in organisms like corals, coralline algae, molluscs, crustaceans and fishes (*high confidence*). Combined warming and ocean acidification reduce calcification in warm water corals (*high confidence*). [6.2.5, 6.3.2, 6.3.5, 6.5.2]

The ongoing expansion of hypoxic regions termed Oxygen Minimum Zones (OMZs) or anoxic “dead” zones constrains the habitat of O_2-dependent animals, plants and microbes while it benefits anaerobic microbial life (*high confidence*). Warming-induced stratification, reduced intensity of ocean circulation and the decomposition of organic matter by heterotrophic organisms create an expansion of these specialized, microbially dominated ecosystems, the regional OMZs (*high confidence*). The removal of fixed nitrogen (denitrification) via the metabolism of selected bacteria and archaea can reduce nutrient inventories and alter the N:P balance. Hypoxia tolerance varies among species and is influenced by temperature, elevated CO_2, food consumption, and O_2-demand (*high confidence*). [6.2.2-6, 6.3.3, 6.3.5]

Intensified ocean upwelling in some eastern boundary systems produce cooler surface waters associated with enhanced productivity (*medium confidence*), but in addition to hypoxia effects consequences for higher trophic levels in those areas remain unknown. [6.1.1, 6.3.3, 6.3.4, 6.3.6]

Geoengineering approaches involving manipulation of the ocean to ameliorate climate change (e.g. purposeful nutrient fertilization, binding of CO_2 by enhanced alkalinity and direct CO_2 injection into the deep ocean) have very large associated environmental footprints (*high confidence*), with some actually requiring purposeful alteration of ocean ecosystems for implementation. Alternative methods focusing on solar radiation management (SRM) leave ocean acidification unabated. [6.4.2]

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

The Oceans cover 71% of Earth’s surface to an average depth of 3,800 m and represents more than 95% of the habitable environment (by volume) of our planet. Marine habitats exhibit natural variability on temporal scales from synoptic to interdecadal but the causes and ecological consequences are poorly understood as long-term series of direct observations from the open ocean are rare. The available information indicates that oceanic ecosystems are particularly sensitive to stresses mediated by climate change, partly because of direct effects on organisms and their interactions and partly because physical and chemical forcings control ocean temperatures, chemistry and the current regime, upper ocean stratification, nutrient supply and light regime and, hence, growth of phytoplankton, availability of food for heterotrophs (live organisms as prey, or their decomposing bodies, i.e. debris or dissolved organic matter) and the structure and function of the food webs. Physical and chemical attributes influence biogeochemical processes, including carbon cycle dynamics. They also shape the biological diversity the oceans support and the services they provide. Some of the knowledge on marine impacts has been assessed in the 4th IPCC assessment report, AR4 WGII Chs. 4-6, 15,16. For the first time in the series of IPCC reports, impacts on the oceans are a focus in AR5, in the present sectoral chapter and a regional chapter (30). This allows for a more differentiated discussion of phenomena and impacts, as well as the associated uncertainties and the levels of confidence in observed and projected changes. For some of those, confidence has changed since AR4.

The present chapter focuses on the general principles and processes characterizing climate change impacts on the ocean system as a whole and its use by human society, so it focuses on global ocean processes rather than those in specific water columns or benthic provinces. It also addresses our understanding of functional mechanisms across all levels of biological organization, from molecular to organismal to ecosystem scale which is required for accurate projections of the ocean's responses to climate change. Division of the oceans into discrete functional units can help to elucidate variability and differences in ongoing and projected changes in key processes and carbon inventories across ocean regions (Figure 6-1). Oceanic ecosystems and the services that they provide must then be assessed on a region-specific basis (see WGII Chs 5, 28 and 30).

In order to assess the available evidence on the relationships between climate and ecosystem change, as well as to project future impacts, we rely on Representative Concentration Pathways (RCP) of climate change scenarios (Moss *et al*., 2010). We begin with a discussion of the variability of the principal physical and chemical parameters of the oceans and build on evidence available from paleo- and historical observations for identifying the forces causing change. Then, a conceptual framework of understanding climate change effects on organisms and ecosystems is developed and used to interpret empirical observations of ecosystem change, to assess the implications of such changes for ecosystem services and to identify plausible socioeconomic consequences.

[INSERT FIGURE 6-1 HERE
Figure 6-1: Productivity in 51 distinct global ocean biogeographical biomes as represented by a grid of thin black lines (after Longhurst, 1998), overlain with an average annual composite plot of chlorophyll *a* concentration, i.e., a proxy for phytoplankton stocks in the upper ocean, from the NASA/Orbimage SeaWiFs satellite (Bailey *et al*., 2006; McClain *et al*., 2004; McClain, 2009). The characteristics and boundaries of each biome are primarily set by the underlying regional physics and chemistry. Together, these provinces or biomes span several orders of magnitude in chlorophyll *a* from < 0.1 mg m^{-3} that characterize the low latitude oligotrophic regions (denoted by purple and blue) up to 10 mg m^{-3} in highly productive coastal upwelling regions in Eastern boundary currents (denoted by red).]

6.1.1. Recent Trends and Projections of Physical and Chemical Parameters

Trends in ocean conditions over the last 50 years reflect significant human impacts beyond natural variability on e.g. temperature or salinity or carbon content of the upper ocean (Pierce *et al*., 2012; WGI Ch.10).

6.1.1.1. Warming

Over the last 43 years average warming has occurred by >0.1 °C/decade in the upper 75 m and by 0.017 °C/decade at 700m depth (WGI Ch. 3), with trends strongest at high latitudes and regional differences between warming rates associated with prominent spatio-temporal structures (WGI Ch. 2) and scales of natural sea surface temperature variability (Figure 6-2), particularly strong at the typical ENSO high and low frequencies, and on multidecadal scales (>25 years). The interannual frequencies are dominant at most tropical oceans, while the multidecadal scale explains most of the high latitude variability. Changes in ENSO activity have been explored through global climate models, but trends in the spatial signature are highly uncertain. Moreover, global observation-based analyses of climate-induced changes in dominant variability frequencies are limited by data availability, especially for the low frequency scale at high latitudes, where the strongest warming is occurring. Temperature variations are accompanied by spatially variable changes in salinity. Both warming and freshening can cause enhanced stratification. Increases in salinity result from reduced precipitation relative to evaporation and have occurred in upper thermoclines of subtropical gyres at mid to low latitudes since 1970 (WGI Ch. 3). In contrast, freshening caused by enhanced precipitation relative to evaporation occurs at higher latitudes, exacerbated by increased sea ice melt. These trends are projected to continue into the 21st century (WGI Figure 12-34), leading to lower salinity intermediate waters sinking at high latitudes (Helm *et al*., 2010; WGI Ch. 3).

[INSERT FIGURE 6-2 HERE
Figure 6-2: Sea surface temperature variability in the last century (1911 to 2011). The top left map shows the sea surface temperature average for the period. The top right map illustrates the temperature range calculated as the difference between the maximum and minimum values for each grid component during the century. The spatial distribution of variability by time scales (left hand map series) was computed by accumulating the relative spectral densities of each 2°x2° grid box frequency-transformed series by frequency windows, corresponding to the multidecadal (period >25 years), bidecadal (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 sum of the six maps at every single box corresponds to 100% of the interannual time series variability. The right hand histograms show the area of the World Ocean (%) at each weight interval, for each frequency window. All computations are based on the Extended Reynolds Sea Surface Temperature (NOAA, 2012).]

6.1.1.2. Acidification

Scenarios of future atmospheric carbon dioxide (CO_2) concentrations (given as partial pressures, pCO_2, in µatm) have been described by SRES and following several RCPs (Moss *et al*., 2010; Meinshausen *et al*., 2011). All RCPs lead to atmospheric pCO_2 levels somewhat less than 500 µatm by 2050. Then, under different RCPs, values between 420 µatm and 940 µatm can be expected by 2100.-On average, rising CO_2 concentrations in air cause significant increases in upper ocean CO_2 levels associated with oceanic drawdown of atmospheric CO_2 (Watson *et al*., 2009). This leads to ocean acidification (OA), an increase in acidity measured as a decline in pH. OA also results in a progressive decrease of carbonate ion (CO_3^{2-}) concentration and thus of the saturation state (Ω) of calcium carbonates ($CaCO_3$; Zeebe and Westbroek, 2003; WGI Chs. 3, 6). Hence, the solubilities of calcite, Mg-calcite, or aragonite increase. These minerals are important components of shells or skeletons in many marine organisms (6.2.2). OA occurs on a background of natural variability of pH and Ω values over time and between sites from pH 8.2 in highly productive pelagic regions to 7.2 in mid-water layers where excess respiration causes low oxygen (O_2) and elevated CO_2 levels. While the physical and chemical basis of ocean acidification is well understood, few field data exist of sufficient duration, resolution and accuracy to document the acidification rate and its geographic and temporal variability (WGI Figure 3-17). Trends in anthropogenic OA clearly deviate from the envelope of natural variability (Friedrich *et al*., 2012). OA presently ranges between -0.0015 and -0.0024 pH units per year (WGI Ch. 3, 6, 12; Dore *et al*., 2009); average surface ocean pH has decreased by more than 0.1 units below the pre-industrial average of 8.17 and is expected to drop until 2100 by -0.13, -0.22, -0.28 to -0.42 pH units, at CO_2 levels of 421, 538, 670, and 936 ppm under the RCP 2.6, 4.5, 6.0 and 8.5 scenarios, respectively (WGI Figure 6-28). The rate of acidification varies regionally and is 50% higher in the Northern North Atlantic than in the subtropical Atlantic (Olafsson, 2009). Ice melt or excess precipitation cause salinity reductions (Jacobs and Giulivi, 2010; Vélez-Belchí *et al*., 2010) and, thereby, an exacerbation of OA (Steinacher *et al*., 2009; Denman *et al*., 2011). In the absence of biota (6.2.2., 6.3.3), the changes in ocean chemistry due to OA will take thousands of years to be buffered through neutralization by calcium carbonate from sediments and tens to hundreds of thousands of years for the weathering of rocks on land to eventually restore ocean pH completely (Archer *et al.*, 2009).

6.1.1.3. Hypoxia

Oceanic O_2 concentrations range from over 500 µmoles kg^{-1} in productive, nutrient rich Antarctic waters (up to 140% saturation relative to equilibrium with the atmosphere; Carrillo *et al.*, 2004) to zero in coastal sediments rich in organic matter and in anoxic deep layers of isolated water bodies such as the Black Sea and the Cariaco Basin. The average value for the ocean is estimated as 178 µmol kg^{-1} (Sarmiento and Gruber, 2006). Large-scale fluctuations of O_2 concentrations have occurred over geological time (Wignall, 2001; Meyer and Kump, 2008), during glacial-interglacial cycles (Schmiedl and Mackensen, 2006; Robinson *et al.*, 2007), on multi-decadal (Yasuda *et al.*, 2006; Whitney *et al.*, 2007) inter-decadal (Arntz *et al.*, 2006), seasonal, synoptic and, in some high productivity regions, diurnal time scales (Grantham *et al.*, 2004; Connolly *et al.*, 2010). In ecological literature, the term hypoxia (see 6.3.3) is commonly used for O_2 concentrations below 60 µmoles kg^{-1}, according to the transition to communities with characteristic hypoxia adaptations. (It should be noted, however, that O_2 can become limiting to animal life once it falls from air saturation to levels well above this threshold (6.2.5) These hypoxic waters presently occupy ~5% of the ocean volume ($7.6x10^{16}$ m^3) (Deutsch *et al.*, 2011). Oxygen minimum zones (OMZs) associated with hypoxia at $O_2 < 22$ µmol kg^{-1} (< 0.5 ml L^{-1}) occupy nearly $30x10^6$ km^2 ($10.2x10^7$ km^3) in the open ocean (Paulmier and Ruiz-Pino, 2009) and cover about $1.15x10^6$ km^2 of the continental margin seabed (Helly and Levin, 2004; Diaz and Rosenberg, 2008). At the oxic-anoxic interface, suboxic waters with very low O_2 concentrations (< 4.5 µmoles kg^{-1}) occupy $4.6x10^{14}$ m^3 (less than 0.05 % of the ocean volume), mainly in the Northeast Pacific (Karstensen *et al*., 2008).

Hypoxia in midwater OMZs stretching over hundreds up to thousands of meters in the main ocean basis, and other O_2 deficient habitats is caused by respiration coinciding with CO_2 accumulation. Over the past 50 years, the mean rate of O_2 decrease was from 0.1 to over 0.3 µmoles kg^{-1} $year^{-1}$ (Stramma *et al.*, 2008; Stramma *et al.*, 2010), but in some OMZs it was much higher, due to warming, stratification and bacterial O_2 demand (WGI Box 6.5, Figure 1). Long-term declines in O_2 by about 7 µmoles kg^{-1} $decade^{-1}$ have been documented at mid water depths over much of the subarctic North Pacific (Keeling *et al.*, 2010). The number of extremely hypoxic coastal regions excluding metazoans, termed 'dead zones' and attributed to eutrophication induced deoxygenation, have increased from 120 in the 1980s to over 400 in 2008 (Diaz and Rosenberg, 2008). A rapid build-up of anoxic zones (void of O_2) has been found in stratified inland water bodies such as the brackish water Aral Sea (Zavialov, 2005; Zavialov *et al.*, 2009). With future warming, the spread of hypoxic zones will *very likely* accelerate, especially in temperate to subpolar regions where increases in ocean stratification due to warming or freshening of the surface layer can reduce the depth of winter mixing and create dense waters in association with ice formation. Most models project a decrease of global ocean oxygen content of 1 to 7 % by 2100 (Keeling *et al.*, 2010; WGI Figure 6-29 under RCP 8.5) implying feedbacks on the volumes of severely hypoxic and suboxic waters as well as key biogeochemical pathways (Deutsch *et al*., 2011). Fluvial runoff into the ocean causing eutrophication and associated hypoxia is projected to increase by 2100 due to climate-related intensification of the global water cycle (e.g. Milly *et al.*, 2008; Ch. 5.2.2.1.7). Figures vary for regions and catchment areas (Kundzewicz *et al.*, 2005). The evolution of low O_2 zones will also be linked to changes to the wind regime (e.g. Vecchi and Soden, 2007; Ren, 2010) and of the intensity, duration and seasonal timing of upwelling events (Snyder *et al.*, 2003). The potential contribution of destabilized gas hydrates and bacterial methane oxidation to exacerbating hypoxia and acidification at high latitudes remains to be explored (Westbrook *et al*., 2009).

6.1.1.4. Other Physical and Chemical Drivers

Most modeling experiments indicate that the depth of the surface mixed layer will become shallower in the coming decades (e.g. Sarmiento *et al.*, 1998; Matear and Hirst, 1999) due to increased and seasonally extended (Holt *et al*., 2010) density stratification of the ocean especially in the tropics, the North Atlantic, the Northeast Pacific, and the Arctic (Capotondi *et al*., 2012). This may lead to decreased vertical transport of nutrients to surface waters (Polovina *et al.*, 2008; Doney, 2010). The resulting reduction in nutrient supply to phytoplankton growth may be partly compensated for by river plumes (Signorini *et al*., 1999), or by nutrient accumulation in the pycnocline as in the North Pacific (Whitney, 2011), or enhanced upwelling (Ch. 5.2.2.1.6) indicated by observations in the Peruvian (Gutiérrez *et al.*, 2011), Californian (Snyder *et al*., 2003; Rykaczewski and Dunne, 2010) and Canary systems (McGregor *et al*., 2007). However, upwelling rates projected by climate models largely diverge (Bakun *et al*., 2010).

6.1.1.5. Conclusions

It is *virtually certain* that with climate change, marine ecosystems are exposed to changing regimes of drivers, e.g. rising temperature, ocean acidification and the expansion of hypoxic zones. Warming of the surface layers *very likely* enhances and prolongs stratification, thereby limiting the nutrient inventory available to phytoplankton. Enhanced upwelling and human-induced eutrophication could partly compensate for the projected reduced nutrient supply in coastal oceans (*limited evidence, medium agreement*). Light availability to phytoplankton will *likely* increase due to shoaling of the surface mixed layer.

6.1.2. Paleo-Records

Paleontological records in marine sediments, from all ages and latitudes, provide information on spatial distributions of organisms and their abundance over time that can be readily related to the concurrent shifts in multiple environmental properties that are also recorded in these sediments. These records give us insights into extinctions, emergences, and changes in abundance and the environmental forcings that organisms are responding to. Temporal trends reveal influences of temperature, hypoxia and food availability on organisms and ecosystems, and changes in seasonal timing (phenology) of different components of the ecosystem (6.1.1, Figure 6-11). Spatial trends, from cores from different geographical locations, provide evidence of expansion of geographical ranges of plankton. These records are complemented by historical data sets of the last centuries of organisms which live for decades or centuries recording natural variability in the ocean system (WGI Ch. 3).

While the geological record often does not allow identification or direct attribution to a single driver of change or their relative importance, it supports by itself future projections on possible changes of a specific driver in extant ecosystems and their services only with *low* levels of *confidence* (6.4). Importantly though, increasing atmospheric CO_2 is causing warming in the surface ocean, altered/enhanced upper ocean stratification and consequently a decrease in dissolved O_2 concentration in the geological past and in the future. Thus, paleo and present day climatic shifts both share the same combination and sign of environmental changes (WGI). Therefore, a combination of data from the geological record and global circulation and carbon cycles models can use coupled warming and ocean acidification and deoxygenation events from the geological past to inform, with *medium confidence*, about future climate change impacts on ocean biota.

[INSERT FIGURE 6-3 HERE
Figure 6-3: Atmospheric CO_2 (bottom, grey) and temperature (middle, red/orange) changes with associated biotic changes (top) for the Paleocene Eocene Thermal Maximum (PETM) and the industrial era. Episodes of largest environmental change are indicated with yellow bars. CO_2 data are based on measurements at Mauna Loa (modern: Keeling *et al.*, 2005) and model output (PETM: Ridgwell and Schmidt, 2010; Zeebe *et al*., 2009). Temperature data are based on proxy data (modern: Wilson *et al.*, 2006; Lea *et al.*, 2003; PETM: Kennett and Stott, 1991) representing the regional temperature changes in the surface ocean. Modern biotic responses include changes in coralline algal growth (Halfar *et al.*, 2011), and coral calcification (De'ath *et al.*, 2009). Evolutionary changes are exemplified by the extinction of benthic foraminifera (Thomas, 2003). Abundance data (top row) of planktonic foraminifera and coccolithophores (modern: Field *et al.*, 2006; PETM: Bralower, 2002) indicate range expansion due to warming.]

The last glacial-interglacial transition is associated with an increase in atmospheric CO_2 of ~0.02 µatm/year on average over the transition (WGI Ch. 5) and hence fifty-fold slower than the current increase by 1 µatm/year on average over the last 100 years. Consequently, the resultant pH change of 0.002 pH units per 100 years during the glacial interglacial transition is small relative to the ongoing anthropogenic perturbation of >0.1 pH unit/century. Overall the glacial ocean was colder, with strong regional differences (WGI Ch. 5) and more O_2 rich than today’s ocean. There is *high confidence* that foraminifera, coccolithophores, diatoms, dinoflagellates and radiolarians showed marked poleward range expansion during the last glacial-interglacial transition and abrupt short-lived events such as the Bølling-Allerød Warming (see WGI Ch. 5) (CLIMAP Project Members, 1976; MARGO Project Members, 2009). Lower CO_2 concentrations in the upper ocean during the glacial interval are associated with increased calcification in planktonic foraminifera (*limited evidence*, *medium agreement)*. In the Santa Barbara basin, changes in oxygenation did not cause extinctions in the benthic foraminifera (Cannariato *et al*., 1999) while in the Arabian Sea, a stronger monsoon and the associated increases in upwelling, productivity and local reduction in O_2 led to a loss in diversity in the benthic foraminiferal assemblages (Schmiedl and Leuschner, 2005).

The last time atmospheric CO_2 was close to today’s was during the Pliocene warm period (3.3 to 3.0 Ma), with atmospheric CO_2 levels between 330-400 µatm (=ppm, Pagani *et al.*, 2010; Seki *et al.*, 2010) and temperatures ~+2 warmer than today (Haywood *et al.*, 2009, WGI Ch. 5) (*medium confidence*). Such a warming trend, occurring over several tens of thousands of years in contrast to 100 years projected for modern climate change, resulted in a poleward geographical expansion of tropical calcifying plankton species (Dowsett, 2007) (*high confidence*); however, no increases in species extinction or emergences compared to background rates has been associated with

Pliocene warming for coccolithophores (Bown *et al.*, 2004), corals (Jackson and Johnson, 2000) or molluscs (Vermeij and Petuch, 1986).

Perhaps the best analogue for the alteration of the future ocean is the Paleocene-Eocene Thermal Maximum (PETM), 55 million years ago (Ma), an event of rapid warming and ocean acidification, though model simulations for the future show 10 times higher rates of CO_2 input and hence ocean acidification in surface waters today than during the PETM (Ridgwell and Schmidt, 2010) (*medium confidence*). Depending on the assumed rate and magnitude of the CO_2 release during the PETM, models project a 0.25 to 0.45 pH unit decline in surface waters (Ridgwell and Schmidt, 2010) and a reduction in surface ocean aragonite saturation from Ω=3 to Ω=2 or even as low as 1.5. During the PETM, warming caused range expansion of warm-water taxa towards higher latitudes (*high confidence)*. While the composition of coccolithophore (Gibbs *et al.*, 2006, 2013) and dinoflagellate assemblages (Sluijs and Brinkhuis, 2009) changed, suggested to reflect the changes in nutrient availability and/or warming (6.2.2.-3), there was no bias in extinction towards more heavily calcifying species. In contrast, the benthic ecosystem recorded a 50% extinction among benthic foraminifera (Thomas, 2007) and a major change in the macrobenthic community (Rodríguez-Tovar *et al.*, 2011). In contrast to sediment dwellers, 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 larger benthic foraminifera (Scheibner and Speijer, 2008) (*medium confidence*). Models for the PETM suggest that the increase in oceanic vertical temperature gradients and stratification led to decreased surface ocean productivity and O_2 depletion in the deep sea (Winguth *et al.*, 2012), particularly in the equatorial zone by weakening of the trade winds and hence reducing upwelling.

The very warm climates of the Mesozoic (251 to 65 Ma) led to a number of oceanic anoxic events (Jenkyns, 2010). For some of these events, anoxia was not restricted to the deep ocean but vertically expanded OMZs led to photic zone anoxia (Pancost *et al.*, 2004). Some of these Cretaceous oceanic anoxic events were associated with extinctions or increased turnover (normalized sum of originations and extinctions) of the marine plankton (an average of 30% for planktonic foraminifera and radiolarians) although the changes were very small for other groups of organisms, e.g. coccolithophores (maximum 7%, Leckie *et al.*, 2002). The causal link between O_2 reduction and the evolutionary change in these groups is tenuous as these events were also associated with warming, changes in nutrient supply and, possibly, ocean acidification (Hönisch *et al*., 2012).

For examples of marine ecosystem collapse at global scale, expansion into the deep record of the past 250 million years (Myr) is required. Some mass extinctions, and in particular the Permian Period extinction 251 Ma ago, have been associated with large scale inputs of carbon into ocean and atmosphere and the associated deep-sea O_2 decline and global warming (Knoll *et al.*, 2007; Kiessling and Simpson, 2011; Knoll and Fischer, 2011) with consequent warming, acidification and O_2 depletion, though the rate of change has not been accurately constrained to date for any of these events. 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). The extinction rate of the end-Permian biological collapse was greater than any projection for coming centuries (Bambach, 2006), but it underscores the differing vulnerabilities of marine life to environmental perturbation among organisms of differing anatomy, physiology and ecology (Knoll and Fischer, 2011).

Of the last 100 Myr, only the last 2 Myr had CO_2 at levels lower than any projected for this decade and only the deep time older than 33 Ma record has CO_2 levels comparable to business as usual projections for the end of 2100 (WGI Ch. 5; Hönisch *et al*., 2012). That marine biota thrived throughout most of this era could imply that the organisms, which make up marine ecosystems, will not be impaired in a future warm, high CO_2 world. However, such comparisons are invalid because the key environmental issue of the 21st century is one of an unprecedented rate of change in CO_2 levels, not simply magnitude (Hönisch *et al*., 2012). The unparalleled rate and magnitude of modern ocean acidification in at least the last ~300 Myr of Earth history highlights the magnitude and scale of the current change in several environmental drivers. The slower events in the geological history provide *robust evidence and high agreement* of environmentally-mediated compositional changes in fauna and flora and, in some cases, of extinction and, to much lesser degree, emergences. Although similarities exist, no past natural climatic event perfectly parallels future projections, emphasizing how unprecedented future climate change is in the evolutionary history of most organisms. In light of the present rate of change the challenges involved may therefore be outside the adaptive capacity of many organisms living in today’s ocean (*low to medium confidence*).

6.1.3. Long-Term Biological Observations

Ocean ecosystems are complex, time and space variable, and non-steady state (Figures 6-4, 6-5). While climate science has benefitted from paleo-observations of tree rings, sedimentary records and ice cores (6.1.2), data sets of oceanic phenomena are rare. Those existing (Table 6-1) provide evidence that spatial and temporal variability are inextricably linked (Stommel, 1963). Therefore, systematic, long-term interdisciplinary observations using repeated, highly calibrated measurements at a given field site are required to distinguish natural ecosystem variability from (long-term) anthropogenic trends. The undersampling of ocean phenomena in time (Henson *et al*., 2010) and space constrains meaningful assessments of current states and projections about future ones.

[INSERT TABLE 6-1 HERE
Table 6-1: Selected examples of long-term biological and ecological observations in the oceans (NPP denotes Net Primary Productivity).

[INSERT FIGURE 6-4 HERE
Figure 6-4: Multiple coupled temporal and spatial scales of variability in physical, physiological and ecological processes in marine systems. Observations over broad time and space scales are necessary to separate natural variability from human-induced impacts, and define appropriate observation tools. The shaded regions depict the approximate boundaries of major processes, and the boxes define the scales of selected measurement/ observation procedures. Langmuir cells are a series of wind-driven shallow, slow, counter-rotating circulations at the ocean's surface. From Karl (2010), as modified from Dickey (1991).]

Historical data sets of organisms with life histories of decades and centuries and high resolution sediment cores covering the last few centuries document the responses of biota to natural variability in the ocean system (such as the North Atlantic Oscillation Index [NAO], the Atlantic Multidecadal Oscillation [AMO], the Arctic Climate Regime Index [ACRI], Pacific Decadal Oscillation [PDO] or the El Niño-Southern Oscillation [ENSO]) but also to warming of the surface ocean since the 1970s (6.3.2). Many examples highlight the influences of temperature, hypoxia and abundance of food on organisms and ecosystems, causing, for example, changes in biodiversity, expansion of geographical ranges of plankton, changes in seasonal timing (phenology) of different components of the ecosystem and changes in macrobenthos calcification (6.2, 6.3; Figures 6-3, 6-5).

[INSERT FIGURE 6-5 HERE
Figure 6-5: Time-series of water column integrated primary production (PP) anomalies at: Northwestern Spain, La Coruña (43° 25.2 N, 8° 26.4 E); HOT (22° 45 N, 158°W); BATS (31° 50 N, 64° 10 W); Monterey Bay, Central California Current (37°N, 122°W); Cariaco Basin, Venezuela (10°30 N, 64°40 W), reproduced from Chavez *et al.* (2011). Anomalies were calculated by integrating over the water column, then interpolating to 14 d, smoothing with a moving average and differencing for each 14-d interval from the grand mean for that interval. All sites except Cariaco seem to show positive (pink) PP anomalies after 2000.]

The research questions presently addressed using long-term data sets range from changing species composition and phenology via investigations of physical and chemical drivers causing these changes to low-frequency events, e.g. regime shifts (abrupt, non-linear and persistent changes in the structure and function of a system, Table 6-1). National programs run by marine stations sampling regional seas provide detailed long-term data sets augmented by several international limited-term scientific programs such as the World Ocean Circulation Experiment (WOCE) and the Joint Global Ocean Flux Study (JGOFS). The ship-based time-series programs in the North Pacific Subtropical Gyre (HOT), the Sargasso Sea (BATS), Ligurian Sea (DYFAMED), Canaries (ESTOC), southwest of Kerguelen Island (KERFIX), northwest of Hokkaido Island (KNOT) and southwest of Taiwan (SEATS) have provided invaluable data on the physical and biogeochemical state of the oceans (Karl *et al*., 2003). Data from these sites have documented decadal scale ecosystem changes, including ocean acidification (Dore *et al*., 2009; WGI Ch. 3). Additional trends will emerge as the time-series programs continue and new sites are added.

Direct observations are complemented by satellite remotely-sensed datasets, with ocean color data (e.g. SeaWiFS) providing estimates of chlorophyll concentrations, used as a proxy for phytoplankton stocks. Because total chlorophyll cannot be measured from space, the near surface chlorophyll (approximately one optical depth) is extrapolated to whole water-column chlorophyll. Large uncertainties persist in the interpretation as chlorophyll estimates from satellite reflect both phytoplankton stocks and their physiological status (Dierssen, 2010; Behrenfeld, 2011). In conjunction with algorithms these chlorophyll estimates are converted to Net Primary Production (NPP) (6.1.3., Saba *et al*., 2011). Behrenfeld *et al.* (2006) using SeaWiFs data, report a prolonged and sustained global NPP decrease of 190 Tg C per year for the period 1999 to 2005 - an annual reduction of ~0.4 % of global NPP. In contrast, a time-series of directly measured NPP between 1988 to 2007 by Saba *et al.* (2010) (i.e. *in situ* incubations using the radiotracer ^{14}C-bicarbonate) revealed an increase (2 % yr^{-1}) in NPP for two low latitude open ocean sites. This indicates uncertainties in either methodology and/or the extent to which discrete sites are representative of oceanic provinces (Saba *et al*., 2010, 2011). Furthermore, modeling studies have argued that the <20 year archive of SeaWiFS is insufficient to distinguish climate-change mediated shifts in NPP from those driven by natural climate variability (Henson et al., 2010).

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

6.2.1. Overview: Ocean Characteristics and Climate Sensitivities

Global scale observation and modeling studies provide evidence, with *high confidence,* of present and future climate-mediated alterations of the ocean environment (6.1.1., WGI Chs. 3, 6; Bopp *et al*., subm) which in turn leads to impacts on ocean ecosystems (Boyd and Doney 2002; Brierley and Kingsford, 2009; Hoegh-Guldberg and Bruno, 2010; Drinkwater *et al*., 2010; Overland *et al*., 2010). An assessment of present findings and projections requires knowledge of the characteristics of ocean biota and ecosystems and the background of their climate sensitivity.

Life on Earth is phylogenetically and metabolically diverse as a result of nearly 4 billion years of evolutionary history. Marine microorganisms are the oldest forms of life, and the most diverse while the more complex organisms are constrained to limited functional types (Table 6-2). As anthropogenic climate change accelerates, a key issue is how quickly organisms can adapt. Evolutionary adaptation is typically thought to depend upon the genetic variation present within a population, and the environment is believed to select the fittest genotypes from within it (Rando and Verstrepen, 2007; Reusch and Wood, 2007). The inherent variability of marine environments (6.1.1) is suggested to ensure that genetic variation within populations is maintained at high levels. However, there is limited information about genetic variation within species, except for a few well-studied species of fishes and bacteria. The capacity of any species to adapt is highly variable, depending on mutation rates, generation time, and whether population size is large enough to harbour sufficient variation. Processes based on DNA point mutations may be too slow to permit adaptation to rapid climate change (Bowler *et al*., 2010). The fitness of marine organisms may, however, also be influenced by epigenetic regulation mechanisms, such as reversible histone modifications and DNA methylation (Richards, 2006), which are transmitted from generation to generation. Such processes are suggested to be remarkably rapid in terrestrial ecosystems (Bossdorf *et al*., 2008). There is currently *limited evidence, medium agreement* and *low confidence* in evolutionary adaptation induced by climate change in recent centuries.

[INSERT TABLE 6-2 HERE
Table 6-2:Variations in metabolism based on sources of energy, electrons and carbon according to Karl (2007a), complemented by the taxa which exploit these pathways. Mode of metabolism may relate to organizational complexity and tolerance to environmental extremes (Figure 6-8).

Metabolic pathways and their rate of use according to energy demand respond to changing temperatures in virtually all cases or to changing irradiance and CO_2 levels, specifically exploited by the respective modes of metabolism. These responses may be involved in direct or indirect effects of climate change and associated drivers (6.1.1) on marine organisms and contribute to set limits to their adaptability (6.2.2).]

6.2.1.1. Pelagic Biomes and Ecosystems

Organisms living in the pelagic biomes are key to biogeochemical processes in the ocean. The fixation of CO_2 via photosynthesis, a process also known as primary production, forms the base of the marine foodweb. Photosynthesis in the surface ocean is controlled by light, temperature, inorganic nutrients (CO_2, nitrate, phosphate, silicate, trace elements including iron, and the temperature dependent formation rate, stability and duration of the surface mixed-layer depth (MLD) (6.1.1., Sverdrup, 1953; Taboada and Anadón, 2012). Temperature and its variability (Figure 6-2) thus are key factors governing the occurrence, diversity, development, reproduction, behaviour and phenology of marine organisms (Edwards and Richardson, 2004; Beaugrand *et al.*, 2009; Brierley and Kingsford, 2009, Tables 6-3, 6-4). The delivery of nutrients from deep water below the euphotic zone is controlled by vertical eddy diffusivity and advection, caused by the combined effects of local winds and thermohaline (density)-driven processes such as ocean circulation (Rykaczewski and Dunne, 2010) which create net upwelling (temperate, subpolar) and net downwelling (subtropical) gyres (Table 6-3). Coastal oceans are nutrient enriched by tidal mixing, estuarine circulation and upwelling. All of these processes are subject to climate-related influences and associated shifts in physical forcing. Changes in environmental conditions and the displacement of organisms by convection cause variability in phytoplankton productivity, competitiveness and natural selection (Margalef, 1978; Margalef *et al.*, 1979) and result in changes in carbon sequestration (Figures 6-1, 6-6). Reduced nutrient availability causes primary production to fall, leading to a reduction in the amount of energy supplied through the web to higher trophic levels, including fish and invertebrates (*high confidence*, Ware and Thomson, 2005; Brander, 2007), and defining fishery yields (Cheung *et al.*, 2008; Friedland *et al.*, 2012). Species replacement might result in a redirection of carbon and energy flows. The wide range of trophic structures in marine foodwebs and the potentially non-linear changes in energy transfer under different primary production and temperature scenarios (Stock and Dunne 2010) make it difficult to accurately predict how changes in primary production will alter higher trophic levels.

[INSERT TABLE 6-3 HERE
Table 6-3: Environmental forcing on biological production by physical, chemical and biological characteristics of major pelagic ecosystems (Adapted from Barber, 2001, based on the original analysis by McGowan, 1974).]

[INSERT FIGURE 6-6 HERE
Figure 6-6: A schematic representation of the ocean's biological pump, which responds to climate change and is a relevant conduit for carbon sequestration. It is difficult to project how the pump might be altered (Table 6-4) and whether it would represent a positive or negative feedback to climate change which causes: A, shifts in NPP (Net Primary Production; Bopp *et al*., 2002); B, floristic and faunistic shifts in the pelagic realm (Beaugrand *et al.*, 2009) that may alter the relationship between OA and ballasting of settling particles (Klaas and Archer, 2002); C, changes in proportion of NPP released as DOM (Dissolved Organic Matter) due to the effects of ocean acidification (Engel *et al.*, 2004); E, warming and faster bacterial enzymatic rates of particle solubilization (Christian and Karl, 1995); and faunistic shifts at depth (Jackson and Burd, 2001). Modified from Buesseler *et al.* (2008) by J. Cook (WHOI).]

[INSERT TABLE 6-4 HERE
Table 6-4: A wide range of processes make up the ocean's biological pump (Figure 6-6). In order to assess how a changing climate will alter the functioning of the pump, and the resulting biogeochemical feedbacks on global climate, the cumulative effects of climate-change mediated alteration of processes from cellular to ocean basin, and from pelagic to mesopelagic, must be quantified. This table illustrates, using published information, 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 (C, Carbon; TEP, Transparent Exopolymer Particle; DOM, Dissolved Organic Matter; POM, Particulate Organic Matter).]

6.2.1.2. Benthic Habitats and Ecosystems

Benthic communities are defined as those that live in, on, or in association with the sea floor. Benthic organisms are classified by their size (mega-, macro-, meio-, microbenthos), their mode of energy supply (Table 6-2) or their mode of food uptake (suspension feeders, deposit feeders, herbivores, carnivores). Their habitats range from the intertidal to the deep sea and are characterized by climate regime, water depth, light penetration, distance from land, topography, substrate (rocky, hard, soft, mixed), sediment grain size and chemistry or by the dominant plant or animal communities that they support. In general, benthic organisms living in shallow waters or the intertidal (where they experience temporary exposure to air) are prone to experience and tolerate the influence of widely fluctuating environmental parameters due to natural or anthropogenic influences, such as temperature extremes, hypoxia, elevated CO_2 or fluctuating sea level including sea level rise (WGI Chs. 3, 12). As benthic systems comprise sessile or slow moving plants and animals, they may be adapted to local conditions. Many of them are unable to escape from unfavorable changes except by means of fertilized eggs or planktonic larvae. In the deep sea, where environmental conditions remain unchanged on large geographical scales, some meiobenthic deep-sea organisms may show extremely wide distribution ranges (Menzel *et al*., 2011; Gooday and Jorissen, 2012).

Benthic ecosystems are coupled to the pelagic realm via the biological pump (Figure 6-6), the chemical exchange of nutrients, gases and by the existence of pelagic and benthic life history stages. Even in abyssal benthic habitats there is a continuous rain of organic detritus and this serves as the primary source of carbon and energy for benthic communities. This inextricable connection to primary marine productivity means that climate impacts on surface marine ecosystems (as oceans stratify, warm and become more acidic) will impact the most remote benthic communities, even if direct changes to the physical habitat do not occur (Smith *et al.*, 2009).

Benthic habitats are influenced by ecosystem engineers (sensu Jones *et al.*, 1994) which can be grouped into two categories. Autogenic engineering species (like corals) form habitat from the structures they produce (e.g. coral skeletons) while allogenic engineering species form habitat through their behaviour (e.g. by mechanical displacement of sediment, a process termed bioturbation). Both types of ecosystem engineers have the potential to influence the regeneration of nutrients and to affect benthic-pelagic coupling. If climate change negatively affects the engineering species, the entire ecosystem may be impacted.

6.2.2. Mechanisms and Principles of Climate Change Impacts across Organism Taxa

This section focuses on the principles of climate impacts known across organism taxa, 6.2.3. to 6.2.6. then report the taxon-specific aspects. A comprehensive understanding of mechanisms responding to climate related environmental factors at ecosystem, whole organism, tissue, cell and molecular levels of biological organization would provide a solid foundation for reliable interpretation and attribution of climate change effects on ocean biology. 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. Empirical studies of marine organism and ecosystem sensitivities have made progress in identifying the mechanisms and processes linking climate to ecosystem changes (Drinkwater *et al.*, 2010; Ottersen *et al.*, 2010). Changes in community composition, species interactions and the food web often build on organismal effects elicited by environmental forcing (e.g. Pörtner and Farrell, 2008; Boyd *et al.*, 2010; Ottersen *et al.*, 2010). Knowledge of the underlying mechanisms in a hierarchy of organismal to molecular effects (Pörtner, 2002a, Pörtner and Knust, 2007; Raven et al., 2012), appears as a major asset for attributing observations to climate and for projections of impacts (Pörtner *et al.*, 2012). Knowledge of overarching similarities across organism domains, archaea, bacteria, and eukarya (Woese *et al*., 1990) or kingdoms (Cavalier-Smith, 2004) would facilitate projections of climate impacts. Microbes, i.e. bacteria and microalgae support many fundamental biogeochemical cycles and may respond by exploiting their large diversity, e.g. undergoing species replacements (Karl *et al*., 2001), and thereby sustaining their biogeochemical roles. Species replacements also occur among macroorganisms (plants and animals), however, for most of them their resilience, well-being, abundance, survival and conservation have been the research foci.

After identifying the principle effects of individual drivers across organism taxa understanding their integrated action is required for comprehending climate change effects (6.3.5). Furthermore, such effects may be compensated for on long time-scales by acclimation and evolutionary adaptation to individual or multiple drivers, as seen in the coccolithophore *Emiliania huxleyi* under high pCO_2 (1100 and 2200 µatm) over 500 asexual generations (Lohbeck *et al*., 2012). In macroorganisms the rate of evolutionary adaptation is constrained by their long generation times but is enhanced by large phenotypic variability among larvae as a pool for selections, with high mortality rates (e.g. Sunday *et al*., 2011). In general, the mechanisms setting limits to acclimation or adaptation capacity are presently unknown for virtually all climate drivers. However, mass extinctions occurring during much slower rates of climate change in earth history (6.1.2) suggest that evolutionary rates in macroorganisms may not be fast enough to cope with various drivers changing. Interactions of drivers like ocean warming, acidification, hypoxia, freshening with each other and with other human-induced drivers like eutrophication are addressed in 6.3.5.

6.2.2.1. Principles of Temperature Effects

Thermal reaction norms describe the temperature dependent changes in performances such as growth and have been used to evaluate sensitivity (Figure 6-7). They apply across organism phyla (Chevin *et al.*, 2010), viruses (Knies *et al.*, 2006), bacteria (Ratkowsky *et al.*, 1983), phytoplankton (Eppley, 1972; Thomas *et al.*, 2012), higher algae and plants (Bolton and Lüning, 1982; Müller *et al.*, 2009, 2011; Vitasse *et al.*, 2010) and animals (Huey and Kingsolver, 1989; Deutsch *et al.*, 2008; Angiletta, 2009). The shape and width of the curves can shift within limits and mirror the large scale distribution boundaries of a species or population. Maximum temperatures tolerated differ largely between organisms, depending on organizational complexity (Figure 6-8). The knowledge of the mechanisms shaping such curves and associated thermal limits appears most advanced in animals (Pörtner *et al.*, 2012; 6.2.5) but these have not been systematically explored in other organism groups (e.g. Green *et al.*, 2008).

