Chapter 6. Ocean Systems

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Executive Summary

This chapter addresses climate change impacts on natural and human systems from the point of view of the global ocean.

Key interrelated factors changing in the oceans with the potential to cause biological and, thereby, human system responses include changes in temperature means and extremes, the oxygen inventory and associated ammonia and sulfide levels, levels of anthropogenic CO_2 and associated ocean acidification, nutrient stocks and their redistribution, ice melt, salinity fluctuations, underwater light regime and food availability (*robust evidence, high agreement, high confidence*). Alteration of oceanographic conditions will be driven by shifts in water mass boundaries and ocean frontal features, along with altered thermohaline stratification (nutrient supply) and mixed layer depth (light regime), ocean warming, acidification and hypoxia (*high confidence*). [6.1.1, 6.2.2.1]

The paleo-record illustrates the sensitivity of ocean ecosystems to climate change and confirms some of the key environmental drivers involved (*high confidence*). Present rates of climate change are unprecedented compared to the paleo-record (linked to ~10 times faster atmospheric CO_2 accumulation than during the Paleocene-Eocene Thermal Maximum (PETM) (*robust evidence, high agreement, high confidence*). Calcification responses in key functional groups point to the role of ocean acidification in bringing about responses of past ecosystems to climate change. Mass extinctions in the marine realm occurred under the effect of combined environmental drivers (*high confidence*), including temperature extremes, nutrient supply, oxygen deficiency and CO_2 enrichments. [6.1.2]

Marine ecosystems respond to climate change, with examples found in virtually all of the world's oceans (*very high confidence*). Individual observations of responses to climate change indicate three kinds of general, interrelated responses of marine species, shifts in distribution (geographic ranges), phenology (timing of seasonal activities) and inter-specific interactions including competition between species and predator-prey system dynamics. Variations in these responses will inevitably lead to feedbacks on population dynamics and may underpin changes in species abundance and community composition (*high confidence*). [6.2, 6.3, 6.5]

The marine environment will be altered in a complex manner by climate change. These changes lead to regional shifts in microbial phenology, regional alteration of biological processes including nitrogen fixation and phytoplankton productivity as well as changes in phytoplankton community structure (*high confidence*). Further biogeochemical processes involving microbes and higher trophic levels and identified as responsive to climate change include carbon sequestration and export production, calcification and respiration. Together they may contribute to oxygen depletion and acidification, especially in subsurface oxygen minimum zones (OMZs). Upscaling to global ecosystems though highlights that identifying which microbial species or groups and processes are affected and how these will be altered by climate change is presently based on *limited evidence*, *low agreement* and *confidence* as these organisms and their reactions to the physical change are extremely diverse. Changes in oceanographic conditions can also cause reduced primary productivity if the areal extent of nutrient-poor gyre increases. The global implications of such observations and projections for biogeochemical cycles have *low confidence*. [6.3, 6.5] In general, there are many unknowns, for example, how adaptation by the biota to these physical changes will manifest itself, or how the different interlinked components of an ecosystem will cumulatively respond to climate change. [6.2, 6.3]

A warming ocean may initially enhance the metabolic rates of microbes but may also begin to challenge their thermal tolerance and affect their abundance, distribution and community structure (*medium confidence*), however, there is *limited evidence* and *low confidence* on which physiological mechanisms are setting differential physiological performances and how microbial tolerances and the interactions between planktonic organisms can be qualified. There is *limited evidence* (*low confidence*) from experimental systems that warming leads to enhanced build-up of heterotrophic bacterial in relation to phytoplankton biomass. The bacteria then absorb a larger proportion of inorganic nutrients and organic matter produced by phytoplankton, causing a strengthening of heterotrophy and microbial carbon flow in coastal systems. [6.2.2.2, *low confidence*] Some phytoplankton groups (coccolithophores) display warming-induced poleward shifts in distribution in the subpolar Southern Ocean and the Bering Sea. At high polar latitudes a longer growing season, due to more sea-ice free days and higher underwater irradiances may have increased phytoplankton productivity in Arctic waters. This contrasts with decreased phytoplankton stocks and productivity in the vicinity of the Antarctic Peninsula, via the interplay of sea-ice and cloud cover along with altered wind velocities. Underwater light climate may thus be altered differently by density stratification and changes to surface mixed layer depth, cloudiness and/or to alteration of sea-ice areal extent and thickness. The capacity for photophysiological acclimation and limits to its plasticity may be involved in the organismal responses to altered light regimes but have *limited evidence* and *low confidence*. Environmental conditions in warming, more nutrient rich coastal oceans may benefit the development of harmful algal blooms or the distribution of pathogens like cholera (*limited evidence, low confidence*). [6.4.2.3] Warming may both increase the grazing rate of zooplankton and affect phytoplankton body size (*medium confidence*). [6.2.2.1, 6.3.2]

The oceans provide about half of global net primary production (NPP). NPP is expected to change in the future, with regional differences and to increase at high latitude (*high confidence*). However, numerical predictions of whether the global surface ocean NPP is changing are made with *low confidence* as there are conflicting trends reported dependent on the methodology used and region studied. Projections from coupled carbon cycle-climate models and empirical models suggest that global primary production will change (*high confidence*) and that NPP will decrease at low to mid latitudes but increase at high latitudes in the 21st century under a range of climate scenarios. The direction, magnitude and regional differences of a global change of NPP in the open ocean as well as in coastal waters have *limited evidence*, *low agreement* and thus, *low confidence* for a decrease by 2100. [6.3.1, 6.5.1]

Complex (macro)-organisms (water breathing animals including zooplankton, seaweeds, seagrasses) specialize on the prevailing regional and local temperature regimes, with the result of differential widths of their windows of thermal tolerance and accordingly, differential thermal sensitivities, sometimes between populations (*high confidence*). Water breathing animals display metabolic stimulation upon warming, their thermal windows show a trend to be narrowest in early and spawning life stages as well as sluggish lifeforms (*medium confidence*). Thermal windows are narrowest in Antarctic animals, widest at temperate mid-latitudes and moderately wide at tropical latitudes (*medium* to *high confidence*). These relationships define temperature dependent biogeography and its response to climate change (*robust evidence, medium agreement* and *confidence*). Marine species that already live close to their upper thermal limits will be most sensitive to climate change (*high confidence*). Among macrophytes, seagrasses may tolerate higher temperatures than seaweeds.

For marine water breathing animals the physiological basis of thermal sensitivity has been unraveled and formulated in the concept of oxygen and capacity limited thermal tolerance (OCLTT). The concept explains the shape and width of the performance curve and identifies which processes cause shifts in energy budget, an early decrease in performance and thereby initiate a loss in fitness, with the respective implications at ecosystem level (*robust evidence, high agreement, high confidence*). Thermal windows change dynamically according to developmental stage, mode of life, body size and activity levels (more mobile or small species displaying high resting metabolic rates and high functional capacities result more eurythermal, i.e. they cover wider temperature ranges), thereby leading to differential sensitivities and biogeographies, possibly with the respective consequences for species interactions (*medium confidence*). The concept supports integration of the effects of further drivers like progressive hypoxia and ocean acidification. Equivalent concepts are not available for other groups of organisms. [6.2.2.1]

Mechanistic insight readily explains why and how animals are affected by temperature extremes through losses in abundance, local extinction and latitudinal shifts (*robust evidence, high agreement, very high confidence*) and how such relationships cause regime shifts, or can be affected through trends in ocean stratification and productivity. [6.3.2, 6.5.2] Once warming temperature approaches their tolerance limits, polar species will be unable to migrate to cooler waters and especially Antarctic species possess limited capacity to acclimate to rising temperatures (*robust evidence, medium agreement, medium confidence*). Some tropical and warm water fish, invertebrates and macrophytes at low to medium latitudes also live close to their upper thermal limits and will respond sensitively to thermal extremes and synergistic drivers like ocean acidification (*robust evidence, medium agreement, medium confidence*). [6.2.2.3, 6.2.2.4, 6.3.2]

Expansion of hypoxic zones (e.g. Oxygen Minimum Zones, OMZs in the pelagic realm) constrains the habitat of oxygen dependent macroorganisms and microbes (the latter in extreme hypoxia) and benefits anaerobic

microbial life now and into the future (*high confidence*). *Robust evidence* indicates that with enhanced warming-induced stratification, reduced ocean circulation and the decomposition of organic matter by heterotrophic organisms, mostly bacteria both create specialized, microbially dominated ecosystems and sustain OMZs by their diversity and plasticity of metabolism (*high confidence*). Warming-induced OMZ expansion may not be continuous but influenced by decadal climate events. Bacterial and archaeal denitrification, by the combined effects of dissimilatory nitrate reduction and anaerobic ammonium oxidation (anammox), is common in OMZs and can lead to the loss of fixed nitrogen (mostly in the forms of N_2 gas and the greenhouse gas N_2O). The resulting hypoxia affects animals by replacing more active, oxygen dependent species with specialists temporarily or permanently adapted to hypoxic environments at low species richness. These specialists are predominantly sluggish life forms that have low oxygen demand and high capacities to exploit available oxygen (*high confidence*). Due to the concomitant elevation of CO_2 partial pressure, calcifiers are largely excluded from OMZs (*high confidence*). Warming reduces tolerance to hypoxia (*high confidence*); small animals are more capable to sustain permanent hypoxia than large ones. Conversely, hypoxia constrains thermal tolerance. Hypoxia tolerance varies dynamically with temperature, food consumption, oxygen demand and other environmental stressors including elevated CO_2 partial pressures (*medium evidence, high agreement, high confidence*). [6.2.2, 6.3.3]

Ocean acidification causes marine organisms to take up accumulating CO_2 passively by diffusion leading to permanently elevated internal CO_2 partial pressures and an ongoing challenge to acid-base regulation, with implications for alteration of the rates of a wide range of physiological processes and associated energy demand and allocation (*medium evidence*, *medium* to *high confidence*). A wide range of sensitivities to projected rates of ocean acidification is evident between and within phyla and genera (*high confidence*). Calcified structures for defence and structural support are found across organismal kingdoms and the sensitivity of calcification to ocean acidification has received the widest attention. Calcifying organisms allocate energy to ion transport and acid-base regulation as relevant for the sustenance of calcification rates, and may result more sensitive with low capacities of ion and acid-base regulation (*limited* to *medium evidence, medium agreement and confidence*). [6.2.2]

Among macrophytes and phytoplankton the physiological effects of ocean acidification may have the greatest potential effect on calcifying species – crustose algae and the coccolithophores (*medium confidence*), but differs largely between groups. In laboratory experiments most macrophytes (seaweeds and macroalgae) respond positively to elevated CO_2 levels by increasing growth (*medium evidence and agreement, high confidence*). Among coccolithophores, responses are species- and strain-specific, also with respect to the response of calcification. Capacities of acid-base regulation have not been compared, preventing any overarching mechanistic understanding among phytoplankton species. A potential for evolutionary adaptation and, thereby, compensation for effects of ocean acidification may exist (*limited evidence, medium confidence*). Elevated CO_2 may cause increased rates of carbon fixation, depending on how the microbes acquire the carbon, and of N_2 fixation (in cyanobacteria). However, responses are variable and influenced by other factors like light, energy, oxygen, nutrient availability and temperature (*limited evidence*, *low agreement*, *low confidence*). [6.2.2.2]

Among animals, the effects of ocean acidification are species- and life stage-specific with a trend for sensitivity to be highest in early life stages (*high confidence*). Sensitivity may depend on the capacity for acid-base regulation and associated compensation of CO_2 induced acidosis (*medium evidence, agreement* and *confidence*). Experimental evidence suggests that such capacity is highest in more active marine animals, especially in fishes and cephalopods and also shallow-water crustaceans (*robust evidence, high confidence*). Feeding status supports individuals to reach their species specific capacities of acid-base and ion regulation and thus resilience. Ocean acidification constrains the dimensions of climate dependent thermal windows (*high confidence*) as shown in representatives from various phyla, with projected consequences for biogeography (range contractions) and species interactions (changes in relative performance, predator-prey relationships, competitiveness) (*limited evidence, low confidence*). The relative sensitivity of species from various climate zones and the degree or velocity of evolutionary adaptation remains poorly understood. Variability among larval genotypes may accelerate such adaptation (*limited* to *medium evidence, medium agreement and confidence*). [6.2.2.4]

Reef-building warm water corals respond sensitively to both warming and acidification and have already encountered a rising frequency of thermally induced bleaching events (loss of symbiotic algae) with the result

of decreased live coral cover (1-2 % per year) **in many reefs (*high confidence*).** Corals and coral reefs live close to their upper thermal limits and respond sensitively to thermal extremes and synergistic stressors like ocean acidification (*robust evidence, high agreement, high confidence*). With even moderate warming, bleaching will occur with ever increasing frequency and severity until it will *likely* occur on an annual basis by mid to late this century, associated with an increase in the area of bleaching and in the fraction of coral colonies bleached under a range of climate scenarios (*very high confidence*). The changing reef will see climate dependent species replacements, according to species-specific sensitivities and a wide heterogeneity of responses. There is *limited evidence* and *low agreement* that corals can rapidly acclimate or adapt to the unprecedented changes in sea temperature such that the *de novo* appearance of more thermally tolerant symbioses and especially their establishment at ecosystem scales remains largely unknown. There is *robust evidence* that the calcification rate of corals is reduced with increasing ocean acidification. Response and resilience to ocean acidification are species-specific; nutrient availability to symbionts and heterotrophic feeding improves resistance (*medium evidence, high agreement, high confidence*). Temperature acts synergistically with the impacts of perturbed sea water chemistry, reducing calcification but also increasing sensitivity to other impacts such as the loss of symbionts (*medium evidence, high agreement, high confidence*). A limited number of experiments in cold water corals has shown significant capacity to compensate for exposure to acidified seawater. [6.2.2.4, 6.3.2, 6.5.2.]

Among animals, air breathing marine birds, mammals, and turtles are not directly affected by ocean acidification or hypoxia, but are indirectly impacted through sensitivities of their prey to these altered conditions [*high confidence*). There is thus no unifying influence of climate change on this group. Detected effects on individual species are mostly mediated through climate dependent changes in habitat structure (sea ice) and food availability, especially in mammals and birds (*robust evidence, high agreement, high confidence*). Modeling projections suggest an increase in cetacean species richness above 40° latitude in both hemispheres and a decrease in both pinniped and cetacean richness at lower latitudes by mid-century 2040-2049 under the SRES A1B scenario. Distribution of loggerhead turtle is projected to expand poleward in the Atlantic Ocean and to benefit from an increase in available habitat in the Mediterranean Sea (*medium confidence*). [6.2.2.4.]

Projected future changes in the physical and biogeochemical conditions of the ocean are expected to cause poleward shifts in the distribution and abundance of marine fishes and invertebrates or equivalent shifts to deeper and cooler waters (*high confidence*). The rate of range shifts is largely determined by the warming trend at regional scales and projected to be three times higher for pelagic than for demersal fishes in the 21st century under a range of climate scenarios (*medium confidence*). As a result, high latitude regions (the Arctic and Southern Ocean) are projected to have high rates of species invasions while high rates of local extinction are projected for the tropic, sub-Arctic and semi-enclosed seas (e.g., Mediterranean Sea, Persian Gulf) (*high confidence*). [6.5.2]

Variability in oceanographic conditions is linked to large fluctuations in ecosystem structure and fish stocks, with a key role for temperature and circulation regimes as drivers (*robust evidence, high agreement, very high confidence*). Long-term observations reveal shifts in phenology, abundance, migration patterns, reduction in body size and largely poleward shifts in biogeographical distribution (20 to 200 km per decade) of zooplankton and fish (*robust evidence, high agreement, very high confidence*). These are mainly attributed to temperature changes during climate variability and change (*very high confidence*), with an as yet unclear contribution of other environmental drivers (*low confidence*), which may become stronger in the future (ocean acidification, expanding hypoxia zones, changing food availability). As a consequence of reduced aerobic scope from warming, hypoxia and ocean acidification, the maximum body size of fishes and invertebrates may decrease (*low confidence*). It is projected that this will alter maximum body size of fishes at individual and community levels in the 21st century under the SRESA2 scenario (*low confidence*). Through species gains and losses correlated with warming, macroorganism diversity increases at mid and high latitudes and will fall at tropical latitudes (*medium confidence*). Such changes in species diversity and composition are projected to continue by 2050 under a range of climate scenarios (*medium confidence*). There is *medium confidence* that the biota in certain regions may be more vulnerable to change than in other regions, e.g., species occurring in semi-enclosed seas in general and, especially those highly endemic and exposed to hypoxic waters and animals at warming high polar latitudes. Therefore, changes in ecosystem characteristics are probably greatest in polar systems (*high confidence*) [6.3.2, 6.5.2.]