[INSERT FIGURE 6-7 HERE
Figure 6-7: Mechanisms linking organism to ecosystem response explain the why, how, when and where of climate sensitivity (based on knowledge for animals, after Pörtner, 2001, 2002a, 2012; Pörtner and Farrell, 2008, blue to red colour gradients illustrate transition from cold to warm temperatures). (A) As all biota, animals specialize on limited temperature ranges, within which they grow, behave, reproduce, defend themselves by immune responses. Optimum temperatures (T_{opt}) indicate performance maxima, pejus temperatures (T_p) the limits to long-term tolerance, critical temperatures (T_c) the transition to anaerobic metabolism, and denaturation temperatures (T_d) the onset of cell damage. These OCLTT thresholds (see text) can shift by acclimatization (horizontal arrows). Under elevated CO_2 levels and in hypoxic waters performance levels can decrease and windows of performance be narrowed (dashed green arrows pointing to dashed black curves). (B) Thermal range widths (horizontal arrows) change between individual life stages of a species. (C) The shift of performance curves between polar, temperate and tropical animal species reflect evolutionary adaptation to the respective climate zones. Via species-specific effects on performance and thermal limits (dashed curves, cf. A), additional stressors and species interactions cause shifts in higher-level processes (seasonal activities in response to light or temperature cues, shifts in predator-prey interactions or competition within changing coexistence ranges of interacting species). (D) Shifts in biogeography result during climate warming (modified after Beaugrand, 2009). The polygon delineates the range in space and time, the level of grey denotes abundance. Species display maximum productivity in southern spring, wide seasonal coverage in the centre and a later productivity maximum in the North. The impact of photoperiod increases with latitude (dashed arrow). During warming, the southern temperature and time window contracts while the northern one dilates (directions and shifts indicated by arrows). Control by water column characteristics or photoperiod may overrule temperature control in some organisms (e.g. diatoms), causing contraction of spatial distribution in the north.]

For animals breathing in water (invertebrates and fish exchange respiratory gases with water rather than air; FAQ 6.II), the dimensions of the thermal niche (Figure 6-7A) have been explained by the concept of oxygen and capacity limited thermal tolerance (OCLTT, Pörtner *et al.*, 2010) which integrates findings from ecosystem to molecular levels and explains thermal specialization and associated limitation. For other organisms the respective knowledge explaining thermal reaction norms is not available. Thermal specialization of animals results from economizing energy use, limiting the functional capacity of tissues. Beyond upper and lower thermal thresholds (T_p, Figure 6-7A) tolerance becomes time-limited. At large body size, O_2 supply limitations are exacerbated in the warmth, causing the organism to reach long-term heat limits at lower temperatures. The widths and positions of acute thermal windows on the temperature scale are changing dynamically over time, during short-term or seasonal acclimatization of the individual over days and weeks, during the life cycle of a species and with increasing body size (Figure 6-7A,B) as well as during long-term evolutionary adaptation, across generations, to a climate regime or local conditions (Pörtner, 2006; Pörtner *et al.*, 2008; Eliason *et al.*, 2011). Both acclimatization and adaptation involve adjustments in biochemical characters (membranes, enzymes), and their functional properties, however, the capacity to shift thermal boundaries (Figure 6-7A) is limited to within the thermal niche (Pörtner *et al.*, 2008, 2012). Such limits are effective in the field (Pörtner and Knust, 2007, Katsikatsou *et al.*, 2012) and may contribute to the reduction of abundances during warming (Pörtner and Knust, 2007), to coral losses (Donner *et al*., 2005), to shifts in the seasonal timing of (zooplankton) biomass formation (Mackas *et al.*, 1998; Goldblatt *et al.*, 1999; Schlüter *et al.*, 2010) or to the reduction of animal body sizes in warming aquatic communities (Daufresne *et al.*, 2009; see examples in 6.3.2) and projected in the 21st century under climate change (Cheung *et al*., 2012; 6.5). Modelling and paleo-studies have adopted the OCLTT concept to project climate effects (6.5) and explain climate-induced mass extinction events and evolutionary patterns in earth history (Pörtner *et al.*, 2005; Knoll *et al.*, 2007; Knoll and Fischer, 2011).

At community and ecosystem levels, differences in thermal sensitivities and shifts in the relative performance of animal species may underlie their changing competitive or trophic interactions and foodweb structure (Pörtner and Farrell, 2008; Figure 6-7 C), also via shifts in reproductive success, larval output, early juvenile survival and thus recruitment. Knowledge of such high-level functions shaping thermal reaction norms in other organism domains would be essential for a comprehensive view of shifting biogeographies, species interactions, abundances as well as community assemblages and foodwebs in space and time (Beaugrand *et al.*, 2003; Parmesan and Matthews, 2005). Mechanism-based insights link physiological impacts with changing species interactions (e.g. Pörtner, 2010, 2012; Harley, 2011), underpinning scenarios of community level responses to temperature change (Urban *et al*., 2012), with respect to niche breadth, ecosystem mixing and the resulting extinction threats (6.3), informing modelling (6.5) as well as having implications for conservation and ocean management (6.3., 6.4).

[INSERT FIGURE 6-8 HERE
Figure 6-8: Ranges of temperatures and O_2 concentrations covered by various domains and groups of free living marine organisms (bacteria to animals, domains and groups modified after Woese *et al*.,1990) in various habitats (Storch *et al*., subm). High organizational complexity enables an increase in body size, associated with decreasing tolerances to hypoxia and heat. In the domain Bacteria, the group Thermotogales comprises obligate anaerobes, displays less complex structures such as a single layer lipid membrane and is most tolerant to high temperatures. Highest temperatures of growth were found at 122°C in hydrothermal vent species under elevated hydrostatic pressure in laboratory experiments. Dashed white arrows denote wide O_2 tolerances in unicellular archeae, bacteria and protists, as compared to animals and plants (multicellular eukarya). Anoxic habitats are conquered by small multicellular and unicellular Eukarya, supported by less complex mitosomes or hydrogenosomes used in energy metabolism. Species richness of animals (upper right) increases with rising O_2 levels reflecting better hypoxia tolerance in small compared to large individuals and their taxa (6.3.3).]

6.2.2.2. Principles of CO_2 Effects in Ocean Acidification

Rising oceanic CO_2 concentrations causing ocean acidification (OA) will have multi-faceted effects on biota. By analogy with thermal stress phenomena, effects mediated by elevated CO_2 levels also range from molecular to systemic, including the neuronal level in animals. OA effects interact with those of other key drivers like temperature and hypoxia (Pörtner, 2010, 2012; Boyd, 2011; Gruber, 2011) and translate from organism into ecosystem level impacts. Meta-analyses of the biological effects of OA indicate that the rate of net calcification (i.e. calcification minus OA-mediated dissolution) is most responsive (Hendriks *et al.*, 2010), however, such meta-analyses cannot resolve for the diversity of species-specific responses, or diverse vulnerabilities of different processes or life stages (Hendriks and Duarte, 2010; Hendriks *et al.*, 2010; Kroeker *et al*., 2010, 2013).

In marine organisms the diffusive uptake of CO_2 leads to elevated CO_2 partial pressures in all compartments (FAQ). CO_2 causes a (respiratory) acidosis in cells and body fluids which can affect various functions. The weak acid distribution characteristics of CO_2 (Pörtner, 2008, 2012) require a high capacity of ion and acid-base regulation (i.e. of the membrane transporters involved) to balance acidification and readjust setpoints in pH through net base accumulation (e.g. Heisler, 1986; Pörtner *et al*., 2000; Claiborne *et al*., 2002; Taylor *et al*., 2011) (Figure 6-10A). In photolithoautotrophic microbes, accumulating CO_2 or bicarbonate may serve as substrates for metabolism, supporting primary production. The formation of carbonate from bicarbonate is essential in calcification, the formation of calcified structures built by the deposition of solid $CaCO_3$ and used across biota for defence and structural support. Calcification usually occurs in separate body compartments, where even in coccolithophores and corals, pH and thus, the concentration of CO_3^{2-} and Ω of $CaCO_3$ (aragonite, calcite, Mg calcite, 6.1.1) are maintained higher than in other body fluids or ambient water (Trotter *et al*., 2011; Taylor *et al*., 2011; McCullough *et al*., 2012a, Venn *et al*., 2013). CO_2 impedes the formation of carbonate at calcification sites such that calcification rate decreases or the effect is compensated for by ion transport, incurring elevated energetic costs. In addition, external carbonate shells rely on ambient seawater being supersaturated with regards to carbonates. Otherwise, shells would be dissolved unless protected from direct contact with sea water by organic coating (periostracum) as in molluscs or brachiopods. Falling calcite/aragonite saturation levelsΩ to below unity in the water, as evident in OMZs, favor the dissolution of carbonate shells (FAQ). Table 6-5 summarizes effects of OA in various organism taxa observed in laboratory studies, field experiments (mesocosms) and natural analogues which include submarine CO_2 venting areas in the vicinity of: Ischia, Italy (Hall-Spencer *et al*., 2008), Papua New Guinea (Fabricius *et al*., 2011) or Puerto Morelos, Mexico (Crook *et al*., 2012). With *medium confidence* some species will be tolerant to OA, however, the capacity of sensitive species to acclimatize or adapt remains largely unidentified.

[INSERT TABLE 6-5 HERE
Table 6-5: Assessment of tolerances to ocean acidification in marine taxa, considering the number of laboratory and field studies, and of parameters and species studied in the pCO_2 range from <650 to >10 000 µatm. (Parameters include growth, survival, calcification, metabolic rate, immune response, development, abundance, behaviour and others). Not all life stages, not all parameters and not 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: most species were negatively affected; tolerant: most species were not affected. RCP 6.0: representative concentration pathway 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 timescales, across generations (see separate reference list). For an assessment of variability between species from the same phylum see Figure 6-10.]

6.2.2.3. Principles of Hypoxia Effects

The term hypoxia refers to a phenomenon, where ambient PO_2 falls below air saturation and constrains life (6.1.1). Hypoxia affects organisms relying on aerobic metabolism; tolerance thresholds determined as the critical O_2 tension (P_c) or concentration (O_2crit) vary across domains (Figure 6-8) and are high for larger organism. For animals, the P_c is traditionally defined at rest, as the O_2 partial pressure, below which energy turnover falls below regulated rates. At the P_c, a progressive transition from aerobic to anaerobic energy production begins (Pörtner and Grieshaber, 1993). In animals, the P_c is determined by the capacity of ventilatory and circulatory systems in relation to O_2 demand, developmental status, and body size. In active animals with a high O_2 demand or at the extremes of their thermal windows functional constraints set in early, under mildly hypoxic conditions. Most animals can only transiently sustain anaerobic metabolism, even if they are energy efficient and sustain long-term tolerance (Grieshaber *et al.*, 1994). Such time-limited tolerance is highest in large individuals, with a higher capacity of anaerobic metabolism than, for example in larvae, where such tolerance is low (Gray *et al.*, 2002; Jessen *et al*., 2009).

6.2.2.4. Principal Effects on Animals Breathing in Air: Marine Reptiles, Mammals, and Birds

Marine reptiles (sea turtles, marine snakes, crocodiles), mammals and seabirds breathe in air but live mostly in water. Therefore, ocean acidification and hypoxia would have minimal direct influences. 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). Hypoxic habitat compression for fishes may enhance the foraging opportunities for their air breathing predators (Hazen *et al*., 2009). Warming waters influence the ectothermic turtles, e.g. through range expansion (McMahon and Hays, 2006) and less so the homeothermic birds and mammals. Large body sizes enable some of these air breathers to travel across the widest aquatic temperature ranges possible and support some of the largest migration ranges on earth. Constraints on thermal tolerance are imposed by various degrees of insulation of the body core in mammals and birds which contributes to constrain their distribution to warmer (poor insulation) or colder waters (high insulation). Their larger independence from physical and chemical drivers in the oceans would make many of these air breathers more resistant to the direct influences of climatic change than fishes or invertebrates but would still expose them to effects mediated via changes in habitat structure or the food web, related to changes in the availability of prey or other, including alternative food items (6.2.5., 6.3). If habitat structures offering retreat or ambush (e.g. sea ice for polar bears or walrusses) become less available, this will enhance the energetic costs of life. If food items are only found in thermally restricted areas or move to large depths, mammals and birds may be constrained to certain distribution ranges or exploitation of their physiological dive limits (McIntyre *et al*., 2011). Compared to oceanic migrators shifts in prey distributions and resultant oceanic habitat may have effects on the physiological costs of finding prey for foragers that are tied to land between trips (Hazen *et al*., 2012; Péron *et al*., 2012).

6.2.2.5. Principal Effects of Changes in Light, Nutrient, and Food Availability

In addition to temperature and CO_2, availability of light and nutrients to photoautotrophs may be altered directly or indirectly with a changing climate, partly through density-related stratification (Figure 6-9), the circulation regime at different spatial scales and the physical displacement of organisms. The supplies of major plant nutrients (macro-nutrients) such as nitrate, and of micronutrients such as iron (Pitchford and Brindley (1999) vary both seasonally (Boyd, 2002), regionally (Moore *et al.*, 2002) and with the current regime and may involve simultaneous limitation (co-limitation) by more than one resource (Saito *et al.*, 2008). Nutrients provide the elemental building blocks for macromolecules needed for cellular physiology. The net result of climatic change affecting all of these processes may be changes in primary productivity due to changing rates of photosynthesis and other physiological processes, as well as changes in community composition. For heterotrophs, from bacteria to fish, mammals and birds, the uptake of organic material as food, ultimately provided by primary production, is central not only to productivity but also for fueling energy consuming functions including the resistance of organisms to environmental change and pathogens (6.2.5., 6.3.6). 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 (Figure 6-7A,C).

6.2.2.6. Conclusions

Integrating findings across levels of biological organization, molecule to ecosystem, support a comprehensive cause and effect understanding of climate change effects on marine biota (*high confidence*). Some of the respective understanding is emerging but is fragmentary for many organism groups. Experimental observations therefore are largely empirical and cannot easily be scaled up to projecting species-specific responses. The principles of thermal reaction norms are not yet widely applied across organism domains (*medium evidence, limited agreement*) but the recent emergence of converging approaches from empirical, modeling and ecological studies enhances *confidence* to *high* as to their usefulness for developing coherent approaches in all organisms.

6.2.3. Microbes – Link to Biogeochemical Processes

The phylogenetic and metabolic diversity of the microbial world (6.2.1) sustains many unique cellular and key ecosystem processes such as CO_2 fixation and O_2 production, the conversion of nitrogen into ammonia (N_2 fixation), and the use of nitrate, sulphate, CO_2 and metals (Fe and Mn) as terminal electron acceptors in metabolism when O_2 is absent. Microorganisms also catalyze the horizontal transfer of genetic information between unrelated individuals, thereby enhancing biodiversity (McDaniel *et al*., 2010). Microorganisms also catalyze the horizontal transfer of genetic information between unrelated individuals, thereby enhancing biodiversity. The development of a better understanding of climate-induced alterations in the functioning of microorganisms builds on laboratory, mesocosm, and in situ studies as well as modeling. Together, these data will eventually inform us of what regions and which taxonomic groups are more susceptible to climate change and consequently where in the ocean to look for the biological imprint of a changing ocean (Boyd *et al.*, 2011).

6.2.3.1. Temperature – Related Processes

A warming ocean may initially enhance the metabolic rates of microbes (Banse, 1991) and stimulate their overall growth as in phytoplankton (Bissinger *et al*., 2008) but eventually challenge their thermal tolerance –as described by organismal performance curves (i.e. fitness versus environment) for different groups (Chevin *et al.*, 2010), leading to competitive advantages and species replacements. Ocean surveys of phytoplankton size structure revealed increasing fractions of small cells in warmer waters (Morán *et al.*, 2010). 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.

A coastal experimental microcosm study reports that resident heterotrophic bacteria are more responsive to warming than a laboratory-reared phytoplankter and hence this study illustrates the potential biogeochemical implications of a non-linear ecological response to warming, i.e. greater stimulation of bacterial rate processes relative to that for phytoplankton, within upper ocean foodwebs (Wohlers-Zöllner *et al*., 2011). Consistent with the finding of a warming induced shift to heterotrophy along a high to low latitude survey transect in both the North and South Atlantic (Hoppe *et al*., 2002), it has been hypothesized that heterotrophy might then play a bigger role in warmer oceans and hence microbially-mediated carbon flow to the atmosphere (i.e. CO_2 efflux,or outgassing) might increase (Sarmento *et al*., 2010). The underlying principles and wider applicability of these findings remain to be established (Kirchman *et al*., 2009) in further comparative studies (*limited evidence, low agreement*).

6.2.3.2. Irradiance

The range and mean level of underwater irradiances (light climate) encountered by phytoplankton will be altered by a changing climate (Doney, 2006), due to changing surface mixed layer depth, cloudiness and/or to alteration of sea-ice areal extent and thickness. The physiological response of phytoplankton to higher or lower irradiances caused by the predicted shallowing of the mixed-layer depth (6.1.1) and loss of ice cover, involves photophysiological acclimation via changes in cellular chlorophyll which is however constrained by unidentified limits to its plasticity (Falkowski and Raven, 1997). A longer growing season, due to more sea-ice free days, may have increased productivity (based on a time-series of satellite ocean color and a primary productivity algorithm) in Arctic waters (Arrigo and van Dijken, 2011). This study showed that the average annual NPP increased by an average of 8,1 Tg C yr^{-1} between 1998 and 2009, strongest between 2003 and 2007. In addition, massive under-ice blooms have been observed favored by light penetrating surface melt ponds and first-year ice (Arrigo *et al*., 2012). Little is known about expected shifts from sea-ice algae to free-drifting phytoplankton with a decrease in sea-ice cover and increased irradiance in polar waters in the coming decades. As some krill predominantly feed on sea ice algae, it is unclear (*low confidence*) whether they will be able to adapt to feeding on free drifting phytoplankton (Smetacek and Nichol, 2005).

6.2.3.3. Stratification – Nutrient and Irradiance Controls on Primary Production

A stronger vertical density gradient will reduce the communication between the sunlit upper ocean where photosynthesis takes place and the underlying nutrient-rich waters (Doney, 2006; Figure 6-9). Lower chlorophyll concentrations at warmer sea surface temperature in nutrient-poor low latitude waters, based on ocean color data, have in fact been interpreted as an effect of increased stratification on phytoplankton stocks (Boyce *et al.*, 2010). In contrast, higher chlorophyll concentrations at warmer sea surface temperature were found at high latitudes (Boyce *et al.*, 2010). It has thus been suggested based on *limited evidence* and *low agreement* due to methodological uncertainties (6.1.3) that expanding, permanently stratified, low chlorophyll, tropical regions (WGI Ch. 3), will result in declining phytoplankton stocks in the warming oligotrophic waters of the N and S Pacific and N and S Atlantic (Polovina *et al.*, 2008; Signorini and McClain, 2012; 6.3.1). Furthermore, increased frequency of, or a transition to, permanent El Niño favorable conditions in a warmer future world (Wara *et al.*, 2005) and further expansion of subtropical ocean gyres (Polovina *et al.*, 2008), may lead to lower global ocean NPP.

[INSERT FIGURE 6-9 HERE
Figure 6-9: Projected alteration of oceanic properties and atmospheric events due to a changing climate. Properties will be altered across the water column, from the mid-water stratum to the sunlit surface layer, and will influence the fitness of the residence biota. Changes in storm activity and dust deposition will influence ocean physics and chemistry, with consequent effects on ocean ecosystems (courtesy of Boyd and Law, 2011).]

However, projections of a global decrease in phytoplankton biomass have been refuted (McQuatters-Gollop *et al*., 2011; Mackas, 2011; Rykaczewski and Dunne, 2011). Time series with shorter than 20 years of observations do not resolve impacts of bidecadal 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 of carbon fixation by phytoplankton on most shelves (Sherman and Hempel, 2009; Chavez *et al*., 2011; Bode *et al*., 2011), possibly caused by both climate change and by anthropogenic eutrophication. As satellite trends do not encompass the variability in subsurface chlorophyll (6.1.3) the putative enhancement of primary productivity at the nutricline (Whitney, 2011) remains undetected. Recent field studies point to a growing fraction of primary production derived from atmospheric N in large ocean basins (e.g. Mouriño-Carballido *et al*., 2011). In the presence of sufficient phosphate, fixation of atmospheric N may gain importance in warmer and stratified tropical and subtropical oceans (e.g. Sohm *et al*., 2011).

6.2.3.4. Ocean Acidification – Effects of Anthropogenic CO_2 Concentrations and Water pH

The physiological effects of ocean acidification (OA) appear to be species- and even population-specific. Elevated surface ocean CO_2 partial pressures (pCO_2) may lead to fertilization of phytoplankton but effects are species- or taxon-specific possibly depending on how they acquire carbon (i.e., the presence and in particular the type, capacity and energetic costs of carbon-concentrating mechanisms (CCM’s, Giordano *et al.*, 2005; Kranz *et al.*, 2011; 6.2.2). Diatoms are considered to be relatively insensitive to elevated CO_2 with regard to growth and fixation rates (Rost *et al.*, 2003; Trimborn *et al.*, 2008), yet there are indications for CO_2-induced stimulation of primary production rates (Tortell *et al.*, 2008b). For dinoflagellates, relatively little is known with regard to their sensitivity to elevated CO_2 (Hansen *et al.*, 2007) although in one species carbon fixation rates were enhanced at 750 µatm CO_2 while growth remained unaffected (Fu *et al.*, 2008).

Changes in calcification under OA are species-specific. Overall, there is *medium evidence and low agreement* that CO_2 induced OA will result in exoskeletons that are insufficiently calcified for sustained structural support and protection. In coccolithophores, the response is highly variable, uncertainty is high as the function(s) of calcification are not known and consequences of lowered calcification are difficult to be estimated (e.g.Trimborn *et al*., 2007; Rost *et al*., 2008). Reductions, increases and unchanged shell architecture or calcification rate have been documented for RCP 8.5 CO_2 conditions projected around 2100 in different coccolithophore species (Riebesell *et al.*, 2000; Zondervan *et al.*, 2001; Langer *et al.*, 2006; Iglesias-Rodriguez *et al.*, 2008) with species-specificity (Langer *et al.*, 2006) and strain-specificity for calcification in *Emiliana huxleyi* (Langer *et al.*, 2009; Hoppe et al., 2011; Langer *et al.*, 2011) (see Table 6-6 for details). Low light (Zondervan *et al.*, 2002) or nitrogen limitation (Sciandra *et al.*, 2003) are suggested to limit the beneficial effect of OA on photosynthesis and to have a strong negative effect on calcification (Sciandra *et al.*, 2003; Rokitta and Rost, 2012). Nutrients and light cause functional adjustments through gene expression (Dyhrman *et al*., 2006; Richier *et al*., 2009).

[INSERT TABLE 6-6 HERE
Table 6-6: Selected ocean acidification effects on microbes and associated processes.]

Likewise, laboratory studies on planktonic N_2 fixing cyanobacteria (termed diazotrophs) indicate that some of these organisms respond to changing CO_2. In particular, strains (genetically distinct populations of the same species) of offshore cyanobacteria belonging to the genera *Trichodesmium* and *Crocosphaera* increased rates of carbon and N_2 fixation under elevated CO_2 (Lomas *et al*., 2012). However, the resulting responses in N_2 fixation have varied widely (Barcelos e Ramos *et al.*, 2007; Hutchins *et al.*, 2007; Levitan *et al*., 2007; Kranz *et al.*, 2010; Lomas *et al*., 2012) and not all marine N_2 fixing cyanobacteria increase rates of N_2 fixation under elevated pCO_2. Laboratory studies using the bloom-forming cyanobacteria *Nodularia* (an organism largely found in stratified, eutrophic waters) revealed decreased growth and N_2 fixation under elevated CO_2 conditions (Czerny *et al.*, 2009). To date, the mechanisms underlying these observed physiological responses, especially those in open ocean nitrogen fixers, remain unknown. Cyanobacteria may reallocate energy from their costly CCMs toward N_2 fixation and acquisition of growth limiting nutrients (Kranz *et al.*, 2010; Levitan *et al.*, 2010b). However, evidence for such diversion of energy from CCMs toward N_2 fixation is lacking. *Confidence* is thus *low* based on *limited in situ evidence* and *medium agreement* that there is an increase in nitrogen fixation with progressive ocean acidification.

6.2.3.5. *Bacterial Life in Hypoxia and Anoxia – Oxygen Minimum Zones (OMZ)*

Heterotrophic energy yield with O_2 is largest and is generally preferred over the use of alternate electron acceptors. It has only recently been shown that some bacteria can still grow aerobically and efficiently at even nanomolar O_2 concentrations (Stolper *et al.*, 2010). This has important implications for the formation of ‘oxygen minimum (or even free) zones’ (OMZs). R*obust evidence* indicates that bacteria both create and sustain OMZs by their diversity and plasticity of metabolism. Wherever the consumption of organic matter supporting bacterial metabolism exceeds the rate of O_2 re-supply, an OMZ will be formed, also characterized by elevated pCO_2 and enhanced acidification. With *high confidence*, OMZs are therefore a consequence of high organic loading or restricted water movement, or both (6.1.1; WGI Box 6.5, Figure 1). Most marine sediments also have OMZs due to limited penetration and exchange of dissolved O_2 with the bottom water. OMZs have also been detected in coastal waters downstream of regions of high inorganic nutrient or organic matter loading. Natural variation in thermocline depth can counter effects of OMZ expansion in the open sea (6.1.1., 6.3.3) by limiting oxidative demand in deepened, warmer, low O_2 thermocline waters (Deutsch *et al.*, 2011). Therefore, OMZ expansion may not be manifested as a monotonic change, but rather be complicated by decadal climate events.

6.2.3.6. *Conclusions*

While various physiological processes are known to respond to changes in irradiance, nutrient supply, temperature, CO_2 or hypoxia in microbes, the knowledge base on how these processes may be altered does not (yet) include a conceptual foundation suitable to support an integrated understanding of climate impacts on individual species and in turn on communities. The data available are patchy and the reported data trends are often in different directions, partly due to the application of different experimental protocols and/or the over-reliance on species or strains of microbes that are readily culturable and hence have been used for decades in laboratory research. *High confidence* is thus presently limited to the attribution of specific physiological responses of microorganism species, such as primary production, N_2 fixation, or calcification, to environmental drivers associated with climate change.

6.2.4. *Macrophytes - Effects of Temperature and Ocean Acidification*

Macrophytes (seaweeds and seagrasses) in the transition zone to coastal waters (WGII Ch. 5) cover only 0.6 % of the world's marine areas (Smith, 1981) but their production amounts to almost 10 % of total oceanic production (Charpy-Roubaud and Sournia, 1990). Their thermal growth-response curves (Figure 6-7) show a clear link between production and the local temperature regime. Temperate species with wide windows of thermal tolerance (Figure 6-2) acclimatize by shifting these windows following the seasonal temperature change (Kübler and Davison, 1995). Antarctic or tropical macroalgae are exposed to permanently low or high temperatures and have consequently specialized on limited temperature variability, paralleled by a low acclimatization potential (Pakker *et al.*, 1995; Eggert and Wiencke, 2000; Eggert *et al.*, 2006; Gómez *et al.*, 2011). In the tropics, observations indicate that seagrasses tolerate higher temperatures than seaweeds (Campbell *et al*., 2006). As in other organisms, the molecular basis of acclimatization and its limitation in relation to the climate regime require further study.

Primary production, shoot density, reproductive output and/or below-ground biomass of seagrasses generally respond positively to elevated pCO_2, indicating CO_2 limitation of their productivity. Such effects were identified in the laboratory and the field in the range above 720 to 1800 µatm (*high confidence*, e.g. Palacios and Zimmerman, 2007; Hall-Spencer *et al.*, 2008; Andersson *et al.*, 2011). Similarly, most non-calcifying seaweeds exhibit significantly increased production, growth and recruitment at CO_2 levels above 700 to 900 µatm (Kroeker *et al.*, 2010). In some macroalgae, such stimulation only occurs in combination with elevated temperature (Connell and Russell, 2010) or not at all (Porzio *et al.*, 2011). In experiments, calcifying algae show complex and species-specific responses of photosynthesis and/or carbon production to elevated CO_2, but calcification is highly impacted beyond species-specific thresholds of pCO_2 (*medium confidence*, Anthony *et al.*, 2008; Ries *et al.*, 2009, Ragazzola *et al.*, 2012). Calcification by temperate coralline red and calcareous green algae increased with rising CO_2 levels up to 900 µatm and only decreased at the highest concentration applied (2850 µatm) but did not fall below control rates (Ries *et al.*, 2009). During 3 months of CO_2 exposure, growth of cold water *Lithothamnion glaciale* decreased progressively with rising CO_2 levels. Structural integrity was weakened beyond 590 µatm (Ragazzola *et al.*, 2012).

In conclusion, *confidence* is *high* that macrophytes specialize on limited temperature ranges, are sensitive to temperature extremes and that CO_2 stimulates primary production of some macroalgae and seagrass species. With *medium confidence*, calcifying species do not benefit and will be less competitive in a high CO_2 ocean.

6.2.5. Animal Performance and Sensitivities – Fitness and Interactions in Various Climate Zones

Climate change has the potential to affect all animal phyla, from ectotherms (like turtles, with a body temperature that fluctuates with ambient temperature) to endotherms (like mammals and seabirds which generate metabolic heat to sustain a constantly elevated body temperature) through effects on individual organisms, populations and communities or on species interactions and the food web. Existing knowledge of the principles of effect increases confidence in projections of future change (6.2.2).

6.2.5.1. Temperature-Dependent Biogeography and Species Interactions

The distribution, abundance and population dynamics of marine fishes and invertebrates correlate with climate change and climate variability monitored by hydro-climatic indices such as AMO or NAO (6.1.2). Ecosystem shifts attributed to climate change (Hoegh-Guldberg and Bruno, 2010) have mostly been related to temperature. Although temperature means are still most commonly used in marine attribution studies, temperature extremes rather than means are most often mediators of effects (Easterling *et al.*, 2000; Grebmeier *et al.*, 2006; Pörtner and Knust, 2007; Wethey *et al.*, 2011; Wernberg *et al*., 2013; Figure 6-7; 6.2.2). During heat exposure near biogeographical or equivalent limits (including the high intertidal or warming surface waters), reductions in growth, activity and abundance of fish and invertebrate populations set in with even small (<0.5°C) shifts in ambient temperature extremes (Takasuka and Aoki, 2006; Pörtner and Knust, 2007; Farrell, 2009; Nilsson *et al.*, 2009; Neuheimer *et al.*, 2011). Local extinction events follow due to mortality or behavioral avoidance of unfavorable thermal environments (Breau *et al.*, 2011). Shifted biogeographies follow clines from high to low temperature, along latitudes, an equivalent lateral gradient (Perry *et al*., 2005) or even a vertical gradient to deeper waters (Dulvy *et al*., 2008; Graham and Harrod, 2009, Figure 6-7).

In marine animals, the widths of thermal windows roughly match ambient temperature variability (Figure 6-2) according to climate regime and seasonality (Sunday *et al*., 2012). A comparison of fishes across latitudes suggests that high latitude polar species have narrow windows (stenotherms), species at temperate mid latitudes have the widest windows (eurytherms) and ranges are intermediate at tropical latitudes (Pörtner and Peck, 2010). Higher variability in atmospheric and ocean temperatures characterizes the Northern versus the Southern hemisphere (Jones *et al*., 1999, Figure 6-2), resulting in wider temperature ranges in Northern invertebrates and fishes and making them less vulnerable to warming than Southern ones, especially at sub-polar latitudes.

Wide thermal windows are often associated with higher energetic costs, reflected in high resting metabolic rates, as seen in sub-Arctic (Pörtner, 2006), small or highly mobile species (Pörtner, 2002b). Conversely, polar species with narrow thermal windows have low levels of energy demand. Variability in thermal windows between coexisting species is even found among Antarctic stenotherms (Peck *et al.*, 2009) and has implications for their relative climate sensitivity, their potential interactions (Milazzo *et al*., 2013) and community composition. Such principles (6.2.2) may underlie “regime shifts“ between coexisting species (Pörtner, 2012; Table 6-7). Critical mismatches between predator and prey organisms may cause abundance losses or local extinctions (Figure 6-7D; Beaugrand, 2009).

In the lifecycle of species, early life stages or adult spawners may be more sensitive to warming because of their narrower thermal windows, e.g..on the cold side for winter spawning Atlantic cod (Table 6-7). For bigeye, bluefin or skipjack tuna, effects during early life stages are less clear, their thermal window is also narrow, but at high temperatures. If adults spawning at high temperature need to prevent overheating, a compensatory shift in location to cooler (deeper) waters may occur (Lehodey *et al*., 2011). Indirect effects of warming, such as the changing composition and biomass of food, depend on ocean stratification and productivity, or expanding OMZs (6.3.2.-3).

[INSERT TABLE 6-7 HERE
Table 6-7: Examples illustrating species vulnerabilities and underlying mechanisms to changing temperature, hypoxia, ocean acidification (OA).]

Local adaptation may be strong in organisms living in heterogeneous environments like the intertidal (Kelly *et al*., 2012), causing functional differentiation. Functional and genetic differentiation into populations supports the wide biogeographical ranges of species like Atlantic cod and its ongoing invasion of Arctic waters (Pörtner *et al*., 2008). Acclimatization capacity is small in high polar, e.g. Antarctic species (Peck *et al*., 2010). In general, species at their warm or cold distribution limits have exploited their acclimatization capacity. Tropical reef fishes undergo rapid warm acclimation across generations (Donelson *et al*., 2012); again, mechanisms and capacities are poorly known.

6.2.5.2. Hypoxia Effects

Animal life in low oxygen conditions (hypoxia) requires adaptations leading to a reduction in O_2 and energy demand, and the improved ability to efficiently extract O_2 from the water and transport it to tissues. This lowers the minimum oxygen content in the water that is needed to sustain life. This critical O_2 threshold (P_c, 6.2.2) varies with life stage, body size, temperature, consumed food, O_2 demand and is influenced by other environmental stressors (Pörtner, 2002b; Ekau *et al.*, 2010; Seibel, 2011). On average, large, more active animals have high O_2 demands, for example fishes, crustaceans and muscular squids, associated with high P_c thresholds and are, therefore, sensitive to permanent hypoxia. However, even in high activity animal groups some specialists such as Humboldt squid or bigeye tuna have adapted to live temporarily in hypoxic environments (Childress and Seibel, 1998; Richards *et al*., 2009; Seibel, 2011). Time-limited tolerance is sustained 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 reduces tolerance to high temperature extremes, because oxygen demand and P_c rise with increasing temperature, reflecting increasing difficulty for animals to get enough oxygen and fuel their activities. This may occur fastest in warm oceans, where metabolic rates are higher and animals live closer to upper thermal limits (Pörtner, 2010). Conversely, high oxygen availability alleviates thermal stress (Mark *et al.*, 2002; Pörtner *et al.*, 2006) and acclimation to hypoxia increases thermal tolerance (Burleson and Silva, 2011), for example by enhancing blood pigment content or reducing energy demand.

Permanent life in the OMZ relies on energy demand being covered exclusively by aerobic metabolism. This is supported by cold temperature which causes energy demand to be low and, thereby, supports P_c thresholds to remain below ambient O_2 levels. Finally, low O_2 levels support a high abundance of meiofauna (very small fauna, <1mm), because their O_2 extraction from the water is facilitated by the combination of reduced energy demand and small body size (Yang *et al.*, 1992; Vetter *et al.*, 1994; Childress and Seibel, 1998; Pörtner, 2002b; Levin *et al.*, 2009). Moreover, food is abundant and predation by larger organisms reduced (Levin, 2003). Under extreme hypoxia (suboxia) only specialists can survive, resulting in a loss of biodiversity (Vaquer-Sunyer and Duarte, 2008). Once approaching anoxia, the centres of pelagic OMZs and benthic dead zones exclude animal life (Levin, 2003). Calcifiers, due to the lowering of metabolic rates at elevated pCO_2 are marginalized in OMZs (Levin, 2003).

6.2.5.3. *Effects of CO_2-induced Ocean Acidification*

The responses of invertebrates and fish to CO_2 imply sometimes positive but mostly negative effects on fitness with variable sensitivities between species and life stages within and across phyla. Present findings indicate a key role for extracellular pH in modulating the responses of various processes to elevated CO_2 (Figure 6-10A). The effects of a lowered pH (acidosis) on processes in organs like muscle or liver may explain when whole organism energy demand falls (Pörtner *et al*., 1998; Michaelidis *et al*., 2005; Langenbuch *et al*., 2006; Pörtner, 2008; Liu and He, 2012), probably paralleled by reduced rates of ion exchange, protein synthesis, growth and feeding (Table 6-7).

The acidosis can be fully or partially compensated for and animal performance maintained by the stimulation of acid-base regulation and associated ion exchange (Figure 6-10A). Compensation, however, may cause increased energy demand and metabolic rates. Costs may increase for ion exchange or for calcification or growth. In fact, at mildly elevated CO_2-levels in rock oysters (Parker *et al*., 2011) or in krill (Saba *et al*., 2012) energy turnover and ingestion rate (krill) increased, indicating significant capacity to resist the CO_2-induced depression of performance. Stimulation of growth induced by CO_2 has also been reported (cf. Gooding *et al*., 2009; Munday *et al*., 2009b; Dupont *et al*., 2010) and might involve not only sufficient compensation but also enhanced energy efficiency under CO_2. Full exploitation of this ability depends on the availability and quality of food which in turn may support fitness and stress resistance (Gooding *et al*., 2009, Melzner *et al*., 2011). A decrease in food quality of a diatom led to slower growth and reproduction of the copepod *Acartia tonsa* (Rossoll *et al*., 2012).

Sensitivity to CO_2 then relates to the capacity of acid-base regulation (Figure 6-10A). Such capacity can be upregulated during acclimatization, indicated by enhanced gene expression of ion exchange proteins as seen in echinoderm larvae (O'Donnell *et al*., 2010; Martin *et al*., 2011), or in fishes (Deigweiher *et al*., 2008; Tseng *et al*., 2013). In general, such capacity is higher in more active marine animals with high metabolic energy turnover, among fishes, cephalopods and also copepods, coastal crabs when compared to sessile, more inactive species (Table 6-7), Pörtner *et al*., 2005, 2011; Ishimatsu *et al*., 2008; Melzner *et al*., 2009; Ishimatsu and Dissanayake, 2010). The capacities of acclimatization and adaptation processes, as well as their limits in shifting tolerances remain to be explored.

[INSERT FIGURE 6-10 HERE
Figure 6-10: Top: Responses of a schematized marine animal (blue line) to ocean acidification (OA). Effects are mediated via diffusive entry of accumulating CO_2 (dark green, black arrows) into body compartments, resulting in a drop in compartmental pH (highlighted in red) and its effects (red dashed arrows) on various processes (light blue) as well as calcium carbonate saturation state (Ω) at calcification sites (after Pörtner, 2008). Variable sensitivity depends on the degree of pH decline and compensation, depending on the capacity of transmembrane ion transport. Bottom: % fraction of studied scleractinian coral, echinoderm, molluscan, crustacean and fish species affected negatively, positively or not at all by various levels of ambient CO_2. Effects considered include those on life stages and processes reflecting physiological performance (O_2 consumption, aerobic scope, behaviours, scope for behaviours, calcification, growth, immune response, acid-base balance, gene expression, fertilization, sperm motility, developmental time, production of viable offspring, morphology). As not all life stages, parameters 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 CO_2 range, variable species numbers result (on top of columns). The total number of species studied for a given group is represented as the number above the control column. Horizontal bars above columns represent frequency distributions significantly different from controls (from Wittmann and Pörtner, subm).]

In some cases, species might not be able to compensate despite a rise in whole organism metabolic cost. Possibly, extracellular acidosis persists and/or imbalances in energy budget result; e.g. some tissues like epithelia or calcification compartments may display enhanced costs, exceeding the downregulation of metabolism in others, e.g. muscle or liver. Enhanced calcification can then occur at the expense of somatic growth (Wood *et al*., 2008; Beniash *et al*., 2010; Thomsen and Melzner, 2010; Parker *et al*., 2011). It was recently discovered that elevated CO_2 can cause behavioral disturbances in larval and juvenile coral reef fishes, while growth was reportedly undisturbed or even stimulated (Munday *et al*., 2009b, 2011b). The behavioral disturbances would make fishes as sensitive as the other animal phyla (Figure 6-10B; Munday *et al.*, 2010; Ferrari *et al.*, 2011; Devine *et al.*, 2012; Domenici *et al.*, 2012). The neural sensitivity to moderate CO_2 increases seen in tropical reef fishes (Nilsson *et al*., 2012) warrants study of its long-term persistence and in species from other climate zones before general conclusions can be drawn.

Changes in calcification rates seen in experiments on animals vary largely but meta-analyses show a decrease to be the most uniform response (Box CC-OA). Reduced calcification and weakened calcified structures were seen in corals (see below, Box CC-CR), echinoderms, molluscs and, possibly, crustaceans (Kurihara and Shirayama, 2004; Arnold *et al.*, 2009; Comeau *et al.*, 2009; Lischka *et al.*, 2011). Some species enhanced calcification above control rates in the range of $p\mathrm{CO}_2$ from 600 to 900 µatm (Ries *et al.*, 2009). Enhanced calcification in juvenile cuttlefish (cephalopods) and fishes (Gutowska *et al.*, 2008; Checkley Jr *et al.*, 2009; Munday *et al.*, 2011a) yielded stronger cuttlebones or otoliths. The role of enhanced calcification for fitness remains unclear.

Studies analyzing animal sensitivities to OA during their whole life cycle or during critical transition phases (e.g. fertilization, gastrulation, egg hatching, metamorphosis, moulting) are scarce (Table 6-7). In sensitive species from various phyla, early life stages appear most vulnerable. With delayed development, extended predator exposure of larvae may lead to enhanced mortalities. Effects on one life stage may carry over to the next one. Moulting success into the final larval stage was reduced in a crab (Walther *et al.*, 2010). In a sea urchin, negative impact was found to accumulate from larvae to juveniles and during 4 months acclimation from adults to larvae. This latter impact was, however, compensated for during extended acclimation of females for 16 months (Dupont *et al*., 2012), emphasizing the need for long-term acclimation studies to realistic scenarios. In an oyster species, however, enhanced resistance was carried over to offspring when parents were pre-exposed to elevated CO_2 levels (Parker *et al.*, 2012). It remains to be explored whether and to what extent animal species undergo evolutionary adaptation to progressive ocean acidification over generations. While this process is constrained by long generation times, it is facilitated by high phenotypic variability among larvae (Parker *et al*., 2011, 2012; Sunday *et al.*, 2011). This may also explain the selective mortality seen in Atlantic cod larvae under elevated CO_2 (Frommel *et al*., 2012).

A meta-analysis of responses to CO_2 showed species- and taxon-specific sensitivity distributions in metazoa (Figure 6-10B), with various processes affected (Table 6-7; Box CC-OA). Echinoderms, the molluscan bivalves and gastropods as well as corals begin to respond negatively at lower CO_2 levels than crustaceans or cephalopods (Figure 6-10B). This sensitivity pattern resembles observations for 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 sensitivity are not met by similar observations in the fossil record. Evolutionary adaptation may thus eliminate or minimize reported effects.

In general, effects of ocean warming, acidification and hypoxia may operate through interrelated physiological mechanisms (Pörtner, 2012). Such knowledge helps to reconcile apparently contrasting findings. For example, warming below the thermal optimum stimulates physiological processes beneficial for resistance to OA; compensation of CO_2 induced disturbances of growth and calcification has in fact been observed (Brennand *et al.*, 2010; Findlay *et al.*, 2010; Walther *et al.*, 2011). Warming to above optimum temperatures, however, exacerbates sensitivity to CO_2 and conversely, CO_2 enhances heat sensitivity in crustaceans (Walther *et al.*, 2009; Findlay *et al.*, 2010), coral reef fishes (Munday *et al.*, 2009a) and corals (via CO_2-enhanced bleaching; Anthony *et al.*, 2008; 6.2.2., Figure 6-7), causing a narrowing of the thermal niche (Walther *et al.*, 2009; Figure 6-7; 6.3.5).

The climate zone may thus shape CO_2 sensitivity due to differences in temperature, ocean chemistry and organism physiology. Elevated energy turnover in Northern hemisphere ectotherms (see above) may improve resistance, associated with a higher capacity in acid-base regulation. In contrast, low energy expenditure in Southern, deep sea and high polar, e.g. Antarctic species, may cause enhanced sensitivity (e.g. crustaceans, Pane and Barry, 2007). Reported patterns of acid-base regulation in Antarcic fishes under OA are unusual and their influences on sensitivity unclear (Strobel *et al*., 2012). Polar calcifiers are exposed to higher CO_2 solubility and lower carbonate saturation levels, possibly exacerbating sensitivity (Orr *et al.*, 2005). Tropical species may again be specialized and more sensitive than species from temperate regions (Pörtner *et al.*, 2011). This rough differentiation is complicated by local adaptation from within species genetic variability. At present, it is unclear if evolutionary adaptation to elevated CO_2 levels has occurred in polar waters, OMZs or marine sediments, possibly with reduced reliance on the strength of calcified structures (Clark *et al.*, 2009; Walther *et al.*, 2011; Maas *et al*., 2012).

6.2.5.4. Sensitivities of Warm and Cold Water Reef-building Corals

Tropical corals differ from most other animals by forming an endosymbiosis with dinoflagellates of the genus *Symbiodinium*, which enable their hosts to build and sustain carbonate reefs and their functions (Box CC-CR). *Symbiodinium* provides the host with organic carbon from photosynthesis (Trench, 1979; Pernice *et al*., 2012) and is provided with inorganic nutrients which are in short supply in clear tropical waters (Muscatine and Porter, 1977; Muscatine and D'elia, 1978). Unusual changes in light or salinity and small changes in temperature correlate with 'bleaching', the loss of symbionts and tissue color, possibly caused by Reactive O_2 Species (ROS). Damage to the symbionts involves disturbed excitation processing within the light harvesting centers of photosynthesis (Glynn and D'croz, 1990; Hoegh-Guldberg and Smith, 1989) and ROS release, also affecting CO_2 fixation by Rubisco (Ribulose Bisphosphate carboxylase, Jones *et al*., 1998) and/or photosystem II (PSII) functioning (Warner, 1999). Mass bleaching is correlated with small temperature anomalies (+1-2 °C of the long-term summer maximum, satellite observations), causing mortalities (Goreau and Hayes, 1994; Strong *et al*., 1997, 2011) and an observed average decrease in coral abundance by 1-2 % per year (Carpenter *et al*., 2008; Box CC-CR). It is debated whether corals adapt to warming (Box CC-CR), by considering shifting heat tolerances across coral genera (Hoegh- Guldberg and Salvat, 1995; Loya *et al*., 2001), the exchange of genetic clades of *Symbiodinium* with more tolerant varieties (Baker, 2001, 2004; Jones *et al*., 2008; Ulstrup and Van Oppen, 2003), as well as acclimatization phenomena (Howells *et al*., 2012). It remains unexplored whether such mechanisms can sustain reef formation.

OA causes genera-specific reductions in calcification (Kleypas et al., 1999, Hoegh-Guldberg *et al*., 2011; Kleypas and Langdon, 2006; Langdon and Atkinson, 2005; Leclercq *et al*., 2002). Coral communities around natural CO_2 seeps have lower growth, calcification and biodiversity (Manzello *et al*., 2008; Fabricius *et al*., 2011) and display a shift from net accretion to net erosion, depending on ambient CO_2 levels (Box CC-CR). Nutrient availability to symbionts may sustain calcification. Females may sacrifice calcification more than males due to energetic tradeoffs with reproduction (Holcomb *et al*., 2010, 2012). Heterotrophic feeding supporting resilience (Edmunds, 2011) shows the energy dependence of coral calcification and acid-base regulation (Figure 6-10).

Temperature extremes acting synergistically with CO_2 reduce calcification and increase sensitivity to bleaching (Anthony *et al*., 2008; 6.3.5). Combined warming and OA following B2 and A1FI AR4 scenarios in mesocosms caused losses of symbionts and corals, and a nocturnal decalcification of the reef community in summer (Dove *et al.*, subm). Wide changes occur in gene expression including ones involved in carbonate deposition and skeleton formation (Kaniewska *et al*., 2012). Mechanisms of temperature and OA impacts clearly require further study.

Studies of the climate sensitivity of cold water corals are scarce. Findings that *Lophelia pertusa* respond strongly to 3°C warming, with a three-fold increase in metabolic rate (Dodds *et al.*, 2007) indicate that these have narrow thermal windows (cf. Pörtner, 2006). Three studies provided proof for resilience of *L. pertusa* to ocean acidification. In short-term ship-board incubations and with pH reductions of between 0.15 and 0.3 units, (Maier *et al.*, 2009) found calcification rates reduced by 30-56 %, especially in young, fast growing polyps. However, not only was net calcification maintained at water aragonite saturation <1, but acclimation to enhanced pCO_2 equivalent to pH reductions by 0.1 units led to calcification rates being maintained over six months (Form and Riebesell, 2012), likely due to upregulation of pH and carbonate saturation at calcification sites (McCulloch *et al*., 2012). The role of the aragonite saturation horizon in defining the distribution of cold water corals is thus not clear (Guinotte *et al*., 2006).

6.2.5.5. Sensitivities of Marine Reptiles, Mammals, and Birds to Climate Change

Long-term data sets indicate that some species of seabirds, marine mammals and sea turtles are responding to the anomalous ocean climate of the 20th century (Hughes, 2000). The reptiles, being ectotherms, are more responsive to temperature effects than seabirds and marine mammals (6.2.2). There is insufficient information to assess the risks for sea snakes or crocodiles. For turtles, poleward distribution shifts 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), warming and abundance being inversely correlated in various species and regions (Chaloupka *et al.,* 2008; Mazaris *et al.,* 2009 b; Balazs and Chaloupka, 2004; Saba *et al*., 2007;

Broderick *et al*., 2001). Extreme weather causes nest flooding, considerably reducing hatching success (Van Houtan and Bass, 2007). Those capable of changing nesting sites (Fish and Drews, 2009; Hawkes *et al*., 2009) will be less impacted than those with high fidelity to nesting and foraging sites (Cuevas *et al*., 2008). During continued warming, modulated by changing rainfall (Santidrián Tomillo *et al*., 2012), turtle sex ratios may be skewed towards output of females, combined with higher egg and hatchling mortality (Fuentes *et al.*, 2009; Saba *et al*., 2012), earlier onset of nesting (Pike *et al*., 2006; Weishampel *et al*., 2004; Mazaris *et al.*, 2008), decreasing nesting populations (Chaloupka *et al.*, 2008) and shifts in dietary breadths (Hawkes *et al.*, 2009), leading to projected recruitment declines for, e.g. the 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 (Broderick *et al*., 2000; Godfrey *et al*., 1999; Hays *et al*., 2003; Marcovaldi *et al*., 1997; Poloczanska *et al.*, 2009). The absence of sea turtles in certain regions may, however, 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). Northern-temperate species have shifted their ranges to higher latitudes (Robinson *et al.*, 2005; La Sorte and Jetz, 2010). Southward range expansion or population growth are reported in the southern hemisphere, (e.g. Dunlop 2001; Bunce *et al.*, 2002). Some species like the king penguin follow shifting foraging zones (Péron *et al*., 2012), others are affected by changing habitat structure like sea ice (e.g. the emperor penguin, Jenouvrier *et al*., 2012). Trans-hemispheric migratory seabirds such as the sooty shearwater *Puffinus griseus*, which spend the austral winter off the coast of California, probably shifted towards the central, equatorial Pacific waters, where increasing SSTs may have enhanced primary productivity and prey availability (Hyrenbach and Veit, 2003). Warming causes many bird species to breed earlier (Sydeman and Bograd, 2009). Extant high-latitude, cool-water species experience extended breeding seasons (Chambers *et al.*, 2005, 2011). Nevertheless, there is often no clear agreement (Heath *et al.*, 2009) whether those changes solely reflect ocean warming or a combination of human-induced climate change and natural variations or other synergistic factors like fishing pressure on seabirds' prey species, sea level rise and pollution (Heath *et al.*, 2009; Galbraith *et al.*, 2005; Votier *et al.*, 2005). Most of the changes in range shifts and seasonal activity involve shifts in trophic relationships. Seabirds with narrow geographic domains and limited phenotypic plasticity are expected to be more susceptible to climate change (Chambers *et al.*, 2005; Grémillet and Boulinier, 2009); even leading to the local extinction of populations (e.g. the Galápagos penguin *Spheniscus mendiculus*, Vargas *et al.*, 2007; and the marbled murrelet *Brachyramphus marmoratus*, Becker *et al*., 2007).

Predator-prey dynamics or impacts on specific habitats also shape the effects of climate change on the distribution, phenology and migration timing of marine mammals (Calambokidis *et al.*, 2009; Salvadeo *et al*., 2011). Some marine mammals shift their distribution poleward to follow the movement of their prey (Simmonds and Isaac, 2007). There is *medium evidence* and *agreement* suggesting that expected patterns may already be occurring, in case of dolphin, porpoise and whale species showing a northward shift in distribution (Salvadeo *et al.,* 2010; MacLeod *et al.,* 2005; Springer *et al*., 1999; Calambokidis *et al*., 2009; Moore and Barlow, 2011). As in birds, vulnerability is high for marine mammals with narrow geographic ranges and high habitat dependence. Examples are the critically endangered vaquita (*Phocoena sinus*) endemic to the Northern Gulf of California, which cannot move north because of the land barrier; or the polar bear (*Ursus maritimus*, Laidre *et al.*, 2008; Rode *et al.*, 2010, 2012) and the walrus (*Odobenus rosmarus*) that 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 and ice-associated species in the Arctic (fin whale; minke whale, *Balaenoptera acutorostrata*; gray whale; killer whale, *Orcinus orca*, humpback whale, *Balaenoptera novaeangliae*; and bowhead whale, *Balaena mysticetus*) may benefit from the net loss of sea ice, due to better access to a pelagic-dominated ecosystem (Moore and Huntington, 2008).

6.2.5.6. Conclusions

Physiological knowledge indicates with *high confidence* that animals specialize on restricted temperature and predicts how the species-specific capacity for performance and associated energy turnover shape sensitivity to climate induced ocean warming, acidification and hypoxia, thereby supporting attribution of effects to climate change. Increased food availability and sustained feeding capacity improve resilience (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*). These trends are exacerbated by the growing influence of OA and hypoxia, leading to mechanism based projections of faster range contractions than with warming alone (*medium confidence*), however, quantitative conclusions have *low confidence*. The synergistic effects of stressors cause relative changes in the performance of interacting species and lead to shifts in species interactions and food webs (*limited evidence*, *medium agreement*). High sensitivities to OA are associated with low metabolic rates and functional capacities of marine animal species. Calcification rates in sensitive invertebrate groups including corals, echinoderms and molluscs decrease under OA, especially if combined with temperature extremes (*high confidence*). Polar species sensitive to warming will be marginalized, with no possibility for that fauna to escape to colder regions (*high confidence*), however, formal loss of a polar species has not been recorded yet. Some tropical species such as corals or ecosystems such as coral reefs exist close to their upper thermal limits. *Confidence* is *low* for direct attribution of changes in life history and population dynamics of marine mammals, birds and turtles to climate drivers. Conversely, *confidence* is *high* that climate effects on reptiles, birds, and mammals are mostly mediated through climate-dependent changes in habitat structure and food availability.

6.3. Trends in Biological Field Observations: Attribution to Climate Change?

Mechanistic knowledge (6.2) and long-term observations (6.1.2.-3) support attribution to climate change of impacts including: (i) changes in abundance and overall biomass, (ii) loss of habitat, (iii) changes in community composition and species richness, (iv) changes in species biogeographical ranges, (v) alterations to phenology and the frequency of events like exposures to extreme temperatures, (vi) changes in connectivity among populations and habitats (e.g. Carson *et al*., 2010) and (vii) propensity for change, including frequency and severity of waterborne diseases. For warming and hypoxia, effects are accelerated by exposures of organisms and ecosystems to shifting seasonal or even diurnal extremes and their frequency (*medium evidence* and *agreement*) (e.g. Pörtner and Knust, 2007; Diaz and Rosenberg, 2008). This may also apply to effects of anthropogenic OA (*low evidence* and *agreement*), as indicated by the detrimental effects of upwelling high CO_2 waters on oyster cultures in the Northeast-Pacific (Barton *et al*., 2012). This section analyzes how physical and chemical forces (6.1.1) shape biological responses in the field, as a result of their physiology (6.2). Modeling approaches and the resulting global projections are discussed under 6.5.

6.3.1. Contrasting Observations and Projections on Primary Production

Observations indicate significant alterations of net primary production (NPP) in the ocean when environmental controls are altered due to natural perturbations, shifts in ocean currents, volcanic eruptions and enhanced iron supply, as in high-nitrate low-chlorophyll (HNLC) waters of the NE Pacific (Hamme *et al.*, 2010). Climate variability can drive pronounced changes in primary productivity (Chavez *et al.*, 2011), such as during the El Niño to La Niña transition in Equatorial Pacific, when nutrient and trace element supply are enhanced (Chavez *et al.*, 1999). As outlined in 6.1.3. and 6.2.3., the limited temporal extent of the satellite datasets, and the contrasting evidence from satellite and field based time series data in low latitude waters lead to *medium confidence* that there has been a small but significant increase in global NPP over the last two decades, but this increase may be linked more closely to shifts in environmental variability than to climate change. At high latitudes, there is *medium confidence* based on *limited evidence* and *medium agreement* from satellite images and modeling studies of an observed trend of higher rates of NPP (6.2.3).

6.3.2. Temperature-Mediated System Changes

Temperature effects on ecosystems are built on organismal responses, direct or indirect via competing species or the foodweb (6.2.2) or via additional changes in the physical environment. Direct organismal responses include changes in distribution, abundance, phenology and body size, which are related to physiological responses that affect species' performances in growth and reproduction (6.2.2.-5). Marine ecosystems are also indirectly affected by temperature through changes in stratification, sea-ice extent and interactions with other drivers like OA and hypoxia

(6.3.3). Species responses to temperature depend on location, the respective climate regime and, potentially, local adaptation (6.2.2). Geographical shifts of marine species from similar locations vary (Genner *et al*., 2004; Perry *et al*., 2005; Simpson *et al*., 2011b) emphasizing that thermal window widths and associated thermal sensitivities are species- specific, related to mode of life, phylogeny and associated metabolic capacities (6.2.5). Differences between species-level changes affect community and ecosystem responses to temperature-mediated effects.

6.3.2.1. Species Abundance, Biogeography, and Diversity

There is *high confidence* that recent changes in abundance and distribution of marine species and the associated shifts in biomes and diversity patterns are resulting, at least partly, from temperature-mediated biological responses (Table 6-8). In pelagic systems (Box 6-1), plankton abundance is related to water temperature (6.3.1, Ch. 30). For example, data from the Continuous Plankton Recorder (6.1.3) in the Northeast Atlantic from 1960 to 1995 show that warmer temperature enhances phytoplankton growth (Edwards *et al*., 2001), and that plankton distribution in the North Atlantic shifted poleward at a mean rate of hundreds of km per decade since the 1950s (Beaugrand *et al.*, 2009; Beaugrand *et al.*, 2002; Bonnet *et al.*, 2005; Lindley and Daykin, 2005; Richardson *et al.*, 2006; Figure 6-11, Box 6-1). Coccolithophore blooms (*E. huxleyi*) were observed for the first time in the Bering Sea during the period 1997-2000, probably in response to a 4°C warming cue, combined with a shallower mixed layer depth, higher light levels and low zooplankton grazing (Merico *et al*., 2004). Warming may also have caused the southward movement of coccolithophores in the Southern Ocean in the 2000s (Cubillos *et al.*, 2007).

[INSERT TABLE 6-8 HERE
Table 6-8: Examples of observed biological responses resulting from temperature and temperature-mediated changes in the ocean.].

Similarly, the distribution of pelagic and demersal fishes and macroinvertebrates has shifted poleward at tens to hundreds of km per decade during warming since the 1970s, although the range shifts have not been uniform across taxa or ocean regions (Johns *et al.*, 2001; Johns *et al.*, 2003; Mackas and Beaugrand, 2010; McGinty *et al.*, 2011). In the Northeast Pacific, the center of distribution of forty fishes and invertebrates shifted north by an average of 34 ± 56 km since the early 1980s (Mueter and Litzow, 2008; WGII Ch. 28). A general increase in the frequency of southern species moving northward occurred with El Niño associated warming events in the late 50s, early 80s and late 90s and, with a general interdecadal climatic regime shift in the California Current, beginning in the late 70s (McGowan *et al.*, 1998). In the North Sea, marine species have been moving polewards by 22 km decade^{-1} and to deeper water by 3.6 m decade^{-1} in relation to warming from the 1970s to 2000s (Perry *et al*., 2005; Dulvy *et al*., 2008). A global meta-analysis including 311 marine species from non-single species studies estimated an average poleward shift of 8.9 km decade^{-1} (Przeslawski *et al*., 2012). These distribution changes are mostly attributed to temperature change, but may be influenced by other factors such as sea-ice extent, nutrient enrichment and overfishing. For comparison, average terrestrial species distribution shifts ranges from 6.1 km per decade (Parmesan and Yohe, 2003) to 16.9 km per decade (Chen *et al*., 2011), with a high diversity of range shifts among species. Shifts to cooler depths in marine environments are the equivalent of altitudinal shifts in terrestrial environments (Dulvy *et al*., 2008; Burrows *et al*., 2011). Poleward distribution shifts resulted in increased species richness in high latitude regions (Hiddink *et al*., 2008) and in changing community structure (Simpson *et al*., 2011), causing polar and temperate ecosystems to become more temperate and subtropical, respectively (Philippart *et al.*, 2011). In semi-enclosed seas such as the Mediterranean geographical barriers constrain range shifts and may cause a loss of endemic species (Ben Rais Lasram *et al*., 2010), with associated niches filled by alien species, either from nearby or artificially introduced (Philippart *et al*., 2011).

[INSERT FIGURE 6-11 HERE
Figure 6-11: **A**. Long-term changes in the ecosystem state based on 5 biological parameters (phytoplankton colour index, mean size of calanoids, mean calanoid diversity, an index of change in plankton composition and cod recruitment). The orange line denotes the mean ecosystem state for the period prior and after the abrupt ecosystem shift. **B**. Long-term changes in the multiscale temporal local variance of the ecosystem state (in red). High values indicate pronounced year-to-year changes in the ecosystem state. The light gray band shows the unstable period (1980-1989). **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 (9-10°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 colour bar is 10-fold inferior for warm-temperate pseudo-oceanic species because these species are less frequently observed than their temperate counterparts. From Beaugrand *et al*. (2008) and Beaugrand *et al*. (2009).]

Field observations show changes in abundance, distribution and diversity of ocean benthos in response to climate change, especially in intertidal organisms and coral reefs (WGII Ch. 5, *robust evidence*, *high agreement*) but also in other benthos (*medium confidence*), shaped by exposures to temperature extremes (WGII Ch. 5; cf. Figure 6-7). Phenomena in sedentary organisms and benthic macroalgae are complicated by the influence of local dynamics and topographic features (islands, channels, coastal lagoons, e.g. of the Mediterranean, Bianchi, 2007) on biogeographic boundaries (Poloczanska *et al.*, 2011). Considerable poleward shifts of warm water species including macroalgae (Table 6-8; van den Hoek, 1982; Müller *et al*., 2009, 2011; Fernández, 2011) or corals (Precht and Aronson, 2004; Yamano *et al*., 2011) have been observed over last decades (*high confidence*) and are projected to continue (Müller *et al*., 2009, 2011). In corals during the last interglacial this was paralleled by the equatorial deterioration and retreat of coral reef ecosystems (Kiessling *et al*., 2012), likely due to associated bleaching (6.2.5; Box CC-CR). This confirms that shallow-water reef-building corals and their low latitude ecosystems are among the most sensitive to warming (Veron *et al*., 2009). However, a large scale survey found diverse coral reef types along a climatic gradient, but no consistent latitudinal response to climatic drivers (Hughes *et al*., 2012). The distribution of sublittoral benthos may respond more slowly to warming than that of fishes, plankton and intertidal organisms, but immigration and proliferation of species from warmer waters has been observed in selected areas like the British channel (Hiscock *et al*., 2004; Hinz *et al.*, 2011) or the North Sea coastal area (Reise and van Beusekom, 2008). The diversity of these findings indicate various environmental influences and pathways of changing species composition.

6.3.2.2. Phenology

There is *robust evidence* from long-term observations that warming and other temperature-mediated changes have resulted in shifting phenologies of marine species (Table 6-8), ranging from phytoplankton and zooplankton blooms, to reproduction and migration of invertebrates, fishes and seabirds, with many biological events advanced in timing under warming. In the waters around the U.K., 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} (Thackeray *et al*., 2010). This rate of phenological shift is not statistically different from shifts observed for freshwater and terrestrial species. Overall, the average rate of shift across species in all biomes is estimated to be 0.39 d yr^{-1}. Patterns of phenology shifts are different between trophic groups, potentially causing trophic mismatch and disruption of interspecific interactions.

6.3.2.3. Body Size

There is *medium evidence* from long-term observations that warming and other temperature-mediated changes affect the body size of marine organisms (Table 6-8). Weight-at-age of some juvenile or younger fish populations were shown to increase with temperature, as warmer water increases growth rates (e.g. Brunel and Dickey-Collas, 2010; Neuheimer and Grønkjær, 2012). However, spatial and temporal comparisons of observed maximum body sizes of invertebrates and fish populations suggest a decrease in maximum body size as temperature increases (6.2.2., Box 6-1, e.g. Daufresne *et al*., 2009). Changes in body size observed in a local population under warming may be complicated by effects on energy budget through temperatures drifting outside of a species' optimum range, the availability and changing body size of prey, species interactions or effects of fishing (Cheung *et al*., 2012).

6.3.2.4. Trophic Interactions

There is *high confidence* that temperature affects marine trophic interactions through changes in the distribution and timing of peak abundances of prey and predator, their growth and consumption rates (grazing or predation; Table 6-8). A time series for four commercial fish species and their zooplankton prey in the Norwegian and Barents Seas showed that climate shapes population growth rates through complex influences early in life, including direct temperature effects on growth, further effects through prey and delayed feedback effects through predators (Stige *et al.*, 2010). In a study of temperature effects on five trophic levels, species interactions of primary producers (microalgae), primary, secondary and tertiary consumers (zooplankton, fishes and jellyfishes) and benthic detritivores (echinoderms and bivalves) were modified through trophic amplification due to differential species responses to temperature (Kirby and Beaugrand, 2009). There is *high confidence* that the responses of various plankton functional groups, diatoms, dinoflagellates or copepods to warming are not synchronous, resulting in predator – prey mismatches that carry over to higher trophic levels (Edwards and Richardson, 2004; Costello *et al.*, 2006; 6.3.5., 6.3.6). In the intertidal, the relative ranges of predator and prey change in response to warming lead to shifts in dominance through interactions and modifications in predator pressure (Harley, 2011).

6.3.2.5. Conclusions

Overall, there is *very high confidence* that temperature is directly affecting marine organisms, their biogeography and community structure in both pelagic and benthic systems. Effects are complemented by indirect effects, e.g. *via* stratification, sea ice melt and freshening (*high confidence*). In a warming world, ecosystems adapted to the coldest temperatures or existing at their upper thermal limits are more sensitive (6.2.5). Long-term field observations and experimental research have identified, with *high confidence* and building on *robust evidence* and *high agreement*, that shallow-water reef-building corals and their reefs are among the marine ecosystems most affected by climate change and especially associated warming. However, other factors change concomitantly, such that quantification of the fraction of ecosystem change attributable to temperature has not always been possible.

_____ START BOX 6-1 HERE _____

Box 6-1. The Atlantic Example: Long-Term Responses of Pelagic Organisms and Communities to Temperature

Long-term observations (6.1.3) encompassing the whole pelagic Northeast Atlantic over a 50 year period show changes in the seasonal abundance of phytoplankton and rapid northerly movements of temperate and subtropical species of zooplankton (e.g. calanoid copepods) and phytoplankton (e.g. dinoflagellates and diatoms) and changes in the ecosystem functioning and productivity (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 and functional groups (Edwards and Richardson, 2004). Fluctuations in climate indices like the Northern Hemisphere Temperature (NHT) and the North Atlantic Oscillation (NAO) over multidecadal periods accompanied these changes. In cooler regions increased phytoplankton activity caused by warming probably favored growth and 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 (6.2.3; Richardson and Schoeman, 2004). Hinder *et al*. (2012) attributed a recent decline in dinoflagellates in relation to diatoms to warming, increased summer windiness and thus, turbulence. In the Northwest Atlantic sub-polar region, shifts in plankton distribution may be limited by the prevailing flow from the north, in addition to sea-ice extent and temperature (Head and Pepin 2010).

In line with the increased understanding of physiology (6.2.2., 6.2.5) warming in the temperate to polar North Atlantic was paralleled by a reduction in the average body lengths of about 100 copepod species, from 3-4 mm to 2-3 mm. Warming also led to an increase in species richness among copepods and in the dinoflagellate genus *Ceratium* (Beaugrand *et al.*, 2010). For diatoms as major contributors to carbon export (Armbrust, 2009), warming and decreasing annual variability in SST were associated with 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. Global outbreak frequencies of jellyfish aggregations may follow rising SSTs (Mills, 2001; Purcell, 2005; Purcell and Decker, 2005), however, evidence is inconclusive. Some studies report an increasing trend (Brotz *et al*., 2012) and others do not support this view (Condon *et al*., 2013) (*low confidence)*.

The ecosystem regime shift observed in North Sea plankton in the late 1980s involved an increase in phytoplankton 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 North Sea regime shift was paralleled by the northward propagation of a critical thermal boundary (CTB) between the temperate and the polar biomes (Figure 6-1; Beaugrand *et al*., 2008). Surpassing the CTB led to 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 Atlantic cod in the North Atlantic Ocean (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).

Regions of high vulnerability exist where mild warming can trigger rapid and substantial ecosystem shifts, offering a way to anticipate future shifts in all of the North Atlantic sector. Recent findings indicate a regime shift in the Bay of Biscay, the Celtic and the North Seas in the mid to end 1990s (Luczak *et al.*, 2011) when a shift in plankton composition and in the abundance of both sardine and anchovies and of the Balearic shearwater (*Puffinus mauretanicus*, an endangered seabird) paralleled stepwise warming. In contrast, changes in SST, plankton composition and productivity in the southern Bay of Biscay were less marked in areas influenced by seasonal upwelling (Valdés *et al*., 2007; Bode *et al.*, 2009, 2011). In the North Sea, a further shift discovered at the end of the 1990s (Beaugrand *et al*., revised) impacted about 40% of the phytoplankton and zooplankton species and thus had the same magnitude as the North Sea regime shift in the 1980s.

Changes in local and regional species richness, abundance and community composition result from species-specific latitudinal range shifts, depth distribution and the associated change in the structure and functional properties of ecosystems, such as productivity, energy flows and invasion resistance (*high confidence*, Stachowicz *et al.*, 2002; Duffy, 2003; Simpson *et al*., 2011b). Similar to plankton, northward range extensions or redistributions in fishes were largest along the European Continental shelf and attributed to regional warming, e.g. by 1.05°C from 1977 to 2001 in the North Sea, with winter warming being effective for Atlantic cod (Perry *et al*., 2005; 6.2.5). In the Northwest Arctic winter and spring warming caused expansion of the thermal optimum area covering 4–8°C, associated with greater growth in Atlantic salmon (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 extend to western Norway, and Mediterranean and north-west African species extend to the south coast of Portugal (Brander *et al.*, 2003; Beare *et al.*, 2004; Genner *et al.*, 2004).

The cooling and freshening of the Northwest Atlantic during the late 1980-early 1990s had the opposite effect, causing capelin and their predator, Atlantic cod to shift farther south (Rose and O'Driscoll, 2002). Between the early 1990s and mid-2000s in the Northwest Atlantic sub-polar gyre, phytoplankton increased, due to warming induced stratification. 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 throughout the region for reasons likely unrelated to climate (DFO 2011a,b). Further south, Arctic freshwater inflow caused freshening and associated 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* (de Young *et al.*, 2004; Pershing *et al*., 2005, 2010). Various fish species showed poleward shifts in distribution (Table 6-8). This was associated with reduced survival of larval cod (Mountain and Kane, 2010), fewer right whale calves (Greene *et al*., 2003), but increased herring abundance (Greene and Pershing, 2007).

_____ END BOX 6-1 HERE _____

6.3.3. Effects of Hypoxic Events and Expansion of Oxygen Minimum Zones (OMZs)

Hypoxic or anoxic conditions in both water and sediments strongly impact marine biota (6.2.2). O_2 deficiency in expanding OMZs will shift pelagic communities from diverse midwater assemblages to diel migrant biota that return to oxygenated surface waters at night (Seibel, 2011). Expanding OMZs will cause habitat loss to groundfishes and pelagic predators, affect the distribution of key zooplankton and nekton species and influence their diurnal and ontogenetic vertical migrations (Auel *et al.*, 2005; Ekau *et al.*, 2010). Major effects of expanding OMZs thus are habitat compression or abundance losses for intolerant taxa such as billfishes and other pelagic fishes with a high O_2 demand (Prince and Goodyear, 2006; Prince *et al.*, 2010; Stramma *et al.*, 2012; cf. 6.2.5), large benthic invertebrates like crabs (Chan *et al.*, 2008), mesopelagic fishes (Koslow *et al.*, 2011) and groundfishes (McClatchie *et al.*, 2010). Hypoxia effects propagate along the food chain and thereby affect fish stocks and top predators (Stramma *et al.*, 2010). Conversely, hypoxia supports range expansions or population growth in tolerant taxa like anaerobic bacteria (Ulloa *et al.*, 2012), gelatinous zooplankton (medusae, ctenophores) and selected fishes (gobies, hake), or possibly selected cephalopods (Gilly *et al.*, 2006; Zeidberg and Robinson, 2007; Bazzino *et al.*, 2010), characterized by slow growth rates, low O_2 demand and high capacities to exploit available O_2. Overall, expanding hypoxia will result in a lower biodiversity (Levin, 2003; Levin *et al.*, 2009a; Ekau *et al.*, 2010; Gooday *et al.*, 2010).

Upwelling events can be associated with exposures to hypoxic high CO_2 deep water causing strong ecosystem responses (*high confidence*), such as hypoxia induced biomass reduction in fish and invertebrate fauna (Keller *et al.*, 2010) and increases in sulphide-oxidizing bacterial mats (Chan *et al.*, 2008). Shifts in upwelling activity with climate change coincide with an apparent increase in the frequency of submarine gas eruptions of methane and hydrogen sulphide, caused by enhanced formation and sinking of phytoplankton biomass to the hypoxic to anoxic sea floor (Bakun *et al.*, 2010). These eruptions and the combined factors acting have been blamed for extensive mortalities of coastal fishes and invertebrates (Bakun and Weeks, 2004) and reductions in fishing productivity, particularly of Cape hake (*Merluccius capensis)*, Namibia’s most valuable fishery (Hamukuaya *et al.*, 1998).

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 (<10m), while sardines actively avoid such conditions (Bertrand *et al*., 2010). High susceptibility of early life stages to hypoxia in both pelagic and benthic ecosystems (Ekau *et al*., 2010), threatens population survival. In benthic ecosystems, the expansion of OMZs will, with *high confidence*, shift microbial and faunal composition, reduce diversity and alter the functional attributes of upper slope and shelf environments (Levin *et al*., 2009a; Stramma *et al*., 2010).

As CO_2 increases in parallel to O_2 depletion, marginalization of calcifiers is observed in OMZs (Levin, 2003), indicating interactions of hypoxia with acidification (6.2.2). Furthermore, significant correlations between H_2S concentrations and climate change indicators such as sea surface temperature and sea level pressure have been documented at interannual and interdecadal scales for the open part of the Black Sea (Daskalov, 2003; Faschuk, 2011). There is *medium confidence* that climate associated processes may change the parameters of anoxic and OMZs and of zones poisoned by hydrogen sulphide and thus influence corresponding pelagic and bottom faunal distributions, trophic relations, energy flows, and productivity (Figure 6-12).

[INSERT FIGURE 6-12 HERE
Figure 6-12: Schematic illustrating the principal mechanisms underlying the formation of hypoxic conditions and their biological background (modified from Levin *et al.*, 2009a; Levin and Sibuet, 2012). The buoyancy flux from fluvial discharges produces sharp density stratification at the base of the freshened layer (also valid for icemelt, 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 phytoplankton blooms. The enhancement of oxygen consumption due to respiratory catabolism of sinking organic matter results in hypoxic conditions of OMZs. Heating of the upper layer further increases stratification, while the wind-driven upwelling of hypoxic, nutrient-rich water from deeper layers adds to the formation of the oxygen minimum zone.]

With the expansion and enhanced variability of OMZs, both (dissimilatory) nitrate reduction and anaerobic ammonium oxidation (anammox) will cause enhanced loss of fixed nitrogen 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).

In conclusion, there is *medium confidence* that OMZ expansion is causing habitat loss to groundfishes and pelagic predators and affecting the distribution of key zooplankton and nekton species as well as influencing their diurnal and ontogenetic vertical migrations. There is *high confidence* that effects of OMZ expansion will propagate along the food chain. If O_2 levels decline and OMZs expand further, a community change toward hypoxia-tolerant fauna will occur in midwater (*high confidence*). The diversity of macroorganisms will decrease and, finally, higher marine organisms will disappear and heterotrophic microorganisms will dominate (*high confidence*).

6.3.4. Effects of Anthropogenic Ocean Acidification

The strongest evidence for effects of ocean acidification (OA) on ocean biology stems from short (h) to medium term (several months) perturbation experiments in the laboratory or, more recently, the field and the assessment of organism responses after exposures to elevated CO_2 levels (6.2.2.-5). The long-term progressive nature of anthropogenic OA over years, even centuries indicates that results obtained during such acute exposures may not be easily scaled up to effects on longer timescales. Depending on the organism studied and its generation time perturbation studies measure tolerance and acclimation, but rarely adaptation or natural selection.

At ecosystem level shell thinning in planktonic foraminifera was attributed to anthropogenic ocean acidification in Southern Ocean species (Moy *et al*., 2009) and to both anthropogenic OA and upwelling of CO_2 rich deep waters for planktonic foraminifera in the Arabian Sea (de Moel *et al.*, 2009) or for pteropods in the Southern ocean (Bednarsek *et al*., 2012; *limited evidence, medium agreement*). An eight year trend of (variable) pH decline in coastal waters and the observation of species replacements in communities associated with local pH dynamics support the projection of shifts from shelled species like mussels to fleshy algae and barnacles with acidification along the Northeast Pacific coast (*medium confidence*, Wootton *et al*., 2008). Otherwise, contributions of OA to climate-induced alterations in the field have not yet been clearly established, partly because OA is still early in the process and has a much smaller effect than other drivers like temperature. For example, declines in calcification reported in corals (De'ath *et al.*, 2009) were elicited by thermal extremes and associated declines in performance, but may include an as yet unclear contribution by OA. Species-specific declines in calcification were also correlated with average annual sea surface temperature but at different temperature ranges characterizing the respective reef (Carricart-Ganivet *et al*., 2012).

Field studies at the demographic/metapopulation level are presently limited to natural analogues (CO_2 vents; Kroeker *et al*., 2011; Fabricius *et al*., 2011), indicating losses in diversity, biomass and trophic complexity of benthic marine communities. These studies cannot fully project future changes.

6.3.4.1. Bacterial Communities and Nutrient Cycles

Existing studies on the effect of OA (either through reduced pH or increased CO_2) on autotrophic and heterotrophic bacterial production have provided inconsistent results emphasizing that these responses are still poorly known and complex. 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) which makes projections of their reaction to ocean acidification on an ecosystem level very difficult. Processes discussed are: (1) cellular elemental stoichiometry (C-N-P ratios, Riebesell, 2004; Fu *et al*., 2007), (2) rates of CO_2 and N_2 fixation (Riebesell, 2004; Riebesell *et al*., 2008; Hutchins *et al*., 2007; Hutchins *et al*., 2009), (3) rates of nitrification (Beman *et al*., 2011), and (4) changes in the proportion of dissolved to particulate photosynthate carbon production and the implied efficiency of the biological carbon pump (Kim *et al*., 2011; 6.4.1). Field experiments led to the projection that nitrification rates (ammonia oxidation to nitrite and nitrite oxidation to nitrate) of ammonium oxidizing bacteria and archaea will be reduced by 3–44% in response to pH decrements by 0.05–0.14 (Beman *et al.*, 2011). Such a decrease in pH corresponds to a rise in atmospheric CO_2 concentration by approximately 100 µatm as projected for the next 30 to 40 years (WG I AnnexII). The reported decrease in nitrification occurred regardless of natural pH variability providing no evidence for acclimation of the nitrifiers to reduced pH, e.g. in upwelling areas. However, potential changes in cell abundance, for example, due to lower per cell nitrification rates could further decrease or restore, respectively, the total volumetric rate of nitrification. While effects have been observed in the laboratory and in coastal mesocosm studies (Weinbauer *et al*., 2011) or in field experiments (Beman *et al.*, 2011), there is no evidence as yet for a reduction in abundances or metabolic activities of microbial communities in the field at either extreme of extant pH variability (Joint *et al*., 2010). Krause *et al.* (2012) documented a change in composition, without loss in abundance for a coastal bacterial community at pH 0.4 and 0.5 below ambient for the North Sea. Liu *et al.* (2010) propose 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 OA and maintain function, 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 such that projections of future changes are not yet possible.

6.3.4.2. Phyto- and Zooplankton Communities

While there is *high confidence* in systematic changes in plankton abundance and community structure over recent decades (6.1.2, 6.3.1), most of these changes were caused by both the direct and indirect effects of warming and are driven in many cases by climate variability (Chavez *et al.*, 2011). The specific effects of anthropogenic OA are much less clear. Physiological rates and growth of some groups benefit from “fertilization” by CO_2 and may gain predominance (Rost *et al.*, 2008; Hutchins *et al.*, 2009, Table 6-6). Such shifts may be influenced by light and nutrients (6.2.2). For natural phytoplankton assemblages there is *medium confidence* to date that NPP is stimulated by increased CO_2 concentrations (Riebesell *et al.*, 2008; Tortell *et al.*, 2008b). As responses to elevated CO_2 may influence the competitive abilities of species, small differences in CO_2 sensitivity may lead to pronounced shifts in the dominance of species (Tortell *et al*., 2008b, Beaufort *et al*., 2011).

Quantification of the calcite mass of the coccolithophore community in the present ocean and over the last 40 kyr revealed patterns of decreasing calcification with increasing $p\mathrm{CO}_2$, which in large parts was 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 *E. huxleyi* morphotypes in upwelling systems characterised by low pH, a finding which highlights the complexity of assemblage-level responses. For example, a shift from 'overcalcified' to weakly 'calcified' coccolithophores *Emiliania huxleyi* at higher latitudes may not reflect effects on cellular calcification rates but a temperature-related shift in ecotype dominance (Cubillos *et al*., 2007; 6.3.2). Due to the complexity in response patterns, an up-scaling of effects of calcification in coccolithophores from monospecific culture experiments cannot be achieved. Projections of OA impacts on phytoplankton become even more complicated by synergistic interactions with other drivers (Boyd, 2011; 6.3.5).

For zooplankton, field and laboratory studies lead to *medium confidence* that pteropods (planktonic molluscs with aragonite shells) at high latitudes will experience reduced calcification in response to OA until the end of the century (Orr *et al*., 2005; Comeau *et al.*, 2009; Comeau *et al.*, 2010; Lischka *et al*., 2011; Bednarsek *et al*., 2012). This may have severe impact on Subarctic Pacific and Southern Ocean ecosystems as pteropods form an integral part of the foodweb as grazers and prey for fishes like pink salmon (Bathmann *et al.*, 1991; Armstrong *et al.*, 2005; Hunt *et al.*, 2008). The comparison of decreasing calcification and shell weight found in extant planktonic foraminifera exposed to elevated CO_2 (Bijma *et al.*, 1999; Russell *et al.*, 2004; Lombard *et al.*, 2010) with findings in historical specimens (Moy *et al*., 2009) and during glacial interglacial cycles (Barker and Elderfield, 2002) supports *high confidence* in projections of future reductions in net calcification in foraminifera.