Climate change will lead to large-scale redistribution of global catch potential for fishes and invertebrates (*high confidence*). Depending on whether a decrease in global ocean NPP occurs, overall fisheries catch potential may decrease. In association with faunal displacements it will shift from low and mid to higher latitudes. [6.2.2.4, 6.3.2, 6.4, 6.5] Such changes are projected to comprise an average of 30–70% increase in yield of high-latitude regions (>50° N in the northern hemisphere), but a drop of up to 40% in the tropics by 2055 relative to 2005 under the SRES A1B scenario (*high confidence* for the general trend, *low* to *medium confidence* for the magnitude of change). [6.5]

Observations show enhanced ocean upwelling in Californian, Humboldt and Canary eastern boundary systems, which produce cooler surface waters associated with enhanced productivity, but unclear trends for higher trophic levels in those areas (*medium confidence*). If associated with exposures to hypoxic and corrosive (high CO_2) deep water, upwelling can be accompanied by significant ecosystem responses, such as a reduction in biomass of fish and invertebrate fauna. The effect of climate change on upwelling systems through stronger winds, altered current patterns or enhanced ocean acidification remains unclear. Extrapolation of such effects to the global level is currently not possible (*low confidence*). [6.1.1, 6.3.3, 6.3.4, 6.3.6]

Climate change has drivers (e.g. temperature, ocean acidification, hypoxia) causing effects on the oceans that are often influencing and amplifying each other. Additional human-induced drivers like pollution, nutrient input and associated eutrophication, as well as overfishing, result in enhanced vulnerability of natural systems to climate related forcings (*high confidence*). As a consequence, a decrease or shift in ecosystem services, e.g., through the availability of marine living resources will be accelerated and felt regionally. [6.3.6, 6.4, 6.5]

Human societies benefit from and depend on ecosystem services, including provisioning of food and other goods, climate and natural hazards regulation, cultural and supporting services, some of which may be affected by climate change (high confidence). There is *robust evidence and high agreement* that climate change will impact the marine ecosystems and their services. With *limited evidence* and *low confidence*, socio-economic consequences of drivers such as ocean acidification may be evident. The provision of open waterways for shipping is a specific supporting service that is very *likely* to change in specific, measurable ways in the next several decades. Reductions in sea ice in the Arctic may allow new trade passages such as the North West Passage to be established, thereby raising the possibility of economically viable trans-Arctic shipping, as well as increasing access to regional resources supporting natural resource extraction and tourism. [6.4]

Physical effects of climate change may act, under some circumstances, as an additional conservation pressure that can, however, not be mitigated by a reduction in human activities like fishing (*high confidence*). As an example, a reduction in the accidental capture of turtles in fishing gear may not successfully protect the population if a significant number of nesting beaches are impacted by sea-level rise or storm surges. Additional 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. [6.4]

All geoengineering approaches involving manipulation of the ocean to ameliorate climate change (fertilization by nutrient addition, binding of CO_2 by the addition of 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 focussing on solar radiation management (SRM) are fraught with the shortcoming that atmospheric CO_2 release and ocean acidification are left unabated unless SRM is combined with CO_2 emission reductions. [6.4]

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

The Ocean covers 71% of Earth's surface to an average depth of 3,800 m and represents more than 95% of the habitable environment of the planet. Approximately half of total annual planetary production of organic matter derives from marine plants, mostly microorganisms (Field *et al*., 1998). Ecological processes in the oceans have long been investigated, and yet many features important for biogeochemistry and ecological functioning on large scales, including environmental controls on photosynthesis, respiration and carbon storage are poorly known as most oceanic regions have never been sampled. Even in the areas studied extensively, for example, the North Atlantic Ocean, variability on temporal scales ranging from synoptic to interdecadal is poorly understood as long-term series of ecological data from the open ocean are generally rare. However, the available information indicates that oceanic ecosystems are particularly sensitive to stresses mediated by climate change, because physical forcing primarily controls nutrient supply and light regime and, hence, growth of phytoplankton, food availability for heterotrophs and the structure and function of the food webs.

The ocean in its entirety is simply too large and diverse to allow for exhaustive coverage by *in situ* observations. The concept of a minimal set of functional subunits (ecosystems) could be used to track and model the global ocean and climate change impacts as a whole. Barber (2001) saw “considerable heuristic power in the ecosystem concept because understanding gained in one ocean ecosystem can be used to predict the response of another ecosystem of the same kind that is geographically distinct from it.” Ecosystems are shaped by physical and chemical variables and are distinguished by their modes of energy capture and transfer to organisms in the food web, as well as by community succession that optimizes energy transfer and material cycling. Physical and chemical attributes therefore relate to biogeochemical processes, including carbon cycle dynamics. The ability to scale ecological knowledge in space and time is especially important for predicting the response of oceanic ecosystems to natural and anthropogenic climate variability and change.

Division of the ocean into discrete functional units may help to elucidate the ongoing and projected changes in key processes and carbon inventories (Figure 6-1). The oceans can be subdivided into biomes, which are distinct habitats controlled by complex interactions of specific physical and biological processes. Odum (1971) defined a biome as “the largest community unit which is convenient to recognize”. Longhurst (1998) identified 4 major ocean biomes (i.e., “*Westerlies”*, “*Trades”*, “*Polar”* and “*Coastal”*)*,* distinguished mainly by different physical mechanisms shaping the conditions in the upper mixed layer and then further subdivided these 4 biomes in each major ocean basin into a total of 51 provinces (Figure 6-1). Benthic habitats have also been classified based on total benthic organism biomass, sedimentary oxygen flux estimates and hard and sediment substrate structures (e.g. Jahnke, 1996; UNESCO, 2009, Levin *et al*., 2010). Marine benthos includes all organisms that live just above, on or in the seafloor including both soft sediment and hard substrates. Benthic organisms are usually less mobile than pelagic organisms, implying that dispersal and gene flow are more limited, also in forms that spend part of their lifecycles in the pelagic realm. All these organisms and ecosystems, as well as many semi-enclosed and marginal seas and numerous coastal habitats, must be assessed on a region-specific basis (see WGII, Chs 5, 28 and 30). The present chapter, however, is intended to focus on the general principles and processes characterizing the climate change impact on the ocean system as a whole and its use by human society. A broad understanding of functional mechanisms across all levels of biological organization, from molecular to organism to ecosystem must be achieved in order to accurately predict the ocean’s response to climate change.

[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 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).]

In order to assess the available evidence on the relationships between climate and ecosystem change, as well as to project future impacts, the chapter relies on climate change scenarios according to the concept of Representative Concentration Pathways (RCP, Moss *et al*., 2010). It starts with a discussion of the variability of the principal physical and chemical parameters of the oceans and builds 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.

6.1.1. Recent Trends and Projections of Physical and Chemical Parameters

6.1.1.1. Warming

The primary role of the world's ocean in the global climate system is related to its capacity to store heat. Over the period from 1970 to 2009 the ocean has absorbed more than 90% of the total increase in the heat content of the planet (Bindoff *et al.*, 2007, WGI Ch. 3). 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. Warming trends are strongest at high latitudes (WG1 Ch. 3). The consequence of the warming is intensified thermal stratification of the upper ocean, which has increased by about 4 % over the past 40 years (WGI Ch. 3), associated with a shoaling of the mixed water layer and hence increased light exposure of the phytoplankton that inhabit that zone. Coastal regions display large spatial variability in their temperature changes. For example, observations over 100 years in the Japan and East China Seas revealed warming trends by +0.7 to 1.7 °C/century, larger than the global average (+0.5 °C/century, Yamano *et al.*, 2011). Temperature rises in other semi-enclosed seas (Baltic Sea, North Sea, Black Sea) are also higher than the global average (Belkin, 2009) emphasizing the need to understand local effects of warming for an assessment of ecosystem impacts. The warming trend is accompanied by spatially variable changes in salinity. Increases in salinity result from reduced precipitation versus 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. This leads to lower salinity intermediate waters sinking at high latitudes, e.g. the Southern Ocean and North Pacific (Helm *et al.*, 2010, WGI Ch. 3). Warming and freshening may cause a weakening of the formation of intermediate waters at high latitude and of the formation of abyssal waters in polar regions (WGI Ch. 3) but long-term projections are not available (e.g. Matei *et al.*, 2012).

Attribution of temperature change to natural climate variability or anthropogenic warming, therefore, is relevant in identifying the anthropogenic influence on marine ecosystems. For example, approximately half the temperature variance in the North Atlantic can currently be accounted for by natural climate variability assessed from hydro-climatic indices during the period 1850-2007 (Atlantic Multidecadal Oscillation [AMO], East Atlantic [EA] Pattern, North Atlantic Oscillation [NAO]; Cannaby and Hüsrevoglu, 2009). The relative influence of hydro-climatic variability varies between regions. For example, during the period 1958-2005 in the extra-tropical part of the North Atlantic east of 20°W, the increase in sea temperature co-varied positively with the Northern Hemisphere temperature rise explaining 46% of the total variance in temperature, while the natural sources of hydro-climatic variability such as the NAO and an index of the Subarctic Gyre circulation only accounted for 26% of the total variance in temperature (Beaugrand *et al.*, 2009). It should be noted that global warming probably also acts on and through changes in these meteo-oceanic processes (Stephenson *et al.*, 2006), making it difficult to quantify the relative influence of natural and anthropogenic forcings.

[PROJECTIONS TO BE ADDED AFTER FOD]

[INSERT FIGURE 6-2 HERE
Figure 6-2: Last Century sea surface temperature variability. The top left map shows the long-term (1911 to 2011) sea surface temperature average. The top right map illustrates the temperature range calculated as the difference between the historical maximum and minimum values for each grid component. 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. Right hand histograms show 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).]

6.1.1.2. Acidification

Long term (i.e. decadal) observations from open-ocean time series sites and ships-of-opportunity have shown significant increases in upper ocean carbon dioxide concentrations (Watson *et al.*, 2009) and consequently, reductions in pH (Dore *et al.*, 2009, WGI, ch. 3). Scenarios of future atmospheric pCO_2 have been described by SRES and for forcings of climate change according to several RCPs (representative concentration pathways, Moss *et al.*, 2010, Meinshausen *et al.*, 2011). RCPs encompass non-CO_2 greenhouse gases and project different atmospheric concentrations of CO_2. All RCPs lead to atmospheric CO_2 levels (given as partial pressures, pCO_2, in μatm, 10^{-6} of atmospheric pressure, or the mole fraction in ppm (10^{-6}) of CO_2 in the humidified gas mixture) somewhat less than 500 μatm by 2050. Under RCP 2.6 this is followed by a decrease to 420 by 2100 before it falls to 360 μatm by 2300. By 2100, RCP 4.5 projects stabilization at around 540 μatm. under RCP 6.0 pCO_2 reaches 670 μatm and is projected to reach 750 μatm by 2300, while RCP 8.5 yields 940 by 2100 and 1960 μatm by 2300, respectively. The oceans serve as a large sink of anthropogenic CO_2 and thereby reduce global warming. At present the oceans continuously absorb 25% of the CO_2 emitted by human activity. Anthropogenic carbon was 151 ± 26 PgC in the global ocean in 2010, corresponding to an annual global uptake rate of 2.5 ± 0.6 PgC yr^{-1} (WGI, Ch. 3).

However, equilibration of sea water with rising CO_2 concentrations in air causes ocean acidification (OA), an increase in acidity, i.e. hydrogen ion (H^+) concentration in sea water, measured as a decline in pH ranging between -0.0015 and -0.0024 per year (WG1 Ch. 3, 6). Anthropogenic OA has started with the industrial revolution and is projected to reach all oceanic regions, surface and deep oceans. At present, OA has already led to a detectable rise in surface ocean pCO_2 and a decrease in pH (Dore *et al.*, 2009). Average surface ocean pH has decreased by more than 0.1 units relative to pre-industrial levels and is expected to drop by another 0.3 units by 2100 under the SRES A1B scenario (Caldeira and Wickett, 2003, 2005). OA also leads to a decrease of carbonate ion (CO_3^{2-}) concentration and of the saturation state (Ω) of calcium carbonates ($CaCO_3$; Zeebe and Westbroek, 2003; WGI, Ch. 3). Ω values >1 indicate an oversaturation of calcium carbonates in sea water (Ω is the ratio of products of in situ concentrations of calcium (Ca^{2+}) and carbonate ion (CO_3^{2-}) over the solubility products (SP) K^*_{SP} of $CaCO_3$ in aragonite or calcite, which are different mineralogical forms of carbonate at *in situ* temperature, salinity and pressure; $\Omega = [Ca^{2+}][CO_3^{2-}]/K^*_{SP}$). Ω is smaller for aragonite than calcite at a given carbonate ion concentration reflecting that aragonite is more soluble than calcite. The magnesium (Mg) content of calcite determines the solubility of this mineral phase such that high Mg calcite can be more soluble than aragonite. All of these minerals (calcite, Mg-calcite, or aragonite) are important components of shells or skeletons in many marine organisms (6.2.2.).

CO_2 levels are spatially and temporally variable, for example in oxygen deficient sediments and stratified water layers, including upwelling systems (Feely *et al.*, 2008). 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 variability. The few data sets that do exist are from long-term ocean stations (e.g., HOT, BATS, ESTOC; WGI, Figure 3-17). Variability in pH is higher in coastal areas than in the open ocean (Dore *et al.*, 2009, Wootton *et al.*, 2008; Hofmann *et al.*, 2012). The rate of acidification is 50% higher in the Northern North Atlantic than in the subtropical time series at BATS and ESTOC (Olafsson, 2009). The pH of the present day pelagic ocean varies by approximately one unit (10-fold in terms of hydrogen ion concentration) from 8.2 in highly productive regions to 7.2 in mid-water layers where excess respiration causes low oxygen and elevated CO_2 levels. In low flow environments, further CO_2 and thus pH variability can be introduced by the formation of boundary layers with pH values of 7.7 that are as low as those projected by ocean acidification models by the year 2100 under business as usual IS92A, close to RCP 8.5 (Hurd *et al.*, 2011). Ocean acidification adds to existing CO_2 levels and the resulting water pH values clearly deviate from the natural variability of pH (Friedrich *et al.*, 2012). Ω values also display natural variability. Recent observations indicate that oceanic waters under-saturated for aragonite have seasonally emerged in the Arctic Ocean (Yamamoto-Kawai *et al.*, 2009) and in upwelling areas of the Eastern North Pacific (Feely *et al.*, 2008). Modeled distribution maps of aragonite saturation (Figure 6-3) (Feely *et al.*, 2009) show pre-industrial Ω values larger than 4 in the tropical areas and higher than 1.5 in the cold oceans. Ω has decreased to present levels of 3.8 to 4.1 in tropical (Kleypas *et al.*, 1999) and of lower than 1.5 in the polar oceans (McNeil and

Matear, 2008, Azetsu-Scott *et al.*, 2010)**.** This matches acidification trends, which by deep water formation in the North-Atlantic are rapidly transferred to mid-water layers (Vázquez-Rodríguez *et al.*, 2012). Ice melt or the excess of precipitation over evaporation cause locally variable salinity reductions (Jacobs and Giulivi, 2010; Vélez-Belchí *et al.*, 2010) and, thereby, an exacerbation of ocean acidification already favored by low temperatures and high gas solubility at high latitudes (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 largely 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).

[INSERT FIGURE 6-3 HERE
Figure 6-3: CCSM3-modeled decadal mean aragonite saturation (Ω) at the sea surface, around the years 1875, 1995, 2050, and 2095 following the SRES A2 emission scenario (left panel). The mean atmospheric CO_2 concentration in 2100 approximates around 850 μatm, somewhat below levels according to RCP 8.5 and mean aragonite saturation state at 2°C will drop to almost 0 by 2300 (Meinshausen *et al.*, 2011, right panels). Deep coral reefs are indicated by darker gray dots; shallow-water coral reefs are indicated with lighter gray dots. White areas indicate regions with no data (Feely *et al.*, 2009) (TO BE DEVELOPED FURTHER AFTER FOD).]

6.1.1.3. Hypoxia

The distribution of dissolved oxygen in the world ocean is a net balance between gas solubility and exchange at the air-sea interface, of ocean circulation and mixing and the net community production (NCP, defined as the difference between gross primary production [GPP], accompanied by the evolution of oxygen, and community respiration, the consumption of oxygen [R]; NCP = GPP-R). The amount of oxygen available to marine organisms is a major determinant in their distribution, abundance, metabolism and survival. Oxygen concentrations range from greater than 500 μmoles kg^{-1} (equivalent to 11 ml L^{-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 isolated, permanently anoxic 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). Because oxygen solubility is determined by temperature and salinity, polar waters contain about 60 % more dissolved oxygen than tropical waters at 100% air saturation. Large-scale fluctuations of oxygen 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, over diurnal time scales (Grantham *et al.*, 2004; Connolly *et al.*, 2010). Most of the respiration in the ocean is attributable to bacteria that oxidize dissolved organic matter (DOM). Oxidative metabolism occurs at rates that deplete oxygen faster than it is re-introduced (Rabalais *et al.*, 2009). Once a parcel of sea water is isolated from gas exchange at the surface, oxygen can be added only by NCP, a process usually restricted to the upper 50 m of the water column, or by lateral import via ocean currents. At greater depths, the partial pressure of oxygen (pO_2) is less than 100% of air saturation. In that sense, most of the ocean is hypoxic (below air saturation), and such limitation may affect animal life through constraints on performance as soon as pO_2 falls (6.2.2.4.).

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 displaying characteristic adaptations to long-term severe hypoxia. These hypoxic waters presently occupy ~5% of the ocean volume (7.6×10^{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 ($102x10^6$ 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). Seasonal or permanent OMZs are also found in semi-enclosed basins such as the Baltic and Black Sea, coastal areas and open ocean regions (Justic *et al.*, 1987; Thamdrup *et al.*, 1996; Rabalais and Turner, 2001; Karlson *et al.*, 2002; Kemp *et al.*, 2005; Chan *et al.*, 2008; Pakhomova and Yakushev, 2011). The pO_2 reached depends on the time since the water parcel was in contact with the atmosphere or depending on lateral import or mixing with oxygenated water. At the oxic-anoxic interface, the ocean is said to be suboxic, with very low concentrations of oxygen (<4.5 μmoles kg^{-1}) and still low levels of sulphide. Suboxic waters occupy only 4.6 x 10^{14} m^3 (less than 0.05 % of the ocean volume), mainly in the Northeast Pacific (Karstensen *et al.*, 2008).

Reduced vertical mixing of stratified waters and the weakened lateral advection of aerated waters from high latitudes into the deep contribute to reduce the oxygenation of mid water layers and the deep oceans (WGI Ch. 3). Expansion of midwater OMZs has occurred over the past 50 years at mid to low latitudes between approximately 45 °N and 45 °S due to the combinations of climate warming, enhanced stratification, wind driven upwelling and eutrophication as well as the resulting oxygen demand in excess in of oxygen supply. The rate of oxygen decrease was from 0.1 to over 0.3 μmoles kg^{-1} $year^{-1}$ (Stramma *et al.*, 2008; Stramma *et al.*, 2010). In the California Current System in the Northeast Pacific, the rates of oxygen decrease ranged even up to 2.1 μmoles kg^{-1} $year^{-1}$, and the hypoxic boundary has shoaled by up to 90 m since the mid 1980s (Bograd *et al.*, 2008). Long-term declines in oxygen of 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). If this trend persists at the same rate, a decrease of the average global ocean oxygen content by 10 to 20 % can be expected by 2100. Most models, however, predict a less pronounced decrease by 1 to 7 % (Keeling *et al.*, 2010).