6.3.4.3. Macrophytes and Macrofauna at Ecosystem Level

Laboratory studies (6.2.2., 6.2.4) suggest that most seagrasses and non-calcifying algae respond to OA by increasing growth and recruitment, while calcifying algae experience reduced productivity. In various animal phyla, sensitivity seems to be highest in early life stages or during critical transition phases in the life cycle (6.1.2., 6.2.2., 6.2.5.., Table 6-5). The wide range of responses among macrofaunal calcifiers in experiments (e.g. Ries *et al.*, 2009), in natural settings at volcanic CO_2 vents (e.g. at Ischia, Italy, Hall-Spencer *et al*., 2008 and Papua New Guinea, Fabricius *et al.*, 2011) and in mesocoms (Christen et al 2013) suggests a wide range of ecosystem level consequences. For example, diversity is lower and non-calcifiers increasingly outcompete calcifiers once pH falls to a mean of 7.8 to 7.7 with a loss of calcifiers around pH 7.2 (Christen *et al.*, 2013). Calcitic bryozoans replace coralline algae which have more soluble high calcite skeletons (Martin *et al.*, 2008), corals decrease calcification rates, seagrasses and non-calcifying algae gain competitive advantage (Fabricius *et al.*, 2011) and net calcification changes to dissolution. However, the high pH variability at natural sites with lower pH values than indicated by the average change (Hall-Spencer *et al.*, 2008; Porzio *et al.*, 2011) and recolonization of the seep areas by larvae from neighbouring areas with normal pH or during periods of high pH, limits the use of these sites for analogues of future OA. With *limited evidence* and, thus *medium agreement*, warming probably exacerbates CO_2 effects on communities at the warm edges of their biogeographical ranges and vice versa (6.2.2., 6.2.5). For cold-water corals experimental and observational findings suggest some resilience to OA (*low confidence*, 6.2.5). The reduction of salinity associated with freshwater input results in lower alkalinity, exacerbates OA and may thereby contribute to constrain the distribution of sensitive species further in estuaries or brackish oceans like the Baltic or in freshening polar oceans (6.1.1., *low confidence*, Miller *et al.*, 2009; Denman *et al.*, 2011). It remains to be explored whether organisms in ecosystems characterized by permanently elevated or fluctuating CO_2 levels (6.1.1), like upwelling areas and OMZs, have evolved a higher resistance to increased CO_2 levels than elsewhere.

6.3.4.4. Conclusions

Overall, *confidence* is *high* that ocean acidification will affect marine ecosystems for centuries. The severity of effects will depend on RCP emission scenarios followed and maximum CO_2 levels reached, but the severity of effects cannot be directly related to any scenario at present. Detection, attribution and projection of OA effects at ecosystem level, including large scale ecosystem functions and biodiversity, are limited by the nature and duration of existing laboratory, mesocosm and field studies. The diversity of responses observed in organisms (6.2.5) and communities remain qualitative at best and are fraught with *low confidence*. Thresholds beyond which effects will set in can be quantified only with *low confidence*. While lab and mesocosm experiments provide evidence for differential effects on interacting species, further studies need to explore how OA may change the composition of communities, impact food webs and affect higher trophic levels. Consequences for fitness, abundance, distribution and species interactions cannot be projected to date. Accordingly, *confidence* is *low* that OA will cause a stimulation of phytoplankton primary production overall in the oceans and is *low* to *medium* for the net stimulation of nitrogen fixation by phytoplankton. C*onfidence* is *medium* that CO_2 accumulation associated with OA will stimulate primary production in non-calcifying macrophytes and thus benefit their abundance, but discriminate against calcifying algae. *Confidence* is *low* to *medium* that differential sensitivities and associated shifts in performance and distribution will change the quality of predator prey relationships and competitive interactions.

6.3.5. Concurrent Community Responses to Multiple Drivers

Various environmental drivers will change concurrently, eliciting a variety of responses ranging from organismal physiology to the areal extent and boundaries of biogeographical regions. This complexity is often confounding the clear attribution of biological trends to individual or anthropogenic drivers (Parmesan *et al.*, 2011). Alterations in marine ecosystems worldwide (Pauly *et al.*, 1998; Oguz, 2007; Österblom *et al.*, 2007) have often been linked to human and especially fishing activities (Frank *et al.*, 2005; deYoung *et al.*, 2008; Jackson, 2008; Casini *et al.*, 2009), however, they may involve a contribution of climate variability and change. Table 6-9 provides an attempt to categorize these multiple influences on marine biota – including temperature, CO_2, dissolved O_2 and nutrient concentrations - (e.g. Sarmiento *et al.*, 1998; Matear and Hirst, 1999; Boyd and Doney, 2002; Ekau *et al.*, 2010) – or other human interventions, including the introduction of non-native species, overfishing, chemical pollution, or habitat destruction (Carlton, 2000). The drivers can act individually, or interactively with either synergistic (i.e. amplification of) or antagonistic (i.e. diminution of) effects. A recent metaanalysis of 171 experimental studies that exposed marine systems to two or more drivers identified cumulative effects that were either 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 either warming, hypoxia or salinity changes leading to complex large-scale synergistic influences such as on both coccolithophore calcite production and abundances under warming and elevated CO_2 (Feng *et al.*, 2009, Table 6-9).

Present day OA is developing more than 10 times faster than in comparable paleo-events (6.1.2; Ridgwell and Schmidt, 2010), when similar to today, OA coincided with warming and enhanced stratification of the oceans and, consequently, a stronger deoxygenation of deeper waters (Thomas, 2007; Gattuso *et al.*, 2011), making it again difficult to attribute changes to OA (6.3.5). Furthermore, ocean physicochemical conditions prior to each of those paleo-events were very different from the present situation. Nonetheless, the PETM (55 Ma) provides useful comparative information for plankton and benthic foraminifera (6.1.2). Insight into the fate of animals shows some of them are affected, however, causalities and patterns have not been clearly identified (*low confidence*). The Permian Triassic (251 Ma) displayed similar patterns of sensitivity across animal phyla as projected for marine animal phyla today (6.1.2., 6.2.5).

[INSERT TABLE 6-9 HERE
TABLE 6-9: Potential interactions between modes of anthropogenic forcing (environmental; harvesting; or complex; considering scales and velocity of change, frequency, intensity, and variability of events) on different levels of biological organisation. These interactions, from simple to complex, are illustrated with published illustrative examples, ranging from physiological studies (Pörtner and Knust, 2007) to modelling studies such as Griffith *et al.* (2011). E, O, and M denote studies using manipulation Experiments (lab or field), Observations, or Modelling approaches, respectively; note that there is an insufficient number of studies to assign a level of confidence to each of these findings "???" defines the bounds on our understanding of the relationship between forcing and its effect on organisational level.]

Many microbes in the surface ocean are simultaneously limited by, for example, nitrate and phosphate, cobalt and iron (Saito *et al.*, 2002; Bertrand *et al.*, 2007), or iron and irradiance (Boyd *et al.*, 2010; 6.2.2). Both synergistic and antagonistic effects of multiple drivers on upper ocean biota have been observed in shipboard and/or laboratory manipulation experiments (Boyd *et al.*, 2010), which may result from the interplay of such co-limitations with multiple factors changing (Folt *et al.*, 1999; Gruber, 2011). In phytoplankton warming under high CO_2, photo-physiological rates of the cyanobacterium *Synechococcus* were synergistically enhanced, whereas the cyanobacterial group *Prochlorococus* showed no change (Fu *et al.*, 2007). Such differences may result in floristic phytoplankton shifts with the potential to restructure predator-prey interactions (Table 6-9). For example, 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. Zondervan *et al.*, 2002; Sciandra *et al.*, 2003; Fu *et al.*, 2007; Kranz *et al.*, 2010). As the co-limiting environmental factors vary between different groups, such as nitrogen fixers (e.g. Hutchins *et al*., 2007; Kranz *et al.*, 2010), coccolithophores (e.g. Feng *et al.*, 2009, Rokitta and Rost, 2012) versus diatoms (Boyd *et al.*, 2010), the predictive capacity of climate change effects is currently limited (Boyd *et al.*, 2010). At ocean basin scale, modeling experiments of interactive environmental effects provide the most reliable projections to date. They mainly point to synergistic effects, such as those of reduced pH, hypoxia and/or warming. Projected OA effects involve altering the sinking particles (C:N ratio and/or reduced calcite content and slower sinking) and a knock-on effect on water column O_2 demand (Gruber, 2011).

For complex organisms like animals or higher plants, climate change also involves synergisms and antagonisms of both abiotic and biotic factors. As increasingly understood in animals, the main drivers mediating climate impacts on ocean ecosystems are intertwined in their impact on organisms and, conversely, are shaped by the responses of biota. Warming reduces O_2 solubility and enhances biotic O_2 demand. The critical oxygen threshold P_c rises in animals indicating reduced hypoxia tolerance (Nilsson *et al*., 2010; Vaquer-Sunyer and Duarte, 2011). The consumption of O_2 generates hypoxia, introduces CO_2 and causes acidification (Millero, 1995; Brewer and Peltzer, 2009). O_2 deficiency, in turn narrows the thermal range of animals (Pörtner *et al.*, 2005). As a consequence, midwater mesopelagic and demersal fish stocks may decline with expanding hypoxia and loss of habitat in the North Pacific or California Current Ecosystem and throughout the Southern California Bight at rates much quicker than anticipated due to warming (Koslow *et al*., 2011; McClatchie *et al*., 2010)..Similarly, CO_2 constrains thermal windows, causing biogeographical range contractions, changing phenologies and changes in relative performance, affecting predator-prey relationships or competitive species interactions (Figure 6-7C). Knowledge largely builds on laboratory work (6.2.4.-5) leading to the projection that the narrowing of the thermal niche by CO_2 and hypoxia will cause shrinking biogeographical ranges, (Figure 6-7). Conversely, CO_2 sensitivity is enhanced at thermal extremes. In OMZs, CO_2 has a protective effect and sustains time-limited hypoxia tolerance since it facilitates the reduction in energy demand (Reipschläger *et al*., 1997; Pörtner *et al.*, 1998, 2000). Regions influenced by river runoff and experiencing increased precipitation will see a shift from marine to more brackish and even freshwater species, with unclear consequences for the impacts of other drivers. Reductions in primary production reduce resilience at higher trophic levels causing changes in species interactions (Kirby and Beaugrand, 2009; Stock *et al.*, 2011; 6.3.5). The introduction of non-indigenous species, when supported by climate-induced shifts in competitive interactions, may provoke the displacement of ecotypes and shifts in ecosystem functioning, for example, in the Mediterranean Sea (Occhipinti-Ambrogi, 2007; Coll *et al.*, 2010; Costello *et al.*, 2010). A mechanistic framework, such as oxygen and capacity limited thermal tolerance (OCLTT) in animals (Pörtner, 2010, 2012), would support a comprehensive understanding of the integrated effects of multiple drivers on organisms and ecosystems.

At the level of animal communities synergistic or antagonistic effects of various drivers remain largely unexplored. Adaptation to climate zones and variability may co-define species sensitivities (6.2.2., 6.2.5). This includes the role of CO_2 and temperature in warm water coral reefs (6.2.2., 6.2.5). It also includes the role of light versus temperature in shaping seasonalities and species interactions, for example during latitudinal distribution shifts (Bradshaw and Holzapfel, 2010). In the Pacific, the complex interaction of climate variability (due to ENSO), warming ocean surface, shallowing mixed layer depth in relation to the positioning of the warm pool and its convergence with the Pacific Equatorial Divergence Province, linked to the associated aggregation of macrozooplankton and micronekton, may have contributed to the net eastward shift of skipjack tuna between 1985 and 2010 (Lehodey *et al*., 2011).

Complex interactions also characterize eastern boundary upwelling systems which cover 1% of the ocean surface area but account for about 11% of new production (Monteiro, 2010) and half of the world’s commercial fish catches (Merrett and Haedrich, 1997). Understanding whether upwelling and climate change will impact resident biota in a synergistic or antagonistic manner is highly relevant for projections of climate impacts on these areas and their services to human society. Upwelling in a changing climate will have both beneficial and detrimental effects. Upwelling of hypoxic and acidified waters will combine with anthropogenic impact and negatively affect marine biota and ecosystem structure of the upper ocean. However, under projected scenarios of reduced upward supply of nutrients due to stratification (Steinacher *et al.*, 2010), upwelling of both nutrients and trace elements may become increasingly important in maintaining upper ocean nutrient and trace metal inventories. Upwelling areas may also increase nutrient content and productivity under enhanced stratification (Rykaczewski and Dunne, 2010). Upwelled and partially denitrified waters contain excess phosphate that may select for N_2 fixation (Deutsch *et al*., 2007; Deutsch and Weber, 2012), but field observations of N_2 fixation in these regions have not supported these predictions (Fernandez *et al*., 2011; Franz *et al*., 2012). The role of this process in global primary production thus needs to be validated (*low confidence*).

Observational (Schwing and Mendelssohn, 1997; Demarcq, 2009) and modeling evidence (Bograd and Lynn, 2003; Snyder *et al.*, 2003; Di Lorenzo *et al.*, 2005) indicates increased alongshore upwelling favored by winds over recent decades, as a putative consequence of warming (Bakun, 1990). Some spatial heterogeneity exists as in some areas like the Iberian peninsula, decreased upwelling occurs (Lemos and Sansó, 2006). The productivity of most wind driven upwelling systems has increased during the last decade (Demarcq, 2009). Habitat compression may initially even enhance fisheries catches in coastal regions or tropical OMZs. Upwelling regions sit closer to thresholds for hypoxia and acidification effects where ecosystem states may shift. For example, changes in sea surface temperature in the California Current System have been linked to latitudinal shifts in faunal composition and fisheries regimes and habitat expansion or contraction for the distribution of some species like sardine and anchovies or Humbold squid (Lluch-Belda *et al.*, 2001; Lluch-Belda *et al.*, 2003; Checkley *et al*., 2009b; Zwolinski and Demer, 2012; 6.3.3), or recruitment changes of near-shore invertebrates. Changing the duration, frequency and magnitude of the upwelling were relevant to explain the dynamic of benthos (Iles *et al*., 2012) and fisheries (Rykaczewski and Checkley, 2008). The effect of climate change on upwelling systems through stronger winds, altered current patterns or enhanced OA remains debated (Chavez and Messie, 2009).

6.3.6. Biotic Interactions

Impacts of climate change on marine populations (6.3.1.-5) underlie alterations of species interactions, ecosystems structure and functioning, including changes in trophodynamics and the physical and chemical characteristics of biogenic habitats. Changes in climate and NPP can affect the entire food web structure (Figure 6-13; Utne-Palm *et al.*, 2010) and the different components of the ecosystems, including fish resources (Parsons and Lear, 2001; Brown *et al.*, 2010; Cheung *et al.*, 2010), by altering predation, competition, and food availability. Climate-driven shifts in dominant trophic pathways have been documented for a variety of marine ecosystems (Kirby and Beaugrand, 2009; Moloney *et al.*, 2011), in some cases, these are irreversible (Jarre and Shannon, 2010). As a consequence of warming, consumer control of food web structure may result because respiration of heterotrophic zooplankton and bacteria responds more strongly to changing temperature than photosynthesis of autotrophic phytoplankton (Connor *et al*., 2009; Gross, 2009). Community reassembly under climate change might involve the mixing of ecosystems with strongly altered trophodynamics (Cury *et al.*, 2003; Parmesan and Matthews, 2005; Luczak *et al.*, 2011). Trophic amplification may then drive an ecosystem towards a new dynamic regime.

[INSERT FIGURE 6-13 HERE
Figure 6-13: Schematic diagram of a marine foodweb and the expected responses to climate change including ocean acidification. A coupled pelagic and benthic foodweb is typically structured by the body size spectrum of species. Warming, hypoxia and ocean acidification lead to biogeographical shifts, changes in species abundance and in the dynamics of trophic interactions. The foodweb resulting from climate change includes reductions in the body size of organisms, changes in species composition and the resulting reconfiguration of trophic linkages. Fishing generally removes large-bodied and vulnerable species and truncates the body size spectrum of the community. As a result, the detection and attribution of foodweb responses to climate change are strongly confounded by fishing effects. The arrows represent species interactions (e.g. between predator and prey or competition for food or space). Broken lines (boxes and arrows) indicate the loss of populations and trophic linkages due to climate change.]

There is therefore *high confidence* that climate change will affect biodiversity, with specific differences between biomes and latitudes (Figure 6-1; 6.5., Sala and Knowlton, 2006; Cheung *et al*., 2009) and cause community reassembly in time and space (Parmesan and Matthews, 2005; Parmesan *et al*., 2011). Species may gain predominance and abundance (Occhipinti-Ambrogi, 2007) from fitness benefits due to temperature change (6.2.2) while others become less competitive or easier prey. Shifted geographical distribution of marine species, e.g. to higher latitude or deeper water cause changes in community composition and interactions (Hawkins *et al*., 2009; Simpson *et al*., 2011b; Harley, 2011; Hazen et al., 2012). Reassembly of species might involve the mixing of ecosystems and strongly alter their food web functioning (Murphy, 1995; Anderson and Piatt, 1999; Moloney *et al.*, 2011) through trophic cascades (Cury *et al.*, 2003; Parmesan and Matthews, 2005; Luczak *et al.*, 2011).

Many impacts of climate change on food webs resemble those caused by other factors such as fishing, pollution, eutrophication, hypoxia (6.3.3) and habitat change (Brander, 2007), suggesting that unambiguous attribution to climate remains difficult (Parmesan *et al*., 2011). Conversely, the anthropogenic factors can affect ecosystem responses to climate change. Fishing truncates the age and size structure of populations making them more dependent on annual recruitment (Perry *et al.*, 2010; Genner *et al*., 2010; Botsford *et al.*, 2011) and reducing their ability to buffer environmental fluctuations (Planque *et al.*, 2010). Both adult and larval fishes show greater variability in abundance in exploited than unexploited populations (Hsieh *et al.*, 2006; Hsieh *et al.*, 2008). Both warming (e.g. Molinero *et al*., 2005) and acidification (Richardson and Gibbons, 2008), or removal of top or competing predators (e.g. Richardson *et al*., 2009; Condon *et al*., 2012) are discussed as reasons causing large fluctuations in gelatinous plankton (e.g. jellyfish) populations. Trans-Arctic interchange of species that repeatedly happened in warm periods (Dodson *et al*., 2007) may occur again, facilitated by enhanced trans-Arctic shipping.

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 webs interactions that influence the species and system level responses, which affect stability and resilience of the overall ecosystem to change (Martinez *et al.*, 2006; Neutel *et al.*, 2007; Dunne and Williams, 2009; Romanuk *et al.*, 2009). There is no single approach currently available for any oceanic system that includes the complex links within and among ecosystems, biogeochemistry and climate that are needed to do projections of future states of marine food webs with the certainty needed for management and science (Fulton, 2011; Moloney *et al.*, 2011), and thus there is *low confidence* in the quantitative projections of such changes (for further discussion see 6.5).

Impacts of climate change on species providing structural habitat and support to high biodiversity (i.e. ecosystem engineers) can also result in profound ecosystem alterations. Tropical corals are known to respond to ocean warming and acidification with a variety of potentially deleterious effects on the structure of the biogenic habitat, from increased coral bleaching and impeded calcification rates to increased rates of coral disease (6.2.5; Veron *et al.*, 2009; Veron, 2011). For other benthic ecosystem engineers such as tropical calcified algae, bryozoans, sponges, and tube-forming serpulid worms (Wood, 1999), deep-water or cold-water corals or sponges, the knowledge on climate impacts is much less. However, they rely on productivity in surface waters, making them vulnerable to any alteration in local productivity patterns and food flux associated with climate change. In conclusion, there is *high confidence* that severe stress as projected from increased temperature, hypoxia and ocean acidification will cause reduced performance and increasing mortality in ecosystem engineers. As the number of available studies is scarce, projections of any more specific climate change effects come with *medium* to *low confidence*.

6.3.7. Summary and Conclusions

Except for the attribution of detected climate change effects to temperature, only a few cases allow clear attribution to another driver (6.6). *Robust evidence* from various ocean regions demonstrates with *high agreement and confidence* that temperature governs the geography, diversity, development, reproduction, behavior and phenology of marine organisms as well as the composition of communities and the seasonal timing of relevant processes (phenology). Accordingly, hydro-climatic variability, with a contributing role of the warming trend, causes large-scale changes in the biogeography, abundance and community composition and structure of marine species (*very high confidence*, 6.2.2.-5., 6.3.2). With *medium evidence* and *agreement*, changes in community composition are associated with reduced body body size (6.2.5) and increased diversity in some groups. Individual examples show, with *high confidence*, the specialization of animal species on regional climate regimes and, conversely, their sensitivity to change. Due to differential species responses to temperature, species interactions across trophic levels can be modified through trophic amplification (*medium* to *high confidence*).

Expansion of OMZs in response to climate leads to community shifts which are clearly attributable to exacerbating hypoxia (*high confidence*). Effects of a progressive decline in O_2 levels and gradual effects on communities have been insufficiently explored. In contrast to effects of temperature and extreme hypoxia, very few ecosystem level changes were attributed to anthropogenic or local ocean acidification trends (shell thinning in planktonic foraminifera, local pH dynamics causing species replacements, *medium confidence*). Otherwise, concomitant trends of warming, O_2 depletion, OA and other drivers prevent clear attribution. With *low evidence*, *medium agreement* and thus *medium confidence* community reassembly and ecosystem mixing may lead to new ecosystem states through trophic amplification (*low confidence*). With *limited evidence*, but *high agreement* and thus *medium confidence* climate change can strongly interact with top down human interferences like fisheries or other forms of harvesting which then accelerate such changes. Non-linearities that can operate within an ecosystem make the understanding and projection of marine ecosystem trajectories under climate warming more difficult.

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

6.4.1. Ecosystem Services

Human societies benefit from resources and processes supplied by natural ecosystems, collectively called ecosystem services (e.g. WGII Ch. 5). These are products such as food, fuel and biochemical resources, climate regulation and biogeochemical processes such as CO_2 uptake and carbon storage and water purification, cultural services like recreational and spiritual opportunities or aesthetic enjoyment, and functions supporting all other ecosystem services, such as nutrient cycling, photosynthesis and 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 fisheries and mineral extraction, regulating services via the global carbon cycle and climate regulation, and cultural services via the enjoyment of a healthy ecosystem.

Attributing and forecasting possible climate-change-mediated changes in marine ecosystem services and assessing their effects on human communities is challenging. This is due to the lack of long-term time-series data, the confounding effects from human activities, the multiple and sometimes overlapping roles of marine ecosystem components in contributing to human well-being, and the difficulty of measuring and assessing the services themselves in ways that are comparable among ecosystem service categories. Some of the challenges are also related to the difficulty of projecting how human communities will adapt to changing marine ecosystem benefits.

6.4.1.1. Food from the Sea

Fisheries provide over 1.5 billion people with almost 20 % of their average per capita intake of animal protein. This value ranges up to over 90% in some regions (Bell *et al.*, 2009; Garcia and Rosenberg, 2010). Total World marine capture fisheries catches stabilized in the mid-1990s at between 75 and 85 million tonnes (FAO, 2010). Marine aquaculture contributes over 63 million tons per year to seafood production, mostly concentrated in coastal areas and comprising primarily molluscs and crustaceans. The growth of this industry has decelerated, but is still considered to be a development opportunity and a strong need in regions such as Africa and Latin America (WGII Ch. 7.4.2.2).

Experience based on other anthropogenic impacts on marine systems, indicates with *high confidence*, that shifts in ecosystems and fisheries production will create significant sustainability and management challenges, particularly amongst countries with fewer resources and adaptive capacity (Allison *et al.*, 2009; Worm *et al.*, 2009; Cooley *et al.*, 2012). Fish stock migrations due to warming (6.3.2) have resulted in shifting composition of fisheries catches (Pinsky and Fogarty, 2012; Cheung *et al.*, subm) and may result in shifting stock distribution (Sebatés *et al.*, 2006) with consequent changes in accessibility and fishing operations costs, straddling economic zones, perturbing international fishery agreements and causing excessive exploitation (Hannesson, 2007; Sumaila *et al.*, 2011). Warming may have beneficial effects on fisheries productivity in some regions, such as the North Atlantic because of the poleward distribution shift of exploited species and changes in primary productivity (Arnason, 2007; Stenevik and Sundby, 2007; Cheung *et al.*, 2010), or for some Pacific Islands due to eastward redistribution of tuna stocks (Lehodey, 2000; Lehodey *et al.*, 2010, 2011). Invertebrate fisheries and aquaculture appear most vulnerable to the impacts of OA (Barton *et al.*, 2012).

The potential interactions between warming, OA and other human impacts such as overfishing may exacerbate the impacts on a wide range of ocean processes and services, including marine fisheries (Table 6-9), For example, over-exploitation of fish stocks and the altered demography (Planque *et al.*, 2010; Petitgas *et al.*, 2006) may reduce the capacity of fish populations to buffer changes in climate variability (Fromentin and Fonteneau, 2001; Hilborn *et al.*, 2003; Ottersen *et al.*, 2006), leading to unpredictable non-linear outcomes (WGII Ch. 7.5.1.1.3).

Nations that depend strongly on fisheries and have limited adaptive capacities (Allison *et al.*, 2009), including many low-latitude and small island nations, are particularly vulnerable to climate change and OA impacts (Allison *et al.*, 2009). This will be exacerbated if increases in the frequency and severity of extreme events (e.g. floods or storms) effect citizens by 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). Economic losses in landed catch value and the costs of adapting fisheries resulting from a 2°C global temperature increase by 2050 have been estimated at US$ 10-31 billion globally, with countries in East Asia and the Pacific being the most affected (Sumaila and Cheung, 2010; Sumaila *et al.*, 2011). Globally, the impacts will partially depend on the flexibility and response capacities of food production systems (Elmqvist *et al.*, 2003; Planque *et al.*, 2011a); however, the specific implications for the fishing industry are still poorly known, as *confidence* in future projections of shifts in primary production and knock-on effects through foodwebs and into fisheries is *low* (Brander, 2007; 2009; Planque *et al.*, 2011b; Stock *et al.*, 2011). Management and socioeconomic challenges may also result from increasing stock fluctuations, although modelling exercises illustrate that in general, management issues have a greater impact on biological and economic conditions than climate change is expected to have (Eide and Heen, 2002; Eide, 2007; 2008; Merino *et al.*, 2010).

6.4.1.2. Other Provisioning Services

Opportunities for marine industries may arise or disappear as systems change. For example, reductions in marine biodiversity due to climate change and other anthropogenic stressors (Tittensor *et al.*, 2010), like OA (CBD, 2009) and pollution, might have an overall negative effect on the discovery of genetic resources from marine species useful in the 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 winds and wave power, although ecosystem impacts of the respective infrastructure need to be considered (6.4.2).

6.4.1.3. Climate Regulation

Climate regulation refers to the maintenance of the chemical composition of atmosphere and oceans by organisms and chemical as well as physical processes (Beaumont *et al.*, 2007). For 800,000 years prior to 1800, the interplay of biogeochemical processes on land and in the ocean (Sigman and Boyle, 2000) have resulted in relatively stable levels of atmospheric CO_2 level (between 170 and 276 µatm; Siegenthaler *et al.*, 2005; Lüthi *et al.*, 2008). Even over the last millions of years, proxy data suggest maximum CO_2 concentrations of 400 µatm (Pagani *et al.*, 2010; Seki *et al.*, 2010). There is *high confidence* that the effect of climate change on marine biota will alter the magnitude of many, if not all of the regulatory mechanisms in which organisms play a key role, such as the balance between photosynthesis and respiration (Johnson *et al.*, 2010), the biological pump (Volk and Hoffert, 1985; Feely *et al.*, 2008; Falkowski, 1997), the modulation of greenhouse gases with high warming potential such as nitrous oxide (N_2O; Jin and Gruber, 2003; Law, 2008) and other climatically reactive gases such as dimethylsulphide (DMS; Vogt *et al.*, 2008). In the geological past, during the PETM (6.1.2) warming of the global ocean and acidification led to changes in phytoplankton composition and in significant biologically mediated feedbacks. In coastal regions, increases in weathering and the hydrological cycle, and hence in runoff from land, led to eutrophication of shelf regions and increased freshwater runoff (Sluijs and Brinkhuis, 2009), while concomitantly open ocean productivity decreased (Gibbs *et al.*, 2006). At the onset of the PETM decreased carbon isotopic gradients between surface and deep waters are interpreted to be a result of increased stratification, reduced nutrient supply and a less efficient biological pump (Zachos *et al.*, 2003). The benthic foraminiferal fauna suggests that there was no reduction in export production reaching the deep ocean, suggesting better organic carbon preservation due to lower O_2 conditions (Thomas, 2007). There is no evidence for decreased biological carbonate production despite higher atmospheric CO_2 levels during the PETM (Gibbs *et al.*, 2010; 6.1.2). Simulations from coupled ocean-atmospheric carbon cycle and climate models suggest that climate change may decrease global ocean NPP (*low confidence*, 6.5.1). Such changes in NPP are projected to lead to a decrease in the export of biogenic carbon to the deep ocean (Bopp *et al*., 2002; Boyd and Doney, 2002; Hashioka and Yamanaka, 2007), which can have a positive feedback on climate change (WGI Ch. 6). However, the effect of a changing climate on some potentially important feedbacks such as the ocean's biological pump cannot be reliably modelled, as many of the factors controlling the functioning of this pump are poorly understood (Figure 6-6).

6.4.1.4. Natural Hazard Regulation

Natural hazards are generally increasing alongside global warming, with floods and storm surges accounting for over two-thirds of the natural disasters affecting people (SREX). The role of natural ocean structures and organisms in reducing the effects of natural hazards has been undervalued. For example, empirical and modeling studies show that coral reefs contribute to buffering the impact of tsunamis (Fernando *et al.*, 2005; Kunkel *et al.*, 2006; WGII Chs. 5, 30). Field and laboratory experiments and climate models indicate that climate change and OA may slow coral growth by nearly 50% by 2050 (Hoegh-Guldberg *et al.*, 2007; WGII Ch. 5). With *high confidence* anthropogenic climate change including OA that threaten coral reefs will make some islands and coastal areas more vulnerable with respect to tsunamis, as well as storm surges. Similar to coral reefs, wetlands and mangroves provide biologically diverse buffer zones that protect coastal regions from storm surges and wave activity (WGII Ch. 5), The impacts of OA and other climate related changes as well as pollution, deoxygenation and other overlapping stressors on mangroves or wetlands have not been determined (Cooley *et al*., 2009; Cooley, 2012), and some of these stressors enhance each other's effects (Cai *et al*., 2011; Howarth *et al*., 2011; Feely *et al*. 2010).

6.4.1.5. Cultural Services

Recreation and support of tourism can be economically assessed using indirect valuation methods, but other cultural services relating to spiritual and heritage issues are extremely difficult to assess. Nevertheless, cultural services are often cited by coastal users as primary reasons for preservation. Marine biodiversity is an important component of ecosystem services, including cultural services. In many tropical countries, coral reefs and their enormous biodiversity sustain substantial tourist industries that attract millions of SCUBA divers every year. Annual net benefits from global reef tourism amount to about US$ 9.6 billion (Cesar *et al.*, 2003; Box CC-CR). If degradation of cultural ecosystem services occurs because of climate change, coastal visitors could choose to spend their recreational budgets on terrestrial attractions (UNWTO, 2008). New tourism opportunities could arise as people travel to see disappearing ecosystem types (e.g. Antarctic tourism, Liggett *et al.*, 2011) or newly open previously inhospitable areas as peak seasons shift (e.g. Amelung *et al.*, 2007; Moore, 2010) or as the locations of key attractors shift (e.g. cetaceans, Lambert *et al.*, 2010), but these opportunities seem short-lived and unsustainable.

Many cultures depend on spiritual and aesthetic benefits from marine ecosystems. While environmental change endangers harvests of culturally important species, cultural forces are putting simultaneous pressure on indigenous traditions, raising ethical questions about cultural preservation (e.g. Nuttall, 1998). In less remote coastal communities, aesthetic benefits from marine ecosystems influence economically measurable factors, such as the relationship of better water quality and lower instances of harmful algal blooms with higher real estate prices and shellfish landings (Jin *et al.*, 2008). Impacts of climate change on coastal habitats (Ch. 5) affect the aesthetic benefits of wetlands, sandy beaches and, in general, natural coastlines.

Heritage benefits of preserving marine ecosystems are extremely difficult to assess. Not only is the challenge because some heritage benefits will be enjoyed by future generations who derive economic benefits from a healthy, diverse ecosystem, but it is also because losses are presently being avoided by maintaining a bank of resources that could be tapped if needed. 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). Any biodiversity loss or pollution of marine ecosystems would decrease the benefits associated with the "insurance policy" of having untapped resources and those associated with the legacy of offering healthy systems to future generations. As with spiritual and aesthetic benefits, maintaining heritage benefits poses challenges for managers who have to consider present-day issues of equity and ethics as well as multigenerational (and possibly multi-cultural) ethical questions.

6.4.1.6. Supporting Services

These services form the foundation of all other ecosystem services. Identifying all supporting services in the marine environment is virtually impossible, as they are so diverse in nature and scales. However, potential changes in marine ecosystems due to climate change and OA can highlight the role of organisms and processes that are especially important in providing supporting services. For example, damage to calcifying algae and corals will reduce habitat for other marine species (6.3.5) and the biodiversity they sustain, the cultural and leisure values of these landscapes and their climate regulation capacity. The provision of open waterways for shipping is a specific supporting service that is expected to change in measurable ways in the next several decades (WGII Ch. 30.6.3.3). Reductions in sea ice in the Arctic may allow new trade passages such as the North West Passage to be established (Wilson *et al.*, 2004; Granier *et al.*, 2006), thereby raising the possibility of economically viable trans-Arctic shipping, as well as increasing access to regional resources supporting natural resource extraction and tourism. Accompanying the positive aspects of this development are negative consequences as well, such as increasing emission of greenhouse gases and other pollutants (Lauer *et al.*, 2009; Corbett *et al.*, 2010), and more potential for invasion of non-indigenous species due to hulls and ballast waters (Lewis *et al.*, 2004).

6.4.1.7. Conclusions

Human societies benefit from and depend on ecosystem services, including the provisioning of food and other goods, climate and natural hazards regulation, cultural and supporting services (*high confidence*). Attributing and projecting their climate-change-mediated shifts remains a challenge, partly because of the intrinsic difficulties of assessing these services, lack of long time-series data and confounding human impacts. However, available evidence from empirical and modeling studies provides *high confidence* that climate change impacts marine ecosystems, leading to changes in provision, regulation and supportive services, while there is *limited evidence* and *medium agreement* that climate change affect cultural services. Food production from the sea is already facing diverse stressors, such as overfishing and habitat degradation, which are expected, with *high confidence*, to interact with climate change phenomena, including temperature rise (6.3.2), ocean deoxygenation (6.3.3), and ocean acidification (6.3.4), causing significantly negative effects in particular to developing nations in tropical regions. The more northerly (and developed) nations may benefit from climate change, at least initially. There is *medium evidence* and *agreement* that climate change is affecting capture fisheries, although projections of such impacts into the future have *low confidence* partly because of the *low confidence* in marine primary production (6.5). Based on evidence from the geological past (*robust evidence*) and the present data (*limited evidence*), there is *high agreement* and *confidence* that marine ecosystems regulate climate through mechanisms such as the biological pump, the balance between photosynthesis and respiration and modulation of greenhouse gases. There is *high confidence* that the effect of climate change on biota will alter the magnitude of many, if not all of these processes. Projections on the direction and magnitude of specific biotic feedbacks to climate change are presently at an early stage of development and have l*ow confidence*.

6.4.2 Management-Related Adaptations and Risks

6.4.2.1. Ecosystem Management

Biophysical and socio-economic effects of climate change will pose new questions and elicit new strategies in the already highly demanding enterprise of managing ocean resources (Eide and Heen, 2002; Eide, 2007). There is *high confidence* that a changing climate will have both positive and negative socio-economic and geopolitical consequences affecting the future management of ocean resources (6.4.1). Ecosystem-based management (EBM), or the ecosystem approach (EA), is already being increasingly adopted globally (FAO, 2003) to deal with the multitude of human pressures on marine ecosystems (Sherman *et al.*, 2005; Hoel, 2009). Extended EBM would include climate-driven changes, as well as new human activities, as the many different drivers will interact and confound each other (Planque *et al.*, 2010; Eero *et al.*, 2011). Such an extension and integration (Miller *et al.*, 2010) is based on *high confidence* that the effects of different human activities will undermine resilience to other, including climate impacts or the effectiveness of mitigation and adaptation measures, by increasing variability (and reducing predictability), and limiting scope for adaptation (e.g. Hughes, 2004; Eero *et al.*, 2011; Sissener and Bjorndal, 2005). Thus, managing ecosystems under climate change requires increasing the resilience of the ecosystems and adaptive capacity of management systems through reducing other human perturbations (e.g. overfishing) (Brander, 2008).

Climate change effects cannot be completely mitigated by reducing the impacts from other non-climate drivers, highlighting the need for adaptive management accompanied by the detection and attribution of climate change impacts. Increased variability of ecosystems and the low predictability of some biological responses under climate change undermine the effectiveness of existing ocean management and conservation measures. Particularly, climate change may contribute to large-scale ecosystem regime shifts. Although there is potential for the early detection of ecosystem shifts through analysis of time-series of environmental and biological data (Carpenter and Brock, 2006; deYoung *et al.*, 2008), long-term forecast of a regime shift is limited by an insufficient number of observations and limited quantitative understanding of regime shifts. In addition, biogeographical shifts under climate change (*high confidence*, 6.5) present direct challenges to the objectives of spatial management, which has become a fundamental part of EBM (Douvere, 2008). This does not invalidate the use of spatial management, but it does mean that “fixed in law forever” site attached zoning to protect specific species may need to become more flexible to ensure that the original objectives are maintained as species move or community structure shifts (Soto, 2001; Hawkins, 2012).

6.4.2.2. Geoengineering Approaches

Recent comparative assessments suggest that the main geoengineering approaches involving the oceans may have large associated environmental footprints (Boyd, 2009; Russell *et al.*, 2012). These geoengineering approaches include, Carbon Dioxide Reduction (CDR), Solar radiation management (SRM) and other similar approaches (see Table 6-10; IPCC, 2012). CDR removes atmospheric CO_2 by directly sequestrating it into the ocean (Boyd, 2008; Shepherd *et al*., 2009). SRM relies on causing increased albedo, for example via stratospheric sulphur injection (Crutzen, 2006). SRM may reduce warming and cause changes in precipitation and their impacts on ecosystems. The use of SRM is fraught with the shortcoming that CO_2 release and OA are left unabated unless SRM is combined with CO_2 emission reductions or CO_2 removal. Also, the sudden cessation of SRM after its implementation would exacerbate the climate effects on ecosystems (Russell *et al*., 2012).

[INSERT TABLE 6-10 HERE.
Table 6-10: Challenges for the oceans that will arise from the employment of a range of geoengineering methods (SRM, solar radiation management, CDR, carbon dioxide removal).]

CDR techniques involving the ocean include fertilization by nutrient addition, binding of CO_2 and build-up of DIC by the addition of alkalinity and direct CO_2 injection into the deep ocean (Table 6-10; Williamson *et al*., 2012), all of which have potentially negative consequences for marine ecosystems. Ocean fertilization through the addition of iron to high-nutrient low-chlorophyll (HNLC) oceanic waters would increase the net export of organic material to the deep ocean and its coupled decomposition, thereby causing deep water CO_2 accumulation. A further issue with fertilization is that it would affect all major biogeochemical cycles of the ocean with as yet unclear side effects, including the formation of methane (CH_4) and N_2O (Law, 2008) or the stimulation of harmful algal blooms (Trick *et al*., 2010; Silver *et al*., 2010). Enhanced NPP by ocean fertilization would add more carbon to the base of food webs (de Baar *et al.*, 2005) and stimulate growth of, e.g. deep-sea benthos (Wolff *et al*., 2011). The increase in organic material in an ocean region (through fertilization or storage of biomass) may cause enhanced O_2 demand and deep-water O_2 depletion (Sarmiento *et al.*, 2010; Table 6-10), which can add to the increase in level and extent of hypoxia and, consequently, their impacts on marine ecosystems (6.2.2., 6.2.5., 6.3.3., 6.3.5). The synergistic effects of hypoxia and hypercapnia will further exacerbate the biological impacts (*high confidence*). The addition of alkalinity e.g. calcium oxide, to neutralize the increased acidifying water would involve large-scale mining and their consequences on land. The biological effects of enhancing Ca^{2+} ions and dissolved inorganic carbon during alkalization remain insufficiently explored. Direct injection of CO_2 into the ocean and, especially, its localized disposal (deep-sea lake option) causes local effects of CO_2 and associated acidification on deep-sea organisms (6.2.2., 6.2.5., 6.3.4., *high confidence,* Caldeira *et al.*, 2005) but appear less harmful on larger scales than the combined impacts of hypoxia and acidification caused by ocean fertilization (Pörtner *et al.*, 2005; 6.3.3).

6.4.2.3. Health Issues

Human health may be directly impacted by harmful algal blooms (HABs) or the spreading or redistribution of disease vectors. HABs are mostly a natural phenomenon (Dale *et al.*, 2006), although biogeographical range extensions caused by regional climate change may have increased the regional presence of HABs (Edwards *et al.*, 2006), posing a major threat to the functioning of near-shore ecosystems. Range expansion of HABs can be related to warming, nutrient fluctuations in upwelling areas, eutrophication in coastal areas and enhanced surface stratification, which all have species-specific responses e.g. causing shifts in seasonal cycles and blooms (Johns *et al.*, 2001) or increased HABs as in the North Sea (Smyth *et al.*, 2004; Edwards *et al.*, 2006). For nearshore waters, analysis of both planktonic time-series archives and sediment cores, which record HAB cysts, have revealed few examples of strong linkages between altered HABS and climate change (Dale *et al.*, 2006). OA may exacerbate the toxicity of species contributing to HABs in coastal oceans under nutrient limited conditions (Tatters *et al*., 2012; Sun *et al*., 2011). Overall, there is *limited evidence, low agreement* and *low confidence* in how global climate change will impact HABs. However, because of the potential impacts of HABs on human health and different ecosystem services, adaptation measures of human societies have been suggested to include appropriate monitoring of increases and range extensions of biotoxin problems (Hallegraeff, 2010).

Climate change may drive changes in the abundance or distribution of pathogen species (Hoegh-Guldberg and Bruno, 2010), although attribution to climate change is confounded by climate variability and non-climate drivers (Lafferty 2009; Dobson, 2009). Specifically, the distribution of the waterborne bacterium, *Vibrio cholera*, the causative agent of cholera, may be supported by climate change. *V. cholera* is a marine bacterium that associates with marine organisms, especially chitinized zooplankton (Vezzulli *et al.*, 2010). Climate variability can affect the marine host species, and consequently the levels of the pathogen in coastal marine environments. In regions where cholera is endemic (e.g, India, Bangladesh, Latin America), cholera outbreak is correlated with elevated sea water temperature and zooplankton blooms (Lobitz *et al.*, 2000; Lipp *et al.*, 2002). Based on an 18-year climate record for Bangladesh, Pascual *et al.* (2000) reported an interannual component of cholera outbreaks at the dominant frequency of El Niño-Southern Oscillation (ENSO), and the recent reappearance of cholera in Peru has also been linked to the intense 1991-1992 El Niño event (Lipp *et al.*, 2002). There is evidence that an increase in sustained maximum surface temperatures of the temperate Baltic Sea is related to an increase in reported *Vibrio* infections (Baker-Austin *et al*., 2013). Continued warming of coastal habitats, excessive nutrient loading leading to phytoplankton and zooplankton blooms, sea water inundation due to sea level rise and ocean warming in temperate zones are all projected to exacerbate the expansion and threat of cholera (*limited evidence, low confidence*).

The risk of ciguatera-poisoning from seafood consumption is also related to ocean warming. Ciguatera-poisoning may occur when people consume fish, mainly from tropical reefs, that has bioaccumulated ciguatoxins due to exposure to the epiphytic dinoflagellate *Gambier discus* sp. Based on historical records, significant correlations have been reported between fish poisoning and sea surface temperature in South Pacific nations (Hales *et al*., 1999); however, such relationship is non-linear and dependent on the specific thermal window of the specific dinoflagellate (Llewellyn, 2010). Thus any scenario of an increase in ciguatera-poisoning under ocean warming based on linear extrapolations of observed phenomena has *low confidence*.

6.4.2.4. Conclusions

There is *high confidence* that the already challenging task of managing the oceans, their resources and linkages to human societies, will face new questions and difficulties due to the impacts of climate change on marine ecosystems. Fisheries and ecosystem management in the future might have to deal not only with the traditional sustainability goals, but might also have to increase ecosystems resilience to climate variability and change. Active ocean manipulation strategies to amend climate change may prove detrimental for different aspects of the ecosystems, which highlights the need for further research. There is strong interest in elucidating the potential changes of different human health issues related to direct exposure to toxic organisms and pathogens or to the ingestion of marine organisms that have bioaccumulated toxins. However, there is *limited evidence* and *low confidence* on how harmful algal blooms and the prevalence of pathogens will respond to climate change.

6.5. Future Projections of Climate Change Impacts through Modeling Approaches

A range of models are applied to explore climate change effects on marine biota, from primary productivity through to higher trophic levels, and to test hypotheses about responses of marine species, food webs and ecosystems (Rose *et al.*, 2010; Stock *et al*., 2011; Fulton *et al.*, 2011). Models range from empirical approaches to mechanistic models describing population/species responses and/or trophic interactions in marine ecosystems over a range of temporal and spatial scales (Barange *et al*., 2010; Stock *et al*., 2011). Earth System Models that couple atmosphere and ocean as well as climate and carbon cycles project changes in ocean biogeochemistry under a range of CO_2 emission scenarios (WGI Ch. 6). Models that focus on population and species level responses to environmental changes include population dynamic models, species distribution models and models which explicitly link climate change effects from changes in ocean physical and chemical conditions to the interactions between species at different trophic levels and human activities such as resource extraction and aquaculture (Rose *et al*., 2010). Uncertainty in model projections of changes in marine ecosystems is partly contingent on the level of confidence in climatic and oceanographic projections (6.1.1; WGI). Models are currently useful for developing scenarios of directional changes in net primary productivity, species distributions, community structure and trophic dynamics of marine ecosystems, and their implications for ecosystem goods and services under climate change. However, quantitative projections from these models have *low confidence* (Rose *et al.*, 2010; Hannah *et al.*, 2010; Stock *et al.*, 2011).

6.5.1. Ocean Primary Production

The long-term average of global ocean net primary productivity (i.e., NPP) is projected to change with climate, with large variations in the magnitude, direction and pattern of projected changes because of differences in model structure and parameterization (Figure 6-14). Four global coupled climate-ocean biogeochemical Earth System Models (WGI Ch. 6) projected an increase in NPP at high latitudes as a result of alleviated light and temperature limitations particularly in Northern and Southern Hemisphere 'subpolar gyre' biomes (Steinacher *et al*., 2010). However, the increase is more than offset by decreases in primary productivity in the North Atlantic, the tropics and the permanently stratified oceans at mid-latitude due to the reduced input of macro-nutrients into the euphotic zone. Reduced mixed layer depth and slowed circulation cause a decrease in macronutrient flux (Polovina *et al*., 2011; Figure 6-14). These result in a reduction in global mean NPP by 2 to 13% in 2100 relative to 1860 under a high emission scenario (SRES A2, between RCP6.0 and RCP8.5). This is consistent with projections from a more recent analysis that is based on 10 Earth System Models (Bopp *et al.*, subm). The study shows consistent decreases in global NPP that amount to -8.6 (±7.9), -3.9 (±5.7), -3.6 (±5.7), -2.0 (±4.1)% in the 2090s relative to the 1990s, under the scenarios RCP8.5, RCP6.0, RCP4.5 and RCP2.6, respectively. However, the magnitude of projected changes in global NPP varies widely between models (e.g. from 0 to 20% decrease in NPP globally under RCP 8.5). Main reasons for such variations include differences in parameterizations and assumptions between models. In contrast, earlier model projections show changes in global NPP from a decrease of > 10% (Field *et al.*, 1998; Boyd and Doney, 2002) to a slight increase by up to 8.1% under an intermediate scenario (SRES A1B, similar to RCP6.0) (Sarmiento *et al*., 2004; Schmittner *et al*., 2008). These projections do not consider the potential contribution of primary production derived from atmospheric N_2-fixation in tropical and subtropical regions, favored by increasing stratification and reduced nutrient inputs from mixing, although this burst in N_2-fixation is not sustainable without phosphate (e.g. Moore *et al*., 2009; Boyd *et al*., 2010). This may lead to an underestimation of primary production (Mohr *et al*., 2010; Mulholland *et al*., 2012; Wilson *et al*., 2012), however, the extent of such underestimation is unknown (Luo *et al*., 2012). Also, uncertainties in the accuracy of NPP observations further increase the uncertainty of projections, particularly from empirical models (e.g. Sarmiento *et al*., 2004; see 6.1.3). Furthermore, the potentially incomplete understanding of the effects of multiple drivers such as ocean warming, deoxygenation and acidification on NPP renders future projections uncertain. Changes in NPP have direct and indirect implications for higher tropic level organisms and fisheries (6.2., 6.4., 6.5.2., 6.5.3).

[INSERT FIGURE 6-14 HERE
Figure 6-14: Multi-model mean changes of projected vertically-integrated net primary production (small and large phytoplankton). To indicate consistency in the sign of change, regions are stippled where all four models agree on the sign of change. Changes are annual means under the SRES A2 scenario (between RCP6.0 - 8.5) for the period 2080 to 2099 relative to 1870 to 1889, after Steinacher *et al*. (2010).]

6.5.2. Higher Trophic Levels

Projected future changes in physical and biogeochemical conditions of the ocean are expected to affect the distribution and abundance of marine fishes and invertebrates (Figure 6-15). In the global ocean, driven by projected changes in temperature and other physical and chemical oceanographic factors, latitudinal distributions of 1066 species of exploited marine fishes and invertebrates are projected to shift by a median of around 50 km per decade (range limits) to higher latitudes by 2050 relative to 2000 under the SRES A1B (RCP6.0) scenario (Cheung *et al.*, 2009), Some species are projected to shift towards the equator following a regional temperature gradient (Burrows *et al*., 2011; Cheung *et al.*, 2012a). The rate of range shifts is projected to be three times higher for pelagic than for demersal fishes (Cheung *et al*., 2009), with demersal fishes shifting at a rate of around 25 – 36 km per decade (Cheung *et al.*, 2012a). The expansion of hypoxic waters may, however, have a greater impact on demersal fishes than warming (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 experience 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). 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*., 2012b). However, detailed quantitative projections are sensitive to model structure and assumptions (Hare *et al*., 2012; Jones *et al*., 2013). Also, responses of specific populations may differ from average responses at species level (Hazen *et al*., 2012).

[INSERT FIGURE 6-15 HERE
Figure 6-15: Scenarios of climate change effects on the biogeography, biology and fisheries catch potential of marine fishes and invertebrates. (A) Hypothesis of changes in distribution, biology and fisheries catch potential of fish stocks under climate change. (B) Example of a projected rate of shift in distribution range along latitude and depth for 610 exploited demersal fish species from 1991-2010 to 2041 – 2060 under the SRES A2 scenario (Cheung *et al*., 2011; Cheung *et al*., 2012a). (C) Projected change in the maximum body size of 610 species of marine fishes from 2000 to 2050 under the SRES A2 (between RCP6.0 - 8.5) scenario (Cheung *et al.*, 2012a). The white area is not occupied by the sampled species. (D) Example of projections of maximum fisheries catch potential of 1000 species of exploited fishes and invertebrates from 2000 to 2050 under the SRES A1B scenario (redrawn from Cheung *et al*., 2010).]

Available projections suggest high impacts of ocean warming on coral reefs through coral bleaching, although some of the main assumptions in these approaches need to be verified (CC-CR). Coral reefs are projected to undergo long-term degradation by 2020 to 2100 relative to the 2000s under RCP 3, 4.5 and 8.5 or their equivalent. The degree of impact will depend on their adaptability to thermal stress and the interaction of multiple stressors (Hoegh-Guldberg, 1999; Sheppard, 2003; Donner *et al*., 2005; Meissner *et al*., 2012; Teneva *et al*., 2012; CC-CR). Reefs that are projected to be most threatened by bleaching by 2100 under the SRES A1B scenario, based on different indicators, include the Central and Western Equatorial Pacific, Coral Triangle and parts of Micronesia and Melanesia (Teneva *et al*., 2012). Degradation of coral reefs will impact key ecosystem services (Hoegh-Guldberg, 2011; 6.4; Box CC-CR).

Some groups of marine megafauna are projected to shift in distribution and abundance (6.2.5). Cetacean richness is projected to increase above 40° latitude in both hemispheres and both pinniped and cetacean richness to decrease at lower latitudes 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 increase in available 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). Abundance of some seabirds such as Cassin's auklet in the California Current ecosystem or Emperor penguin in Antarctica is projected to decline because of climate induced changes in oceanographic conditions, such as temperature and upwelling intensity (Wolf *et al*., 2010) or summer sea ice conditions (Jenouvrier *et al*., 2012).

6.5.3. Ecosystems and Fisheries

Projected responses of marine ecosystems at different levels of organization are expected to result in large changes in fisheries resources, with increased vulnerability particularly in tropical regions. One of the most direct impacts of climate change on marine ecosystem services is through fisheries (6.4; WGII Ch. 7). Existing projections of impacts on fisheries under climate change are based on changes in ocean net primary production, as well as recruitment, growth, mortality, abundance and distribution of fish stocks. Assuming that the potential fish catch is proportional to net primary production, the fish catch in the North Pacific Ocean subtropical biome is projected to increase by 26% while that in the temperate and equatorial biomes may decrease by 38 and 15%, respectively, 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 also projected to affect fisheries catch potential (Cheung *et al*., 2011), resulting in a decrease in the potential catch of large fishes (0 – 75.8%) in the central North Pacific 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 result in a large-scale redistribution of global catch potential, with an average 30–70 % increase in yield in high-latitude regions, but a 40 – 60% drop in the tropics by the 2050s relative to the 2000s under the SRES A1B (RCP6.0) scenario (Figure 6-15) (Cheung *et al*., 2010; Blanchard *et al*., 2012). This highlights the high vulnerability of national economies of tropical coastal countries through impacts of climate change on fisheries (Allison *et al*., 2009; 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 were 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, catches in the western Pacific are projected to decrease while those in the eastern Pacific will increase (Lehodey *et al*., 2011). Moreover, driven by changes in growth and distribution under warming and changes in O_2 content, maximum body weight of exploited demersal marine fishes is projected to decrease globally by 10-24% under the SRES A2 (RCP6.0 to 8.5) scenario (Cheung *et al*., 2012a, Figure 6-15). The decrease in maximum body size may affect natural mortality rates, trophic interactions, and reduce yield-per-recruit and, thus, potential catch. 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), although the magnitude and direction of the projected socio-economic impacts are poorly quantified.

Identifying responses to climate change is complicated by species interactions and multiple stressors. OA and hypoxia are expected to reduce maximum catch potential by 2050 relative to 2000 in both the North Atlantic and Northeast Atlantic (Ainsworth *et al*., 2011; Cheung *et al*., 2011). Fishery of molluscs is projected to be particularly vulnerable to OA (Cooley and Doney, 2009), with a substantial decline in the global production of molluscs potentially occurring between 2020 and 2060 (Cooley *et al*., 2012). However, these projections admittedly are sensitive to the assumed vulnerability of the modeled organisms to OA (6.2.5., 6.3.4). Responses of exploited marine species and their fisheries may interact with other human stressors such as overfishing, exacerbating the impacts on fisheries catches (e.g. Lindegren *et al*., 2010; Ainsworth *et al*., 2011). 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. Fulton, 2011; Griffith *et al.*, 2011; Le Borgne *et al*., 2011). The complex and non-linear interactions and responses of both biophysical and socio-economic systems to climate change and ocean acidification 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 under-estimated in existing model projections (Williams and Jackson, 2007; Lindenmayer *et al*., 2010).

6.5.4. Conclusions

Current understanding is rudimentary of how different modes of forcing like warming, ocean acidification, de-oxygenation and other human impacts, either individually or together, will interact and affect levels of biological organization, from physiology to biomes (i.e., *limited evidence, medium agreement*). Models that integrate climate and ocean changes with biological responses and interactions, and with human activities, at present, have led to some agreement on species and food web responses to climate change. However, these models do not include biological processes such as trophic interactions and evolutionary adaptation that affect responses of biota to physical and chemical changes. Further insights into understanding the relative roles of bottom up and top down effects and their interplay require consideration of scale-dependency, regional and interspecific differences, and improved acquisition and management of biological data. Such insights would improve model projections.

Most projections on ocean biogeochemistry represent open-ocean systems rather well, but coastal and shelf seas regions only poorly. There is a large variation in estimates of the present-day magnitudes and distribution of primary production in models and observation-based estimates (6.1.3., 6.3.1). Accordingly, there is *low confidence* that primary production will decrease by 2100 under low (SRES B1 or RCP4.5) and high emission scenarios (A2 or RCP6.0 - 8.5), also, there is *limited evidence* and *low agreement* and *confidence* on projecting an increase in global NPP or an increase at high latitudes and a decrease in the tropics, although model results are similar.

Confidence is *high* that the distribution of fishes, invertebrates, cetaceans and some marine megafauna will shift further under most emission scenarios, with the projected rates and directions of range shifts being consistent with observations in the last century. More specifically, *confidence* is *high* that the average shift in distribution is generally poleward at large spatial scales and *confidence* is *medium* in projected shifts of fishes and invertebrates to deeper water, except in areas where hypoxia prohibits deeper movement. Species richness and abundance of warmer-water species will increase at high latitudes (*high confidence*) and decrease in the tropics (*low confidence*). Projections of shifts in abundance and distribution of individual populations and species are more variable and sensitive to model structure and parameters.

Despite some agreement between model results, there is *medium confidence* in the projected direction of fisheries production and *low confidence* in the projected magnitude of changes. Maximum fisheries catch potential is projected to increase at high latitudes and decrease in the tropics by 2050 under SRES B1 (RCP4.5) and A1B (RCP6.0) scenarios (*medium confidence*). *Confidence* in quantifying such projections is *low* due to *low confidence* in projected primary production rates, biological responses such as species interactions, and in projected effects of multiple climate drivers and human activities.

Overall, the projected responses of marine organisms and ecosystems to climate change include changes in primary productivity (*low confidence*), species' life history (*medium confidence*), distribution, abundance and diversity across marine foodwebs (*high confidence*) in a time frame of 20 to 80 years from 2010. These changes increase the vulnerability of human societies, particularly those that are dependent on coastal resources (*limited evidence, medium agreement*) by affecting income, employment and food security through their effects on fisheries, tourism, and regulatory services such as coastal protection (6.4, Box CC-CR, *medium confidence*).

6.6. Chapter Conclusions and Key Uncertainties

This section provides an overview of chapter results on confidence in the detection and projection of climate change effects on ocean systems, as well as in the attribution of effects to the respective forcings (Figure 6-16). Case studies, processes, and concepts relevant in assessing the effects of climate change are represented by their acronyms in text and figure. While the anthropogenic signal is clearly seen in the oceans (6.1.1) clear attribution to anthropogenic influences on climate is not always possible in individual case studies, due to the inherent variability of system characteristics (6.1.3).

[INSERT FIGURE 6-16 HERE
Figure 6-16: Overview of the levels of confidence in detection (left), as well as in projection (right) of climate change effects on ocean systems, in relation to the levels of confidence in attributing these effects to the respective climate forcings. While confidence is often high that there are effects, the direct attribution to one driver in field experiments is difficult as several processes are highly correlated with each other such as warming and changes in stratification and hence nutrient depletion. Some climate change impacts have been condensed into rather broad categories in order not to overpopulate the figures (e.g. **BG**, **B**io-**G**eochemical processes). Note that the term attribution is not only used in the context of detections but also for projections. Projections include both qualitative and quantitative extrapolations and simulations from fundamental principles and models. Experiments (field, laboratory and modeling) simulating future conditions may enhance the respective confidence levels above those for detection which refers to present day observations in the field. The empirical observations resulting from those experiments are directly attributable to the respective drivers. Confidence rises further if these experiments identify the affected mechanisms and their response to future conditions. See text for further discussion of the depicted depicted examples and categories. Confidence assignments focus on the nature and size of effects, not on the capacity of models to reliably quantify their magnitude.]

6.6.1. Drivers of Change and their Effects

Present day observations and those from the **G**eological **R**ecord (**GR**, Figure 6-16) show similar signs in respect to environmental changes, e.g. warm times at high CO_2 levels, and similar ecological consequences in the ocean (*robust evidence, medium agreement* and *confidence*). However, the ongoing rate of anthropogenic CO_2 release and hence ocean acidification is unprecedented in the last 300 Ma (*robust evidence, high agreement and confidence,* 6.1.2).

Long-term observations show **T**emperature **E**ffects (**TE**) through warming-induced species displacements and largely poleward shifts in biogeographical distribution (20 to 200 km per decade) of zooplankton and fishes, paralleled by shifts in seasonal activity, species abundance, migration, and body size (6.3.2., *very high confidence*), and leading to shifts in **C**ommunity **C**omposition (**CC,** *high confidence*). Thermal effects reflect the differential specialization of all life forms on limited ambient temperature ranges. Long-term variability in oceanographic conditions paralleled by observed changes in ecosystem structure and fish stocks also provide *robust evidence* (*high agreement*) for a key role of temperature and changing current regimes in causing these effects. **TE**s are *likely* to continue in the 21st century, causing further changes in **CC** (*high confidence*) and, due to species shifts, decreasing **F**isheries **C**atch **P**otentials (**FCP**) at low to mid and increasing **FCP**s at high latitudes (*high confidence*, 5a in figure). These trends will possibly be strengthened by decreased primary production at low and increased PP at high latitudes but changes in **FCP** due to changes in NPP have *low confidence* (6.5.2., 6.5.3., 6.6.2., 5b in figure). **P**olar **O**rganisms (**PO**) which live at very high latitudes and are unable to migrate, acclimate or adapt to warming (*high confidence*), are becoming marginalized contributing to the projected high species turnover in polar areas (*high confidence*, 6.2.5., 6.5.2).

Hypoxic **Z**ones (**HypZ**), in marine sedimentary habitats and pelagic OMZs presently expand due to restricted water movement (enhanced stratification), warming, elevated microbial respiration, high loading with organic matter and nutrients (*high confidence*). They will continue to expand in the future, due to climate induced warming trends (*high confidence*, 6.1.1., 6.2.3). Vertical expansion of OMZs has led to the compression of habitat for organisms, e.g. pelagic billfishes, with a high O_2 demand (*high confidence*). Overall, there is *medium confidence* that local and regional **H**ypoxia **E**ffects (**HE**) during OMZ expansion are causing habitat loss to groundfishes and pelagic predators and affecting the distribution of key zooplankton and nekton species. Progressive hypoxia is causing shifts in **CC** to hypoxia tolerant species, excluding the calcifiers due to elevated $p\mathrm{CO}_2$ (*high confidence*), benefiting the microbes, and leading to reduced biodiversity and the loss of higher life forms (*robust evidence, high agreement* and *confidence*) (6.2.5., 6.3.3). **HypZ** expansion will cause **HE**s to be exacerbated in the future (*very high confidence*).

Few field observations have detected **O**cean **A**cidification **E**ffects (**OAE**), e.g. through decreases in shell weight of foraminifera (*medium confidence*). Attribution of effects to CO_2 is supported by experimental studies simulating future conditions (*medium confidence*) and showing species-specific sensitivities across phyla (*high confidence*). An acidified surface ocean (due to shifted upwelling and anthropogenic OA) is causing clear negative effects on the oyster aquaculture along the North American west coast (*high confidence* in detection, *low confidence* in attribution to anthropogenic causes), which provides a *high confidence* glimpse into the future of anthropogenic OA and associated **O**yster **E**ffects (**OE**). Projected effects are most harmful in some warm water corals, echinoderms, bivalves, gastropods or crustose algae, and less so in some crustaceans and tropical fishes. Projections from experimental studies and observations at natural analogues indicate shifts in **C**ommunity **C**omposition (**CC**) to more active animals and from calcifiers to non-calcifiers in all organism groups (*high confidence* in both projection and attribution, 6.3.4., 6.2.5).

Climate change involves combinations and synergisms of temperature effects with those of other climate related drivers (ocean acidification, hypoxia, freshening, 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 or other forms of harvesting accelerate and amplify climate induced changes (*high confidence*, 6.2.2., 6.3.5). **S**ynergistic **E**ffects (**SE**) will be exacerbated in the future (*medium confidence*), but have not yet been clearly identified (detected) in the field (*low confidence*). Attribution to such synergisms is supported by experimental evidence, especially in animals or plants (*medium confidence*).

Available evidence from empirical and modeling studies provides *high confidence* that climate change impacts marine ecosystems, leading to present changes in provisioning, regulating and supportive **E**cosystem **S**ervices (**ES,** *medium confidence***)**, while there is *limited evidence* and *medium agreement* that climate change affects cultural services. However, attributing their shifts to climate change remains a challenge (*low confidence*), partly because of the intrinsic difficulties of assessing these services, lack of long time-series data and confounding human impacts. However, in light of *high confidence* in projected climate change impacts and available cause and effect understanding, some services will be affected by future climate change (*high confidence* in projection, *medium confidence* in attribution).

6.6.2. Microbial Responses and Biogeochemical Consequences

Various microbial processes (6.2.3., microbes are archaea, bacteria and protists including phytoplankton) respond to changes in irradiance, nutrient supply, temperature, CO_2 or hypoxia (*high confidence*). Experimental evidence from laboratory and mesocosm studies has identified processes potentially responsive to climate change including impacts of ocean acidification on the N cycle (6.2.3), carbon sequestration and export production, calcification, and respiration with the result of water O_2 depletion and acidification (see **HypZ**). However, the knowledge base is insufficient to build projections on a whole organism understanding of climate impacts on species, strains or communities in the field. A functional **M**icrobial **C**oncept (**MC**) supporting the attribution to climate of detected **M**icrobial **E**ffects (**ME**), from gene to ecosystem to large scale changes in biogeochemistry and also for projections into the future is not available at the current level of understanding (6.3.1., *low confidence*). Overall, *confidence* is *low* in that shifts in **B**io-**G**eochemical processes (**BG**) such as O_2 production, carbon sequestration and export production, nitrogen fixation, climate-feedback by DMS production, nutrient recycling, or calcification are presently happening at detectable scales or will do so in the future, paired with *low confidence* in attribution to climate change (6.3.3., 6.3.4., 6.3.5).

The trends in net primary production (NPP) recently reported for much of the low latitude ocean using satellite observations differ considerably from those few long-term direct estimates of offshore NPP (6.1.3., 6.3.1). The latter indicate a small but significant increase in **g**lobal **NPP** (**gNPP**) over the last two decades (*medium confidence* in detection, *low confidence* in attribution). Higher rates of **NPP** at **h**igh latitudes (**hNPP**, attributable to climate change with *high confidence*, 6.3.1) are indicated by satellite images (*medium confidence*) and may be due to a reduction and thinning of sea-ice. Trends in NPP may be strengthened with further warming. Modeling projects that **gNPP** may decrease by 2100 under SRES A1 and A2 scenarios, however, such global trends cannot presently be quantified with sufficient accuracy and projections are fraught with *low confidence* (6.5.1); for **hNPP**, *confidence* in projections of an increase is equally *low*.

6.6.3. Responses of Animals and Plants and their Implications

Temperature Effects (**TE**) include strong **MA**croorganism **E**ffects (**MAE)**, i.e. effects on animals and plants. Causes and effects are understood for fishes and most invertebrates via their **O**xygen and **C**apacity **L**imited **T**hermal **T**olerance (**OCLTT,** 6.2.2., *robust evidence, medium agreement* and *high confidence*). Such knowledge also supports projections into the future (6.5., *medium confidence*), limited by the unknown potential of organisms to adapt. Alterations in **AB**undance (**AB**) of e.g. corals, fishes or intertidal species result when organisms are exposed to increasing extreme temperatures (*high confidence* in detection and attribution). Such trends will be exacerbated during future warming (*high confidence*, 6.5.2). Multiple drivers (warming, ocean acidification, hypoxia) have **S**ynergistic **E**ffects (**SE**) which can also be understood by analyzing the oxygen and capacity limited thermal tolerance of animals (6.2.6., 6.3.5). The following examples reflect the present predominance of **TE**s. Warming causes shifts in the geographical distribution of North **A**tlantic **C**od (**AC**, 6.3.2., *high confidence* in detection, *medium confidence* in attribution), falling abundance of **E**elpout in the **W**adden **S**ea (**EWS**, 6.2.2., 6.3.2., 6.3.7., *medium confidence* in detection, *high confidence* in attribution), collapsing spawning migrations of **P**acific **S**almon (**PS**, 6.3.2., *high confidence* in detection, *high confidence* in attribution) in the Fraser River, Canada, growth patterns in relation to distribution around New Zealand of **B**anded **M**orwong (**BM**, *high confidence* in detection, *medium confidence* in attribution), and shifts from **S**ardines to **A**nchovies in the Sea of **J**apan (**SAJ**, 6.2.5., 6.3.2., *medium confidence* in detection, *medium confidence* in attribution). Loss of deep habitat and biomass of **M**id-**W**ater **F**ishes (**MWF**, 6.3.3., *medium confidence* in detection) off California is attributed to hypoxia (*high confidence*). At temperate and high latitudes communities display increasing fish **S**pecies **R**ichness (**SR**) resulting from latitudinal shifts of species and loss of sea ice (6.3.7., 6.5.2., *high confidence* in detection, *medium confidence* in attribution). These observed changes have been attributed to warming, although the relative contributions of regional climate variation and long-term global trends have not been quantified. Latitudinal shifts due to **TE**s are projected to continue in the 21st century under all IPCC emission scenarios (*very high confidence* in detection and in attribution, 6.2.5., 6.3.2., 6.3.5., 6.3.7., 6.4.1., 6.5.2).

Regime shifts and regional changes in **P**lankton **P**henology (**PP**, *medium confidence*) cause changes in food composition and availability to animals, in concert with shifts in their own distribution such as of fishes like **A**tlantic **C**od (**AC**, *medium confidence* in attribution to climate change, 6.3.2). As a consequence, changes in **F**ish **C**atch **P**otential (**FCP**, *high confidence*) due to species shifts and changing species composition (5a in figure) are partly attributable to climate change (*high confidence*) and to maintained fishing pressure (6.5.3).

Among **M**arine **A**ir **B**reathers (**MAB**, i.e. mammals, seabirds and sea turtles), detected effects include changing abundance and phenology, species distribution shifts, and turtle sex ratios (*high confidence*), all of which are attributed to climate change (*high confidence*). These effects are rarely directly linked to climate drivers (e.g. temperature driven turtle sex ratio) but mostly to shifting habitat structure (e.g. loss of sea ice), availability of prey organisms, or foraging efficiency, in both mammals (polar bear, walrusses) and birds (penguins, albatrosses), resulting in differential sensitivities of species. Such trends will be exacerbated by future warming (*high confidence*, 6.2.5).

Increased bleaching and decreased calcification displayed by several **R**eef-building **W**arm water **C**orals (**RWC**, *very high confidence*) over the last three decades are, with *very high confidence*, attributed to the ongoing warming trend and the associated rise in extreme temperature events and amplitudes (6.2.5, Box CC-CR). With *very high confidence*, such trends will be exacerbated during future warming, with some amelioration by latitudinal shifts and evolutionary adaptation (6.3.2., *medium evidence*, *low confidence*). The patterns seen may involve an increasing influence of ocean acidification, confirmed by similar phenomena during mass extinctions in earth history.

6.6.4. Key Uncertainties

Key uncertainties on how the global ocean will respond to climate change, result from the limited number and duration of observational time series in the oceans and thus from insufficient sampling and limited capacity and infrastructure in countries around the world to study ocean response to climate change. Research foci differ between research areas (studies of pelagic versus benthic ecosystems, biogeochemical processes, sensitivities of species, families, phyla or organism kingdoms and domains, and studies of special mechanisms of functioning or adaptation). Processes investigated by various biological disciplines also differ largely between studied organisms, plants, animals, phytoplankton, and bacteria. Each of the listed foci is important but they are usually not well integrated and reductionist with respect to the level of organization in focus, i.e. ecosystem, whole organism, tissue, cell or molecular. Furthermore, scaling from physiological studies on individual species to shifts in species interactions or foodwebs has not been successful to date. A unifying approach addressing principles across organism domains is lacking such that an integrated framework of climate sensitivity at ecosystem level presently does not exist. For all climate drivers, especially ocean warming, acidification and hypoxia, studies integrating mechanistic knowledge and evolution over generations, as well as in various climate zones and biomes are needed. Laboratory and modeling experiments need to be inspired by long-term field observations and observations at natural or paleo-analogues. Modeling activities need to better integrate observations and mechanism-based understanding, last not least in order to better project the future interactions between human and natural systems in a changing climate. As a corollary, the coordination of research concepts and approaches is deficient and a coherent picture of climate change effects is thus not available, leaving a strong coordinating role for international (both inter- and non-governmental) organizations.

Frequently Asked Questions

FAQ 6.1: Why is ocean life fundamental to the planet's sensitivity to climate change?

Oceans cover 70 % of the planet and provide important services to humankind. The life they contain creates about half of the oxygen (O_2) we breathe and also consume by the burning of fossil fuels. Oceans currently absorb ~25 % of the carbon dioxide (CO_2) emitted from the burning of fossil fuels, convert it into organic matter and export parts of it to the deep ocean. Oceans take up 93% of the heat accumulating during global warming and thereby play a key role in climate regulation. Fisheries and aquaculture provide on average 20 % of the animal protein to more than 1.5 billion people. The oceans provide habitats for charismatic species and sustain ecosystems valued in tourism and for recreation. The rich biodiversity of the oceans offers resources for innovative approaches like medical drug design or biomechanics. Ocean ecosystems contribute to offsetting the effects of natural hazards - for example, coral reefs are known to protect shoreline and efficiently buffer tsunamis and storm surges.

Climate change in the oceans involves rising temperatures, acidification elicited by accumulating CO_2, changed nutrient supply and the expansion of low O_2 areas. These drivers pose risks for ocean life and may impair the ability of marine biota to perform their vitally important functions. Such effects occur on a background of natural variability of these drivers. Additionally, oceans experience other anthropogenic pressures such as overfishing, pollution, nutrient runoff via rivers and the associated eutrophication. In light of the key role of the oceans in global climate change it is crucial but difficult to clearly identify the combined effects of these multiple drivers. Effects of the various drivers may not only be additive but often synergistic, i.e. the effect of each driver is amplified by the concomitant change of the other drivers, causing important but difficult to predict non-linear effects on a wide range of ecosystem processes.

Some insights into future scenarios can be obtained from analysing past events of climate change and from extrapolating the existing long time series (i.e. decades) of data into the future. State-of-the-art ecosystem models built on empirical observations enable us to obtain estimates for responses of marine biota to climate change. Examples are the projected large scale shift in the distribution of commercially relevant fishes to high latitudes and the loss of their catch potential at their original sites. However, formulating well founded or detailed projections is a challenging task because of the large number of interactive feedbacks that must be taken into account. Furthermore, the current rate of environmental change is unprecedented compared to climate changes in the past and, therefore, demands adaptation in only a small number of generations compared to long-term changes in nearly all of the geological record. Changes may thus be too rapid for adaptation to occur. The resilience of marine ecosystems to climate-change mediated impacts is likely to be reduced by the individual and interactive effects of multiple drivers.

FAQ 6.2: What is special about climate change effects on the oceans and can we predict the consequences?

Although there are many similarities in how climate change will alter the land and ocean ecosystems, for example through warming trends, there are also fundamental differences, primarily due to the aquatic environment and associated physicochemical properties of the ocean, including ocean circulation and sea water chemistry. The anthropogenic CO_2 accumulating in the atmosphere enters the ocean and is acidifying the water (making it less alkaline). CO_2 content will thus increase in both the atmosphere and the warming ocean, and be taken up by the organisms. Animals living and breathing in water (for example, fishes, squids, mussels) have naturally 5 to 20 times lower CO_2 levels in their blood and therefore experience stronger changes and are more sensitive than animals on land including aquatic turtles, mammals, seabirds which also live in water but breathe air at the ocean surface.

The warming of the ocean has significant indirect effects on oceanic properties - for example by forming stable ocean layers separated by density differences, which alter the degree of communication between cold nutrient-rich waters at depth and warm nutrient-poor waters near surface. Increasing respiration by organisms in the mid-water layers of stratified oceans will lead to expanding oxygen-poor waters, so-called oxygen minimum zones (OMZs). Respiration also produces CO_2, enriches it further in the water and causes more acidification in expanding OMZs. Low oxygen waters exclude large, more active fishes from living permanently in these areas. Specialized animals with a low O_2 demand will remain such that the communities living in hypoxic areas are very different from those found in well oxygenated waters. Thus, ocean biota (except for sea birds, turtles, mammals) will have to adjust to a fundamentally different environment and one that may be even more altered than that of the land.

At the moment, the uncertainties in modeling prevent any quantification of how much of the change is caused by climate change and how much of it is caused by other human activities. For improved and more reliable projections of future changes, mechanisms and unifying principles shaping the impacts of climate change on various organism groups or on biogeochemical processes must be better understood and included into mechanism based modeling approaches.

FAQ 6.3: How will marine ecosystems look like under 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 species distributions, species richness and community structure have been attributed to ocean warming. Projected changes in physical and biogeochemical drivers, such as warming, acidification, hypoxia, nutrient supply and sea ice cover, will continue to affect marine biota. Under most climate change scenarios, a shift or expansion of habitat range limits towards higher latitudes by tens of kilometres per decade can be foreseen for many species of plankton, fishes and invertebrates, resulting in shifts of species richness and altered community composition. Organisms that are more tolerant to direct effects of climate change may be affected indirectly through climate change restructuring existing food webs. In polar areas cold-adapted species among invertebrates and fishes may be lost by local extinctions and be marginalized due to warming. Similarly, species in semi-enclosed seas such as the Wadden Sea and the Mediterranean Sea face higher risk of local extinction because distributional shifts in response to warming and other environmental changes are limited by the land-boundary.

Overall, climate change will lead to large-scale shifts in the patterns of marine productivity, biodiversity, community composition and ecosystem structure. Extinction of species that are sensitive to climate change, including ocean acidification, 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 the associated ecosystems, such as coral reefs. Alteration of the seasonal activity (phenology) of marine organisms, their biology and distribution will disturb food web interactions such as the grazing of copepods (small crustaceans) on planktonic algae. Ocean primary production is also expected to change but the global patterns are more difficult to project. Existing model projections suggest an increase in primary production at high latitudes such as in the Southern Ocean (higher mean light levels for photosynthesis at lower ice cover) and decreases in the tropics and at mid-latitudes (reduced nutrient supply). Human stressors such as overfishing, eutrophication and pollution are expected to exacerbate the impacts of climate change. Increasing temperature, nutrient fluctuations, and eutrophication may favor harmful algal blooms in coastal including upwelling areas. Climate change may also cause shifts in the distribution and abundance of pathogens such as for cholera.

FAQ 6.4: Why do marine organisms rely on a sufficiently alkaline ocean?

Many marine species, ranging from microscopic plankton to shellfish and coral reef builders are generically referred to as calcifiers, as they depend on using solid calcium carbonate ($CaCO_3$) to construct their skeletons or shells. Solid calcium carbonate comes in different forms called calcite and aragonite; aragonite is more soluble in water than calcite. Sea water contains ample calcium in solution but this needs to be transported to the sites where calcification occurs. In contrast, the carbonate is not transported from the water to calcification sites but newly formed where it is needed. To form carbonate ions in high concentrations and to thereby calcify more easily, the calcification site is made alkaline, meaning that pH is increased by the organism to values higher than in other parts of the body or in ambient sea water. This process demands energy which the organism has to be able to supply. If high CO_2 levels from outside penetrate the organisms this process is becoming even more challenging and costly. If a lot of energy is needed for calcification, energy for other biological processes like growth might become limiting, making these organisms less competitive, reducing their weight or reproduction, all of which is needed for sustaining ecosystem diversity, and services.

CO_2 accumulating in the seawater can also affect the stability of shells and skeletons (Box CC-OA). At low CO_2 levels, the sea water has high carbonate levels and keeps $CaCO_3$ in solid form. As the oceans acidify, by the anthropogenic accumulation of CO_2, the concentration of carbonate falls making $CaCO_3$ more soluble and this water may start dissolving carbonate shells. Some of these shells are shielded from direct contact with sea water by a special coating (as is the case in mussels). Combined with the increased energy needed for calcification, organisms might struggle to repair their shells which are dissolving in corrosive seawater. Presently, corrosive waters upwelling closer to the Northwest coast of the United States impact the oyster aquacultures and illustrate the principles of such effects.

Ocean acidification not only affects species producing calcified exoskeletons. Ocean acidification affects organisms either directly or indirectly. For most organisms investigated, sensitivity is highest at extreme temperatures and thus, at the edges of their thermal ranges highlighting the potential for combined effects with temperature. Indirect effects might be changes in their prey organisms due to their specific sensitivities to climate change. Ocean acidification therefore has the potential to disturb food webs and fisheries.

Cross-Chapter Boxes

Box CC-CR. Coral Reefs

[Jean-Pierre Gattuso (France), Ove Hoegh-Guldberg (Australia), Hans-Otto Pörtner (Germany)]

Coral reefs are shallow-water structures made of calcium carbonate mostly secreted by reef-building (scleractinian) corals and encrusting macroalgae. They occupy less than 0.1% of the ocean floor yet play multiple important roles throughout the tropics. About 275 million people live within 30 km of a coral reef (Burke et al., 2011) and are likely to derive some benefits from the ecosystem services that coral reefs provide (Hoegh-Guldberg, 2011) including those from provisioning (food, construction material, medicine), regulating (shoreline protection, water quality), supporting services (oxygen supply) and cultural (religion, tourism). This is especially true in small islands (29.3.3.1).

Most human-induced disturbances to coral reefs were local (e.g., coastal development, pollution, nutrient enrichment and overfishing) until the early 1980s when global and climate-related disturbances (ocean warming and acidification) began to occur. Temperature and seawater acidity are two of the most important environmental variables determining the distribution of coral reefs (Kleypas et al., 2001). As corals are centrally important as ecosystem engineers (Wild et al., 2011), the impacts on corals have led to widespread degradation of coral reefs.

A wide range of climatic and non-climatic stressors affect corals and coral reefs and negative impacts are already observed (5.4.2.4, 30.5.3, 30.5.6). Bleaching involves the breakdown and loss of endosymbiotic algae (genus *Symbiodinium*), which live in the coral tissues and play a key role in supplying the coral host with energy and nutrients (Baker et al., 2008) (see 6.2.5 for physiological details and 30.5 for a regional analysis). Mass coral bleaching and mortality, triggered by positive temperature anomalies, is the most widespread and conspicuous impact (Fig. 5X; see Sections, 5.4.2.4, 6.2.5, 25.6.2, 30.5 and 30.8.2). For example, the level of thermal stress at most of the 47 reef sites where bleaching occurred during 1997-98 was unmatched in the period 1903 to 1999 (Lough, 2000). Elevated temperature along with ocean acidification reduces the calcification rate of corals (*high confidence*; 5.4.2.4), and may tip the calcium carbonate balance of reef frameworks towards dissolution (*medium evidence and agreement*; 5.4.2.4). These changes will erode fish habitats with cascading effects reaching fish community structure and associated fisheries (*robust evidence, high agreement*, 30.5).

Around 50% of all coral reefs have experienced medium-high to very high impact of human activities (30-50% to 50-70% degraded; Halpern et al., 2008), which has been a significant stressor for over 50 years in many cases. As a result, the abundance of reef building corals is in rapid decline (1 to 2% per year, 1997-2003) in many Pacific and SE Asian regions (Bruno and Selig, 2007). Similarly, the abundance of reef-building corals has decreased by over 80% on many Caribbean reefs (1977 to 2001; Gardner et al., 2003), with a dramatic phase shift from corals to seaweeds occurring on Jamaican reefs (Hughes, 1994). Tropical cyclones, coral predators and coral bleaching have led to a decline in coral cover on the Great Barrier Reef (about 51% between 1985 and 2012; De'ath et al., 2012).

One third of all coral species exhibit a high risk of extinction, based on recent patterns of decline and other factors such as reproductive strategy (Carpenter et al., 2008). Although less well documented, non-coral benthic invertebrates are also at risk (Przeslawski et al., 2008). Fish biodiversity is threatened by the permanent degradation coral reefs, including in a marine reserve (Jones et al., 2004). While many factors, such as overfishing and local pollution, are involved in the decline of coral reefs, climate change through its pervasive influence on sea temperature, ocean acidity, and storm strength plays a very significant role.