Human activity also supplies excess nutrients and pollutants via river inflow and by precipitation, thereby exacerbating ocean hypoxia in the pelagic zone, on continental shelves and in coastal areas. Extremely hypoxic and anoxic regions excluding metazoans have been termed ‘dead zones’ although they are not devoid of bacterial life (e.g., Orcutt *et al.*, 2011). The increasing number of ‘dead zones’ reflects the progressive deoxygenation of the oceans. Over 400 dead zones worldwide were reported for 2008, compared with 300 in the 1990s and 120 in the 1980s (Diaz and Rosenberg, 2008). In areas where oxygen levels fall to below suboxic levels, hydrogen sulphide is formed by bacterial sulfate reduction. A particularly rapid build-up of anoxic conditions has recently been documented for stratified inland water bodies such as the Aral Sea (Zavialov, 2005; Zavialov *et al.*, 2009), which is highly vulnerable to anthropogenic and climatic pressures.

Ongoing climate change is *likely* to further accelerate the spread of hypoxic zones. Fluvial runoff into the ocean is causing eutrophication and associated hypoxia in many regions and is projected to increase by 30 to 70% by 2100 due to climate-related intensification of the global water cycle (e.g. Milly *et al.*, 2002; Wetherald and Manabe, 2002; Milly *et al.*, 2008), although these figures diverge significantly for different regions and catchment areas (Kundzewicz *et al.*, 2005). Apart from enhanced nutrient load to the coastal regions, the increased buoyant freshwater discharges, as well as the warming of the ocean, will further enhance respiration and the vertical density stratification in some regions and hence reduce oxygen content and the ventilation of subsurface layers, i.e. their contact and mixing with air and air saturated waters. On the other hand, a number of regions which are presently poorly ventilated may actually display improved ventilation as the relative mix of waters entering these areas may comprise more oxygen rich surface water (Gnanadesikan *et al.*, 2007). Global warming may significantly alter the regime of enhanced convection and mixing in winter and associated ventilation of subsurface layers (de Boer *et al.*, 2007). The future evolution of low oxygen zones will also be linked to changes of wind regime accompanying global warming. These changes may be manifested in the reduction of wind energy available for ocean mixing and ventilation (e.g. Vecchi and Soden, 2007; Ren, 2010) as well as in alterations of the intensity, duration and seasonal timing of upwelling events (Snyder *et al.*, 2003).

6.1.1.4. Other Physical and Chemical Drivers

Carbon fixation in the pelagic marine environment is controlled by light, inorganic nutrients (carbon dioxide, nitrate, phosphate, trace elements), vertical mixing and temperature dependent stability of the surface mixed-layer. The upward flux of nutrients from the large deep-water pool is controlled by deep vertical mixing caused by the combined effects of local winds and thermohaline (density)-driven processes. All of these processes are subject to climate-related influences which cause shifts in the physical drivers of biological processes. All climate change modeling experiments indicate that the depth of the surface mixed layer will shoal in the coming decades (e.g., Sarmiento *et al.*, 1998; Matear and Hirst, 1999). Thus, phytoplankton in the future will be growing within a shallower surface layer and more nutrient impoverished mixed layer in which they will encounter higher mean irradiances. Mean irradiance will also rise in polar regions due to reduced sea-ice cover.

All climate change modeling experiments to date predict increased density stratification of the upper ocean in offshore waters (Sarmiento *et al.*, 1998), for example in warming gyres. Enhanced stratification at low to mid latitudes may lead to a reduction the standing stocks of phytoplankton due to a reduced vertical nutrient supply to surface waters (Polovina *et al.*, 2008; Doney, 2010). In coastal oceans this reduced nutrient supply to offshore waters may be compensated for to some extent by enhanced upwelling, as is evident in eastern boundary currents. Observations indicate an intensification of upwelling in the Peruvian (Gutiérrez *et al.*, 2011), Californian (Snyder *et al.*, 2003) and Canary systems (McGregor *et al.*, 2007). Upwelling brings waters with a cluster of altered environmental properties to the surface (Boyd *et al.*, 2010) and is a process that clearly illustrates how various environmental drivers – in this case colder waters with higher carbon dioxide levels (lower pH), higher nutrient and trace metal concentrations and lower oxygen concentrations - exert combined effects on the biota. Shelf hypoxia conditions are increasing in the upwelling corridor of the California Current system, combined with enhanced CO_2 levels (Feeley *et al.*, 2008; Connolly *et al.*, 2010), resembling the conditions already documented for other upwelling systems, like Benguela and Humboldt (Helly and Levin, 2004; Monteiro *et al.*, 2008). Changes in upwelling intensity are not sufficiently corroborated by climate model results which are inconsistent in that the rate of upwelling of deep nutrient-rich water is projected to either intensify or weaken depending on the modeling simulations (Bakun *et al.*, 2010). Accordingly, there is *medium agreement* and *limited evidence* for an intensification of coastal upwelling under climate change.

6.1.1.5. Conclusions

It is *virtually certain* that with climate change, marine ecosystems are exposed to changing regimes of environmental drivers including rising temperature means and extremes (Hoegh-Guldberg and Bruno, 2010), combined with ocean acidification due to CO_2 enrichment from the atmosphere (Caldeira and Wickett, 2005; Orr *et al.*, 2005) and the expansion of hypoxic or anoxic zones (Diaz and Rosenberg, 2008; Stramma *et al.*, 2008; Keeling *et al.*, 2010; Stramma *et al.*, 2010). Where hypoxia develops due to excess respiration, the oxidation of organic material (in sediment and water column) *very likely* leads to an accumulation of CO_2 and acidified water layers (Pelejero *et al.*, 2010) and, at extreme hypoxia or anoxia, of ammonia and hydrogen sulphide (Gray *et al.*, 2002; Kump *et al.*, 2005; Chan *et al.*, 2008; Levin *et al.*, 2009). The magnitude of nutrient inventories available from e.g. nutrient-rich deep waters directly dictate phytoplankton growth, plankton size and community and food web structures (*high confidence*). Warming of the surface layers *very likely* enhances stratification, especially during summer, but also during particularly warm winters, thereby limiting the surface ocean nutrient inventory available to spring phytoplankton blooms. Enhanced upwelling and human-induced eutrophication could compensate for the projected reduced nutrient supply in coastal oceans (*limited evidence, medium agreement* for upwelling). Light availability to phytoplankton will increase due to shoaling of the surface mixed layer (Doney, 2006). Ice melt or an excess of precipitation over evaporation due to climate change cause salinity reductions and, thereby, support enhanced stratification as well as an exacerbation of ocean acidification, with *high confidence*. Conversely, enhanced evaporation causes increased salinities at lower latitudes.

6.1.2. Historical and Paleo-Records

The environmental factors summarized under 6.1.1. have acted in the past and are recorded in the paleo-record stored in marine sediments. Accordingly, the fossil record has the potential to reveal biotic responses to past episodes of global warming, as well as changes in ocean stratification, nutrient distributions, oxygenation, CO_2 and pH (Gooday and Jorissen, 2012; Hönisch *et al.*, 2012). Fossils, however, preserve only a small part of the organismal composition of ecosystems, with a bias towards skeletal organisms from stable, low-energy aquatic environments. Moreover, care is needed when identifying appropriate paleo-analogues for future environmental changes as current global changes are taking place alongside additional local anthropogenic perturbations, and their potential synergies may have no analogue in the fossil record. Additionally, of the last 100 million years (Ma) only the last 2 Myr had atmospheric CO_2 at levels lower than any predicted for the next century. That marine biota, including calcifiers, thrived throughout most of this era could imply that 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, not simply magnitude (Hönisch *et al.*, 2012). Long-term, high CO_2 steady-states of time intervals longer than 10 thousand years (kyr) in the past had a well regulated carbonate saturation state as terrestrial weathering is balanced by the preservation and burial of carbonate in marine sediments and hence a small change in saturation. In contrast, the current anthropogenic perturbation represents a transient event, where sources and sinks cannot balance for the coming centuries and hence fast changes in pH and carbonate saturation occur (Zeebe and Ridgwell, 2011).

Historical data sets of organisms with life histories of decades and centuries and high resolution sediment cores covering the last few centuries document 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 a warming of the surface ocean since the 1970s (WGI, Ch. 3) (6.1.1.). Many examples highlight the influence of associated changes in environmental variables like temperature, hypoxia and food availability on organisms and ecosystems, for example changes in diversity of plankters, protists or macrofaunal tracers (Gooday and Jorissen, 2012), expansion of geographical ranges of plankton, changes in seasonal timing (phenology) of different components of the ecosystem and calcification changes of macrobenthos (Figure 6-4, Sections 6.2, 6.3).

[INSERT FIGURE 6-4 HERE
Figure 6-4: Atmospheric CO_2 (bottom, grey) and temperature (middle, red/orange) changes with associated biotic changes (top) for (panel A) the Palaeocene Eocene Thermal Maximum (PETM), the Pliocene warm period, and (panel B) the last glacial to Holocene transition and the industrial era. Intervals of largest environmental change are indicated with yellow bars. CO_2 data are based on measurements at Mauna Loa (Keeling *et al.*, 2005, modern), ice core records from Antarctica (Petit *et al.*, 1999; Monnin *et al.*, 2004, LGM), proxy reconstructions (Seki *et al.*, 2010, Pliocene) or represent model output (Ridgwell and Schmidt 2010, Zeebe *et al.* 2009, PETM). Temperature data are based on proxy data and models (Wilson *et al.*, 2006, [tropical ocean] modern; Lea *et al.*, 2003, [Caribbean], LGM; Lawrence *et al.*, 2009, [North Atlantic], Pliocene; Kennett and Stott, 1991 [Southern Ocean], PETM) representing the regional temperature changes in the surface ocean. For the recent anthropocene record, the Atlantic Multidecadal Oscillation is shown to highlight natural temperature fluctuations (Enfield *et al.*, 2001). Biotic responses include calcification, e.g. coralline algal growth increment changes (Halfar *et al.*, 2011), coral calcification as a product of density and linear extension (De'ath *et al.*, 2009) [modern] and foraminiferal weight (Barker and Elderfield, 2002), LGM. Evolutionary changes are indicated by turnover of coccolithophores defined as the sum of first and last appearances per 10 kyrs (Gibbs *et al.*, 2005, Pliocene) and extinction of benthic foraminifers (Thomas, 2003). Abundance data (top row) of planktonic foraminifers and coccolithophores (Field *et al.*, 2006, [St. Barbara Basin], modern; Thornalley *et al.*, 2011, [North Atlantic], LGM; Dowsett *et al.*, 1988; Dowsett and Robinson, 2006, [North Atlantic], Pliocene, Bralower, 2002 [Southern Ocean], PETM) indicate the temperature change and consequent range expansion or retraction in all four time intervals.]

Historical records of open ocean benthos rely heavily on benthic foraminifera due to their exceptional preservation/fossilization potential. The benthic fauna of the warm oceans of the past contain high percentages of species from high food/low oxygen environments and, in contrast to the modern ocean, only very rarely phytodetritus-ingesting species (Thomas, 2007).

Biological changes have also accompanied larger scale climate changes associated with the growth and decay of continental ice sheets over the past 3 Ma. There is a large body of evidence showing with *high confidence* that foraminifers, coccolithophores, diatoms, dinoflagellates and radiolarians all showed marked geographical range expansion during the last glacial-interglacial transition and within centuries during Dansgard-Oschger Events such as the Bølling and Allerød Warmings (see WGI, Ch. 5) with warm water species increasing their abundances in warming waters at higher latitudes (CLIMAP Project Members, 1976; MARGO Project Members, 2009; Figure 6-4, top row). The glacial interglacial transition is associated with an increase in atmospheric CO_2 of around ~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 (Figure 6-4, bottom row). 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. Lower CO_2 levels during the glacial interval led to higher carbonate saturation and are associated with increased calcification in planktonic foraminifers (*limited evidence, medium agreement)*, with a shell weight increase of 40-50% (Barker and Elderfield, 2002, middle left); no significant planktonic extinction or originations are associated with the glacial-interglacial transition (Lourens *et al.*, 2005).

The 2 °C deep sea warming from the glacial to the current interglacial has left no impact on the benthic foraminiferal assemblages. In contrast, higher nutrient input and changes in upwelling intensity have altered the foraminiferal assemblage in upwelling areas e.g. off north and southern Africa (Eberwein and Mackensen, 2008; Schmiedl and Mackensen, 1997) and in the North Atlantic (Thomas *et al.*, 1995) during the last glacial (*limited evidence, high agreement*). In the Santa Barbara basin, changes in oxygenation on decadal timescales within the last millennia did not cause extinctions in the benthic foraminifers (Cannariato *et al.*, 1999) while in the Arabian Sea, a stronger monsoon and the associated increases in upwelling, productivity and reduction in oxygen led to a loss in diversity in the benthic foraminiferal assemblages (Schmiedl and Leuschner, 2005).

The last time temperature and CO_2 were as high as predicted for the end of the 21st century was during the Pliocene warm period (3.3 to 3.0 Ma), with temperatures +2 to +3°C warmer than today (Haywood *et al.*, 2009, WG1 Ch. 5) and atmospheric CO_2 levels between 330-400 μatm (=ppm, Pagani *et al.*, 2010; Seki *et al.*, 2010) (*medium confidence*). Such a warming trend, occurring over several tens of thousands of years, resulted in a geographical expansion of tropical calcifying plankton species towards the poles (Dowsett, 2007) (*high confidence*); however, no increases in extinction or origination compared to background rates has been associated with Pliocene warming or early Pleistocene cooling for coccolithophores (Bown *et al.*, 2004; Figure 6-4), corals (Jackson and Johnson, 2000) or molluscs (Vermeij and Petuch, 1986) suggesting that this rate and amplitude of change does not pose physiological limits which can not be adapted to. Environmental change, specifically temperature, pH, oxygen in the last million years led to shifts in organisms and changes in calcification. The rate of change in any of these events was at least an order of magnitude smaller than present day changes and hence slow enough to permit organismal responses such as adaptation to the new environmental conditions (*medium* to *high confidence*). In light of the present unprecedented rate of change the challenges involved may therefore be outside the adaptive capacity of many organisms living in today's ocean (*limited evidence*, *low to medium confidence*).

Learning useful lessons for future oceans from the geological record requires that we analyze eras/epochs in the past when the rates of environmental change were comparable to the present. Perhaps the best analogue is the Paleocene-Eocene Thermal Maximum (PETM), 55 Ma, though model simulations for the future show higher rates of environmental change in surface waters today than during the PETM (Ridgwell and Schmidt, 2010) (*limited evidence, medium confidence*). Depending on the assumed rate and magnitude of the CO_2 release, models project a 0.25 to 0.45 pH unit decline in surface waters in the next 100 years (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 global warming drove migration of warm-water planktonic taxa towards higher latitudes (*limited evidence, high agreement)*. While there is a strong compositional change in the coccolithophore (Gibbs *et al.*, 2006) and dinoflagellate assemblages (Sluijs and Brinkhuis, 2009), suggested to reflect the changes in nutrient availability and/or warming (6.2.2), there is no bias in extinction towards more heavily calcifying species. The PETM sediments record one of the largest known extinctions among benthic foraminifers within a few thousand years (~50% of all species, Thomas, 2007) and a major change in ichnofossils indicates replacements in the macrobenthic community (Rodríguez-Tovar *et al.*, 2011). In contrast to sediment dwellers, ostracods (small pelagic crustaceans) do not show any significant change in composition (Webb *et al.*, 2009). In shallow coastal waters, calcareous red algae and corals declined markedly and were replaced by larger benthic foraminifers (Scheibner and Speijer, 2008) suggesting that the combination of warming, changes in runoff and acidification had a major impact on reef builders despite the smaller rates of change compared to the future (*limited evidence*, *low confidence*). Coupled climate and carbon cycle model for the PETM suggests that the increase in oceanic vertical temperature gradients and stratification led to decreased productivity and oxygen depletion in the deep sea (Winguth *et al.*, 2012). Globally, productivity diminished particularly in the equatorial zone by weakening of the trades and hence upwelling, leading to a decline in food supply for benthic organisms. In contrast, Southern Ocean export of organic matter into the deep sea was enhanced by wind-driven vertical mixing of the upper ocean (Wingut *et al.*, 2012). The combination of ocean acidification, warming (hence higher metabolic demands), changes in nutrient distribution in the surface waters (hence compositional changes in plankton) and reduction in oxygen (6.3.3.) makes the attribution of a cause of this extinction difficult, though similar synergies are expected for the future (6.1.1).

Overall, the benthic foraminiferal fauna of the Paleogene Ocean contained high percentages of high food/low oxygen species and, in contrast to the modern ocean, only very rare species using detritus from phytoplankton (Thomas, 2007). While it seems improbable that export productivity was significantly higher in the Paleogene oceans, its efficiency may have differed. The intense modern bentho-pelagic coupling might be a feature of the modern colder (Zachos *et al*., 2001), more stratified (e.g., Schmidt *et al*., 2004) more seasonal (e.g., Thomas and Gooday, 1996) ocean with large (Finkel *et al*., 2005) diatoms as primary producers (Katz *et al*., 2004). This interpretation is highly speculative as there is no firm consensus on whether warming would result in higher or lower net global productivity (Sarmiento *et al*., 2004; 6.5.2.) or export productivity (Laws *et al*., 2000). François *et al*. (2002) and Klaas and Archer (2002), however, argue that carbonate is the more efficient ballast (6.4.1.2.) and hence the calcareous nannofossil dominated systems of the warm Paleogene ocean combined with increased exudation of sticky polysaccharides could have led to increased deposition of organic carbon (Delille *et al*., 2005) and hence a more efficient export of organic matter.

The very warm climates of the Mesozoic (251 to 65 Ma) have led to a large number of oceanic anoxic events (OAE) particularly at the Permo-Triassic boundary (251 Ma), in the Toarcian (175 Ma), during the Cretaceous (145 to 65 Ma) and, regionally, during the PETM (55 Ma). These OAE are recognizable as episodes of widespread distribution of black shales and/or pronounced carbon isotopic excursions indicating the carbon cycle perturbation and the anoxia in the deep ocean (Jenkyns, 2010). For some of these events, anoxia was not restricted to the deep ocean but expanded oxygen minimum zones led to photic zone anoxia (Pancost *et al*., 2004). Some of these Cretaceous OAEs are associated with extinctions or increased turnover (normalized sum of originations and extinctions) of the marine fossilized plankton (an average of 30% for planktonic foraminifers and radiolarians) although the changes are very small for other groups of organisms, e.g. coccolithophores (maximum 7%, Leckie *et al*., 2002). The causal link between oxygen reduction and the evolutionary change is tenuous as these events are also associated with warming, nutrient changes and, possibly, ocean acidification although the latter strongly depends on as yet non-quantified rates of carbon input into the ocean (Hönisch *et al*., 2012). The combination of these factors also hinders the attribution of the Toarcian reef crisis, which is caused by increased metazoan extinction of, in particular, corals and hypercalcifying sponges (Kiessling and Simpson, 2011) to a specific abiotic cause.