There is *robust evidence* and *high agreement* that coral reefs are one of the most vulnerable marine ecosystems (Chapters 5, 6, 25, and 30). Globally, more than half of the world's reefs are under medium or high risk of degradation (Burke et al., 2011) even in the absence of climatic factors. Future impacts of climate stressors (ocean warming, acidification and sea level rise) will exacerbate the impacts of non-climatic stressors (*high agreement, robust evidence*). Even under optimistic assumptions regarding corals being able to rapidly adapt to thermal stress, one-third (9–60%, 68% uncertainty range) of the world's coral reefs are projected to be subject to long-term degradation under the RCP3-PD scenario (Frieler et al., 2013). Under the RCP4.5 scenario, this fraction increases to two-thirds (30–88%, 68% uncertainty range). If present day corals have residual capacity to acclimatize and/or adapt, half of the coral reefs may avoid high frequency bleaching through 2100 (*limited evidence, limited agreement*; Logan et al., sbm). Evidence of corals adapting rapidly, however, to climate change is missing or equivocal (Hoegh-Guldberg, 2012).

Damage to coral reefs has implications for several key regional services:

- *Resources*: Coral reefs produce 10-12% of the fish caught in tropical countries, and 20-25% of the fish caught by developing nations (Garcia & Moreno, 2003). Over half (55%) of the 49 island countries considered by Newton et al. (2012) are already exploiting their coral reef fisheries in an unsustainable way (13.X.X).
- *Tourism*: More than 100 countries benefit from the recreational value provided by their coral reefs (Burke et al., 2011). For example, the Great Barrier Reef Marine Park attracts about 1.9 million visits each year and generates A$ 5.4 billion to the Australian economy and 54,000 jobs (90% in the tourism sector; Biggs, 2011).
- *Coastal* protection: Coral reefs contribute to protecting the shoreline from the destructive action of storm surges and cyclones (Sheppard et al., 2005), sheltering the only habitable land for several island nations, habitats suitable for the establishment and maintenance of mangroves and wetlands, as well as areas for recreational activities. This role is threatened by future sea level rise, the decrease in coral cover, reduced rates of calcification and higher rates of dissolution and bioerosion due to ocean warming and acidification (5.4.2.4, 6.4, 30.5).

Coral reefs make a modest contribution to the global domestic product but their economic importance can be high at the country and regional scales (Pratchett et al., 2008). For example, tourism and fisheries represent on average 5% of the GDP of South Pacific islands (Laurans et al., 2013). At the local scale, these two services provide at least 25% of the annual income of villages in Vanuatu and Fiji (Pascal, 2011; Laurans et al., 2013).

Marine protected areas (MPAs) and fisheries management have the potential to increase ecosystem resilience and increase the recovery of coral reefs after climate change impacts such as mass coral bleaching (McLeod et al., 2009). Although they are key conservation and management tools, they are less effective in reducing coral loss from thermal stress (Selig et al., 2012) suggesting that they need to be complemented with additional and alternative strategies (Rau et al., 2012). Controlling the input of nutrients and sediment from land is an important complementary management strategy because nutrient enrichment can increase the susceptibility of corals to bleaching (Wiedenmann et al., 2012). There is also high confidence that, in the long term, limiting the amount of warming and acidity is central to ensuring the viability of coral reef systems and dependent communities (5.X.X and 30.5).

[INSERT FIGURE CR-1 HERE
Figure CR-1: A and B: the same coral community before and after a bleaching event in February 2002 at 5 m depth, Halfway Island, Great Barrier Reef. Coral cover at the time of bleaching was 95% bleached almost all of it severely bleached, resulting in mortality of 20.9% (Elvidge et al., 2004). Mortality was comparatively low due in part because these communities were able shuffle symbiont types to more thermo-tolerant types (Berkelmans and van Oppen, 2006; Jones et al., 2008). C and D: three CO2 seeps in Milne Bay Province, Papua New Guinea show that prolonged exposure to high CO2 is related to fundamental changes in coral reef structures (Fabricius et al., 2011). Coral communities at three high CO2 (Fig. XB; median pHT 7.7, 7.7 and 8.0), compared with three control sites (Fig. XA; median pHT 8.02), are characterized by significantly reduced coral diversity (-39%), severely reduced structural complexity (-67%), low densities of young corals (-66%) and few crustose coralline algae (-85%). Reef development ceases at pHT values below 7.7. Photo credit: R. Berkelmans (A and B) and K. Fabricius (C and D).]

CC-CR References

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Box CC-OA. Ocean Acidification

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Introduction

Anthropogenic ocean acidification and climate change share the same primary cause at the global level, the increase of atmospheric carbon dioxide (WGI, 2.2.1). Eutrophication and upwelling contribute to local ocean acidification (5.3.3.6, 30.5.4). Past and futures changes in chemistry are well known in the surface open ocean (WGI, 3.8.2 and 6.4.4) but are more difficult to project in the more complex coastal systems (5.3.3.6 and 30.5.2).

Chemistry and Projections

The fundamental chemistry of ocean acidification has long been understood: the uptake of CO_2 into mildly alkaline ocean results in an increase in dissolved CO_2 and reductions in pH, dissolved carbonate ion, and the capacity of seawater to buffer changes in its chemistry (*very high confidence*). The changing chemistry of surface seawater can be projected at the global scale with high accuracy from projections of atmospheric CO_2 levels. Time series observations of changing upper ocean CO_2 chemistry support this linkage (WGI Table 3.2 and Figure 3.17; WGII Figure 30.5). Projections of regional changes, especially in coastal waters (5.3.3.6), and at depth are more difficult; observations and models show with high certainty that fossil fuel CO_2 has penetrated at depths of 1 km and more. Importantly, the natural buffering of increased CO_2 is less in deep than in surface water and thus a greater chemical impact is projected. Additional significant CO_2 increases and pH decreases at mid-depths are expected to result from increases in microbial respiration induced by warming. Projected changes in open ocean, surface water chemistry for year 2100 based on representative concentration pathways (WGII, Figure 6.28) compared to preindustrial values range from a pH change of -0.14 unit with RCP 2.6 (421 ppm CO_2, +1 ºC, 22% reduction of carbonate ion concentration) to a pH change of -0.43 unit with RCP 8.5 (936 ppm CO_2, +3.7 ºC, 56% reduction of carbonate ion concentration).

Biological, Ecological, and Biogeochemical Impacts

The effects of ocean acidification on marine organisms and ecosystems have only recently been investigated. A wide range of sensitivities to projected rates of ocean acidification exists within and across organism groups and phyla with a trend for higher sensitivity in early life stages (*high confidence*; Kroeker et al., in press; 6.2.3-5, 6.3.4). A pattern of impacts, some positive, others negative, emerges for some processes and organisms (*high confidence*; Fig. X.C) but key uncertainties remain from organismal to ecosystem levels (Chap. 5, 6, 30). Responses to ocean acidification are exacerbated at high temperature extremes (*medium confidence*) and can be influenced by other drivers, such as oxygen concentration, nutrients, and light availability (*medium confidence*).

Experimental evidence shows that lower pH decreases the rate of calcification of most, but not all, sea-floor calcifiers such as reef-building corals (Box CC-CR, coralline algae (Raven, in press), bivalves and snails (Gazeau et al., in press) reducing their competitiveness compared to, e.g. seaweeds (Chap. 5, 6, 30). A reduced performance of these ecosystem builders would affect the other components of the ecosystem dependent on the habitats they create.

Growth and primary production are stimulated in seagrass and some phytoplankton (*high confidence*) and harmful algal blooms could become more frequent (*limited evidence, medium agreement*). Ocean acidification may significantly stimulate nitrogen fixation in the oceans (*limited evidence, low agreement*; 6.2.3, 6.3.4). There are few known direct effects on early stages of fish and adult fish remain relatively undisturbed by elevated CO_2. Serious behavioral disturbances were reported, mostly on larval and juvenile coral reef fishes (6.2.4).

Projections of ocean acidification effects at the ecosystem level are limited by the diversity of species-level responses. Natural analogues at CO_2 vents indicate decreased species diversity, biomass and trophic complexity of communities living on the sea-floor. Shifts in community structure have been documented in rocky shore environments (e.g., Wootton et al., 2008), in relation with rapidly declining pH (Wootton and Pfister, 2012). Differential sensitivities and associated shifts in performance and distribution will change predator-prey relationships and competitive interactions (6.2-3), which could impact food webs and higher trophic levels (*limited evidence*, *high agreement*).

There is *limited evidence* and *medium agreement* that some phytoplankton and mollusks can adapt to ocean acidification, indicating that the long-term responses of these organisms to ocean acidification could be less than responses obtained in short-term experiments. However, mass extinctions during much slower rates of ocean acidification in Earth history (6.1.2) suggest that evolutionary rates are not fast enough for sensitive animals and plants to adapt to the projected rate of change (*high confidence*).

The effect of ocean acidification on global biogeochemical cycles is difficult to predict due to the species-specific responses to ocean acidification, lack of understanding of the effects on trophic interactions, and largely unexplored combined responses to ocean acidification and other climatic and non-climatic drivers, such as temperature, concentrations of oxygen and nutrients, and light availability.

Risks

Climate risk is defined as the probability that climate change will cause specific physical hazards and that those hazards will cause impacts (19.5.2). The risks of ocean acidification to marine organisms, ecosystems, and ultimately to human societies, includes both the probability that ocean acidification will affect key processes, and the magnitude of the resulting impacts. The changes in key processes mentioned above present significant ramifications on ecosystems and ecosystem services (Fig. 19.3). For example, ocean acidification will cause a decrease of calcification of corals, which will cause not only a reduction in the coral's ability to grow its skeleton, but also in its contribution to reef building (*high confidence*; 5.4.2.4). These changes will have consequences for the entire coral reef community and on the ecosystem services that coral reefs provide such as fisheries habitat (*medium confidence*; 19.5.2) and coastal protection (*medium confidence*; Box CC-CR). Ocean acidification poses many other potential risks, but these cannot yet be quantitatively assessed due to the small number of studies available, particularly on the magnitude of the ecological and socioeconomic impacts (19.5.2).

Socioeconomic Impacts and Costs

The biological, ecological and biogeochemical changes driven by ocean acidification will affect several key ecosystem services. The oceans will become less efficient at absorbing CO_2, hence less efficient at moderating climate change, as their CO_2 content will increase (*very high confidence*). The impacts of ocean acidification on coral reefs, together with those of bleaching and sea level rise, will in turn diminish their role of shoreline protection in atolls and small island nations as well as their direct and indirect benefits on the tourism industry (*limited evidence, high agreement*; Box CC-CR).

There is no global estimate of the observed or projected economic costs of ocean acidification. The production of commercially-exploited shelled mollusks may decrease (Barton et al., 2012) resulting in an up to 13% reduction of US production (limited evidence, low agreement; Cooley and Doney, 2009). The global cost of production loss of mollusks could be over 100 billion USD by 2100 (Narita et al., 2012). The largest uncertainty is how the impacts on prey will propagate through the marine food webs and to top predators. Models suggest that ocean acidification will generally reduce fish biomass and catch (*limited evidence, high agreement*) and that complex additive, antagonistic and/or synergistic interactions will occur with other environmental (warming) and human (fisheries management) factors (Branch et al., 2012; Griffith et al., 2012). The annual economic damage of ocean-acidification-induced coral reef loss by 2100 has been estimated, in 2009, to be 870 and 500 billion USD, respectively for A1 and B2 SRES emission scenarios (Brander et al. 2012). Although this number is small compared to global GDP, it represents a large proportion of the GDP of some regions or small island states which rely economically on coral reefs.

Adaptation and Mitigation

The management of ocean acidification comes down to mitigation of the source of the problem and adaptation to the consequences (Rau et al., 2012; Billé et al., sbm). Mitigation of ocean acidification through reduction of atmospheric CO_2 is the most effective and the least risky method to limit ocean acidification and its impacts. Climate geoengineering techniques based on solar radiation management would have no direct effect on ocean acidification because atmospheric CO_2 would continue to rise (6.4.2). Techniques based on carbon dioxide removal could directly address the problem but their effectiveness at the scale required to ameliorate ocean acidification has yet to be demonstrated. Additionally, some ocean-based approaches, such as iron fertilization, would only re-locate ocean acidification from the upper ocean to the ocean interior, with potential ramifications on deep water oxygen levels (Williamson and Turley, 2012; 6.4.2; 30.3.2.3 and 30.5.7). Mitigation of ocean acidification at the local level could involve the reduction of anthropogenic inputs of nutrients and organic matter in the coastal ocean (5.3.4.2). Specific activities, such as aquaculture, could adapt to ocean acidification within limits, for example by altering the production process, selecting less sensitive species or strains, or relocating elsewhere. A low-regret approach is to limit the number and the magnitude of drivers other than CO_2. There is evidence, for example, that reducing a locally determined driver (i.e. nutrient pollution) may substantially reduce its synergistic effects with a globally determined driver such as ocean acidification (Falkenberg et al., 2013).

[INSERT FIGURE OA-1 HERE

Figure OA-1: A: Overview of the chemical, biological, socio-economic impacts of ocean acidification and of policy options (adapted from Turley & Gattuso, 2012). B: Multi-model simulated time series of global mean ocean surface pH (on the total scale) from CMIP5 climate model simulations from 1850 to 2100. Projections are shown for emission scenarios RCP2.6 (blue) and RCP8.5 (red) for the multi-model mean (solid lines) and range across the distribution of individual model simulations (shading). Black (grey shading) is the modelled historical evolution using historical reconstructed forcings. The models that are included are those from CMIP5 that simulate the global carbon cycle while being driven by prescribed atmospheric CO_2 concentrations. The number of CMIP5 models to calculate the multi-model mean is indicated for each time period/scenario (IPCC AR5 WG1 report, Figure 6.28). C: Effect of near future acidification on major response variables estimated using weighted random effects meta-analyses, with the exception of survival which is not weighted (Kroeker et al., in press). The effect size indicates which process is most uniformly affected by ocean acidification but large variability exists between species. Significance is determined when the 95% bootstrapped confidence interval does not cross zero. The number of experiments used in the analyses is shown in parentheses. * denotes a significant effect.]

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Table 6-1: Selected examples of long-term biological and ecological observations in the oceans (NPP denotes Net Primary Productivity).

Region	Name of time series	Duration covered	Type of information	Interpretation
Global	SeaWiFS (Sea-viewing Wide Field-of-view Sensor)	1997-2011	Near surface chlorophyll	Direct and indirect effects of warmer oceanic conditions, associated with climate variability, result in lower chlorophyll concentrations and decreased rates of NPP (Behrenfeld *et al.* 2006a). Satellite time-series is insufficient to make robsut projections on the effect of climate change on chlorophyll concentrations or rates of NPP (Henson *et al.*, 2010)
English Channel and later into the open sea	CPR (Continuous Plankton Recorder)	1920s - ongoing	Zoo- and phytoplankton abundance/ presence absence	• changes in the seasonal abundance of phytoplankton (Edwards *et al.*, 2001) • rapid northerly movements of temperate and subtropical species of zooplankton and phytoplankton (Beaugrand *et al.*, 2009) • climate induced trophic mismatch between phytoplankton and zooplankton and its impact on fisheries (6.3.2.; Edwards and Richardson, 2004)
North Sea	Helgoland Roads (Alfred Wegener Institute)	1962 - ongoing	salinity, secchi disk depth, macronutrients, phytoplankton, zooplankton, intertidal macroalgae, zoobenthos and bacterioplankton	• Increase in green algae, decrease in brown algae, increased number of invaders on macrofauna, changing foodweb and bloom dynamics (Wiltshire *et al.*, 2010)
California	CalCOFI (California Cooperative Oceanic Fisheries Investigations)	1949 - ongoing (quarterly, 1969-1984 triennial) on variable grid	Ecological assessment	• El Niño impacts marine invertebrates and fishes (Chelton *et al.*, 1982; Butler, 1989; Rebstock, 2001) • decline in zooplankton biomass during periods of warming (Roemmich, 1992; Roemmich and McGowan, 1995a; Roemmich and McGowan, 1995b) • multidecadal shifts in the pelagic ecosystems (sardines and anchovies) (Brinton and Townsend, 2003; Lavaniegos and Ohman, 2003; Chavez *et al.*, 2003).
North Pacific Subtropical gyre	Climax HOT (Hawaii Ocean Time-series)	1968 - 1985 and 18 expeditions, mostly in summer months 1988 - ongoing monthly	ecosystem structure and variability	• Doubling of ship-measured chlorophyll a concentrations during period 1968-1985 (Venrick *et al.*, 1987). • Change from large eukaryotic to small photosynthetic prokaryotes (Karl *et al.*, 2001) • Decrease in dissolved phosphate concentrations due to proliferation of nitrogen fixing microorganisms (Karl 2007b)

Fisheries data series	Various	Various, see to the right	Fish stock assessments	• from 1950, fisheries landings and aquaculture production statistics, FAO: http://www.fao.org/fishery/statistics/en • from 1950, Sea Around Us project: www.seaaroundus.org, • from 1950, Global fishing effort database, Anticamara *et al*., 2011; • from 1970, ICES Trawl Surveys – DATRAS, ICES: http://datras.ices.dk/Home; • from 1950, RAM Legacy Stock Assessment Database (Ricard *et al*., 2012) • from 1903, British landings and effort data for major exploited fish stocks (Engelhard, 2005, ICES, 2010, 2011)

Table 6-2: Variations in metabolism based on sources of energy, electrons and carbon according to Karl (2007a), complemented by the taxa which exploit these pathways. Mode of metabolism may relate to organizational complexity and tolerance to environmental extremes (Figure 6-8).

Source of Energy[1]	**Source of Electrons**	**Source of Carbon**	**Domain / Taxon**
Sunlight *photo-*	Inorganic *-litho-*	CO_2 *-autotroph*	Bacteria, Archaea, Eukarya (algae and higher plants)
	Organic *-organo-*	Organic *-heterotroph*	Bacteria
Chemical *chemo-*	Inorganic *-litho-*	CO_2 *-autotroph*	Bacteria Archaea
	Organic *-organo-*	Organic *-heterotroph*	Bacteria Archaea Eukarya (Protozoa, Metazoa)

[1] A “mixotroph” is an organism that has the ability to use more than one source of energy, electrons or carbon

Table 6-3: Environmental forcing on biological production by physical, chemical and biological characteristics of major pelagic ecosystems (Adapted from Barber, 2001, based on the original analysis by McGowan, 1974).

	Size		**Stratification**			**Nutrient**[1]	
System	**Area (km^2x10^6)**	**%**	**Degree of**	**Duration**	**Productivity and Pattern**	**Level**	**Source**
Low-latitude gyre	164	52	Strong	Permanent	Low to to medium (debated)	Low	Eddy diffusion
Southern Ocean	77	25	Very weak, except strong when ice melts in summer	Seasonal	Moderate to high in summer only, Strongly seasonal	High	Mixing and upwelling
Equatorial upwelling	22	7	Aperiodic, upward vertical transport (temporally variable ranging from active upwelling to permanent stratification)	Permanent	High, Continuous	High	Upwelling and horizontal mixing
Subarctic gyre	22	7	Moderate stratification following winter mixing	Seasonal convective mixing	Low in winter, Strongly seasonal	High	Convective mixing and eddies
Eastern Boundary Current	21	7	Medium	Permanent	Moderate, Seasonal	Medium	Upwelling and lateral advection
Coastal upwelling	6	2	Strong stratification following vertical transport	Continuous	High, Weakly seasonal	High	Upwelling

[1] Nitrate and phosphate

Table 6-4: A wide range of processes make up the ocean's biological pump (Figure 6-6). In order to assess how a changing climate will alter the functioning of the pump, and the resulting biogeochemical feedbacks on global climate, the cumulative effects of climate-change mediated alteration of processes from cellular to ocean basin, and from pelagic to mesopelagic, must be quantified. This table illustrates, using published information, the complexity of the integrated knowledge platform needed to provide evidence of these biogeochemical ramifications and thus the limits to clear conclusions about climate induced effects on the biological pump (C, Carbon; TEP, Transparent Exopolymer Particle; DOM, Dissolved Organic Matter; POM, Particulate Organic Matter).

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

Table 6-5: Assessment of effects of ocean acidification on marine taxa with the number of laboratory and field studies, processes, parameters and total number of species studied in the range from $p\text{CO}_2$ <650 to >10000 µatm. Processes and parameters investigated in multiple life stages include growth, survival, calcification, metabolic rate, immune response, development, abundance, behaviour and others. Not all life stages, not all parameters and not 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. E.g. most species of calcifying macroalgae were negatively affected when exposed to a $p\text{CO}_2$ of 670 µatm (RCP 6.0 in 2100), considering e.g. calcification or growth, which renders the group as vulnerable with *medium confidence*. +: denotes that possibly more species or strains were studied, as only genus or family were specified; beneficial: most species were positively affected; vulnerable: most species were negatively affected; tolerant: most species were not affected. RCP 6.0: representative concentration pathway with projected atmospheric $p\text{CO}_2$ = 670 µatm in 2100; RCP 8.5: representative concentration pathway with projected atmospheric $p\text{CO}_2$ = 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 timescales, across generations (see separate reference list). For an assessment of variability between species from the same phylum see Figure 6-10.

Taxon	No. of studies	No. of para-meters studied	Total no. of species studied	$p\text{CO}_2$ where the most vulnerable species is negatively affected or investigated $p\text{CO}_2$ range* (µatm)	Assessment of tolerance to RCP 6.0 (*confidence*)	Assessment of tolerance to RCP 8.5 (*confidence*)
Cyanobacteria	8	5	5+	370-1000*	Beneficial (*low*)	Beneficial (*low*)
Coccolithophores	20	6	4+	800	Tolerant (*low*)	Vulnerable (*low*)
Diatoms	9	5	7+	400-820*	Tolerant (*low*)	Tolerant (*low*)
Dinoflagellates	5	4	3+	350-750*	Beneficial (*low*)	Beneficial (*low*)
Foraminifers	7	4	5	800	Tolerant (*low*)	Vulnerable (*low*)
Seagrasses	3	6	4	300-21000*	Beneficial (*medium*)	Beneficial (*medium*)
Macroalgae (non-calcifying)	5	5	3+	350-20812*	Beneficial (*medium)*	Beneficial (*low*)
Macroalgae (calcifying)	15	10	19+	550	Vulnerable (*medium*)	Vulnerable (*medium*)
Corals	25	17	22+	560	Tolerant (*low*)	Tolerant (*medium*)
Annelids	4	6	4+	2800	Tolerant (*medium*)	Tolerant (*medium*)
Echinoderms	33	29	29+	600	Tolerant (*medium*)	Vulnerable (*high*)
Molluscs	54	33	40+	600	Vulnerable (*low*)	Vulnerable (*high*)
Bryozoans	2	3	5+	2900	Tolerant (*medium*)	Tolerant (*medium*)
Crustaceans	33	27	37	700	Tolerant (*low*)	Tolerant (*medium*)
Fish	30	24	25	700	Vulnerable (*low*)	Vulnerable (*low*)

Table 6-6: Selected ocean acidification effects on microbes and associated processes. The experiments were conducted throughout more than a decade which large changes in experimental setup and data reporting (Riebesell *et al*., 2010) though information is still underreported in more recent papers, e.g. Krause *et al*, 2012, report pH values but not CO_2 or other carbonate system parameters. Therefore, pH as a common variable is reported in this table and not CO_2. The CO_2 values range from 150ppm (in this example pH 8.52) to 1500 ppm (pH 7.69) but changes in dissolved inorganic carbon (DIC) and total alkalinity (TA) do not allow a direct conversion from CO_2 to pH. Also note that the pH scale used was not always reported which can lead to errors up to 0.15 pH units between the NBS and free scale.

Organism	pH	Effect	Synergistic effects	reference
Archaea and ammonium oxidizing **bacteria**	pH reductions by 0.05–0.14 in water samples from various field sites	Decreased nitrification rates		Beman *et al.*, 2011
Batch bacterial community	8.22-8.15, 7.82, 7.67	Community shift No change in abundance		Krause *et al.*, 2012
Cyanobacteria	8.4, 7.8	Prochlorococcus/ Synechococcus – no clear change in C-fixation Trichodesmisum – enhanced rates of N_2 and C fixation	With excess Fe, P	Lomas *et al.*, 2012
Trichodesmium	8.52 to 7.69	Enhanced rates of photosynthesis, higher cell division rates, altered nutrient utilization (C:N and C:P ratios) and enhanced rates of N_2 fixation	Under P limitation	Barcelos e Ramos *et al.*, 2007; Hutchins *et al.*, 2007; Kranz *et al.*, 2010
Trichodesmium	8.35-7.80	Decreased N_2 fixation rates and growth	under iron limitation	Shi *et al.*, 2012
Trichodesmium erythraeum	8.28-8.01	No increase in N_2 fixation No increase in CO2 fixation	High light Low light	Garcia *et al.*, 2011
Synechococcus	8.05, 7.80	Increased cell division higher photosynthetic rate	Ambient temperature versus 4°C warming	Fu *et al.*, 2007
Prochlorococcus	8.05, 7.80	No change	Ambient temperature versus 4°C warming	Fu *et al.*, 2007
Diatom				
Pseudo-nitzschia fraudulenta	8.4, 8.2, 7.9	Increased toxicity Higher growth rate	Si limitation	Tatters *et al.*, 2012
Pseudo-nitzschia multiseries	8.38, 7.94	Increased toxicity		Sun *et al.*, 2011
Diatom-dominated assemblages		Increased primary production		Tortell *et al.*, 2008
Thalassiosira weissflogii	8.10, 7.8			Shi *et al.*, 2009

Coccolithophores				
Emiliania huxleyi	Various levels	Increased growth		Riebesell *et al.*, 2000; Rost *et al.*, 2003; Leonardos and Geider, 2005
Dinoflagellates				
Prorocentrum minimum	8.28 to 8.01 (based on T, DIC, CO_2)	Higher carbon fixation rates growth unaffected		Fu *et al.*, 2008

		CALCIFICATION	
Species	pH	Effect	Reference
Emiliania huxleyi	8.2-7.75 ~8.5-~7.9	Reduced calcite production Increased POC production reduced PIC/POC	Riebesell *et al.*, 2000; Zondervan *et al.*, 2001; For list see Ridgwell *et al.*, 2009 and Hoppe *et al.*, 2011
Emiliania huxleyi Strain NZEH	8.15, 8.13, 7.96, 7.85, 7.77	Increased PIC production by 80% Increased POC by 150% No change in PIC/POC	Iglesias-Rodriguez *et al.*, 2008
Emiliania huxleyi Strain RCC1256 Strain NZEH	Numerous experiments 8.44 - 7.2	No change in POC production 10% Reduced calcification between 288 to 1206 µatm, lower growth No change in growth, slightly reduced calcification and POC	Hoppe *et al.*, 2011;
Emiliania huxleyi Strain NZEH	8.10, 7.8	36% increase in PIC 69% increase in POC	Shi *et al.*, 2009
Emiliania huxleyi	Various experiments from 8.45 to 7.77	35% reduction in calcification between 200 and 900 µatm No change in POC Optimum response in POC	Langer *et al.*, 2009
Emiliania huxleyi		Independent of light limitation reduction in PIC/POC, POC independent of light PIC decrease with increasing CO2 at high light, Unaffected at low light	Zondervan *et al.*, 2002
Emiliania huxleyi	8.02, 7.82	Under nitrogen limitation: reduced calcite production and reduced POC, smaller cell volume	Sciandra *et al.*, 2003
Emiliania huxleyi mescosm		40% decrease in net community calcification from 175 to 600 ppmV CO_2 no change in NPP Calcite formation decreased with CO_2 concentration, reduction of weight of liths, Increased TEP formation from 190, 410 to 710 ppmV CO_2	Delille *et al.*, 2005; Engel *et al.*, 2005
Calcidiscus leptoporus	8.74, 8.44, 8.27, 8.13, 7.93, 7.86 8.33, 8.34, 7.72, 7.6, 7.49, 7.86	Optimum calcification at 400ppm Optimum calcification between 400-900 ppm various methods in altering carbonate chemistry	Langer *et al.*, 2006 Langer *et al.*, 2011
Coccolithus pelagicus	8.56, 8.22, 7.81	No significant change	Langer *et al.*, 2006
Gephyrocapsa oceanica	8.2-7.75	Reduced calcite production, reduced PIC/POC	Riebesell *et al.*, 2000; Zondervan *et al.*, 2001

Table 6-7: Examples illustrating species vulnerabilities and underlying mechanisms to changing temperature, hypoxia, ocean acidification (OA).

General pattern	Phenomenon	Driver	Mechanism / Sensitivity	References
Species displacement, regime shifts abundance losses	Northward shift in the distribution of North Sea cod (*Gadus morhua*) stocks	Winter/spring warming (*high confidence*)	Bottlenecks of high sensitivity during early life stages as well as adult spawning stage in winter/early spring	Perry *et al.*, 2005; Pörtner *et al.*, 2008
	Decreased abundance of northern temperate species, increased abundance of southern species in the Bay of Biscay (France)	Increasing annual mean temperatures at 100 m depth.	Bottlenecks of high sensitivity during recruitment	Hermant *et al.*, 2010
	Shift from sardines (*Sardinops melanostictus*) to anchovies (*Engraulis japonicus*) in the Sea of Japan observed between 1993 and 2003	Warming (*high confidence*) at the interdecadal scale	Thermal windows of growth and reproductive output are found at higher temperatures for anchovies than sardines, food preferences of the competing species being similar.	Li *et al.*, 1992; Takasuka *et al.*, 2007, 2008
	Bigeye (*Thunnus obesus*), skipjack (*Katsuwonus pelamis*), albacore (*T. alalunga*), yellowfin (*Thunnus albacares*) or bluefin tuna (*T. maccoyli*), mildly affected by warming trends, shifting core habitat, abundances, and heat stress of spawners projected.	Wide specific thermal ranges (Bigeye 11-29, skipjack 17-30, yellowfin 18-31 or bluefin tuna 10.5-21, albacore 13-25°C; optimal thermal window narrowest and warmest during spawning, effects of reduced primary productivity.	– Eurythermal tissue characteristics, large body size, wide roaming ranges. – Larvae most sensitive to water temperature, widening their thermal habitat as they grow. – Adults at spawning stage need to prevent overheating, a shift in location to cooler waters may occur to maintain spawning success, e.g. in surface-dwelling skipjack tuna.	Katz, 2002; Pörtner, 2004; Lehodey *et al.*, 2011; Hazen *et al.*, 2012
	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}).	Species specific exposures and tolerances to hypoxia, related to feeding activity in hypoxic zones.	Oxygen transport via hemoglobin is adapted to be highly efficient supporting high metabolic rates as needed during feeding in the OMZ.	Lehodey *et al.*, 2011; Seibel, 2011
	Variable sensitivities to OA within and across animal phyla (Figure 6-9 B)	Anthropogenic OA, Sea water acidification by elevated $p\text{CO}_2$ in OMZs, upwelling areas, involving	– Lowered extracellular (blood plasma) pH causing a lowering of the rates of ion exchange and metabolism in muscle	Reipschläger and Pörtner, 1996; Pörtner *et al.*, 2000; Vezzoli *et al.*, 2004; Langenbuch and Pörtner, 2003;

		anthropogenic ocean acidification.	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	Fernández-Reiriz *et al.*, 2011; Langenbuch and Pörtner, 2002; Langenbuch *et al.*, 2006; Michaelidis *et al.*, 2005; Pörtner *et al.*, 1998; Stumpp *et al.*, 2012
			Further affected fitness-relevant processes: – gonad maturation, – egg fertilization, – egg haching, – brooding success, – larval development, – critical transition phases in development (onset of feeding, moulting), – larval and adult calcification and growth, – neuronal metabolism and functioning, behaviors (feeding, disorientation and distortions in olfactory and acoustic perceptions) – immune response, – exercise performance	Bibby *et al.*, 2008; Boyd and Burnett, 1999; Chan *et al.*, 2011; Dupont *et al.*, 2008; Kurihara and Shirayama, 2004; Kurihara, 2008; Havenhand *et al.*, 2008; Hernroth *et al.*, 2011; Kawaguchi *et al.*, 2011; Michaelidis *et al.*, 2005; Munday *et al.*, 2009c, 2010; Nilsson *et al.*, 2012; Pörtner, 2002b; Reuter *et al.*, 2011; Reipschläger *et al.*, 1997; Sewell and Hofmann, 2011; Shirayama and Thornton, 2005; Simpson *et al.*, 2011; Walther *et al.*, 2010.

Table 6-8: Examples of observed biological responses resulting from temperature and temperature-mediated changes in the ocean.

Responses and attribution	**References**
Species abundance, biogeography and diversity	
Observations by the European Large Marine Ecosystems study report the northward movement of species and the conversion of polar into more temperate and temperate into more subtropical system characteristics. Effects are attributed to climate change but may be influenced by nutrient enrichment and overfishing. Due to the lack of geographical barriers and to advective processes, the mean poleward movement of plankton reached up to 200–250 km per decade between 1958–2005.	Beaugrand *et al.*, 2009; Philippart *et al.*, 2011
Retreat of colder water plankton to the north in the Northeast Atlantic between the 1950s and 2000s.	Beaugrand *et al.*, 2002
Between 1960 and 2000 the Newfoundland Shelf in the Northwest Atlantic saw an increase in the abundance of arctic boreal plankton species, notably the copepods *Calanus hyperboreus* (Kroyer), *Calanus glacialis* (Jaschnov) and the dinoflagellate *Ceratium arcticum* due to an increased contribution of Arctic water via the shelf branch of the Labrador Current. In 1996, a dramatic drop in the NAO allowed a flood of cool Labrador slope water to round the tail of the Grand Bank, carrying *C. hyperboreus* along the Scotian shelf-break, to reach Georges Bank two years later.	Johns *et al.*, 2001; Greene and Pershing, 2003
In the Southwest Atlantic sector and the Bellingshausen Sea a historical analysis of the distribution of Antarctic macrozooplankton between 1925 and 1951 demonstrated the key role of temperature and differential thermal windows in setting distribution ranges. Food (chlorophyll *a*) availability codefined the distribution of krill (*Euphausia superba*).	Mackey *et al*., 2012
NAO-driven variability in growth rate has been documented for the Atlantic quahog, *Arctica islandica* from Iceland, the coralline alga *Clathromorphum compactum* off Newfoundland and the bivalve *Clinocardium ciliatum* in the Barents Sea (combined NAO and ACRI). A role for temperature has yet to be unequivocally demonstrated.	Schöne *et al.*, 2005; Carroll *et al.*, 2011; Halfar *et al.* 2011
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, with early disappearance of the largest individuals.	Pörtner and Knust, 2007
Studies of tropical coral reefs document large scale bleaching (6.2.2.4.4.), growth reductions and decreased calcification in *Porites* and other corals over the last two decades, a change unprecedented in the last centuries largely induced by warming.	Lough, 2008; De'ath *et al*., 2009; Cooper *et al*., 2012
The giant kelp *Macrocystis pyrifera* off the eastern north Pacific has shown changes in both distribution and abundance during major El Niño events (Tegner and Dayton, 1987; Tegner et al., 1996), with particularly strong consequences and widespread mortality at its southernmost distribution limit off Baja California.	Ladah *et al*., 1999; Valdez *et al*., 2003
In the Northwest Atlantic the majority of fish caught in trawl surveys show a northward movement in response to warming since the 1960s, with some of the shifts being correlated with the AMO.	Nye *et al*., 2009; Lucey and Nye, 2010; Nye *et al*., 2011

Responses and attribution	**References**
Phenology	
In the waters around the U.K., 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}	Thackeray *et al*., 2010.
Migration time of pink salmon (*Oncorhynchus gorbuscha*) in Alaska is almost two weeks earlier now relative to 40 years ago which is related to warming. This is related to the rapid microevolution for earlier migration timing.	Kovach *et al*., 2012
Body size	
Asymptotic size of different populations of Atlantic cod (*Gadus morhua*) and Atlantic Herring (*Clupea harengus*) are negatively related to temperature.	Taylor, 1958, Brunel and Dickey-Collas, 2010
Decrease in asymptotic size of haddock (*Melanogrammus aeglefinus*) in the North Sea from the 1970s to the 2000s is significantly related to changes in sea surface temperature.	Baudron *et al*., 2011
Trophic and competitive interactions	
Both warming and the decreasing spatial extension of krill habitat benefits the salp (Pakhomov, 2004) and may also govern the on-going reductions in Adelie and chinstrap penguin populations via reductions in prey availability.	Trivelpiece *et al*., 2011.
Direct effects of warming on both, the Atlantic cod and the putative copepod prey species of juvenile cod are involved in climate effects on Atlantic cod (*Gadus morhua*) populations in the Eastern North Atlantic. The regime shift in the North Sea, from the larger copepod *Calanus finmarchicus* to ones forming lower biomass including *C. helgolandicus* represent an unfavorable shift to less energy dense food particles for juvenile cod and to a later timing for reproduction, such that *Calanus* eggs and nauplii are less abundant as food for newly hatched cod larvae. This shift was thereafter shown to be largely caused by temperature.	Beaugrand *et al*., 2003; Helaouët and Beaugrand, 2007
Significant community-wide changes in abundance and composition among 150 intertidal and subtidal algae and invertebrates resulted from direct effects of temperature on key taxa as well as indirect effects through ecological interactions after long-term warming by 3.5 °C from 1985 to 1995 at a power station in temperate California. In the Californian intertidal after warming by 0.79-1.26 °C within 60 years (1931-1933 vs. 1993 -1996) southern species increased and northern decreased in abundance, in line with range-related community shifts.	Sagarin *et al.*, 1999
The relative ranges of predator (sea stars) and prey (mussels and barnacles) change in response to climatic differences reflecting and leading to associated changes in interactions and modifications in predator pressure.	Harley, 2011
In tropical seas, turf algae can rapidly colonize thermally damaged corals depending on the extent to which coralline red algae, which are the most important substrate for coral recruitment, suffer from ocean acidification.	Doropoulos and Diaz-Pulido, 2013; Fricke *et al*., 2011; Hoegh-Guldberg *et al*., 2007

Table 6-9: Potential interactions between modes of anthropogenic forcing (environmental; harvesting; or complex; considering scales and velocity of change, frequency and variability of events, intensity) on different levels of biological organisation. These interactions, from simple to complex, are illustrated with published illustrative examples ranging from physiological studies (Pörtner and Knust, 2007) to modelling studies such as Griffith *et al.*, (2011). E, O, and M denote studies using manipulation Experiments (lab or field), Observations, or Modelling approaches, respectively; note there are an insufficient number of studies to assign a level of confidence to each of these findings “???” defines the bounds on our understanding of the relationship between forcing and its effect on organisational level.]

Anthropogenic Forcing

Biological Organisation studied at ecosystem level				
	Single Environmental Driver	*Multiple Environmental Drivers*	*Fishing / Foodwebs*	*Fishing / Climate change*
Individual species	Lab experiments and field observations show that warming alters organismal physiology and thereby, in situ abundance (Pörtner and Knust, 2007) E & O	Shipboard manipulation experiment addressing interactive effects of temperature and CO_2 on coccolithophore calcification (Feng *et al.*, 2009) E	Interactive effects of multiple drivers on larval fish (Perry *et al.*, 2010; Runge *et al.*, 2010) O & M	???
Population	Lab cultures show how altered pH elicits different responses of coccolithophore species (Langer *et al.*, 2006) E	Lab cultures show differential responses of cyanobacterial groups to temperature and CO_2 (Fu *et al.*, 2007) E	Altered maturation age and growth rate of populations due to fishing (Fairweather *et al.*, 2006; Hseih *et al.*, 2006) O	???
Ecosystem	Mesocosm experiments simulating the effect of individual drivers (e.g. ocean acidification, benthic: Christen *et al*. 2013; pelagic: Riebesell *et al.*, 2013) E, O or M	Mesocosm experiments studying differential effects of light and temperature, on copepods versus diatoms (Lewandowska and Sommer, 2010) E	Effects of fishing on ecosystem structure – trophic cascades (Frank *et al.*, 2005) O	Interplay of fishing and climate pressures on ecosystems promotes lower trophic levels (Kirby *et al.*, 2009) O; enhances diversity loss in benthic communities (Griffith *et al.*, 2011) M
Biome	Time-series observations on warming and the alteration of zooplankton biomes (Beaugrand *et al.*, 2009) O	???	???	???

Table 6-10: 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 per cent of sunlight, by various techniques, is able to offset the global mean temperature effects of a doubling of atmospheric carbon dioxide content from preindustrial 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, 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
Artifical upwelling or downwelling	Ocean fertilization by bringing nutrient rich deep water (from 200 - 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 which 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

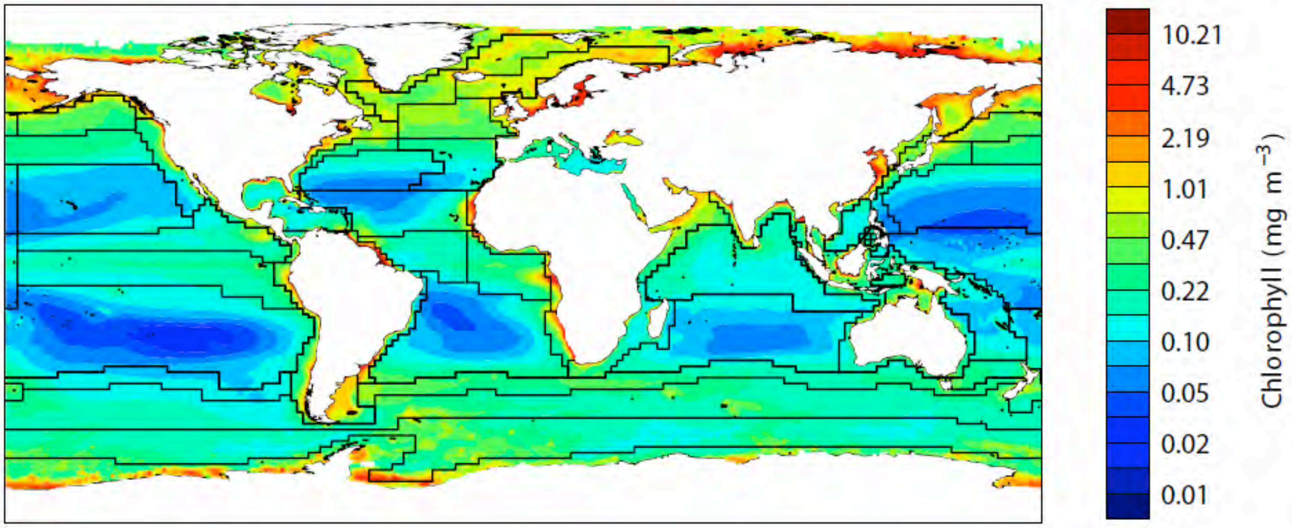


Figure 6-1: Productivity in 51 distinct global ocean biogeographical biomes as represented by a grid of thin black lines (after Longhurst, 1998), overlain with an average annual composite plot of chlorophyll *a* concentration, i.e., a proxy for phytoplankton stocks in the upper ocean, from the NASA/Orbimage SeaWiFs satellite (Bailey *et al*., 2006; McClain *et al*., 2004; McClain, 2009). The characteristics and boundaries of each biome are primarily set by the underlying regional ocean physics and chemistry. Together, these provinces or biomes span several orders of magnitude in chlorophyll *a* from < 0.1 mg m^{-3} that characterize the low latitude oligotrophic regions (denoted by purple and blue) up to 10 mg m^{-3} in highly productive coastal upwelling regions in Eastern boundary currents (denoted by red).