To observe examples of global scale ecosystem collapse in the oceans, we need to expand into the deep historical record of the past 500 Ma. Sedimentary rocks record a handful of mass extinctions, at least some of which have been associated with perturbations in the carbon cycle, deep-sea oxygen decline and global warming (Kiessling and Simpson, 2011; Knoll and Fischer, 2011). In particular, mass extinction at the end of the Permian Period 251 Ma ago fits the biological predictions of global change induced by CO_2 (Knoll *et al*., 2007) with consequent pH reduction and strong oxygen depletion in subsurface water masses. The mass extinction preferentially affected reef organisms such as corals and sponges resulting in a 4 Myr long reef gap (Kiessling and Simpson, 2011). The scale of end-Permian biological collapse was greater than any predictions for coming centuries (Bambach *et al*., 2006), but it underscores the differing vulnerabilities of marine life to environmental perturbation as well as the heterogeneous nature of responses among organisms of differing anatomy, physiology and ecology (Knoll and Fischer, 2011).

In conclusion, we can deduce with *high confidence* from the geological record that the current rate of (mainly fossil fuel) CO_2 release and the associated rate and magnitude of modern ocean acidification are unparalleled in at least the last ~300 Myr of Earth history. This highlights the magnitude and scale of the current environmental change. The smaller and much slower events in the geological history provide *robust evidence* of compositional changes in fauna and flora and, in some cases, of extinction and, to much lesser degree, emergences. Although similarities exist, no past event perfectly parallels future projections, emphasizing how unprecedented future climate change is in the evolutionary history of most organisms. As the geological record does often not allow identifying clearly direct attribution to a single driver of change or their relative importance, it supports by itself future projections on possible changes in extant ecosystems and their services only with *low* levels of *confidence* (6.4). Importantly though, increasing atmospheric CO_2 in the geological past and in the future is causing warming in the surface ocean and upper ocean stratification and consequently a decrease in dissolved oxygen concentration and hence 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 past coupled warming and ocean acidification and deoxygenation events to inform, with *medium confidence*, about future climate change impacts on ocean biota.

6.1.3. Recent Trends in Long-Term Biological Observations

It is undeniable that ocean ecosystems are complex, time and space variable, non steady-state habitats that need to be studied as such. The current undersampling of ocean phenomena constrains our abilities to make meaningful assessments of current states and predictions about future ones. Existing open ocean time series data sets provide evidence that spatial and temporal variability are inextricably linked (Stommel, 1963; Figure 6-5. Systematic, long-term interdisciplinary observations are required to distinguish natural habitat variability from (long-term) environmental change arising from human activities. For example, the documentation of acid rain by the Hubbard Brook laboratory (Likens *et al*., 1977) or increasing atmospheric carbon dioxide concentrations at Mauna Loa Observatory (Keeling, 1998) both required repeated, highly calibrated measurements at a given field site.

[INSERT FIGURE 6-5 HERE
Figure 6-5: 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. From Karl (2010), as modified from Dickey (1991). (TO BE DEVELOPED FURTHER AFTER FOD)]

6.1.3.1. The Role of Ocean Time Series Observations

While climate science has benefitted from paleo-observations of tree rings, sedimentary records and ice cores, contemporary observational data sets of oceanic phenomena are rare. 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. Most 20th century ocean time-series programs have already been terminated (Duarte *et al*., 1992), including the successful International Ocean Weathership Program that began in the late 1940s as an aid to commercial aviation (Dinsmore, 1996). At its peak, the Weathership program supported 22 North Atlantic and 24 North Pacific stations where daily (or more frequent) atmospheric and ocean observations were made. In 2009, funds supporting the final weathership, Mike, in the Norwegian Sea (66° N, 2° E) were terminated. National programs run by marine stations sampling regional seas remain and provide detailed long-term data sets. A program to study plankton and its impact on fisheries was initiated by Sir Alister Hardy in the 1920s and led to the Continuous Plankton Recorder (CPR) supported by the Sir Alister Hardy Foundation for Ocean Science (SAHFOS). Since 1962, the Helgoland Roads plankton and environmental data set in the North Sea has been used to monitor temperature increases, changing foodweb and bloom dynamics (Wiltshire *et al*. 2010).

In the mid-1980s, in response to a growing awareness of the ocean's role in global climate and potential impacts on marine biological processes, several international scientific programs were established. The World Ocean Circulation Experiment (WOCE) and the Joint Global Ocean Flux Study (JGOFS) both emphasized field observations, including time-series. JGOFS sponsored physical and biogeochemical ship-based time-series programs in the North Pacific Subtropical Gyre (HOT), the Sargasso Sea (BATS), Ligurian Sea (DYFAMED), near Gran Canaria (ESTOC), southwest of Kerguelen Island (KERFIX), northwest of Hokkaido Island (KNOT) and southwest of Taiwan (SEATS) as part of a coordinated global effort (Karl *et al*., 2003). Data from these sites have documented decadal scale ecosystem changes, including ocean acidification (Dore *et al*. 2009, also WGI report). Additional trends will probably emerge as the time-series programs continue and new sites are added.

6.1.3.2. Examples of Long-Term Observations

We briefly introduce four examples where multiple decade-long ocean observations have detected evidence for variations in ecosystem structure and function forced by climate variability and change. The first three examples are ongoing, ship-based observation programs and the final example is derived from a 9-year satellite derived study of ocean color. Additional programs are usually run by marine stations sampling regional seas.

6.1.3.2.1. Continuous Plankton Recorder (CPR)

The Continuous Plankton Recorder (CPR) collected plankton samples in the English Channel and later into the open sea. The purpose of this observation program was to track coupled coastal and open ocean ecosystem productivity and changes that might be attributable to climate (Reid *et al.*, 2003). One of the most important results of the CPR program to date is the hypothesis that effects of climate variability and change in the North Sea may involve a trophic mismatch between phytoplankton and zooplankton in the pelagic ecosystem resulting in differential responses by the various trophic levels, and ultimately in a potential decoupling in the seasonal synchrony of primary and secondary production, with an impact on fisheries (6.3.2.; Edwards and Richardson, 2004)..

6.1.3.2.2. The California Cooperative Oceanic Fisheries Investigation (CalCOFI)

CalCOFI was initiated in 1949 to investigate the sharp collapse of the sardine fishery off California, from 718,000 metric tons in 1936–37 to 118,000 metric tons in 1947–48 (Radovich, 1981). The founding motivation of the program was to understand the physics, chemistry and biology of the biome of the Pacific sardine. In order to obtain the necessary field data, a comprehensive, ship-based investigation of the coastal and bordering oceanic regions was established. During the intervening 60 years, both the extent of the sampling grid and the frequency of observations have been reduced, due largely to funding considerations. For example, in 1969, the sampling program was restricted to once every three years and this imposed serious limitations on the ability to detect climate-related impacts on ecosystem dynamics (Chelton *et al.*, 1982). Both the 1976-1977 phase shift in the PDO and the major 1982-1983 El Nino event were missed by the triennial sampling design. In 1984, the grid was significantly reduced in order to revert back to a quarterly sampling schedule which is maintained to the present. Despite the limitations imposed by the reductions in sampling frequency and geographic coverage, the program has proved to be a key historical information source to understand several processes at different scales.

The program has provided indispensable contributions to the taxonomy, biogeography and ecology of holoplankton and early stages of fish and invertebrates and to knowledge on the functioning of the oceanographic system (Reid *et al.*, 1958; Lynn and Simpson, 1987, Sette and Isaacs, 1960). The program has also produced several fishery-independent estimates of historical variability of populations and communities, including reconstructions from collections (e.g., Butler *et al.*, 2003), calibration of bio-optical algorithms for remote sensing of oceanic phytoplankton (O'Reilly *et al.*, 1998; Kahru and Mitchell, 1999), continuous underway fish egg sampling (Checkley *et al.*, 1997), development of the daily egg production method for estimating spawning stock biomass of epipelagic fishes (Lasker, 1985) and paleoreconstructions from fish scales deposited in varved sediments (Soutar and Isaacs, 1974; Baumgartner *et al.*, 1992). These estimates, among others, have been used to document how El Niño impacts marine invertebrates and fishes (Chelton *et al.*, 1982; Butler, 1989; Rebstock, 2001) and causes the declines in zooplankton biomass during interdecadal periods of warming, associated with increased sea level in the California Current (Roemmich, 1992; Roemmich and McGowan, 1995a; Roemmich and McGowan, 1995b), and multidecadal shifts in the pelagic ecosystems of the North Pacific, including shifts in the biomass of sardines and anchovies (Brinton and Townsend, 2003; Lavaniegos and Ohman, 2003; Chavez *et al.*, 2003).

6.1.3.2.3. The North Pacific Subtropical Gyre (NPSG)

Subtropical gyres are extensive, coherent regions covering nearly 40% of the Earth's surface. The NPSG (area = 2 x 10^7 km^2) is the largest circulation feature on our planet (Sverdrup *et al.*, 1946). The NPSG is a very old, relatively isolated and permanently oligotrophic (low nutrient, low phytoplankton biomass and low productivity) environment. In 1968, scientists from the Scripps Institution of Oceanography began a sampling program in the NPSG near 28°N, 155°W, in an area they dubbed the "Climax region." Between 1971 and 1985, an additional 18 major expeditions were conducted (Hayward, 1987). Despite the fact that the observations were biased by season (70% of the cruises were in summer and 35% were in August alone) and were discontinuous (there were no observations in 1975, 1978-9, 1981 or 1984), the Climax program provides a unique data set on ecosystem structure and variability thereof. In 1987, Venrick reported that the average euphotic zone (0-200 m) chl *a* concentration in the NPSG during summer had nearly doubled during the period 1968-1985. The sampling frequency was not sufficient to determine whether the increase had been continuous over time or whether there had been a step function increase between 1973 and 1980 (Venrick *et al*., 1987). The authors hypothesized that the decade-scale increase in phytoplankton standing stock had been caused by large scale atmosphere-ocean interactions that led to a change in the carrying capacity of the ecosystem.

In 1988, sampling in the NPSG was continued by scientists at the University of Hawaii with the establishment of the Hawaii Ocean Time-series (HOT) program (Karl and Lukas, 1996). That monthly sampling program extended the sampling and confirmed that the year round chl *a* concentrations in the 1990s were much higher than reported from cruises conducted prior to 1976. Furthermore, there appears to have been a major shift in the size structure of the phytoplankton community from mostly large eukaryotic phytoplankton to mostly small (< 2 μm) photosynthetic prokaryotes (*Prochlorococcus* and *Synechococcus*; Karl *et al*., 2001). Finally, the dissolved phosphate concentrations appear to be decreasing and this has been linked to the selection and proliferation of nitrogen fixing microorganisms. It has been hypothesized that these changes began in 1976 and are linked to more frequent El Niño and fewer La Niña events leading to more stratified surface waters in the NPSG and reduced deep water nutrient delivery. The replacement of fixed nitrogen by N_2 fixing microbes can only continue as long as all other macro- and trace elements are available for their growth. Continued stratification, driven by climate variability and change, may eventually lead to a reduction in surface chl *a* as has been reported by Polovina *et al*. (2008) based on satellite data (6.3.4.).

6.1.3.2.4. Remote sensing of ocean color: SeaWiFS

A detailed time-series of global maps of phytoplankton stocks has been widely available over more than a decade based on satellite remotely sensed ocean color data sets for chlorophyll (e.g. SeaWiFS), which is used as a proxy for phytoplankton stocks. Because whole water column chlorophyll cannot be measured from space, the near surface chlorophyll (0-25 m, approximately one optical depth in the clearest ocean waters) must be extrapolated to total chlorophyll using an algorithm based on nearly 4000 ship-collected open ocean profiles (i.e. case 1 waters; Morel and Berthon, 1989). Finally, net primary production (NPP) was estimated from information on total chlorophyll, incident light, water column optical properties and assumptions regarding the physiology of the phytoplankton assemblages. A variety of models have been used for the purpose of extrapolating total chlorophyll to NPP (Campbell *et al*., 2002; Carr *et al*., 2006). Climate mediated changes in primary production across major oceanographic provinces over the period 1997 to 2006 have been reported by Behrenfeld *et al*. (2006). For their analysis, (Behrenfeld *et al*., 2006) used two independent, temperature-dependent descriptions of phytoplankton physiology including the standard Vertically Generalized Production Model (Behrenfeld and Falkowski, 1997) and the exponential model developed by Morel (1991) and based on the temperature-dependent growth relationships first described by Eppley (1972). The most significant finding from Behrenfeld *et al*. (2006) was the strong correlation between temporal changes in the strength of the El Niño/Southern Oscillation (ENSO) cycle (as measured using the Multivariate ENSO Index, MEI) and NPP where warmer conditions result in lower total chlorophyll and decreased rates of NPP (Behrenfeld *et al*., 2006, 6.3.4.).

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

6.2.1. Overview: Ocean Characteristics and Climate Sensitivities

All global scale modeling experiments to date provide evidence, with *high confidence*, of present and future climate-mediated alterations of the environmental properties of the oceans (Sarmiento *et al*., 1998; Matear and Hirst, 1999; Doney *et al*., 2004; Doney, 2010; Steinacher *et al*., 2010; Gruber, 2011; Friedrich *et al*., 2012) which in turn point to climate change impacts on ocean biota and ecosystems (Boyd and Doney 2002; Brierley and Kingsford, 2009, Hoegh-Guldberg and Bruno, 2010). An assessment of these observations and the resulting projections require knowledge of the characteristics of ocean ecosystems and the background of their climate sensitivity.

6.2.1.1. Adaptability of Life in the Sea

All living organisms on Earth can be placed into one of three main phylogenic categories: archaea, bacteria or eukarya. Viruses have no independent metabolism or self-reproduction but do play an important role in population dynamics and evolution of other groups. Archaea and bacteria are grouped as 'prokaryotes' and contain no intracellular organelles. Most eukarya are also single-celled and microscopic, but also include macroscopic marine plants, invertebrates and vertebrates. Typically a threshold of approximately 100 μm is used as the upper size limit to define microorganisms. Although small, marine microbes are the dominant contributors to biomass, metabolism (production/respiration) and biodiversity in all marine ecosystems. Higher marine organisms, i.e. plant and animals, comprise the charismatic species and the marine resources important for human interest and economy including food and recreation industries. While assessments of climate sensitivity among microbes usually focuses on their role in biogeochemical processes and the foodweb, sensitivities at organism level represent the more important focuses for higher marine life. These sensitivities shape the existence, abundance and biomass of individual species and the functional characteristics of the ecosystems sustaining them. Climate change effects on organisms and communities may be direct, via changing abiotic parameters, and/or indirect, via changes in species interactions including food availability.

Classification of marine life follows phylogenetic (evolutionary), biogeographical or trophic (feeding) relationships, including symbioses. Classification according to metabolic characteristics distinguishes autotrophs from heterotrophs and thereby, whether survival was dependent upon preformed organic matter (i.e., heterotrophic) or not (Table 6-1). This leads to the commonly used terms bacteria, phytoplankton/plants and animals (including zooplankton, invertebrates, fish, reptiles, birds and mammals). Because the flow of carbon and energy in the sea are fundamental processes affected by climate change, we need a much more accurate consideration of metabolism, based on how an organism obtains its energy, electrons and cell carbon (Table 6-1). For example, if an organism uses sunlight (photo-) as the energy source to split water molecules to obtain electrons (litho-) for the reduction of CO_2 (autotroph) to sugar as is the case in the well known process of 'green plant' photosynthesis, then the organism is a photolithoautotroph. If on the other hand an organism uses organic substrates as the source of both electrons and cell carbon, as all animals do, the metabolic pathway is termed chemoorganoheterotrophic. Many other pathways include mixed or hybrid metabolism and, at least for microorganisms, may be the most common in the sea.

[INSERT TABLE 6-1 HERE
Table 6-1:Variations in metabolism based on sources of energy, electrons and carbon according to Karl (2007). 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.).]

A key issue is how quickly organisms can adapt to environmental change. Local adaptation is typically thought to depend upon the standing stock DNA sequence 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). Concomitantly, the variability of marine environments ensures that variation within conspecifics is maintained at high levels. However, the extent of standing stock variation within a given species and also, the extent to which the environment can generate new variation are currently unresolved. DNA sequence variations may not provide sufficient leverage upon which the environment can select, because point mutation-based processes may be too slow to permit adaptation to rapid climate change (Bowler *et al.*, 2010). Fitness of marine organisms may therefore be due to the adaptive dynamics conferred by epigenetic regulation mechanisms, such as reversible histone modifications and DNA methylation (Richards, 2006), transmitted from generation to generation. The recent examination of such processes in terrestrial ecosystems suggests that they are remarkably rapid (Bossdorf *et al.*, 2008), however, generation times differ largely between microbes and macroorganisms, and within animals between zooplankton and megafauna like larger reptiles, fishes and mammals. The role of epigenetic phenomena in marine ecosystems is currently unexplored.

Most marine ecosystems contain species with young that feed on different diets than the adults. This leads to a complex, often stabilizing structure known as a food web where species may be replaced and carbon and energy flows be re-directed if environmental conditions change. The nature of these interdependent and variable marine food webs makes it difficult to accurately predict how changes in primary production will cascade through the heterotrophic components of the food web. With *high confidence*, if decreased rates of photosynthesis and primary production occur, they will lead to a reduction in the amount of energy supplied through the food web and a decrease in the biomass of higher trophic levels, including fish (Ware and Thomson, 2005; Brander, 2007). The number of trophic levels in a marine ecosystem determines the potential for energy transfer to higher trophic levels such as fish. High-latitude spring-bloom systems are characterised by high phytoplankton production and can potentially transfer energy efficiently in one trophic transfer from phyto- to the herbivore mesozooplankton level (Cushing, 1990). Ecosystems, such as those at high latitudes, that select for large phytoplankton and support high phytoplankton production and short (at most 3-4 trophic levels) food chains (e.g., coastal upwelling systems) support some of the largest fisheries in the global ocean (6.3.). Furthermore, if upwelling were strongly reduced, the entire trophic structure in the upwelling system would be altered, with *high confidence*, and fish production would be decreased (Bakun, 1996; Stenseth *et al.*, 2002).