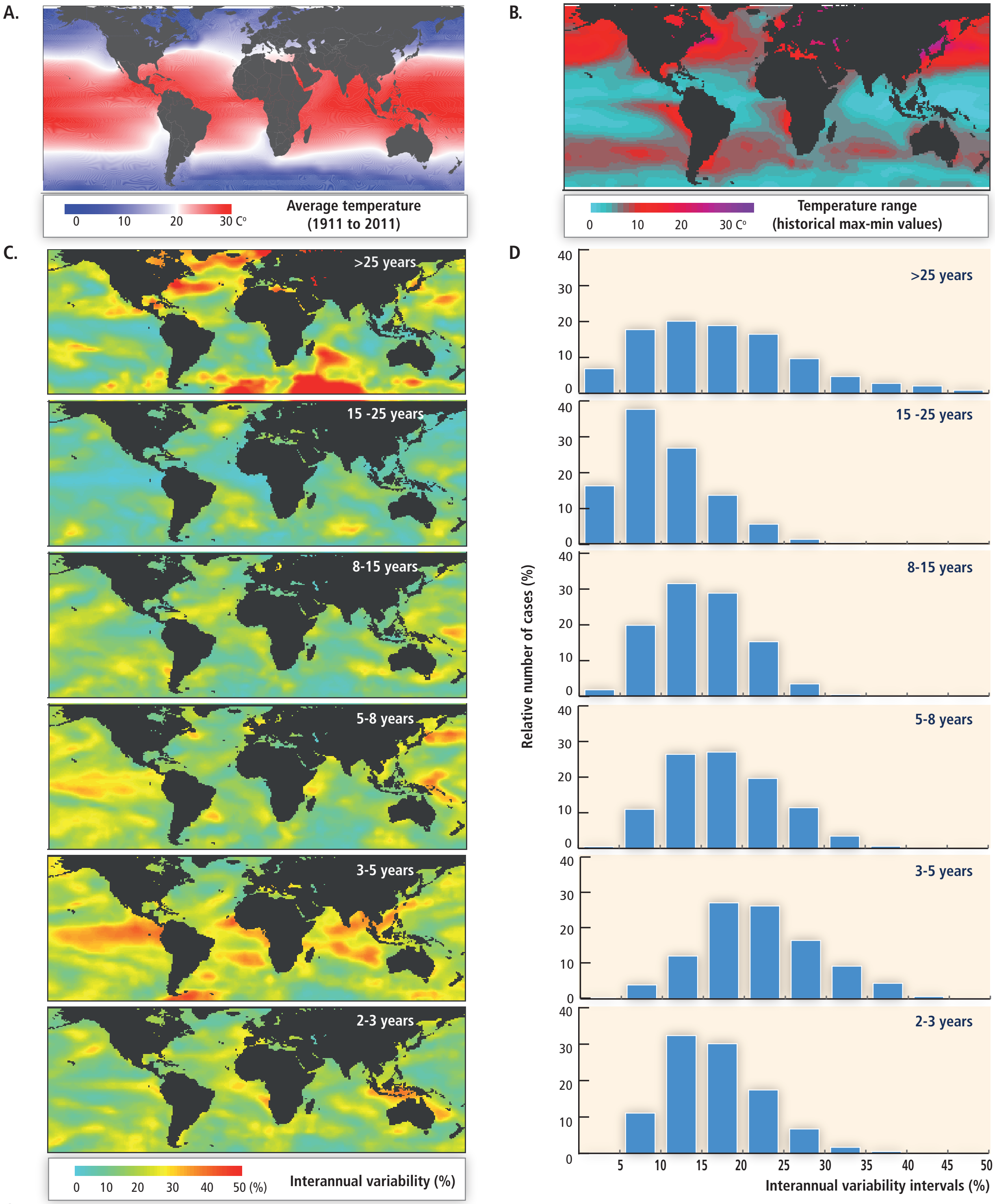


Figure 6-2 | Last Century sea surface temperature variability. A) The long term (1911 to 2011) sea surface temperature average. B) The temperature range calculated as the difference between the historical maximum and minimum values for each grid component. C) The spatial distribution of variability by time scales was computed by accumulating the relative spectral densities of each 2°x2° grid box frequency-transformed series by frequency windows, corresponding to the multidecadal (period >25 years), bidecadal (15 to 25 years), decadal (8 to 15 years), low ENSO frequency (5 to 8 years), high ENSO frequency (3 to 5 years) and very high frequency (2 to 3 years) scales. The sum of the six maps at every single box corresponds to 100% of the interannual time series variability. D) The relative number of cases (grid boxes) at each temperature class intervals. The class intervals represent fractions of the temperature range at each variability scale. The sum of all cases for each histogram accounts of the 100% of the area, and the sum of all the temperature fractions from all histograms accounts for the total temperature ranges shown in the upper right map. All computations are based on the Extended Reynolds Sea Surface Temperature (NOAA, 2012).

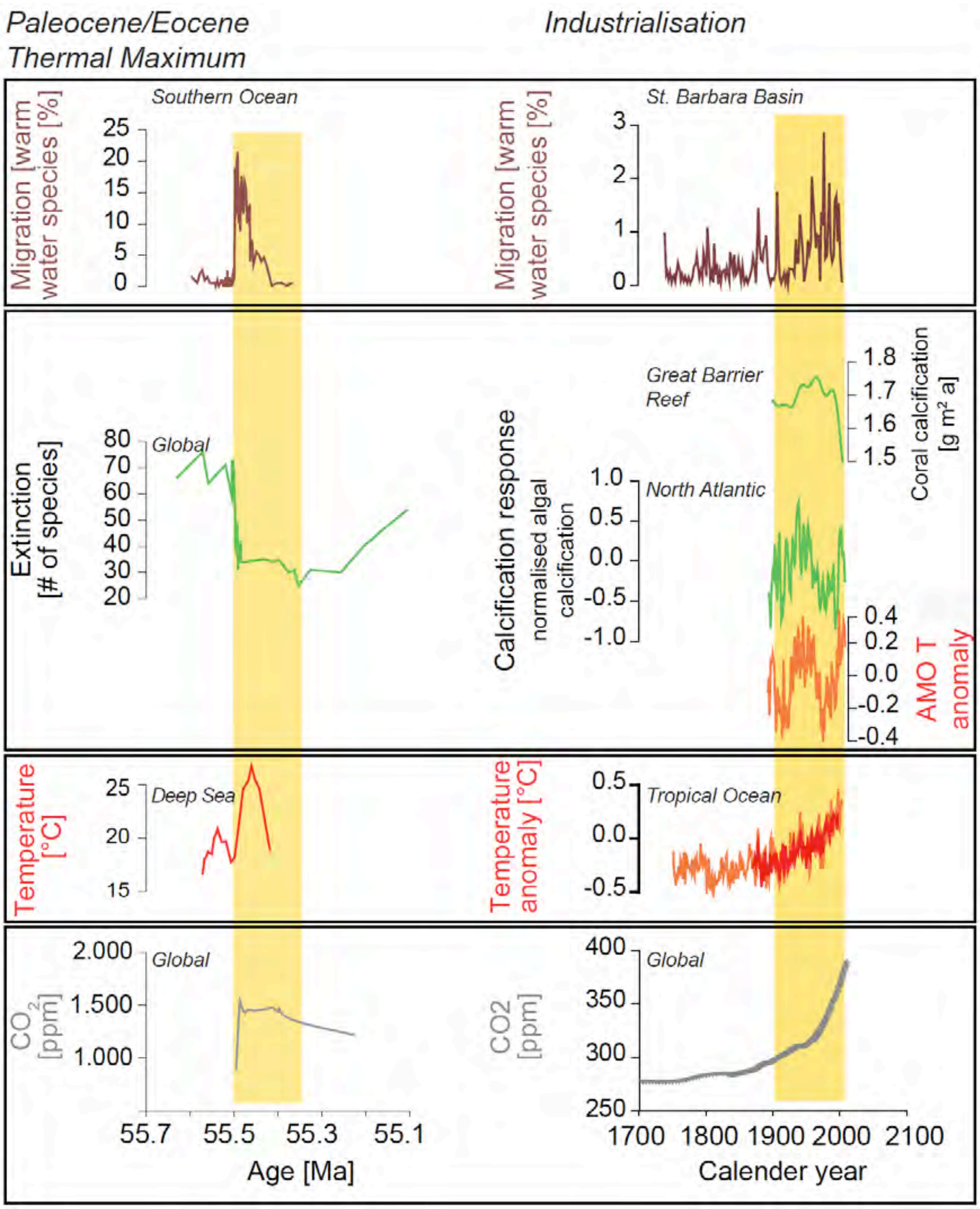


Figure 6-3: Atmospheric CO_2 (bottom, grey) and temperature (middle, red/orange) changes with associated biotic changes (top) for the Paleocene Eocene Thermal Maximum (PETM) and the industrial era. Episodes of largest environmental change are indicated with yellow bars. CO_2 data are based on measurements at Mauna Loa (modern: Keeling *et al.*, 2005) and model output (PETM: Ridgwell and Schmidt, 2010; Zeebe *et al.*, 2009). Temperature data are based on proxy data (modern: Wilson *et al.*, 2006; Lea *et al.*, 2003; PETM: Kennett and Stott, 1991) representing the regional temperature changes in the surface ocean. Modern biotic responses include changes in coralline algal growth (Halfar *et al.*, 2011), and coral calcification (De'ath *et al.*, 2009). Evolutionary changes are exemplified by the extinction of benthic foraminifera (Thomas, 2003). Abundance data (top row) of planktonic foraminifera and coccolithophores (modern: Field *et al.*, 2006; PETM: Bralower, 2002) indicate range expansion due to warming.

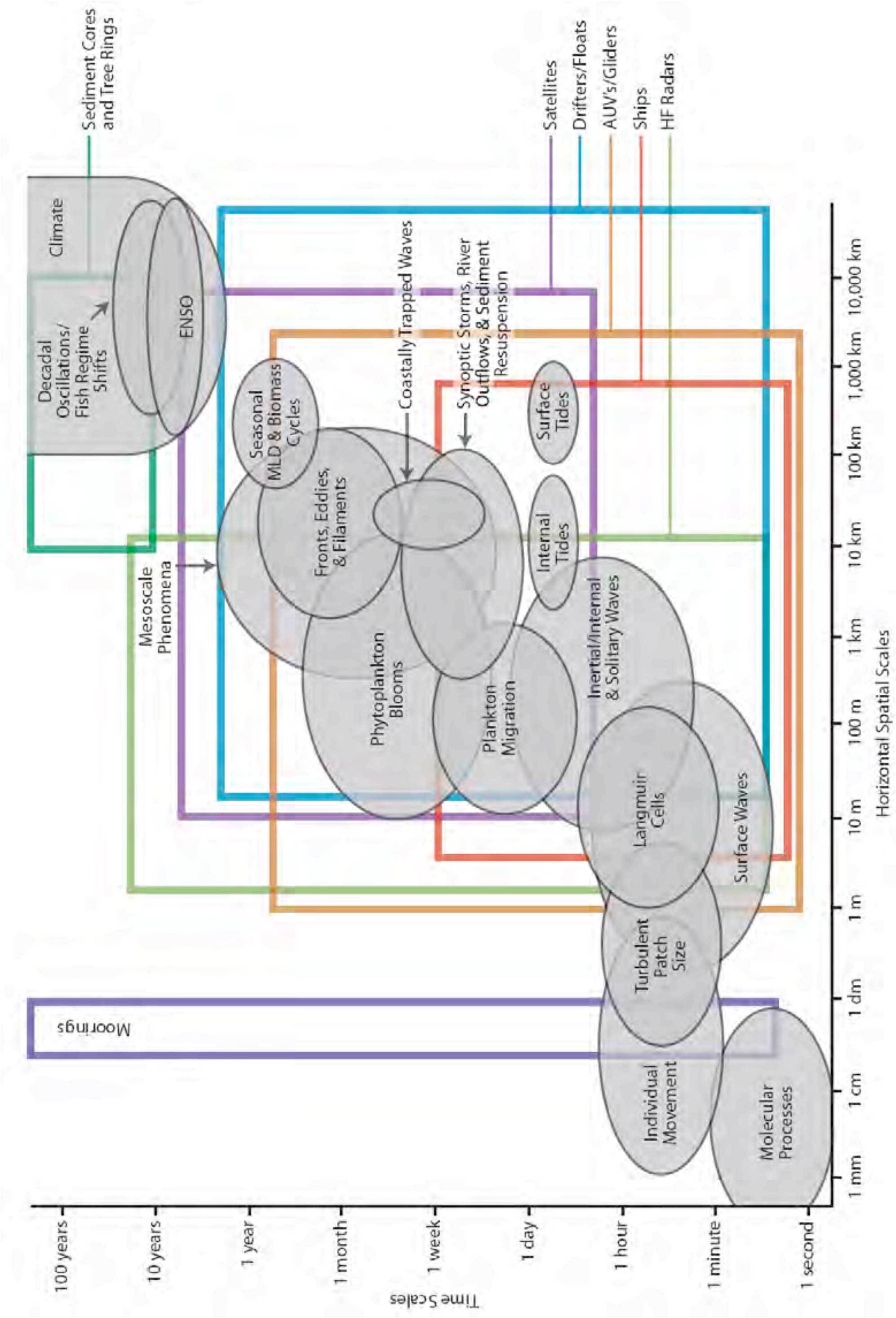


Figure 6-4: Multiple coupled temporal and spatial scales of variability in physical, physiological and ecological processes of interest in contemporary marine system research. Observations over broad time and space scales are necessary to separate natural variability from impacts due to human-induced effects, and define the observation tools that are necessary to obtain relevant data. The shaded regions depict the approximate boundaries of major processes of interest, and the boxes define the scales of selected measurement/observation procedures. Langmuir cells are a series of wind-driven shallow, slow, counter-rotating circulations at the ocean's surface. From Karl (2010), as modified from Dickey (1991).

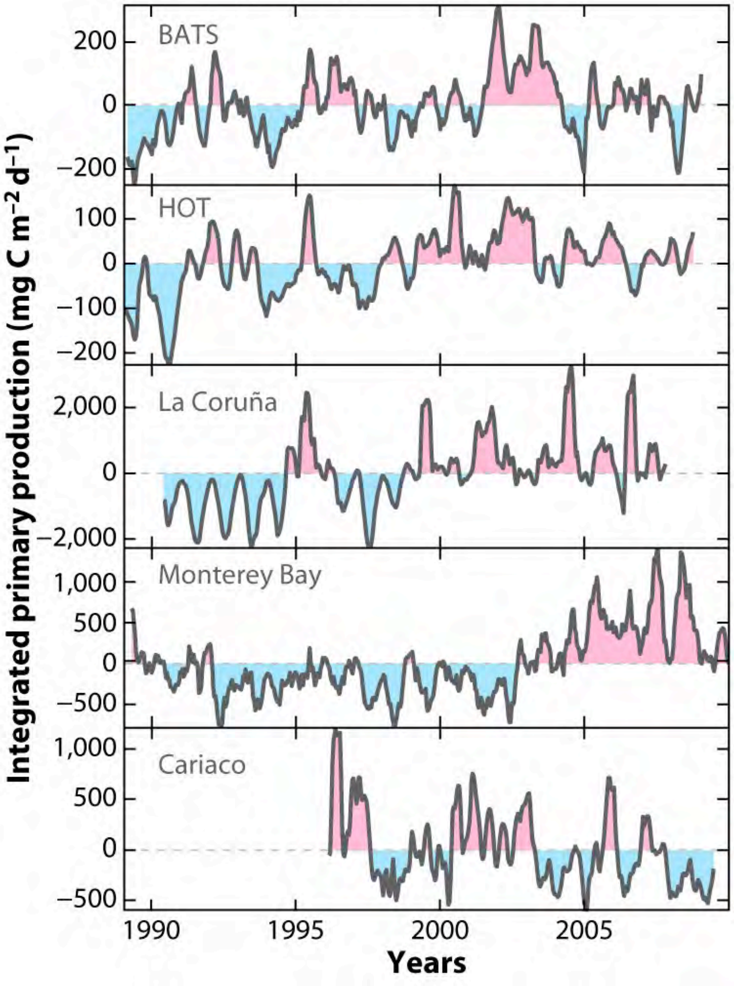


Figure 6-5: Time-series of water column integrated primary production (PP) anomalies at: Northwestern Spain, La Coruña (43° 25.2 N, 8° 26.4 E); HOT (22° 45 N, 158°W); BATS (31° 50 N, 64° 10 W); Monterey Bay, Central California Current (37°N, 122°W); Cariaco Basin, Venezuela (10°30 N, 64°40 W), reproduced from Chavez *et al.* (2011). Anomalies were calculated by integrating over the water column, then interpolating to 14 d, smoothing with a moving average and differencing for each 14-d interval from the grand mean for that interval. All sites except Cariaco seem to show positive (pink) PP anomalies after 2000.]

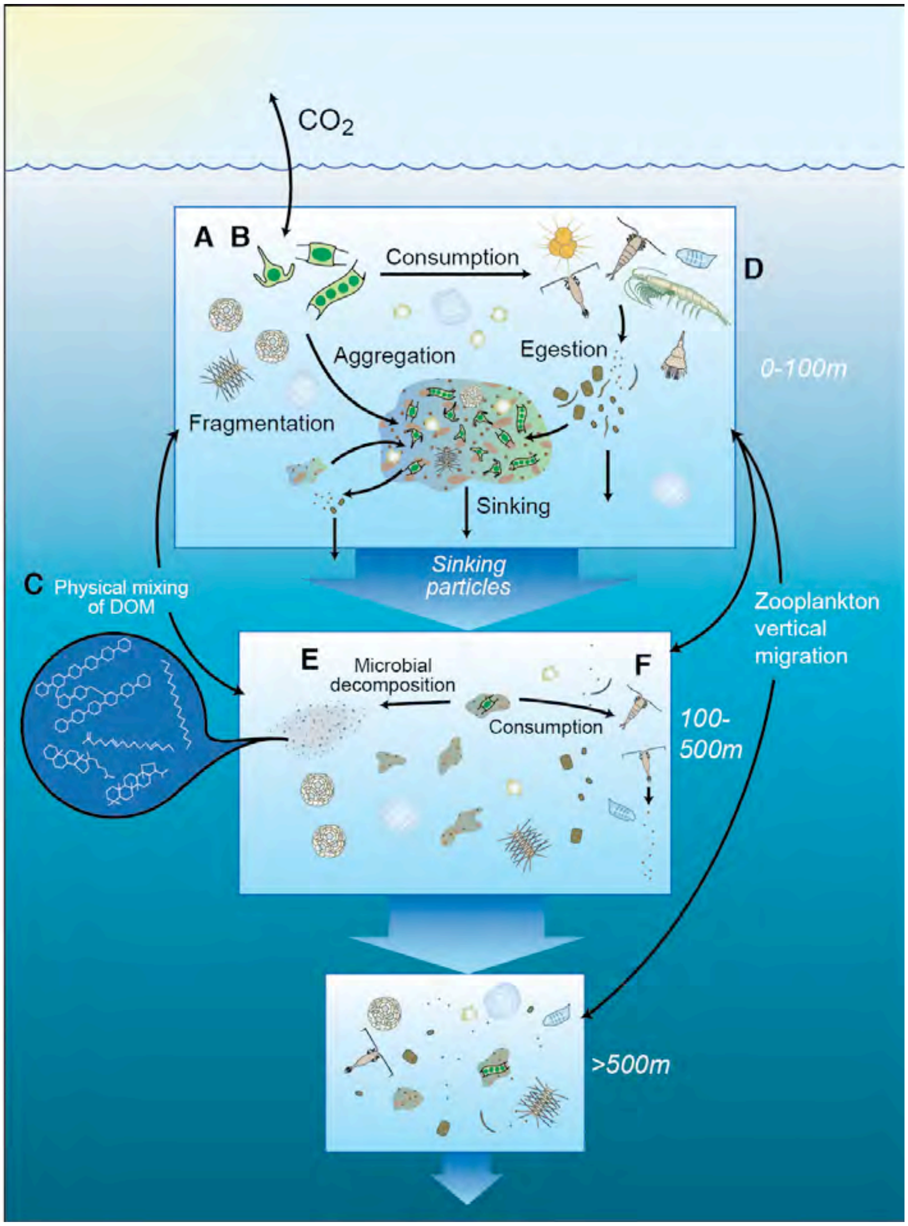


Figure 6-6: A schematic representation of the ocean's biological pump, which responds to climate change and is a relevant conduit for carbon sequestration. It is difficult to project how the pump might be altered (Table 6-4) and whether it would represent a positive or negative feedback to climate change which causes: A, shifts in NPP (Net Primary Production; Bopp *et al*., 2002); B, floristic and faunistic shifts in the pelagic (Beaugrand *et al*., 2009) that may alter the relationship between OA and ballasting of settling particles (Klaas and Archer, 2002); C, changes in proportion of NPP released as DOM (Dissolved Organic Matter) due to the effects of ocean acidification (Engel *et al*., 2004); E, warming and faster bacterial enzymatic rates of particle solubilization (Christian and Karl, 1995); and faunistic shifts at depth (Jackson and Burd, 2001). Modified from Buesseler *et al.* (2008) by J. Cook (WHOI).

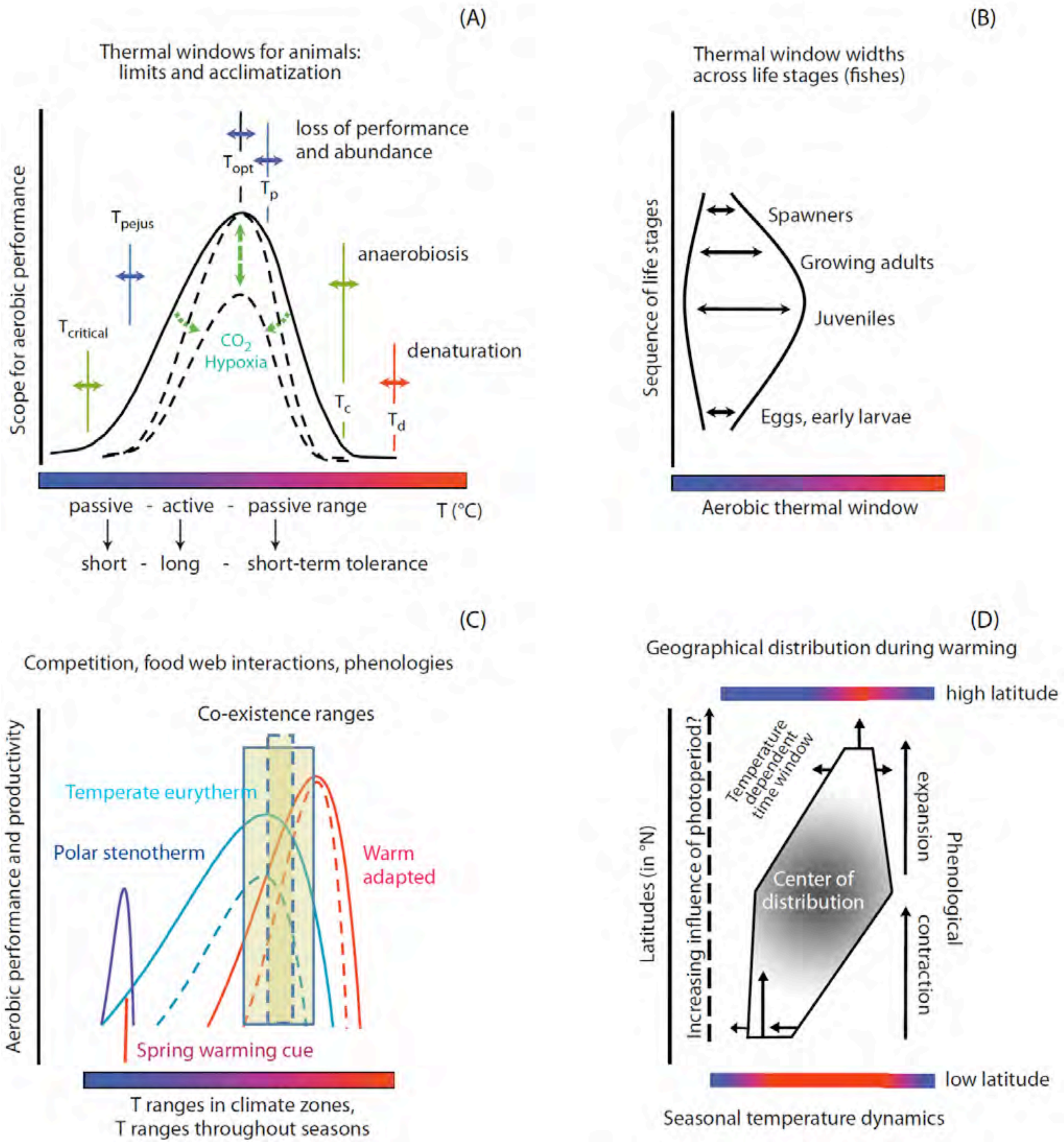

(A)
Thermal windows for animals: limits and acclimatization
Scope for aerobic performance
loss of performance and abundance
T_{opt}
T_p
T_{pejus}
$T_{critical}$
anaerobiosis
CO_2
Hypoxia
T_c
denaturation
T_d
passive - active - passive range
T (°C)
short - long - short-term tolerance
(B)
Thermal window widths across life stages (fishes)
Sequence of life stages
Spawners
Growing adults
Juveniles
Eggs, early larvae
Aerobic thermal window
(C)
Competition, food web interactions, phenologies
Aerobic performance and productivity
Co-existence ranges
Temperate eurytherm
Polar stenotherm
Warm adapted
Spring warming cue
T ranges in climate zones,
T ranges throughout seasons
(D)
Geographical distribution during warming
high latitude
Latitudes (in °N)
Increasing influence of photoperiod?
Temperature dependent time window
Center of distribution
expansion
contraction
Phenological
low latitude
Seasonal temperature dynamics

Figure 6-7

Figure 6-7: Mechanisms linking organism to ecosystem response explain the why, how, when and where of climate sensitivity (based on knowledge for animals, after Pörtner, 2001, 2002a, 2012; Pörtner and Farrell, 2008, blue to red colour gradients illustrate transition from cold to warm temperatures). (A) As all biota, animals specialize on limited temperature ranges, within which they grow, behave, reproduce, defend themselves by immune responses. Optimum temperatures (T_{opt}) indicate performance maxima, pejus temperatures (T_p) the limits to long-term tolerance, critical temperatures (T_c) the transition to anaerobic metabolism, and denaturation temperatures (T_d) the onset of cell damage. These OCLTT thresholds (see text) can shift by acclimatization (horizontal arrows). Under elevated CO_2 levels and in hypoxic waters performance levels can decrease and windows of performance be narrowed (dashed green arrows pointing to dashed black curves). (B) Thermal range widths (horizontal arrows) change between individual life stages of a species. (C) The shift of performance curves between polar, temperate and tropical animal species reflect evolutionary adaptation to the respective climate zones. Via species-specific effects on performance (dashed curves, cf. A), additional stressors and species interactions cause shifts in higher-level processes (seasonal activities in response to light or temperature cues, shifts in predator-prey interactions and competition within changing coexistence ranges of interacting species). (D) Shifts in biogeography result during climate warming (modified after Beaugrand, 2009). The polygon delineates the range in space and time, the level of grey denotes abundance. Species display maximum productivity in southern spring, wide seasonal coverage in the centre and a later productivity maximum in the North. The impact of photoperiod increases with latitude (dashed arrow). During warming, the southern temperature and time window contracts while the northern one dilates (directions and shifts indicated by arrows). Control by water column characteristics or photoperiod may overrule temperature control in some organisms (e.g. diatoms), causing contraction of spatial distribution in the north.

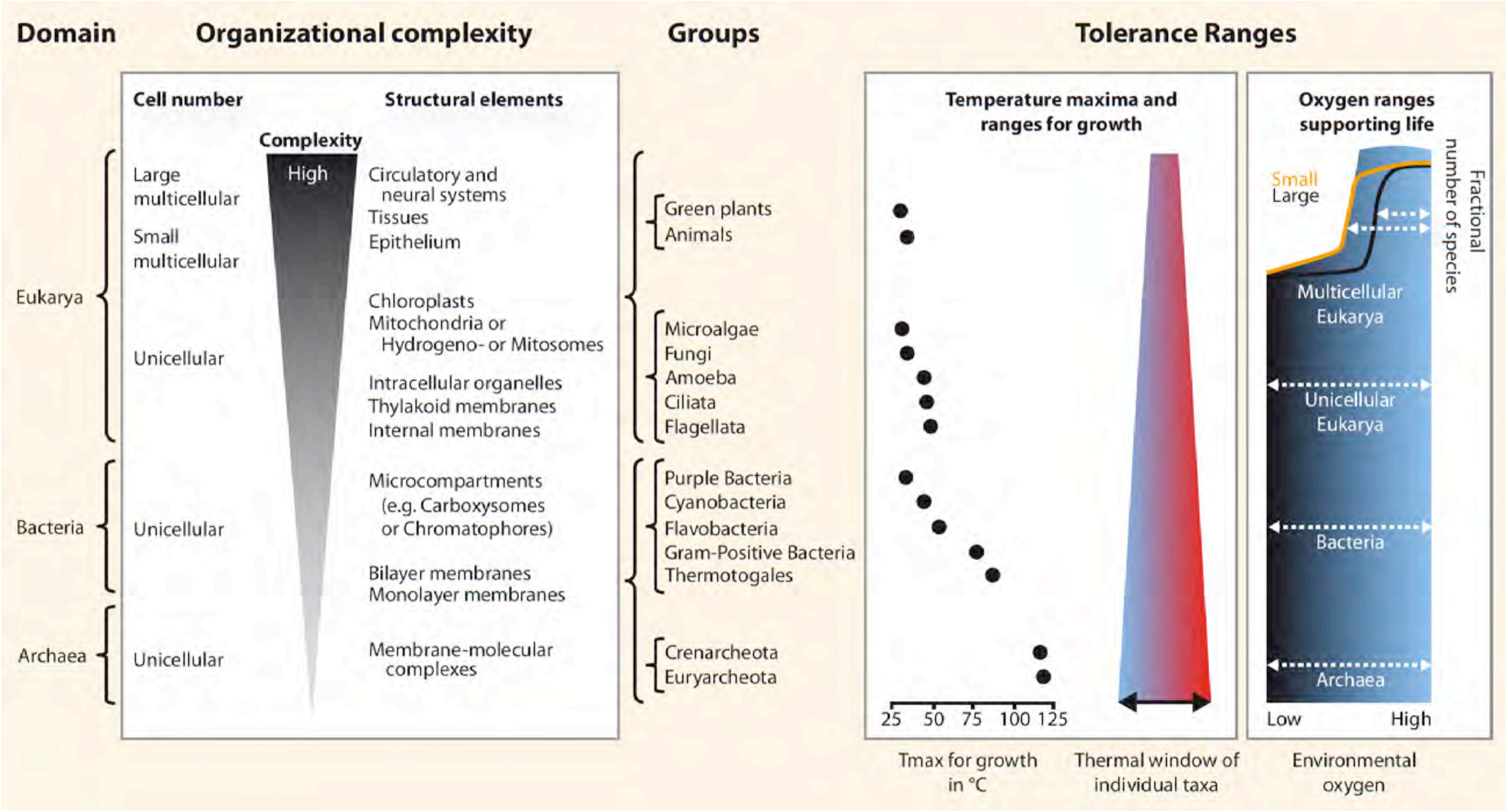

Domain
Organizational complexity
Groups
Tolerance Ranges
Cell number
Structural elements
Complexity
High
Eukarya
Large multicellular
Small multicellular
Unicellular
Bacteria
Unicellular
Archaea
Unicellular
Circulatory and neural systems
Tissues
Epithelium
Chloroplasts
Mitochondria or Hydrogeno- or Mitosomes
Intracellular organelles
Thylakoid membranes
Internal membranes
Microcompartments (e.g. Carboxysomes or Chromatophores)
Bilayer membranes
Monolayer membranes
Membrane-molecular complexes
Green plants
Animals
Microalgae
Fungi
Amoeba
Ciliata
Flagellata
Purple Bacteria
Cyanobacteria
Flavobacteria
Gram-Positive Bacteria
Thermotogales
Crenarcheota
Euryarcheota
Temperature maxima and ranges for growth
25
50
75
100
125
Tmax for growth in °C
Thermal window of individual taxa
Oxygen ranges supporting life
Fractional number of species
Small
Large
Multicellular Eukarya
Unicellular Eukarya
Bacteria
Archaea
Low
High
Environmental oxygen

Figure 6-8

Figure 6-8: Ranges of temperatures and O_2 concentrations covered by various domains and groups of free living marine organisms (bacteria to animals, domains and groups modified after Woese *et al.*,1990) in various habitats (Storch *et al.*, subm.). High organizational complexity enables an increase in body size, associated with decreasing tolerances to hypoxia and heat. In the domain Bacteria, the group Thermotogales comprises obligate anaerobes, displays less complex structures such as a single layer lipid membrane and is most tolerant to high temperatures. Highest temperatures of growth were found at 122°C in hydrothermal vent species under elevated hydrostatic pressure in laboratory experiments. Dashed white arrows denote wide O_2 tolerances in unicellular archeae, bacteria and protists, as compared to animals and plants (multicellular eukarya). Anoxic habitats are conquered by small multicellular and unicellular Eukarya, supported by less complex mitosomes or hydrogenosomes used in energy metabolism. Species richness of animals (upper right) increases with rising O_2 levels reflecting better hypoxia tolerance in small compared to large individuals and their taxa (6.3.3.).

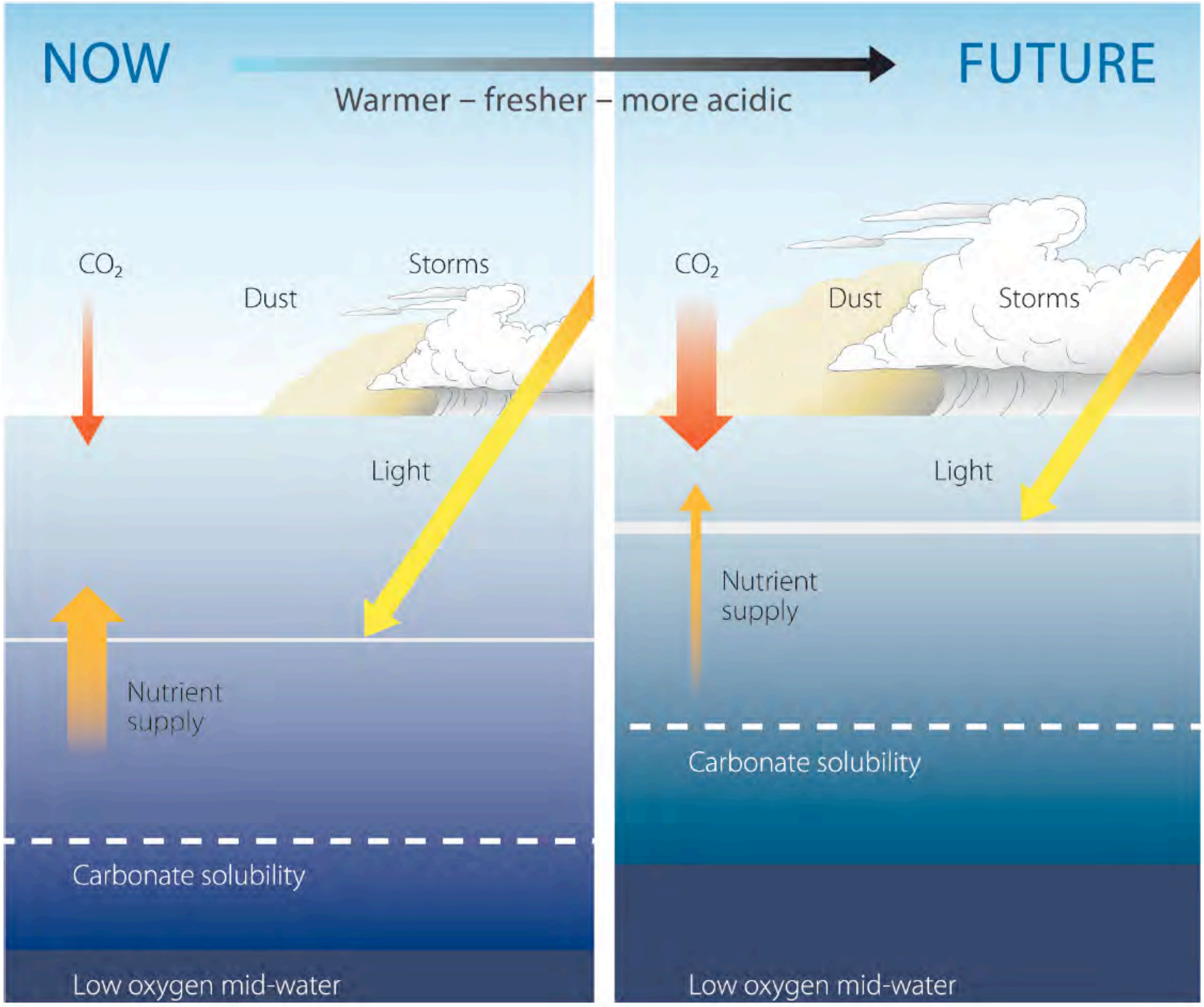


Figure 6-9: Projected alteration of oceanic properties and atmospheric events due to a changing climate. Properties will be altered across the water column, from the mid-water stratum to the sunlit surface layer, and will influence the fitness of the residence biota. Changes in storm activity and dust deposition will influence ocean physics and chemistry, with consequent effects on ocean ecosystems (courtesy of Boyd and Law, 2011).

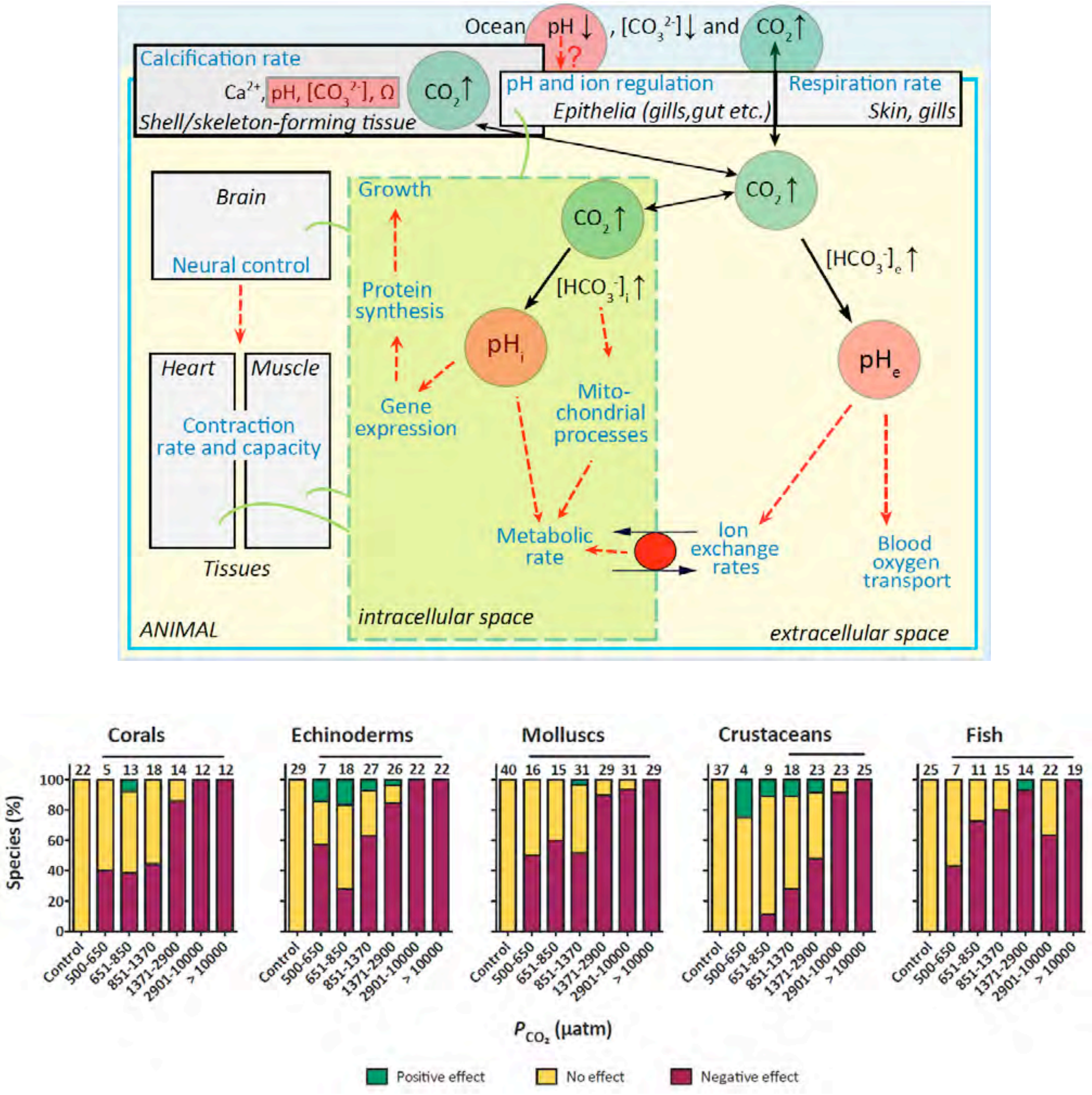


Figure 6-10: Top: Responses of a schematized marine animal (blue line) to ocean acidification (OA). Effects are mediated via diffusive entry of accumulating CO_2 (dark green, black arrows) into body compartments, resulting in a drop in compartmental pH (highlighted in red) and its effects (red dashed arrows) on various processes (light blue) as well as calcium carbonate saturation state (Ω) at calcification sites (after Pörtner, 2008). Variable sensitivity depends on the degree of pH decline and compensation, depending on the capacity of transmembrane ion transport. Bottom: % fraction of studied scleractinian coral, echinoderm, molluscan, crustacean and fish species affected negatively, positively or not at all by various levels of ambient CO_2. Effects considered include those on life stages and processes reflecting physiological performance (O_2 consumption, aerobic scope, behaviours, scope for behaviours, calcification,

growth, immune response, acid-base balance, gene expression, fertilization, sperm motility, developmental time, production of viable offspring, morphology). As not all life stages, parameters 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 CO_2 range, variable species numbers result (on top of columns). The total number of species studied for a given group is represented as the number above the control column. Horizontal bars above columns represent frequency distributions significantly different from controls (from Wittmann and Pörtner, subm.).