6.2.1.2. Pelagic Biomes and Ecosystems

Synthesis of organic material forms the base of the marine foodweb. Most carbon fixation into organic material occurs in the pelagic marine environment and is controlled by light, inorganic nutrients (carbon dioxide, nitrate, phosphate), influenced by vertical mixing and the temperature-dependent stability of the mixed-layer depth (MLD). The upward flux of nutrients from the large deep-water pool is controlled by deep vertical mixing caused by the combined effects of local winds and thermohaline (density)-driven processes. All of these processes are subject to climate-related influences and associated shifts in the physical forcing of biological processes. Changes in environmental conditions and the displacement of organisms by convection cause variable productivity across ocean systems (Figure 6-1) as related to changes in currents and the distribution of water masses. These changes affect primary producers, fish and invertebrates in surface to mid-water depths. Temperature and its variability (Figure 6-2) 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).

A number of characteristics distinguish pelagic ecosystems (Table 6-2) and establish the conditions for plankton growth, phytoplankton diversity and biomass, the balance between photosynthesis and respiration, plankton size structure and the efficiency of trophic transfer through the food web to higher trophic levels as well as the export and storage of organic carbon. The role of climate variables and change in modifying these characters needs to be assessed. While specific impacts of climate change in each of those systems can be identified, an assessment of their relative sensitivity or of hotspots of climate change is not yet possible.

[INSERT TABLE 6-2 HERE
Table 6-2: Environmental forcing on biological production by physical, chemical and biological characteristics of major pelagic ecosystems.]

In a simplified framework Margalef's "mandala" describes how the phytoplankton community structure changes in relationship to turbulence and nutrients, factors which have a strong influence on phytoplankton reproduction and competitiveness (Figure 6-6, Margalef, 1978; Margalef *et al.*, 1979, with additions on harmful algal blooms after Cullen *et al.*, 2007).

[INSERT FIGURE 6-6 HERE
Figure 6-6: Climate impacts on phytoplankton succession. Margalef's "mandala" offers no quantitative predictions, but it is generally consistent with observation, experimentation and theory (Kiørboe, 1993). As turbulence and nutrient supply are expected to be altered by climate change, indirect climate factors (black), direct forcings (red)

and possible feedback mechanisms (blue) on climate and marine ecosystems are highlighted. The arrows indicate the linkages between the processes. Predominantly coastal processes and organisms are indicated in dark green, while processes dominating the open ocean are indicated in light green. Future projections of climate-mediated phytoplankton succession presently rely upon a knowledge base that has *low confidence* and highly depends on regional patterns of change. As an example and based on the mandala, a phytoplankton community that is presently dominated by diatoms and coccolithophores (ellipsoid on the right) may in the future be mainly composed of dinoflagellates and nitrogen fixers (circle on the left) if nutrient supply decreases and stratification intensifies. Conversely, Hinder *et al.* (2012) described a recent decline in dinoflagellates compared to diatoms in the northeast Atlantic and North Sea, associated with warming, increased summer windiness and thus, turbulence (see 6.3.1.).]

6.2.1.3. Benthic Habitats and Ecosystems

Benthic communities differ in their functional characteristics and demand for energy input, partly depending on the prevailing climate regime and on water depth (6.2.2.). Benthic organisms are classified by their size (mega-, macro-, meio-, microbenthos), their mode of energy supply (Table 6-1) or their mode of food uptake (suspension feeders, deposit feeders, herbivores, carnivores). Benthic habitats range from the intertidal zone to the deep sea and can be characterized by the climate regime, water depth, light penetration, distance from land, topography, nature of the substrate (rocky, hard, soft, mixed), sediment grain size and chemistry or by the dominant plant or animal communities that they support. These are, for example, subtidal sand, deep-sea clay, anoxic-sulphidic mudflat, cold and warm water coral reefs, mangroves, saltmarshes or hydrothermal vents and cold seeps. At latitudes below 30° South and North coral reefs are unique sunlit warm water benthic ecosystems in shallow areas and contain a rich diversity of marine organisms (6.2.2.4., Box 5.3). They are exposed to the stronger atmospheric influences and the higher variability of living conditions found in marine surface compared to deeper waters. In general, benthic organisms living in surface waters or the intertidal (where they experience temporary exposure to air) are prone to experience the strongest and immediate influence of environmental parameters changing naturally or due to anthropogenic influences, such as temperature extremes, hypoxia, elevated CO_2 concentrations or fluctuating sea level including sea level rise (WGI, Ch.). As benthic systems comprise sessile or slow moving plants and animals, they may be adapted to local conditions and cannot escape from unfavorable changes as easily as active pelagic swimmers.

Benthic ecosystems are coupled to the pelagic realm via the biological pump, chemical exchange of nutrients, gases and to the existence of pelagic and benthic life history stages. Even in abyssal benthic habitats there is a constant rain of organic detritus and this serves as the primary source of carbon and energy for benthic communities. Bacteria, other microorganisms and animals are involved in the remineralization of the deposited organic matter. Bacteria are typically 2-4 orders of magnitude greater in abundance than they are in the overlying water column. This inextricable connection to primary marine productivity means that climate impacts on surface marine ecosystems (as oceans stratify, warm and become more acidic) can impact even the most remote benthic communities, even if direct changes to the physical habitat do not occur (Smith *et al.*, 2009).

Biogenic habitats are formed in the benthos by ecosystem engineers (sensu Jones *et al.*, 1994) which can be grouped into two categories. Autogenic engineering species (like corals or terrestrial plants) form habitat from the structures they produce (e.g. coral skeletons and tree trunks and branches). Allogenic engineering species form habitat through their behaviour, e.g. by mechanically changing materials. Both types of ecosystem engineers have the potential to influence the regeneration of nutrients, e.g. through bioturbation of sediments, and to affect benthic-pelagic coupling. If climate change negatively affects the engineering species, a whole ecosystem may be detrimentally impacted.

Many benthic ecosystems are characterized by a high productivity and represent a major food resource for pelagic organisms (e.g. Perissinotto and McQuaid, 1990). Vertical migration of zooplankton and the production of pelagic larvae by benthic organisms further connect the two subsystems (Schnack-Schiel and Isla, 2005). Thus, energy flow does not only occur from the pelagic to the benthos, but also vice versa. Furthermore, the presence of benthos can alter pelagic food web structure and productivity (Sullivan *et al.*, 1991). Benthos that lives under stable environmental conditions with little seasonal variability may be especially sensitive to change. Such stenopotency may be highest in Antarctica where laboratory studies indicate that warming trends impact highly specialized cold-stenothermal endemic fauna (Pörtner *et al.*, 2012).

In contrast to a widespread perception, the seemingly monotonous deep sea environment is highly patchy, for example with regards to seasonal and interannual food supply (Berger and Wefer, 1990) and geographical features (Gage, 1996). In areas outside hydrothermal vent regions and cold seeps present deep-ocean biota live in dark environments at temperatures mostly just above 0 °C, at constant salinities and very limited food supply. Hence the organisms living in the deep ocean are generally slow-growing and small (Thomas, 2007).

6.2.2. Principles of Climate Change Effects on Organisms, Populations, and Communities

Empirical studies of marine organism and ecosystem sensitivities to climate change have made progress in identifying the mechanisms and processes linking climate to ecosystem changes (Drinkwater *et al.*, 2010; Ottersen *et al.*, 2010). However, present knowledge is mostly qualitative such that precise attribution of field-observed ecosystem change or elements thereof to relevant factors and processes often remains uncertain. Previous efforts were successful in attributing effects to temperature or hypoxia effects (6.3.). In contrast, attribution of on-going ecosystem change or fractions thereof to anthropogenic ocean acidification has only been attempted for few species. Since specific effects of individual factors may be strongly influenced by synergistic or antagonistic influences of other factors, laboratory studies need to identify the mechanisms and the unifying principles of effect for each of those drivers as well as the mechanisms of their interaction. Such evidence enhances certainty and confidence in identifying and understanding causality in a traceable process for the detection of effects and their attribution to one or more of the climate related drivers.

6.2.2.1. Mechanisms affected by Climate Change - Overarching Principles

Environmental variables influence all levels of biological organization, from genome to ecosystem. Changes in community composition and species interactions often build on organismal effects elicited by physical environmental forcing (e.g., Pörtner and Farrell, 2008; Boyd *et al.*, 2010; Ottersen *et al.*, 2010). Knowledge of the mechanisms affected (e.g., Pörtner and Knust, 2007; Raven et al., 2012), and considering a hierarchy of systemic to molecular effects (Pörtner, 2002a), appear to be a major asset for better predictions on the future of marine ecosystem dynamics (Pörtner *et al.*, 2012). If the principle mechanisms of climate effects apply equally to all types of organisms, with overarching similarities, then one could use this knowledge to predict climate impacts. However, the identification of unifying principles of climate effects has not sufficiently been pursued across organismal kingdoms, in addition to the investigation of the largely different processes characterizing e.g. animals, plants, protozoans, fungi and bacteria (Cavalier-Smith, 2004), or in general, microbes, the macroscopic plants and animals. Microbes have been studied with respect to how they are supporting many fundamental biogeochemical cycles. However, as microbes are characterized by large diversity, they may respond to environmental challenges including climate change by exploiting such diversity, e.g., undergoing species replacements, and thereby sustaining their biogeochemical roles. In contrast, macroorganisms, especially animals, have been looked at from the angle of organismal well-being, abundance and survival, and this reflects where the respective key knowledge foci currently are.

6.2.2.1.1. Principle effects of current regime, light, nutrient, and food availability

For photoautotrophs the availability of light and nutrients may change directly or indirectly with a changing climate, partly depending on its influence on ocean density and stratification, and on the current regime and the physical displacement of organisms. The control on NPP by mean underwater light levels (Sverdrup, 1953) or iron is well established, while other controls, such as the role of the trace element cobalt, have been confirmed only recently (Saito *et al.*, 2002). It is now well known that the controls on NPP vary both seasonally (Boyd, 2002) and regionally (Moore *et al.*, 2002) and that in certain seasons and particular regions more than one environmental driver – referred to as co-limitation or simultaneous limitation – may control NPP (Saito *et al.*, 2008). For heterotrophs the availability of organic material, ultimately provided by primary production, is central to shaping productivity and in maintaining energy consuming functions including those providing resistance to environmental change. As food items comprise live organisms or their decomposing cells and tissues any direct influence of climate related drivers on those organisms will translate to indirect effects on the foraging species (Figure 6-7.).

[INSERT FIGURE 6-7 HERE
Figure 6-7: Mechanisms linking organism to ecosystem response, generalizing from the principles identified in animals (after Pörtner and Farrell, 2008; Pörtner, 2001, 2002a, 2010). Wider applicability of such reaction norms to bacteria, phytoplankton, macrophytes requires exploration. (A) Concept of oxygen and capacity limited thermal tolerance (OCLTT) characterizing the specialization of animals on limited thermal windows set by (aerobic) performance (shaping fitness, growth, specific dynamic action (SDA), exercise, behaviours, immune capacity, reproduction) and, as a consequence, the why, how, when and where of climate sensitivity. Optimum temperatures (T_{opt}) indicate performance maxima, pejus temperatures (T_p) indicate limits to long-term tolerance, critical temperatures (T_c) quantify the borders of short-term passive tolerance and the transition to anaerobic metabolism. Denaturation temperatures (T_d) indicate the onset of cell damage. (B) Thermal specialization and response is dynamic between individual life stages in animals. (C) Performance curves of polar, temperate and tropical animal species reflect evolutionary adaptation to the respective climate zones. The effect of additional stressors and species interactions can be understood through dynamic changes in performance capacity and thermal limits (dashed curves), causing feedbacks on higher-level processes (phenology, interactions). Temperature-dependent performance forms the basis of shifts in phenologies, namely the seasonal timing of biological processes, of changes in thermal ranges of species co-existence and interactions (competition, predator-prey). (D) Shifts in biogeography result during climate warming (modified after Beaugrand, 2009). Here, the black line surrounding the polygon delineates the range in space and time, the level of grey denotes abundance. Thermal specialization causes species to display maximum productivity in spring toward southern distribution limits, wide seasonal coverage in the centre and a maximum in late summer in the North. The impact of photoperiod increases with latitude (dashed arrow). During climate warming, the southern time window shifts and contracts while the northern one dilates (direction and magnitude of shift indicated by arrows), until control by other factors like water column characteristics or photoperiod may overrule temperature control in some species (e.g. diatoms), above the polar circle causing contraction of spatial distribution in the north.]

6.2.2.1.2. Principles of temperature effects

The following analysis assumes that an overarching understanding can be developed for the effects of temperature on various organisms (cf. Chevin *et al.*, 2010). The knowledge base appears most advanced for animals. Here, performance curves (reaction norms) have traditionally been used in evolutionary analyses of thermal biology and sensitivity to climate change (also termed reaction norms; Huey and Kingsolver, 1989, Deutsch *et al.*, 2008; Angiletta, 2009). The shape and width of the curves on the temperature scale, i.e. the temperature range they cover in relation to the climate regime, is dynamic within limits that set the large scale boundaries of species distribution. Such thermal reaction norms may be unifying across organismal kingdoms (Chevin *et al.*, 2010) and be applicable to bacterial phages (Knies *et al.*, 2006), bacteria (Ratkowsky *et al.*, 1983), phytoplankton (Eppley, 1972) and higher plants (Bolton and Lüning, 1982; Müller *et al.,* 2009; Vitasse *et al.*, 2010, 6.2.2.2.). Maximum temperatures tolerated differ between organism domains, depending on organizational complexity (Figure 6-8), however, the respective mechanistic underpinning has not been systematically explored and compared between most groups (e.g. Green *et al.*, 2008).

[INSERT FIGURE 6-8 HERE
Figure 6-8: Ranges of temperatures and oxygen concentrations covered by various domains and groups of free living marine organisms (archaea to animals), reflecting a narrowing of environmental regimes tolerated with rising levels of organizational complexity and increasing body size ([Storch and Pörtner, to come], extending from Pörtner, 2002a,b). High organizational complexity enables an increase in body size, at the expense of decreasing hypoxia and heat tolerance (reflected in falling upper temperature limits of detected growth). Anoxic habitats can be conquered by small multicellular Eucarya (3 known species at < 0.5 mm body size, with about 10,000 differentiated cells, Danovaro *et al.*, 2010) and unicellular Eucarya, by means of special adaptations, e.g. using less complex

hydrogenosomes or mitosomes instead of mitochondria in energy metabolism. Domains and groups are modified after Woese *et al.* (1990). In the domain Bacteria, the group Thermotogales is most tolerant to temperature. It comprises obligate anaerobes and displays less complex structures indicated by a single layer lipid membrane. In the various domains, most heat tolerant representatives are as follows: **Eucarya**: Animals *Alvinella pompejana* (Chevaldonnè *et al.,* 2000) and *Paraalvinella sulfincola* (Girguis and Lee, 2006); Plants *Cymnodocera rotundata, C. serrulata* and *Halodule uninervis* (Campbell *et al.,* 2006); Flagellate *Heterocapsa circularisquama* (Yamaguchi *et al.,* 1997); Fungus *Varicosporina ramulosa* (Boyd and Kohlmeyer,1982); Microalga *Chlorella pyrenoidosa (Eppley, 1972*); Amoeba *Marinamoeba thermophila* (Jonckheere *et al.,* 2009); Ciliate *Trimyema minutum* (Baumgartner *et al.,* 2002); **Bacteria**: Purple Bacteria *Rhodovulum iodosum* sp. Nov. (Straub *et al.,* 1999); Cyanobacterium *Halomicronema excentricum* (Abed *et al.,* 2002); Flavobacterium *Thermonema rossianum* (Tenreiro *et al.,* 1997); Green Nonsulfur Bacterium *Chloroflexus aurantacus* (Madigan 2003); Gram-Positive Bacterium *Thermaerobacter marianensis* (Takai *et al.,* 1999); Thermotogales *Thermotoga maritima* (Huber *et al.,* 1986); **Archaea**: Crenarchaeota *Pyrolobus fumarii* (Kashefi and Lovley (2003); Euryarchaeota *Metanopyrus kandleri* Strain 116 (Takai *et al.,* 2008). Highest exposure temperatures at 122°C of growing species were found under high hydrostatic pressure. Black arrows denote the wide range of oxygen tolerances in unicellular Archae, Bacteria and Eucarya. Species richness of animals (upper right graph) increases with oxygen levels and reflects the higher hypoxia tolerance in small compared to large individuals/taxa (6.2.2.4.2., 6.3.3.). (TO BE DEVELOPED FURTHER AFTER FOD)]

For water breathing animals, explanations of the shape and width of the performance curve and thus of thermal sensitivity have been provided by the concept of oxygen and capacity limited thermal tolerance (OCLTT, Figure 6-7). The concept integrates findings from ecosystem, whole organism, tissue, cellular to molecular levels that are important in setting the levels and thermal limits to performance. It has been shown to explain thermal stress and associated consequences in the field (eelpout, Pörtner and Knust, 2007, mussels, Katsikatsou *et al*., 2012). Thermal specialization results from the need to minimize energy demand, which in turn causes an early loss in performance capacity at extreme temperatures. Here tolerance becomes time limited due to insufficient functional capacity of tissues, unfavorable shifts in energy allocation and molecular stress events. Overall, narrow thermal windows result which encompass ambient temperature variability (Pörtner *et al*., 2010). The OCLTT concept also integrates the (limited) capacity of molecular to organismal mechanisms to shift and change the width and shape of thermal performance curves, which may occur short-term through seasonal acclimatization of the individual and long-term through evolutionary adaptation over generations to a climate regime or during local adaptation to variable local conditions (Pörtner *et al*., 2008; Eliason *et al*., 2011), e.g. to various climate zones (Pörtner, 2006). Both short-term acclimatization over days and weeks and evolutionary adaptation over generations involve adjustments in enzyme quantities, their functional properties and the fluidity of membranes. The widths and positioning of thermal windows on the temperature scale are thus dynamically changing over time. This is also true during the lifetime of an individual, due to functional constraints during development or during subsequent growth and the resulting increase in body size (Pörtner and Farrell, 2008). At large body size, oxygen supply limitations are exacerbated causing the organism to reach heat tolerance limits at lower temperatures, resulting in a narrowing of thermal windows (Pörtner *et al*., 2008). Again, these principles may be overarching and contribute to explaining the overall reduction of body sizes observed in warming aquatic communities (Daufresne *et al*., 2009) and projected in the 21st century under climate change. They may also be operative in terrestrial environments where warming such as during PETM occurred to a similar extent as projected by some models during the next century and may have caused dwarfing such as in mammals, e.g. early horses (Secord *et al*., 2012). In general, paleo-studies have adopted the OCLTT concept to 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, OCLTT related performance shifts may also underlie changing interactions of animal species with differential thermal sensitivities causing changes in relative performance, in the temperature range of coexistence, or causing changing phenologies, the seasonal timing of biological processes (Pörtner and Farrell, 2008, Figure 6-7 C) or trophic interaction and foodweb structure. Some examples reported are in line with such reasoning (6.2.2.4.), however, the physiological basis of shifts in species interactions (competition, predator-prey relationships) has not been investigated to date. Again, knowledge of high-level functions shaping performance curves is sparse in other groups. Once this becomes available, cause and effect in changing interactions between species from various organism taxa will become accessible. These mechanism-based insights link direct physiological impacts of various stressors with those through changing species interactions (e.g. Pörtner, 2010; Harley, 2011). They also match those developed for community level scenarios by Urban *et al.* (2012) with respect to niche breadth, ecosystem mixing and the resulting extinction threats (6.3.).

Altered phenology and biogeography of individual species elicited by warming trends will trigger community reassembly in time and space (Parmesan and Mattews, 2006) with shifting species composition and predominance. At distribution boundaries set by the warm end of thermal window local abundance falls via direct effects of warming on affected species (Pörtner and Knust, 2007). Other species maintaining abundance, new species immigrating or replacing sensitive ones feedback on species interactions and food webs as in the North Atlantic (Beaugrand *et al*., 2003). Shifts in the timing of zooplankton biomass, as recorded in the Subarctic North Pacific or the North Sea over the past 50 years, were also attributed to warming (Mackas *et al*., 1998; Goldblatt *et al*., 1999; Schlüter *et al*., 2010). Patterns may become understandable from species-specific thermal niches and phenologies. Warm-adapted species may gain predominance from fitness benefits and competing or prey species may experience relative losses in performance and then reduced abundances (6.2.2.4).

6.2.2.1.3. Ocean acidification: Principles of CO_2 effects

Specific effects of ocean acidification caused by elevated CO_2 partial pressures also show similarities and differences across organismal kingdoms. Mechanisms specifically responding to CO_2 and associated pH changes have been identified and range from molecular to systemic mechanisms, including those at the neuronal level in animals (6.2.2.4.). Effects at organism levels will exert ecosystem level effects, by analogy with our understanding of thermal stress phenomena. OA will also be interacting with the systemic effects of other key environmental drivers like temperature and hypoxia (Pörtner, 2010; Boyd 2011; Gruber 2011). Meta-analyses of the literature indicate that among affected processes, the rate of net calcification is most responsive across organism groups (Hendriks *et al*., 2010). However, such meta-analyses have been unable to resolve for the diversity of species-specific responses (within and between phyla) or the existence of critical processes or life stages as bottlenecks (Hendriks and Duarte, 2010; Hendriks *et al*., 2010, Koeker *et al*., 2010).

Available information suggests some unifying effects of OA on all marine organisms (water breathing, i.e. they exchange respiratory gases with water rather than air). One of them is the passive uptake of accumulating CO_2 by diffusion leading to permanently elevated CO_2 partial pressures in body fluids (extra- and intracellular in animals, intracellular in unicellular organisms) and a permanent challenge to acid-base regulation in the various (body or cellular) compartments. During acute exposure this causes a deviation of compartmental pH from set values, i.e. a disturbance in acid-base status. The organism strives to compensate for the respiratory acidosis by use of proton equivalent ion exchange and the readjustment of pH (e.g. Heisler, 1986; Claiborne *et al*., 2002). The organism allocates energy to ion transport and acid-base regulation as shown in animals (Pörtner *et al*., 2000) for maintaining transmembrane ion gradients (protons, bicarbonate) between intracellular compartments and the surrounding extracellular fluid (in case of animals) or ambient water (in unicellular organisms) and in animals also, transepithelial gradients between extracellular fluid and ambient water (Figure 6-9A). Coccolithophores adjust H^+ conductance in the plasma membrane to support and control the efflux of H^+ (Taylor *et al*., 2011) by use of a recently identified proton channel encoded by a gene previously known only in metazoa. Activation of the voltage-gated channel leads to elevated pH_i. The energetic costs of transmembrane transport are influenced by the pH (i.e., proton concentration), relevant ion concentrations, and CO_2 concentrations of surrounding body fluids (or water) and the costs of transepithelial transport in turn by those of ambient sea water. Furthermore, the capability to compensate for the disturbance depends on the capacity of ion and acid-base regulation (i.e. of the membrane transporters involved), in relation to the leakiness of membranes and epithelia for passive ion fluxes. Tolerance to OA may require permanent compensation which occurs through the net accumulation of base in body fluids (6.2.2.4.). Another unifying effect of OA is the accumulation of substrate (CO_2 or bicarbonate) for carboxylation reactions in primary metabolism, an aspect in focus for understanding responses in photolithoautotrophic organisms like algae since primary production may benefit from elevated CO_2 levels (6.2.2.2).

[INSERT FIGURE 6-9 HERE

Figure 6-9: (A) Unifying physiological principles characterizing the responses of a schematized marine water breathing animal (dashed blue line) to elevated partial pressures of CO_2. Effects are permanent if the animal is sensitive to ocean acidification (OA) or transient during acute CO_2 exposure if sensitivity is low. Effects are mediated via entry of CO_2 (black arrows) into the body, resulting in a permanent drop in extracellular pH and its putative effects (red dashed arrows) on various tissues (boxes surrounded by solid black lines) and their processes, including calcification as well as performance and fitness of the whole organism (simplified and updated from Pörtner, 2008). Sensitivity is reduced with efficient extracellular pH compensation and/or pH compensation in each of the compartments exerting specific functions including calcification. Variability of responses according to the capacity of compensating mechanisms is indicated by + (stimulation) or – (depression). Many of these elements are similar across organism kingdoms but the link to performance-related processes has only been tested for animals. (B) % fraction of studied scleractinian coral, echinoderm, molluscan, crustacean and fish species affected negatively, positively or not at all by various levels of elevated ambient CO_2 (6.1.1.). Effects considered include those on various life stages and processes reflecting changes in physiological performance (oxygen consumption, aerobic scope, behaviours and scope for behaviours, calcification, growth, immune response, maintenance of acid-base balance, gene expression, fertilization rate, sperm motility, developmental time, production of viable offspring, morphology). Note that not all life stages, parameters and ranges of CO_2 partial pressures were studied in all species. Two assumptions were made to partially compensate for missing data within CO_2 ranges: 1) Species with negative effects at low pCO_2 will remain negatively affected at high pCO_2. 2) If a species is positively or not affected at both low and high pCO_2, it will show the same effect at intermediate pCO_2. Note that it was not possible to derive the response of each species for each CO_2 category, such that variable species numbers (on top of columns) result in each category. Bars above columns represent frequency distributions significantly different from the control treatment (Fisher's exact test, $p < 0.05$; (Literature base added separately, from [Wittmann and Pörtner, to come]).]

Adjustment of compartmental pH values by transmembrane or –epithelial ion exchange to reach suitable setpoints is important for maintaining and integrating various molecular and cellular functions and also for providing the *milieu interieur* (suitable internal conditions) for the process of calcification (e.g., Pörtner, 2008, Figure 6-9). The use of calcified structures for defence and structural support is found across organismal kingdoms. The deposition of solid $CaCO_3$ used for building the shell or other calcified structures usually occurs in body compartments, where the concentrations of Ca^{2+} and CO_3^{2-} and thus the saturation levels Ω of $CaCO_3$ (aragonite, calcite, Mg calcite, 6.1.1.) together with alkalinity and pH are maintained at higher values than in body fluids or ambient water. These generalizations are emphasized by recent findings of up-regulated pH at calcification sites within corals and coccolithophorids (Trotter *et al.*, 2011; Taylor *et al.*, 2011; McCullough *et al.*, 2012). CO_2 thus not only impedes acid-base regulation in general, but also the formation of alkaline fluids at calcification sites and here, compensation may result incomplete or incur especially high energetic costs.

Falling saturation levels Ω to below unity in the water favor the dissolving of carbonate shells unless they are protected from the direct contact of the carbonates with sea water (as is the case by use of the periostracum in mussel shells). Under "normal" alkalinity conditions, the sea water above a certain depth is supersaturated with respect to $CaCO_3$ (e.g. at Sta ALOHA, Hawaii, the site of HOT, the depth where aragonite is 100% saturated is about 500 m; for calcite the depth is closer to 700 m), reflecting conditions which support the precipitation of calcite and aragonite at calcification sites and protect carbonate shells from dissolution.

Table 6-3 lists the processes and mechanisms affected by ocean acidification in various organism kingdoms and taxa, where effects may be mediated through the principles outlined here (see also Figure 6-9). Laboratory studies, field experiments (mesocosms) and natural analogues offer possibilities to study the effects of OA at temperatures unchanged from the control or reference site or reference situation. Natural analogues include CO_2 venting areas as the ones around Ischia (Hall-Spencer *et al.*, 2008), close to Papua New Guinea (Fabricius *et al.*, 2011) or Puerto Morelos, Mexico near the Mesoamerican Reef (Crook *et al.*, 2012). Furthermore, experimental enclosures allow to precisely control the interaction between variables by controlling both CO_2 and hypoxia or temperature levels.

[INSERT TABLE 6-3 HERE

Table 6-3: 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 pCO_2 <650 to >10000 μatm.

Processes and arameters 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. +: 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 $pCO_2 = 670\ \mu$atm in 2100; RCP 8.5: representative concentration pathway with projected atmospheric $pCO_2 = 936\ \mu$atm in 2100 (Meinshausen *et al.*, 2011). Note that *confidence* is limited by the short to medium-term nature of various studies and the common lack of sensitivity estimates across generations, on evolutionary timescales (see separate reference list).]

6.2.2.1.4. Principle hypoxia effects

The term hypoxia refers to a situation where the oxygen partial pressure (Po_2) in the water falls below air saturation and constrains life (6.1.1.). Hypoxia affects virtually all organisms relying on aerobic metabolism. Thresholds for effects of hypoxia vary across organism kingdoms, depending on body size and mode of metabolism (Figure 6-8). In animals, the developmental status of ventilatory and circulatory systems (during ontogeny) and, in general, the capacity of these systems in relation to oxygen demand and body size shape sensitivity thresholds to water oxygen content. Thus, for active swimming animals with a high oxygen demand or for animals at the borders of their thermal windows constraints set in early, under mildly hypoxic conditions. Traditionally, hypoxia tolerance has been quantified by identifying the critical oxygen tension P_c at rest. P_c is traditionally seen as the oxygen partial pressure, below which the capacity to maintain constant energy turnover fails in a resting organism. The P_c can also be defined as the Po_2, at which an organism switches progressively from aerobic to anaerobic energy production (Pörtner and Grieshaber, 1993). Most aerobic heterotrophs can sustain anaerobic metabolism only transiently, even if energy efficient to sustain long-term tolerance (Grieshaber *et al.*, 1994). Such time-limited tolerance is highest in large individuals, which have a higher capacity of anaerobic metabolism, than, for example larvae, where extreme hypoxia tolerance is low (Gray *et al.*, 2002, Jessen *et al.*, 2009). The P_c is temperature dependent meaning that warming reduces tolerance to hypoxia (Nilsson *et al.*, 2010, Vaquer-Sunyer and Duarte, 2011).

Hypoxia is extraordinarily interactive with changes in climate (warming, acidification) and human-induced drivers like eutrophication. Warming reduces oxygen solubility and exacerbates biotic oxygen demand causing oxygen limitation. Oxygen deficiency can narrow the tolerance windows of organisms for other environmental stress conditions (Pörtner *et al.*, 2005). The processes that generate hypoxia usually introduce CO_2 and thus drive down pH and calcium carbonate saturation state (Millero, 1995; Brewer and Peltzer, 2009).

6.2.2.1.5. Integration towards a comprehensive picture of climate change effects

For animals the OCLTT concept integrates the effects of various climate related drivers like hypoxia or ocean acidification (see below for their specific effects), which are temperature dependent and interfere with the levels of thermal tolerance (Figure 6-7A). These insights have led to the suggestion that a comprehensive picture of climate change effects at organism level should build on a thermal matrix of performance (Pörtner 2010). Development and extension of such concept to other organism groups has not been undertaken. For example, enhanced CO_2 sensitivity at thermal extremes may represent a unifying principle (Pörtner and Farrell, 2008). With *high confidence*, this hypothesis has been supported by results from laboratory and field studies in crustaceans (Metzger *et al.*, 2007; Walther *et al.*, 2009; Findlay *et al.*, 2010; Zittier *et al.*, 2012), fishes (Munday *et al.*, 2009), bivalves (Lannig *et al.*, 2010; Schalkhausser *et al.*, 2012), corals (CO_2-enhanced bleaching, Anthony *et al.*, 2008, 2011, calcification, Rodolfo-Metalpa *et al.*, 2011) and coralline algae (calcification, necroses, Martin and Gattuso, 2009). As a consequence, OA constrains the dimensions of climate dependent thermal windows, with projected consequences for biogeography (range contractions) and species interactions (changes in relative performance, predator-prey relationships, competitiveness). As a consequence of warming-induced species shifts and integrative effects of further drivers, semi-enclosed systems such as the Mediterranean tend to lose their endemic species, and the associated niches may be filled by alien species, either from nearby systems or artificially introduced (Phillipaert *et* *al*., 2011). Regions highly influenced by river runoff and experiencing increased precipitation will see a shift from marine to more brackish and even freshwater species. Evolutionary adaptation might compensate for some of these effects and has been investigated in one preliminary study on experimental evolution of the coccolithophore *Emiliania huxleyi* under elevated CO_2 tensions (1100 and 2200 μatm) over 500 asexual generations (Lohbeck *et al*., 2012). Evidence is unavailable whether such compensation can mitigate climate change effects at least partially in macroorganisms. The rate of evolutionary adaptation in macroorganisms is constrained by their long generation times but is enhanced by large phenotypic variability among larvae which offers a pool for selections and are characterized by high mortality rates (e.g. Sunday *et al*., 2011). Findings of mass extinctions during much slower rates of climate change in earth history (6.1.2.) suggest, however, that evolutionary rates may not be fast enough for all macroorganisms to cope.

It should be noted that changes in species interactions and food webs are not only brought about by direct influences of climate variations on individuals and populations but also by changes in ocean primary production, as well as complex indirect, potentially non-linear and delayed impacts through the food web (Kirby and Beaugrand, 2009; Stock *et al*., 2011, 6.3.5.1.). The introduction of non-indigenous species, when supported by climate (including warming-) induced alterations of competitive species interactions, may further provoke the displacement of ecotypes and shifts in ecosystem functioning, for example, in the Mediterranean Sea (Occhipinti-Ambrogi, 2007, Coll *et al*., 2009; Costello *et al*., 2010).

In conclusion, there is *robust evidence* and *high confidence* for the applicability of the OCLTT concept to integrating findings across levels of biological organization, molecule to ecosystem, for a comprehensive cause and effect understanding of climate change effects on marine animal species, as observed in the field. There is *medium evidence* for the suitability of this concept to integrate the effects of multiple drivers, such as OA and hypoxia into a comprehensive whole animal picture of climate related constraints. The associated principles of temperature dependent performance or thermal reaction norms are not yet widely applied across organism kingdoms (*limited evidence*) but the recent emergence of converging approaches from empirical, modeling and ecological studies enhances *confidence* as to their usefulness for developing coherent approaches in all organisms.

6.2.2.2. Microbes – Link to Biogeochemical Processes

Microorganisms including phytoplankton, bacteria, archaea, protozoa are responsible for nutrient cycling and net ecosystem productivity (Falkowski *et al*., 2008). A hallmark of the microbial world is diversity, both in terms of phylogeny and metabolism. Many key ecosystem processes such as CO_2 fixation and oxygen evolution, the conversion of nitrogen into ammonia, (N_2 fixation), the use of nitrate, sulphate, CO_2 and metals (Fe and Mn) as terminal acceptors for electrons when oxygen is absent and the horizontal transfer of genetic information between otherwise unrelated individuals are primarily or uniquely attributable to marine microbes. The development of a better mechanistic understanding of climate-induced alterations in the functioning of marine microorganisms builds on experiments in laboratories and mesocosms as well as in situ studies and modeling. A wide range of environmental drivers, including temperature, light climate, pH and nutrient supply (see below), were identified which cause microbial/phytoplankton groups to vary regionally (Boyd *et al*., 2010). Models have provided projections of which of these environmental variables will be altered (and at what rate) due to a changing climate (Doney, 2006). Together, these data and information streams 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).

6.2.2.2.1. Temperature – related processes

A warming ocean may initially enhance the metabolic rates of microbes (Banse, 1991) and also eventually challenge their thermal tolerance –as is described by organismal performance curves (i.e. fitness versus environment) for different groups (Chevin *et al*., 2010). Short-term (days) manipulation experiments provide some insights into temperature sensitivities, however, the physiological mechanisms setting performance and whole organism tolerances have not yet been identified. Modeling studies point to the pivotal biogeochemical role that differential temperature sensitivity across a range of organisms could play in ocean ecosystems by changing the composition of microbial foodwebs and advocate a better understanding of such sensitivities (Taucher and Oschlies, 2011). However, there is *limited* experimental *evidence* and even more *limited* observational *evidence* (Giovannoni and Vergin, 2012) to support the model projections of differential responses to warming by different organisms such as that by Taucher and Oschlies (2011).