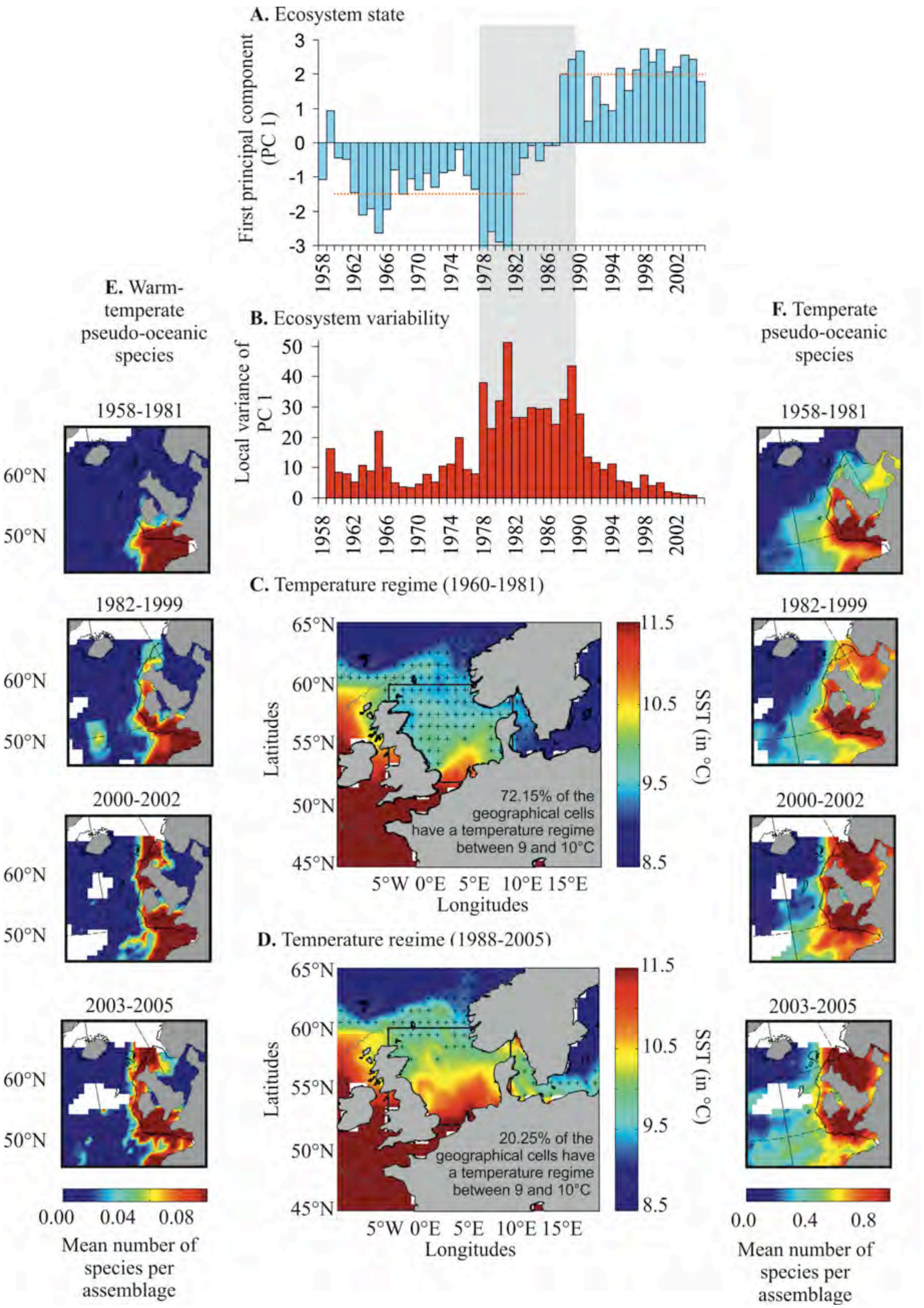

A. Ecosystem state
First principal component (PC 1)
3
2
1
0
-1
-2
-3
1958
1962
1966
1970
1974
1978
1982
1986
1990
1994
1998
2002
B. Ecosystem variability
Local variance of PC 1
50
40
30
20
10
0
C. Temperature regime (1960-1981)
65°N
60°N
55°N
50°N
45°N
Latitudes
5°W 0°E 5°E 10°E 15°E
Longitudes
72.15% of the geographical cells have a temperature regime between 9 and 10°C
11.5
10.5
9.5
8.5
SST (in °C)
D. Temperature regime (1988-2005)
20.25% of the geographical cells have a temperature regime between 9 and 10°C
E. Warm-temperate pseudo-oceanic species
1958-1981
1982-1999
2000-2002
2003-2005
60°N
50°N
0.00
0.04
0.08
Mean number of species per assemblage
F. Temperate pseudo-oceanic species
0.0
0.4
0.8

Figure 6-11

Figure 6-11: **A**. Long-term changes in the ecosystem state based on 5 biological parameters (phytoplankton colour index, mean size of calanoids, mean calanoid diversity, an index of change in plankton composition and cod recruitment). The orange line denotes the mean ecosystem state for the period prior and after the abrupt ecosystem shift. **B**. Long-term changes in the multiscale temporal local variance of the ecosystem state (in red). High values indicate pronounced year-to-year changes in the ecosystem state. The light gray band shows the unstable period (1980-1989). **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 (9-10°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. From Beaugrand *et al*. (2008) and Beaugrand *et al*. (2009).

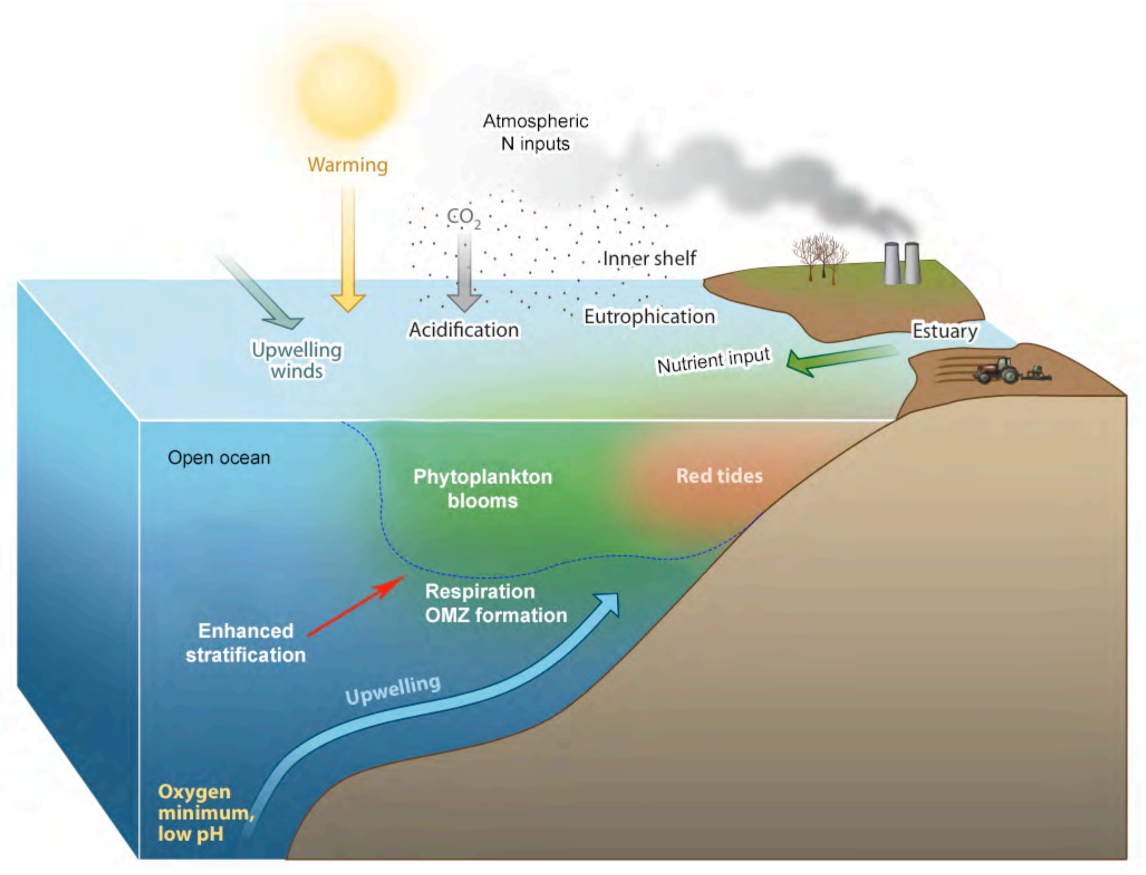
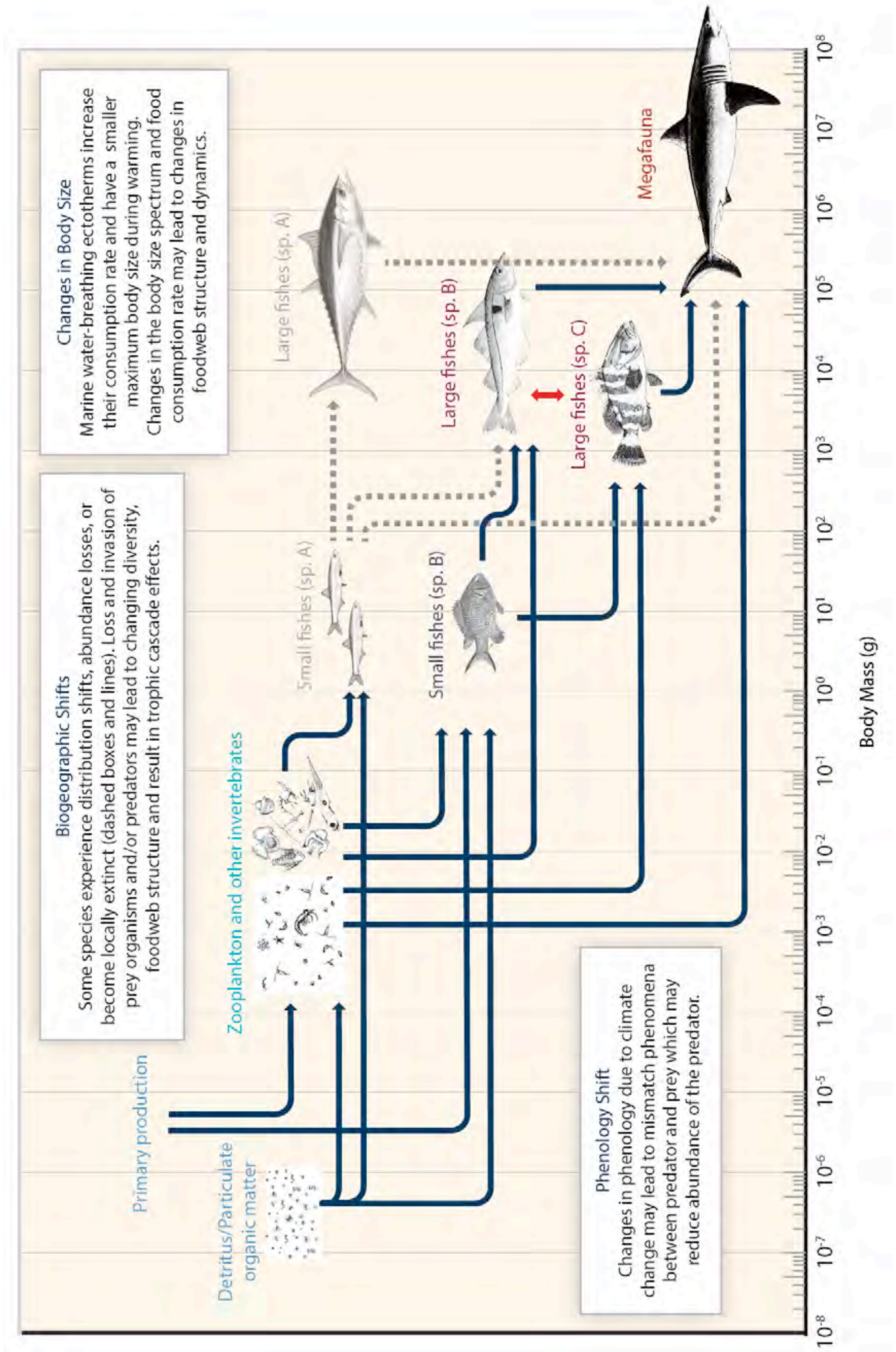


Figure 6-12: Schematic illustrating the principal mechanisms underlying the formation of hypoxic conditions and their biological background (modified from Levin *et al.* 2009; Levin and Sibuet, 2012). The buoyancy flux from fluvial discharges produces sharp density stratification at the base of the freshened layer (also valid for icemelt, 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 phytoplankton blooms. The enhancement of oxygen consumption due to respiratory catabolism of sinking organic matter results in hypoxic conditions of OMZs. Heating of the upper layer further increases stratification, while the wind-driven upwelling of hypoxic, nutrient-rich water from deeper layers adds to the formation of the oxygen minimum zone.



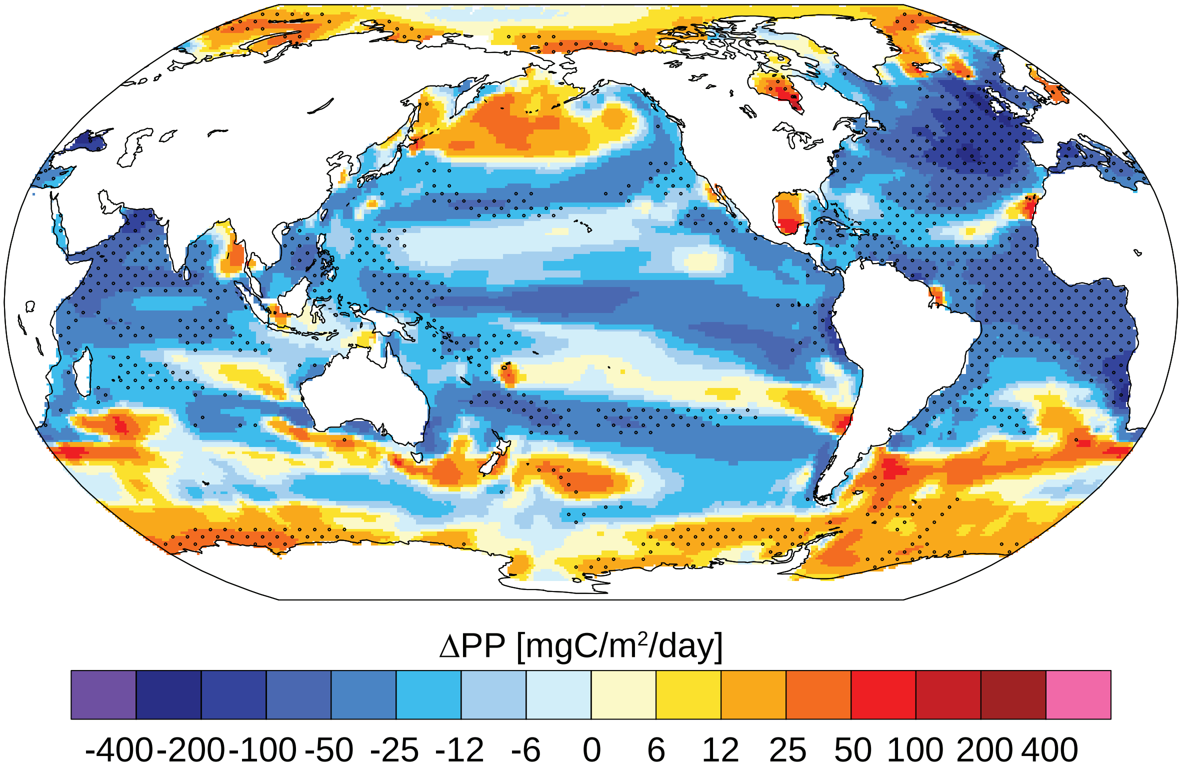
Biogeographic Shifts
Some species experience distribution shifts, abundance losses, or become locally extinct (dashed boxes and lines). Loss and invasion of prey organisms and/or predators may lead to changing diversity, foodweb structure and result in trophic cascade effects.

Changes in Body Size
Marine water-breathing ectotherms increase their consumption rate and have a smaller maximum body size during warming. Changes in the body size spectrum and food consumption rate may lead to changes in foodweb structure and dynamics.

Phenology Shift
Changes in phenology due to climate change may lead to mismatch phenomena between predator and prey which may reduce abundance of the predator.

Figure 6-13

Figure 6-13: Schematic diagram of a marine foodweb and the expected responses to climate change including ocean acidification. A coupled pelagic and benthic foodweb is typically structured by the body size spectrum of species. Warming, hypoxia and ocean acidification lead to biogeographical shifts, changes in species abundance and in the dynamics of trophic interactions. The foodweb resulting from climate change includes reductions in the body size of organisms, changes in species composition and the resulting reconfiguration of trophic linkages. Fishing generally removes large-bodied and vulnerable species and truncates the body size spectrum of the community. As a result, the detection and attribution of foodweb responses to climate change are strongly confounded by fishing effects. The arrows represent species interactions (e.g., between predator and prey or competition for food or space). Broken lines (boxes and arrows) indicate the loss of populations and trophic linkages due to climate change.



Color: Multi-model mean change
Stippling: Areas where all models agree on sign

Figure 6-14: Multi-model mean changes of projected vertically-integrated net primary production (small and large phytoplankton). To indicate consistency in the sign of change, regions are stippled where all four models agree on the sign of change. Changes are annual means under the SRES A2 scenario (between RCP6.0 - 8.5) for the period 2080 to 2099 relative to 1870 to 1889, after Steinacher *et al*. (2010).

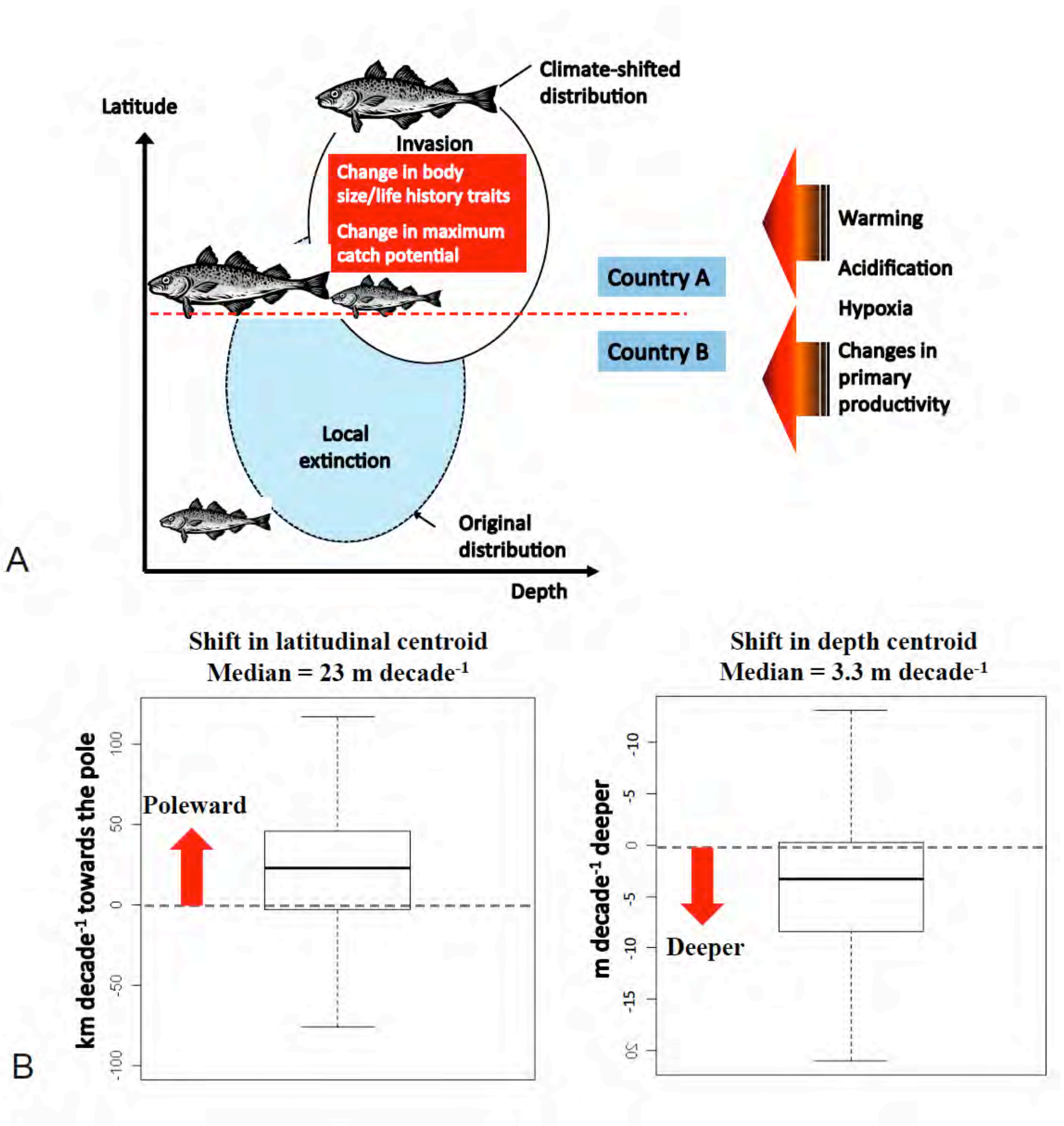


Figure 6-15 A, B

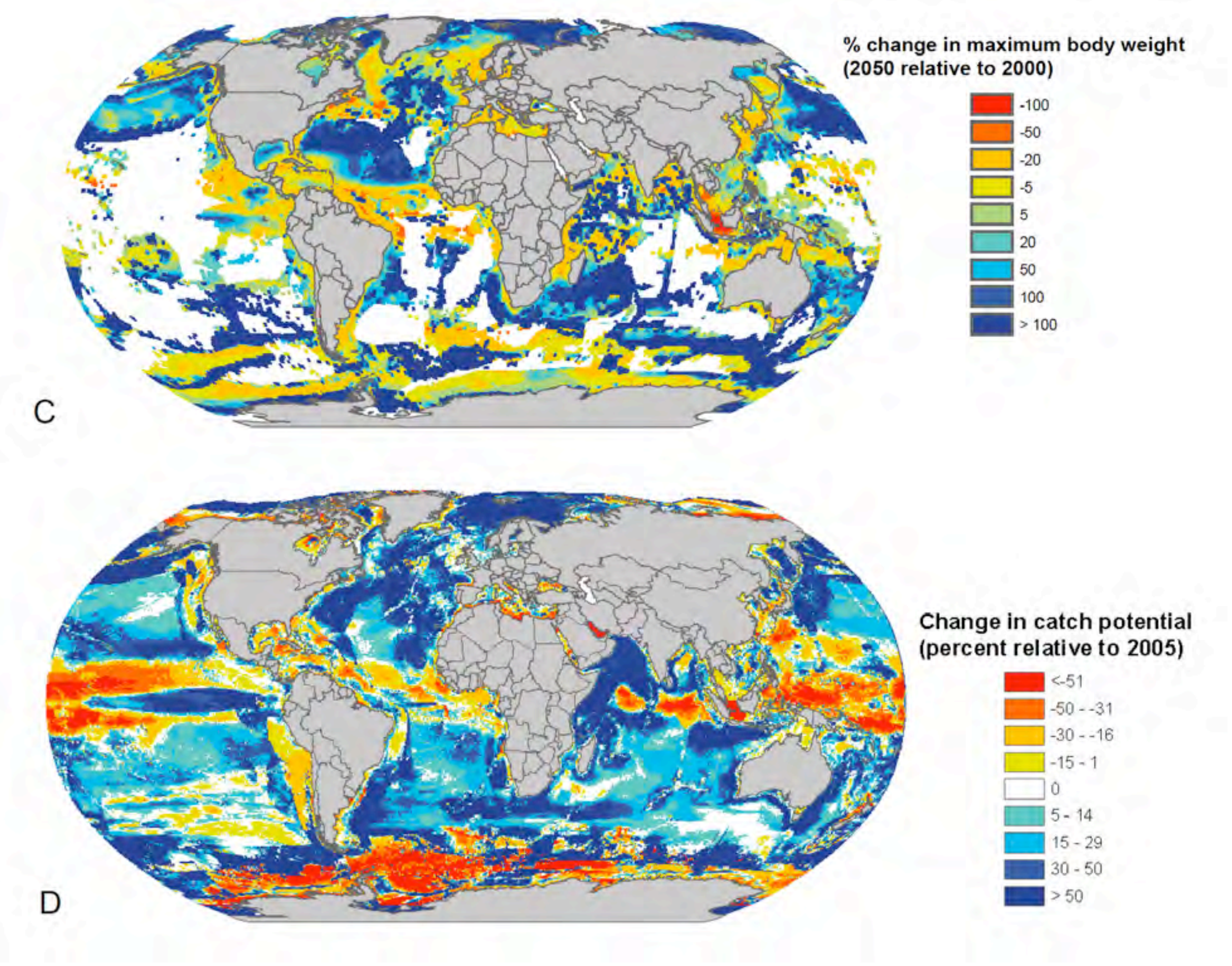


Figure 6-15: Scenarios of climate change effects on the biogeography, biology and fisheries catch potential of marine fishes and invertebrates. (A) Hypothesis of changes in distribution, biology and fisheries catch potential of fish stocks under climate change. (B) Example of a projected rate of shift in distribution range along latitude and depth for 610 exploited demersal fish species from 1991-2010 to 2041 – 2060 under the SRES A2 scenario (Cheung et al., 2011; Cheung et al., 2012a). (C) Projected change in the maximum body size of 610 species of marine fishes from 2000 to 2050 under the SRES A2 (between RCP6.0 - 8.5) scenario (Cheung et al. 2012a). The white area is not occupied by the sampled species. (D) Example of projections of maximum fisheries catch potential of 1000 species of exploited fishes and invertebrates from 2000 to 2050 under the SRES A1B scenario (redrawn from Cheung et al., 2010)

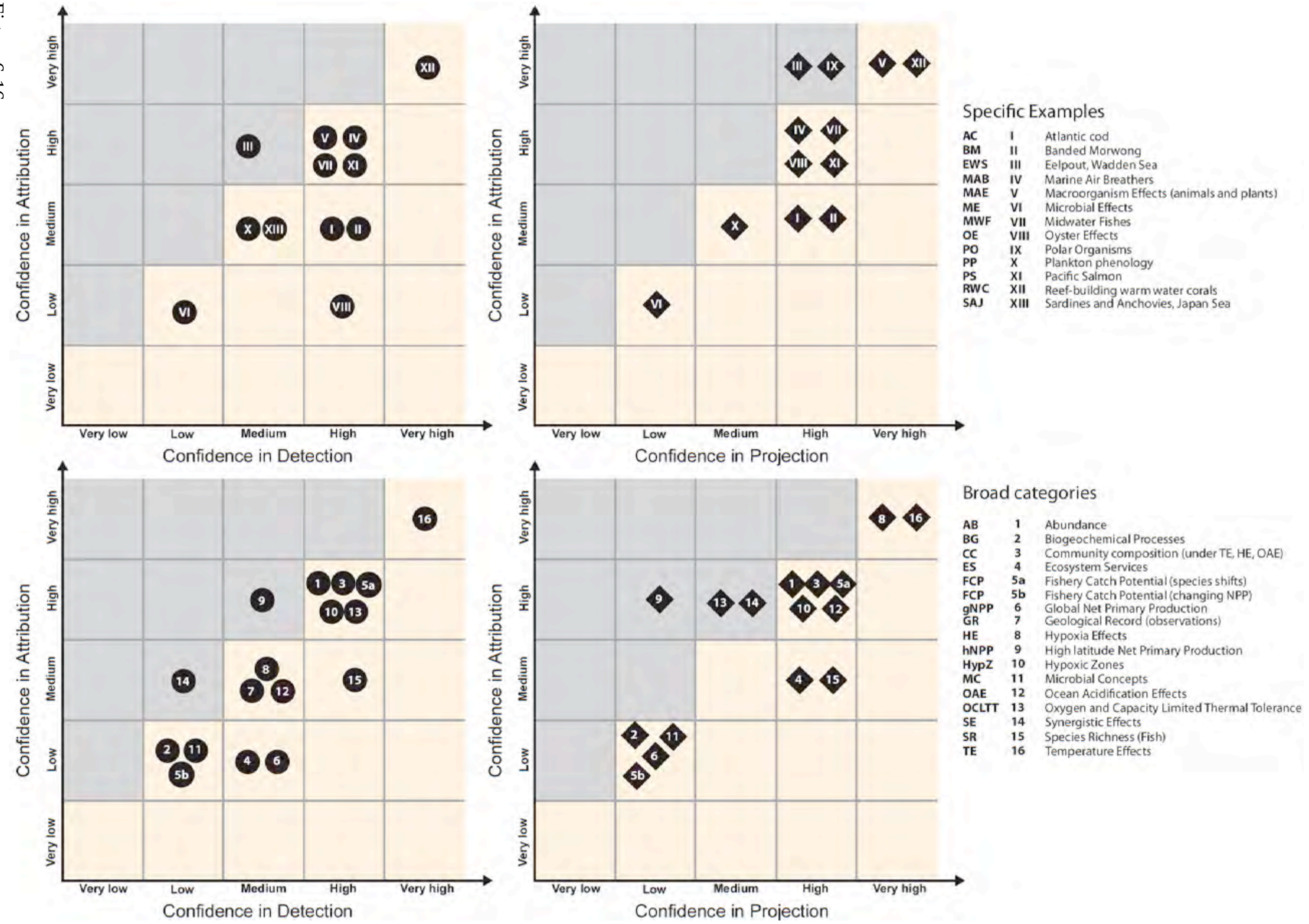

Confidence in Attribution
Very low
Low
Medium
High
Very high
Confidence in Detection
Confidence in Projection
XII
III
V
IV
VII
XI
X
XIII
I
II
VI
VIII
IX
16
9
1
3
5a
10
13
14
8
7
12
15
2
11
5b
4
6
Specific Examples
AC I Atlantic cod
BM II Banded Morwong
EWS III Eelpout, Wadden Sea
MAB IV Marine Air Breathers
MAE V Macroorganism Effects (animals and plants)
ME VI Microbial Effects
MWF VII Midwater Fishes
OE VIII Oyster Effects
PO IX Polar Organisms
PP X Plankton phenology
PS XI Pacific Salmon
RWC XII Reef-building warm water corals
SAJ XIII Sardines and Anchovies, Japan Sea
Broad categories
AB 1 Abundance
BG 2 Biogeochemical Processes
CC 3 Community composition (under TE, HE, OAE)
ES 4 Ecosystem Services
FCP 5a Fishery Catch Potential (species shifts)
FCP 5b Fishery Catch Potential (changing NPP)
gNPP 6 Global Net Primary Production
GR 7 Geological Record (observations)
HE 8 Hypoxia Effects
hNPP 9 High latitude Net Primary Production
HypZ 10 Hypoxic Zones
MC 11 Microbial Concepts
OAE 12 Ocean Acidification Effects
OCLTT 13 Oxygen and Capacity Limited Thermal Tolerance
SE 14 Synergistic Effects
SR 15 Species Richness (Fish)
TE 16 Temperature Effects

Figure 6-16

Figure 6-16: Overview of the levels of confidence in detection (left), as well as in projection (right) of climate change effects on ocean systems, in relation to the levels of confidence in attributing these effects to the respective climate forcings. Some climate change impacts have been condensed into rather broad categories in order not to overpopulate the figure (e.g. **BG**, **B**io-**G**eochemical Processes). Note that the term attribution is not only used in the context of detections but also for projections. Projections include both qualitative and quantitative extrapolations and simulations from fundamental principles and models. Experiments (field, laboratory and modeling) simulating future conditions may enhance the respective confidence levels above those for detection which refers to present day observations in the field. The empirical observations resulting from those experiments are then attributable to the respective drivers. Confidence rises further if these experiments identify the affected mechanisms and their response to future conditions. See text for further discussion of the depicted examples and categories. Confidence assignments focus on the nature and size of effects, not on the capacity of models to reliably quantify their magnitude.

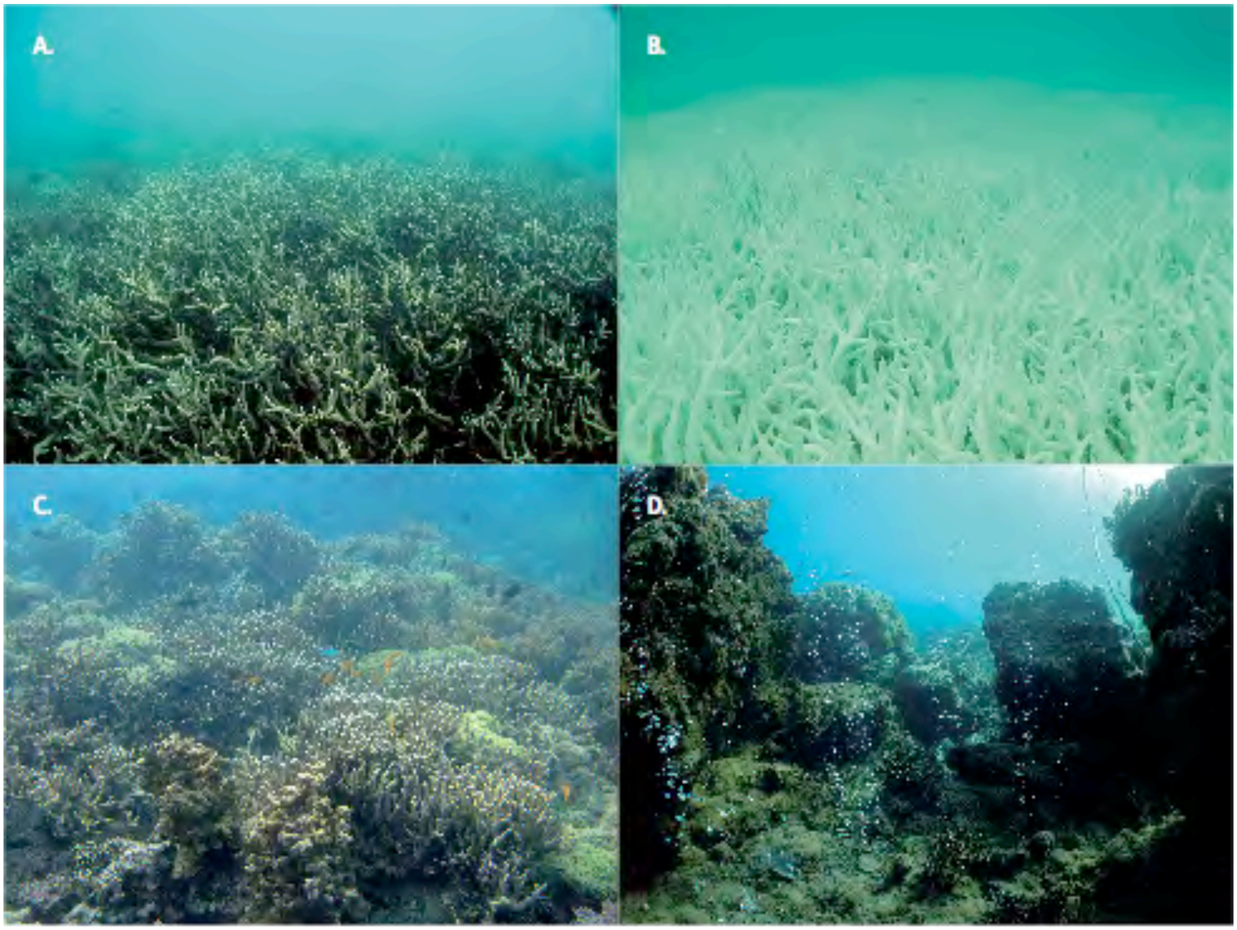


Figure CR-1: A and B: the same coral community before and after a bleaching event in February 2002 at 5 m depth, Halfway Island, Great Barrier Reef. Coral cover at the time of bleaching was 95% bleached almost all of it severely bleached, resulting in mortality of 20.9% (Elvidge et al., 2004). Mortality was comparatively low due in part because these communities were able shuffle symbiont types to more thermo-tolerant types (Berkelmans and van Oppen, 2006; Jones et al., 2008). C and D: three CO2 seeps in Milne Bay Province, Papua New Guinea show that prolonged exposure to high CO2 is related to fundamental changes in coral reef structures (Fabricius et al., 2011). Coral communities at three high CO2 (Fig. XB; median pHT 7.7, 7.7 and 8.0), compared with three control sites (Fig. XA; median pHT 8.02), are characterized by significantly reduced coral diversity (-39%), severely reduced structural complexity (-67%), low densities of young corals (-66%) and few crustose coralline algae (-85%). Reef development ceases at pHT values below 7.7. Photo credit: R. Berkelmans (A and B) and K. Fabricius (C and D).

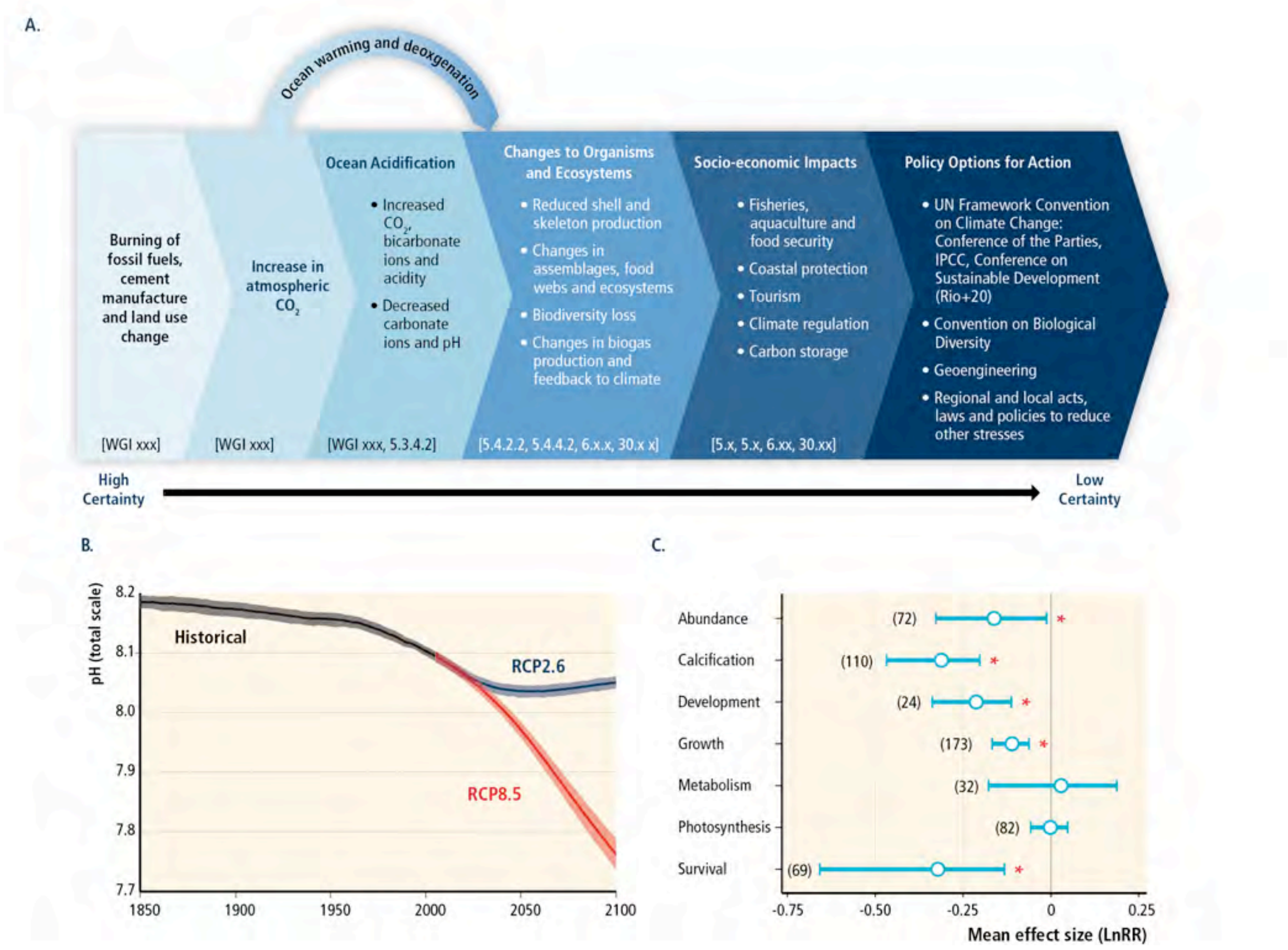


Figure OA-1: A: Overview of the chemical, biological, socio-economic impacts of ocean acidification and of policy options (adapted from Turley & Gattuso, 2012). B: Multi-model simulated time series of global mean ocean surface pH (on the total scale) from CMIP5 climate model simulations from 1850 to 2100. Projections are shown for emission scenarios RCP2.6 (blue) and RCP8.5 (red) for the multi-model mean (solid lines) and range across the distribution of individual model simulations (shading). Black (grey shading) is the modelled historical evolution using historical reconstructed forcings. The models that are included are those from CMIP5 that simulate the global carbon cycle while being driven by prescribed atmospheric CO$_2$ concentrations. The number of CMIP5 models to calculate the multi-model mean is indicated for each time period/scenario (IPCC AR5 WG1 report, Figure 6.28). C: Effect of near future acidification on major response variables estimated using weighted random effects meta-analyses, with the exception of survival which is not weighted (Kroeker et al., in press). The effect size indicates which process is most uniformly affected by ocean acidification but large variability exists between species. Significance is determined when the 95% bootstrapped confidence interval does not cross zero. The number of experiments used in the analyses is shown in parentheses. * denotes a significant effect.