A coastal experimental microcosm study reports that resident heterotrophic bacteria are more responsive to warming than a lab cultured phytoplankton 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). Such a scenario could result in increases in bacterial abundance, reducing the drawdown of inorganic carbon and absorbing a larger proportion of inorganic nutrients and organic matter (Wohlers *et al*., 2009). In line with the finding of a warming induced shift to heterotrophy along both a north to south (northern hemisphere) and a south to north (southern hemisphere) cline in the Atlantic (Hoppe *et al*., 2002) it has been hypothesized that heterotrophy might then play a bigger role in warmer oceans and carbon flow to the atmosphere involving microbes might increase (Sarmento *et al*., 2010). The wider applicability of these findings remains to be established in further comparative studies (*limited evidence, low agreement, low confidence*).

Among the few available studies of temperature effects, coccolithophores in the NE Atlantic, displayed no change in physiological rates with higher temperatures (Feng *et al*., 2009). However, coccolithophores of the subpolar Southern Ocean and the Bering Sea (from 1997 to 2000) displayed poleward shifts in distribution (Merico *et al*., 2004; Cubillos *et al*., 2007). In the Arctic Ocean, Li *et al*. (2009) report that smaller phytoplankton are thriving under conditions of a warmer and freshening ocean. Other studies in the coastal ocean have reported warming and also the effects of altered zooplankton grazing, leading to more phytoplankton with smaller cell size (Sommer and Lewandowska, 2011). Ocean time-series data, such as the Continuous Plankton Recorder survey reveal little change in the seasonal timing (phenology) of the diatom spring bloom, which may depend more on changing light levels. In contrast, earlier emergences over the growth season for dinoflagellates may be the result of them responding to a warming North Sea (Edwards and Richardson, 2004, Figure 6-7 C, 6.3.2.).

6.2.2.2.2. Irradiance

There is *medium confidence* that 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 changes to mixed-layer depth or ice cover, involves photophysiological acclimation via changes in cellular chlorophyll which is however constrained by unidentified limits to its plasticity (Falkowski and Raven, 1997). Long-established oceanic time-series indicate that the only pronounced changes to phytoplankton productivity related to irradiance globally have resulted from reduced sea-ice cover rather than from altered mixed layer depths (Arrigo and van Dijken, 2011; Chavez *et al*., 2011). 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 by up to 27.5 Tg C yr^{-1} (mean) since 2003 (Arrigo and van Dijken, 2011). However, at high latitudes in the Southern Ocean, Montes-Hugo *et al*. (2009) reported decreased phytoplankton stocks and productivity (based on time-series of satellite-derived and measured chlorophyll concentrations) N of 63°S i.e., around the Antarctic Peninsula, but they observed increases in these properties to the S of 63°S. The authors explained these trends suggesting alteration of the mixing regime of the upper ocean via the interplay of sea-ice and cloud cover along with altered wind velocities. 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 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).

6.2.2.2.3. Stratification – nutrient and irradiance controls on primary production

Nutrient input modifies the influence of the light regime and also shapes the additional influence of temperature. Data from satellite archives of ocean color (a proxy for chlorophyll concentrations) suggest a positive relationship between chlorophyll concentrations and sea surface temperature at high latitudes (Boyce *et al*., 2010). In contrast, a strong negative correlation between chlorophyll concentrations and increased sea surface temperature at low latitude has been interpreted as an effect of increased stratification on phytoplankton stocks (Boyce *et al*., 2010). It has been reported with *limited evidence* and *low agreement*, due to uncertainties in the interpretation of chorophyll measurements from satellite (Dierssen, 2010, Behrenfeld, 2011) that the areal extent of low chlorophyll in the oligotrophic waters of the N and S Pacific and N and S Atlantic is expanding, reflecting a decline in phytoplankton stocks, which was suggested to be due to a warming ocean (Polovina *et al.,* 2008, Signorini and McClain, 2012).

Behrenfeld *et al*. (2006) presented a correlative analysis that demonstrated a statistically significant relationship over a period of 7 years between decreasing rates of NPP with rising sea surface temperature, particularly in low latitude oligotrophic waters. In contrast, an extended growth period due to reduced seasonal sea-ice cover at high latitude was interpreted to cause increased NPP in nutrient-rich water (6.2.2.2.2.). A recent review of trends in both surface chlorophyll and column-integrated chlorophyll at both open ocean and coastal time-series sites points to a suite of more complex regional trends in chlorophyll concentrations, which in some cases are tightly coupled to climate variability signatures such as El Niño (Chavez *et al*., 2011). Another factor that may confound the use of chlorophyll as a robust proxy for phytoplankton stocks is the pronounced influence that cellular physiology (for example nutrient stress) has in altering chlorophyll concentration (Falkowski and Raven, 1997), i.e. independent of biomass, reducing the level of certainty of the above conclusions.

In addition to increased stratification, other factors may influence nutrient and/or trace metal supply in the coming decades: The magnitude of atmospheric nutrient and trace metal supply may be altered (Jickells *et al*., 2005; Duce *et al*., 2008). In a future ocean, projected to be characterised by higher levels of CO_2 and lower concentrations of nutrients and trace metals (Boyd *et al*., 2010) microorganisms (including bacteria and archaea) may thrive which are capable of converting the relatively inert nitrogen gas (N_2) into biologically available ammonia.

6.2.2.2.4. Ocean acidification – effects of anthropogenic CO_2 concentrations and water pH

While comparative studies of the mechanisms and capacity of acid-base regulation in algae are still in their infancy (Taylor *et al*., in revision), the use of CO_2 in marine algal metabolism has been extensively explored. Through CO_2 fixation in metabolism elevated CO_2 concentrations may lead to fertilization of phytoplankton processes but this may depend on how they acquire carbon (i.e., presence and in particular the type and physiological cost of a carbon-concentrating mechanisms (CCM's), Giordano *et al*., 2005; see 6.3.3.2). The most comprehensive study so far, from Southern Ocean waters, suggests that virtually all species investigated (diatoms and *Phaeocystis*) operate CCM's (Tortell *et al*., 2008a). The physiological effects of OA may differ between phytoplankton groups (Rost *et al*., 2008) and may have the greatest potential effect on calcifying species – the coccolithophores (Riebesell and Tortell, 2011; Gattuso *et al*., 2011), with species specific and even strain-specific responses. Hence, responses to OA may vary considerably between species and even populations (Beaufort *et al*., 2012). Recent studies have investigated whether high CO_2 or low pH causes reduced calcification, but to date there is *low agreement* based on *limited evidence*. In one study, Langer and Bode (2011) identified CO_2 as the parameter of the carbonate system, which causes both aberrant morphogenesis in the coccolith *Calcidiscus leptoporus* and, at levels higher than 1500 μatm (i.e. > three times present levels), aggregation of cells. In another study on a different coccolithophore species (*E. huxleyi*) Bach *et al*. (2011) concluded that reduced calcification and increased malformation was caused by low pH rather than high CO_2. Thus, as for calcification studies there appear to be major inter-specific differences in responses to OA that are currently preventing any overarching mechanistic understanding. An additional issue that may influence research into OA and altered calcification in phytoplankton is that of the potential for misattribution of cause and effect (Boyd, 2011) since other environmental factors influencing rates of calcification have been reported including light (Richier *et al*. 2009) and nutrients (Dyhrman *et al*., 2006).

Laboratory studies on planktonic N_2 fixing (termed diazotrophs) cyanobacteria indicate that some of these organisms demonstrate physiological sensitivity to changes in CO_2. In particular, several studies found that strains of offshore cyanobacteria belonging to the genera *Trichodesmium* and *Crocosphaera* increased rates of carbon and N_2 fixation under conditions of elevated CO_2. However, the resulting responses in N_2 fixation have varied widely; rates of N_2 fixation have been reported to increase between 30% to >100% with 2- to 3-fold changes in pCO_2 (Barcelos e Ramos *et al.,* 2007; Hutchins *et al.,* 2007, Levitan et al., 2007; Kranz *et al.,* 2010). In some cases, these increases in N_2 fixation were also accompanied by increases in growth and cellular carbon and nitrogen quotas. Stimulation of N_2 fixation by CO_2 in strains of *Trichodesmium* does not increase intracellular concentrations of nitrogenase (Levitan *et al.,* 2010b), the enzyme required for N_2 fixation, suggesting CO_2 does not alter the efficiency of the enzymatic conversion of N_2 to ammonia. For unknown reasons, under conditions of elevated CO_2, *Trichodesmium* prolongs the daily period of active N_2 fixation (Kranz *et al.*, 2010).

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 relegated to 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; attention has focused on reallocation of cellular energy toward N_2 fixation under conditions of elevated CO_2. Specifically, cyanobacteria may reallocate cellular energy from their highly costly CCMs toward N_2 fixation and acquisition of growth limiting nutrients (Kranz *et al.*, 2010; Levitan *et al.*, 2010). However, evidence for such diversion of energy from CCMs toward N_2 fixation is lacking, and both *Trichodesmium* and *Crocosphaera* are capable of growth on both HCO_3^- and CO_2, with some evidence of preference for HCO_3^- (Kranz *et al.,* 2009). Further evidence of a direct interaction between CO_2 and energetics of diazotroph growth derives from studies revealing CO_2 stimulation of N_2 fixation is greater at low irradiances (Garcia *et al.,* 2010, Kranz *et al.*, 2010, 2011). Many of the laboratory studies examining how CO_2 influences the physiological activities of N_2 fixing cyanobacteria have been conducted with cultures grown at relatively low irradiances (<100 μmol quanta m^{-2} s^{-1}); however, both *Crocosphaera* and *Trichodesmium* are often most abundant and active in the near-surface ocean where irradiance can exceed 500 μmol quanta m^{-2} s^{-1}.

Although laboratory studies found that specific genera of N_2 fixing cyanobacteria demonstrate a positive response in N_2 fixation to increasing CO_2, to date, there have been no systematic evaluations of how CO_2 availability influences N_2 fixation or the growth of naturally occurring marine N_2 fixing microorganisms in the ocean. Moreover, there are no cultivated representatives for some of the most numerically dominant groups of N_2 fixing microorganisms in the oceans (Moisander *et al.,* 2010) and thus no laboratory model systems for studying the physiologies of these organisms. The physiological activities of naturally occurring N_2 fixing microorganisms are known to be sensitive to the availability of energy, oxygen, nutrients and temperature (Karl *et al.,* 2002) and hence the applicability of laboratory CO_2 studies to naturally occurring N_2 fixing plankton assemblages remains largely unknown. *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.

6.2.2.2.5. Bacterial life in hypoxia and anoxia – the nitrogen cycle and oxygen minimum zones (OMZ)

At depleted oxygen concentrations bacteria capable of using alternate electron acceptors are selected for and multiply, mostly those using the most energetically favorable alternate form, nitrate. When nitrate concentrations are depleted, other less favorable electron acceptors are used (e.g., oxidized iron and manganese, followed by sulphate and carbon dioxide).

Because energy yield is greater with oxygen, it is generally preferred as long as it is available. It has only recently been shown that some bacteria can still grow aerobically and most efficiently at even nanomolar oxygen concentrations (Stolper *et al.*, 2010). This has important implications for the formation of 'oxygen minimum (or even free) zones' (OMZs). Wherever the flux of organic matter capable of supporting bacterial metabolism exceeds the rate of dissolved oxygen re-supply, an OMZ will be formed, also characterized by elevated pCO_2. With *high confidence*, OMZs are therefore a consequence of high organic loading or restricted water movement, or both. In effect, *robust evidence* indicates that bacteria both create and sustain OMZs by their diversity and plasticity of metabolism. Most marine sedimentary habitats also have OMZs at some sediment horizon due to limited penetration and movement of dissolved oxygen. More recently, OMZs have also been detected in coastal waters downstream of regions of high inorganic nutrient or organic matter loading and are predicted to become more common in the open sea as surface waters warm and ocean circulation becomes more sluggish (6.1.1., 6.3.3.).

Nitrogen cycling/biogeochemistry in the ocean is highly dependent on redox reactions carried out by microbes (mostly bacteria and archaea). The key processes are fixed nitrogen assimilation and regeneration from organic matter, N_2 fixation, nitrification, denitrification and the more recently discovered anaerobic ammonia oxidation (anammox) cycle that involves the coupled reduction of nitrite and oxidation of ammonia. Both denitrification and annammox can lead to the loss of fixed nitrogen (mostly in the form of N_2 gas) whereas N_2 fixation can provide fixed nitrogen. Denitrification is common in OMZs. Furthermore, nitrous oxide (N_2O) as a very potent greenhouse gas can be produced by both nitrification and denitrification. The ultimate primary controls on the rates and pathways of N-cycle processes are the concentrations of dissolved oxygen and supply of reduced (oxidizable) organic matter. When oxygen is low and organic matter supply is high, denitrification processes are favored.

Recent field studies conducted in globally dispersed OMZs have yielded different results with respect to the dominant microbial denitrification pathway. In the Black Sea, Bengula upwelling system and the Eastern Tropic South Pacific (ETSP) Ocean annamox appears to be the dominant pathway for N_2 production (Dalsgaard *et al*., 2003, Kuypers *et al*., 2003, Lam *et al*., 2009). However, in the Arabian Sea, heterotophic (organic matter dependent) denitrification dominates (Ward *et al*., 2009). While the microorganisms responsible for both pathways abound in the ETSP, indeed denitrifiers dominate the biomass, the annamox pathways appears to be favored. Ward *et al.* (1990) have hypothesized that aperiodic delivery of oxidizable organic matter not measured during their short-term field expedition may be important for long-term balance since it is difficult to reconcile how annamox can continue in the absence of some process that can resupply the required substrates, especially nitrite. Furthermore, the extent and biochemical mechanisms of denitrification are also important because denitrification, but not annamox, produces N_2O. Finally, because annamox is an autotrophic process, it may also be a net sink for CO_2 (Voss and Montoya, 2009), provided the energy supplying substrate ammonia is available. While the literature mostly focuses on water column denitrification, it is now known that denitrification is also common among benthic foraminifera and gromids (Piña-Ochoa *et al*., 2010, 6.3.3.2.).

Variation in thermocline depth (linked to the PDO) can counter effects of OMZ expansion by limiting oxidative demand in deepened, warmer low oxygen thermocline waters (Deutsch *et al*., 2011). This means that warming-induced OMZ expansion may not be manifested as a monotonic change, but rather be complicated by decadal climate events.

6.2.2.2.6. 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 contradictory, 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. The existence of *robust evidence* and *high confidence* is thus presently limited to the attribution of responses in biological or physiological processes of microorganisms to environmental drivers associated with climate change, such as primary production, N_2 fixation, particle export flux, oxygen depletion, or calcification.

6.2.2.3. Macrophytes - Effects of Temperature and Ocean Acidification

Macrophytes (seaweeds and seagrasses) exist mostly in the periphery of the world’s oceans and play a key role in the transition zone to coastal waters (WGII, Ch. 5). Although marine macrophytes cover only 0.6 % of the area of the world's oceans (Smith, 1981) their production amounts to almost 10 % of total oceanic production (Charpy-

Roubaud and Sournia, 1990). Macrophytes provide habitat structure and protection for macrofauna and their offspring. Moreover, macrophytes play an important trophic role for many suspension feeders, detritivores and herbivores. Additionally, through the provision of gelatinous phycolloids macrophytes are important in medicine, dairy and cosmetic products.

Growth and photosynthesis of macrophytes are strongly temperature dependent. Their growth-response curves reflect specialization on the local temperature regime. Temperate species are often eurythermal; i.e. they display wide windows of tolerance and, moreover, they acclimatize by shifting these windows following the seasonal temperature change (Kübler and Davison, 1995). Species exposed to permanently low or high temperatures over long evolutionary times such as Antarctic or tropical macroalgae have adapted and specialized on limited temperature variability, they are mostly stenothermal species with a low acclimatization potential (Pakker *et al.*, 1995; Eggert and Wiencke, 2000; Eggert *et al.*, 2006; Gómez *et al.*, 2011). Studies of algal heat tolerance limits showed these are firmly set to 30-33 °C and cannot be shifted by acclimatization such that tropical species may face local extinction upon warming beyond those limits (Pakker *et al.*, 1995). In contrast, tropical seagrasses seem to tolerate even higher temperatures. Based on measurements of photosynthesis tropical seagrasses are projected to suffer irreparable effects from short-term/episodic changes only after exposure to temperatures of 40 to 45 °C (Campbell *et al.*, 2006). Cold-adapted polar seagrasses do not exist; optimal growth temperatures range from 11.5 to 26 °C in temperate zone and from 23 to 32 °C in (sub-) tropical species (Lee *et al.*, 2007). Nonetheless, the temperate *Zostera marina* reaches into the Arctic along Canadian, southwestern Greenland, Northern European and Alaskan coasts, indicating survival below the thermal optimum range. Temperature acclimatization in macrophytes involves changes in enzyme quantities and structures, thereby improving their kinetic properties. Membrane fluidity and function vary with temperature and are maintained by changes in lipid composition (Murata and Los, 1997) during thermal acclimatization and adaptation such that cold-adapted polar macroalgae contain extremely high amounts of polyunsaturated fatty acids (Graeve *et al.*, 2002). The molecular basis of physiological acclimatization and its limitation in relation to the climate regime require further study.

Most seagrasses appear limited by the availability of CO_2. The level of *evidence* is *medium* and *confidence high* that their rate of primary production, shoot density, reproductive output and/or below-ground biomass generally respond positively to elevated pCO_2; such effects were identified in the laboratory and the field in the range above 720 to 1800 μatm (e.g., Palacios and Zimmerman, 2007; Hall-Spencer *et al.*, 2008; Andersson *et al.*, 2011). However, not all species of seagrass benefit and the biodiversity of CO_2 enriched habitats such as at volcanic vents is reduced (Martin *et al.*, 2008; Hendriks *et al.*, 2010; Kroeker *et al.*, 2010). Interaction with other stressors is poorly known; in one species light-limiting conditions prevented stimulation by elevated pCO_2 (Palacios and Zimmerman, 2007). Calcareous organisms living on seagrass blades may hamper carbon uptake and limit light supply such that their elimination by OA may support primary production in the seagrass (Martin *et al.*, 2008).

Similar to seagrasses, most non-calcifying algae exhibit increased production, growth and recruitment in response to elevated CO_2 conditions, as seen above 700 to 900 μatm. Overall, the stimulation of growth is statistically significant (Kroeker *et al.*, 2010) even though it sometimes only occurs in combination with elevated temperature (Connell and Russell, 2010) or not at all (Porzio *et al.*, 2011). Experiments investigating the effect of elevated CO_2 on photosynthesis and/or carbon production of calcifying algae show complex and species-specific responses but, with *medium confidence*, calcification remains highly impacted beyond species-specific thresholds of pCO_2 (Anthony *et al.*, 2008; Ries *et al.*, 2009). According to Ries *et al.* (2009) calcification by 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. Anthony *et al.* (2008) reported a decrease in net productivity (oxygen release) of a coralline alga as a function of increasing pCO_2 at 520 to 700 μatm and beyond. The recruitment rate and growth of crustose coralline algae are severely inhibited and carbonate dissolution stimulated under elevated pCO_2 in outdoor mesocoms and in laboratory experiments under combined scenarios of warming (+3 °C) and OA. Effects became strongly visible at about 700 μatm (Kuffner *et al.*, 2007, Martin and Gattuso, 2009).

In macroalgal assemblages CO_2 may change competitiveness depending on the presence and capacity of carbon-concentrating mechanisms (CCMs). Dominant calcifying coralline species may be negatively affected, non-calcareous macroalgae with CCMs display neutral or positive effects and the relatively rare non-CCM species may experience positive effects (Hepburn *et al.*, 2011).

In conclusion, *evidence* is *robust* and *confidence* is *high* for the specialization of macrophytes on limited temperature ranges and their sensitivity to temperature extremes as well as for a CO_2-dependent stimulation of production of some macroalgae and seagrass species. With *medium confidence*, calcifying species may not benefit and rather be less competitive in a high CO_2 ocean.

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

The distribution, abundance and population dynamics of marine fishes and invertebrates correlate with climate change and variability monitored by hydro-climatic indices such as AMO or NAO (6.1.). However, a detailed understanding of contributing factors and drivers is frequently lacking. Empirical and mechanistic studies have identified unifying principles defining sensitivity at various levels of biological organization (molecular to ecosystem), which should increase *confidence* e.g. from *medium* to *high* in associated projections of future change (6.2.2.1., Pörtner, 2002a; Somero, 2011). Climate change has the potential to affect all animal phyla, from ectotherms to endotherms (mammals and birds) through effects on individual organisms, populations and communities as well as species interactions and the food web. Effects on a species are either direct through changes in environmental conditions like temperature or indirect though changing species interactions. Multiple factors can be involved at ecosystem level however, specific effects of each of those drivers would need to be known. The first subsections deal with water breathing fish and invertebrates, while corals and air breathing vertebrates are dealt with separately, due to their special physiologies.

6.2.2.4.1. Temperature dependent biogeography and species interactions

Marine ecosystem changes 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). Effects as felt by the organism at ecosystem level set in when the extremes reach beyond the limits of thermal tolerance and affect fitness indicators characterizing the performance curves and thus the window of thermal tolerance, like growth, exercise capacity and associated behaviours or reproductive output (Figure 6-7; 6.2.2.1.). During heat exposure near low latitude biogeographical limits (or at the edge of an equivalent temperature dependent gradient, e.g. in the high intertidal or at shallow depth), reductions in growth, activity and abundance of fish and invertebrate populations set in immediately 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 due to enhanced mortality or behavioural selection of suitable thermal environments (Breau *et al*., 2011) follow, leading to shifts of biogeographical ranges along clines from high to low temperature which usually means a shift toward high latitudes or an equivalent lateral (Perry *et al*., 2005) or even vertical (deeper waters) displacement (Dulvy *et al*., 2008; Graham and Harrod, 2009).

The width of thermal window is crucial in setting the level of sensitivity to climate change at species level. It roughly matches ambient temperature variability and climate regime as well as seasonality. A comparison of fishes (large juveniles and adults) across latitudes suggests that windows are narrow especially in high latitude polar species, widest at temperate mid latitudes and moderately wide at tropical latitudes (Pörtner and Peck, 2010). The specialization on the thermal regime involves trade-offs at all functional levels, for example in metabolic rate. Higher temperature variability characterizes the atmosphere in the Northern versus the Southern hemisphere (Jones *et al*., 1999) and this also translates to oceans including polar latitudes. At sub-polar latitudes, Northern hemisphere marine species result more eurythermal than Southern hemisphere species. Low levels of energy turnover (in the thermal optimum) in the cold characterize polar (Antarctic) stenotherms, whereas high rates characterize cold adapted eurytherms living in variable sub-polar (Arctic) climates. In cold eurytherms, metabolic rates result even higher than in populations of the same species at lower, temperate latitudes (Pörtner, 2006). Accordingly, more mobile or small species displaying high resting metabolic rates and high functional capacities would also be more eurythermal (Pörtner, 2002b), even among Antarctic stenotherms (Peck *et al*., 2009). The dimensions of the thermal windows thus appear dynamic, due to acclimation or local adaptation under a changing seasonal temperature regime, but also during ontogeny (6.2.2.1.). Backed by the OCLTT concept, findings suggest highest sensitivities to moderate warming in egg and larval stages as well as adult spawners of Atlantic cod (Pörtner *et al*., 2008). Accordingly, winter warming was identified, with *high certainty*, to drive the northward shift in the distribution of North Sea cod (Perry *et al*., 2005).

Local adaptation may be especially strong in heterogeneous environments like the intertidal zone (Kelly *et al*., 2012), causing functional differentiation and specialization on local conditions. On large scales, such adaptation also occurs in populations of widely distributed species like Atlantic cod. Functional and genetic differentiation of Atlantic cod into populations adapted to the regional climate regimes supports its wide biogeographical range and the ongoing invasion of Arctic waters by the cold-eurythermal Northern-more populations (Pörtner *et al*., 2008). Acclimatization capacity is small or nil in high polar, especially Anarctic species (Peck *et al*., 2010) and in general, in species at their warm and cold distribution limits. In tropical reef fishes, rapid transgenerational acclimation to warming was seen (Donelson *et al*., 2012), however, studies of mechanisms underlying acclimatization are scarce overall.

At ecosystem level, interacting species may possess differential, but overlapping thermal performance windows causing differential phenologies or changes in relative performance with climate change (6.2.2.1.). These may lead to a critical mismatch with available prey organisms or a decrease in competitiveness, again causing losses in abundance or local extinction implicating a biogeographical shift (Figure 6-7D; Beaugrand, 2009). Such principles may also underlie the climate-induced “regime shift“ from sardines (*Sardinops melanostictus*) to competing anchovies (*Engraulis japonicus*) in the Japanese Sea observed between 1993 and 2003. This shift is clearly attributable, with *high confidence*, to effects of temperature change. With food preferences of the competing species being similar (Li *et al*., 1992), the thermal windows of growth and reproductive output are found at higher temperatures for anchovies than for sardines (Takasuka *et al*., 2007; Takasuka *et al*., 2008) such that warming causes a shift in relative performance of the two species and favors the anchovies.

For scombrids and especially bigeye or bluefin, or for lamnid shark or billfishes, their wide range of tolerance to variable temperatures suggest that they are eurythermal and that direct effects of climate warming will be mild (Lehodey *et al*., 2011), especially for adults due to the combined use of eurythermal tissues and elevated muscular activity at large body sizes and wide roaming ranges (Katz, 2002; Pörtner, 2004). Effects during early life are less clear. The optimal thermal window is narrowest and warmest during spawning, larvae are most sensitive to water temperature and widen their thermal habitat as they grow. Adults at spawning stage will need to prevent overheating, a shift in location to cooler waters may occur to maintain spawning success, e.g. in skipjack tuna (Lehodey *et al*., 2011). Indirect effects of warming will be mediated through the changing composition and biomass of food available to larvae and adults and thus depend on trends in ocean stratification and productivity or expanding oxygen minimum zones (6.3.2., 6.3.3.).

Overall, the OCLTT concept provides an integrative understanding of climate specialization and sensitivity in marine animals, with *robust evidence* and high *confidence* in the detection of effects and their attribution to climate drivers.

6.2.2.4.2. Hypoxia effects at various temperatures

As the P_c is temperature dependent and exposure to hypoxia constrains aerobic performance, the OCLLT concept predicts that hypoxia reduces the tolerance to temperature extremes. In other words, hypoxia causes an earlier onset of thermal stress. This may occur fastest in warm oceans where oxygen solubility per unit of $P\mathrm{O}_2$ is less, metabolic rates are higher and animals live closer to upper thermal limits (Pörtner, 2010). Conversely, exposure to ambient hyperoxia, an increase in water $P\mathrm{O}_2$ above air saturation, alleviates thermal stress (Mark *et al*., 2002; Pörtner *et al*., 2006). Heat tolerance is enhanced by hypoxia acclimation (Burleson and Silva, 2011), and thus benefits from the improved oxygen supply capacity in relation to demand, for example by enhancing blood pigment content or reducing energy demand.

On evolutionary time scales, adaptation to hypoxia supports the selection for mechanisms like high gill surface area, high blood pigment oxygen binding and low cost cardiocirculatory capacity, which enhance efficient oxygen extraction from the water and oxygen transport to tissues as well as economic use of oxygen and energy turnover. The net effect of adaptation is a lowering of the critical oxygen tension, P_c, the hypoxia tolerance threshold which varies dynamically with life stage, body size, temperature, food consumption, oxygen demand and environmental stressors. (6.2.2.1., Pörtner, 2002b; Ekau *et al.*, 2010; Seibel, 2011). On average, large, more active animals with high oxygen demands have high P_c thresholds and are the most sensitive to permanent hypoxia, for example fishes, crustaceans and muscular squids. As an example, the four species of Pacific tuna are also sensitive to the availability of dissolved oxygen but to various degrees (Lehodey *et al.*, 2011). Only bigeye tuna routinely reach depths where ambient O_2 content is below 1.5 ml L^{-1} ($\approx$ 60 μmoles kg^{-1}). This emphasizes that specialists temporarily or permanently adapted to hypoxic environments are also found in these high activity animal groups (Childress and Seibel, 1998; Richards *et al.*, 2009; Seibel, 2011).

Enhanced hypoxia tolerance may be beneficial during transient exposures to extreme hypoxia, e.g. when migrating into OMZ for feeding (Seibel, 2011, Lehodey *et al.*, 2011), or even to temporary anoxia. For active species like bigeye tuna oxygen transport via hemoglobin is adapted to be highly efficient supporting high metabolic rates as needed during feeding in the OMZ. For species passive in the OMZ, time-limited tolerance is sustained by transient depression of metabolic rate as during periods of arrest (e.g. diapause of copepods; Auel *et al.*, 2005).

Hypoxia developing due to oxidation of organic material in OMZs and other oxygen deficient habitats coincides with CO_2 accumulation. When animals are transiently exposed to hypoxia, concomitant CO_2 exposure has a protective effect by facilitating metabolic depression and associated energy savings (Reipschläger *et al.*, 1997, Pörtner *et al.*, 1998, 2000). In contrast, permanent life in the OMZ and associated hypoxia is only possible above P_c and relies on the capacity to sustain fully aerobic metabolism. Species are favored which maximize oxygen extraction and use and sustain oxygen limitation by reduced metabolic rates, activity levels and body sizes (Yang *et al.*, 1992; Vetter *et al.*, 1994; Pörtner, 2002b; Levin *et al.*, 2009). In line with physiological knowledge, cold temperature plays a key role in sustaining hypoxia tolerance and life in the OMZ. Cold temperature lowers the P_c by facilitating economic oxygen use through low metabolic rates at high oxygen solubilities in water and body fluids. Accordingly, evolutionary adaptation to the OMZ involves further reductions in energy turnover and associated life styles and feeding rates (Childress and Seibel, 1998). Such physiological constraints explain why densities of small meiofauna are maximal at the lowest oxygen levels (Figure 6-8). Here, beneficial effects include abundant food and reduced predation by larger organisms (Levin, 2003). However, once approaching anoxia, the centre of OMZs in the pelagic and the benthic dead zones exclude the presence of higher marine life (Levin, 2003). Finally, extreme hypoxia (suboxia) only spares the suboxia specialists from extinctions and causes a loss in biodiversity (Vaquer-Sunyer and Duarte, 2008).

Permanent life in the OMZ, however, means exposure to permanently elevated CO_2 partial pressures. Adaptation to hypoxia and hypercapnia go hand in hand and suggest the use of mechanisms similar to those providing tolerance to OA (6.2.2.4.3.). It appears, however, that low metabolic rates combined with elevated CO_2 levels contribute to the marginalization of calcifiers observed in OMZs (Levin, 2003) as an increase in the energy demand of calcification as under hypercania may not be sustainable in the OMZ (6.2.2.4.3.).

6.2.2.4.3. Effects of acidification in warming oceans and various climate zones

The responses to CO_2 as identified in various life stages of invertebrates and fish imply sometimes positive but mostly negative effects on fitness (Pörtner *et al.*, 2004; Fabry *et al.*, 2008; Ishimatsu *et al.*, 2008). The degree and thus capacity of compensation for CO_2 induced acidification depends on ambient CO_2 levels and varies between species and life stages within and across phyla. Available *evidence* from experimental studies is *robust* in showing a disturbance of acid-base status to have physiological effects mediated by a lowered extracellular (blood plasma) pH. It causes a lowering of the rates of ion exchange and metabolism in muscle (Reipschläger and Pörtner, 1996; Pörtner *et al.*, 2000; Vezzoli *et al.*, 2004) or liver (hepatocytes; Langenbuch and Pörtner, 2003) of vertebrates and invertebrates. These findings indicate a key role for extracellular pH in modulating the responses to elevated CO_2 at various levels (Figure 6-9A). Reduced energy turnover involves reduced ion exchange, use of more energy efficient transport mechanisms (Pörtner *et al.*, 2000) and reduced protein synthesis (Langenbuch *et al.*, 2006), associated with enhanced nitrogen release from amino acid catabolism and protein degradation (Pörtner *et al.*, 1998; Langenbuch and Pörtner, 2002; Stumpp *et al*., 2012) and, thereby, causes slower growth (Michaelidis *et al*., 2005; Fernández-Reiriz *et al*., 2011). Further processes affected through these mechanisms may include gonad maturation and egg fertilization (Kurihara and Shirayama, 2004; Havenhand *et al*., 2008; Reuter *et al*., 2011), larval development (Shirayama and Thornton, 2005; Kurihara, 2008), larval and adult calcification and growth (Michaelidis *et al*., 2005; Walther *et al*., 2010), neuronal metabolism and functioning (Reipschläger *et al*., 1997; Munday *et al*., 2009c; Nilsson *et al*., 2012) or the immune response (Boyd and Burnett, 1999; Hernroth *et al*., 2011) and exercise performance (Pörtner, 2002b). A general concept was proposed with a whole organism view of how these responses are mediated via disturbed extracellular acid-base status under hypercapnia and how resistance to hypercapnic exposure depends on the capacity of acid-base regulation in relevant body compartments to partially or fully compensate for the respiratory acidosis (Figure 6-9A). Accordingly, sensitivity to progressive OA is low in more active marine animals with a high capacity to regulate ion and acid-base status, especially in fishes and cephalopods and also shallow-water crustaceans as well as copepods (Ishimatsu *et al*., 2008; Melzner *et al*., 2009; Ishimatsu and Dissanayake, 2010; Pörtner *et al*., 2011).

Such capacity depends on the gene expression and protein density of ion exchange mechanisms in membranes and their functional capacities. These relate to the overall level of energy turnover of a species and in turn to its mode of life and bauplan, associated with potential phylogenetic benefits or constraints (Pörtner *et al*., 2005; Melzner *et al*., 2009). Proteins involved in ion and acid-base regulation in fact undergo gene expression changes as seen in echinoderm larvae (O'Donnell *et al*., 2010; Martin *et al*., 2011), or in fishes exposed medium-term (up to six weeks) to elevated CO_2 levels (Deigweiher *et al*., 2008), implying functional adjustments of the respective processes. The capacities of acclimatization processes and their limits in shifting tolerances, as well as the long-term evolutionary consequences of such processes in relation to emission scenarios remain to be explored.

Under hypercapnia the effects of an uncompensated extracellular acidosis on organs like muscle and liver may explain observations when whole organism energy turnover falls (Pörtner *et al*., 1998; Michaelidis *et al*., 2005; Langenbuch *et al*., 2006; Pörtner, 2008, Liu and He, 2012), probably paralleled by reduced ion exchange, protein synthesis, feeding and growth. Partial or full compensation of acid-base disturbances by stimulated ion exchange and associated base accumulation probably contributes to maintaining performance capacity. At mildly elevated CO_2-concentrations in rock oysters, in fact, energy turnover increased (e.g., Parker *et al*., 2011), probably as a consequence of increasing costs for ion exchange in epithelia or for calcification or growth. Such a response indicates significant capacity to invest energy into compensating for the acidosis in relevant body compartments and to thereby resist metabolic depression. Stimulation of growth induced by CO_2 has been reported (cf. Gooding *et al*., 2009; Munday *et al*., 2009b; Dupont *et al*., 2010) and might involve enhanced energy efficiency and sufficient compensation. Full exploitation of this capacity 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).

In some cases, however, the rise in whole organism metabolic cost may not indicate enhanced resistance, possibly involving sustained extracellular acidosis. Enhanced costs in epithelia or calcification compartments in excess of metabolic depression in muscle or liver may reflect imbalances in energy budget. For example, enhanced calcification may occur at the expense of somatic growth (Wood *et al*., 2008; Beniash *et al*., 2010; Thomsen and Melzner, 2010; Parker *et al*., 2011). Further effects with the potential to cause reduced fitness comprise depressed immune functions (Bibby *et al*., 2008) or reductions in the maturation of sexual glands and in fertilization success (Kurihara and Shirayama, 2004; Havenhand *et al*., 2008; Reuter *et al*., 2011) or in the brooding success of echinoderms (Sewell and Hofmann, 2011). Lower reproductive success may also result from delays or abnormalities in larval development and growth (Shirayama and Thornton, 2005; Kurihara, 2008), or disturbances of critical transition phases like the onset of feeding (Dupont *et al*., 2008) or moulting (Walther *et al*., 2010). Disturbances in behaviour include reduced feeding (Chan *et al*., 2011), disorientation and distortions in olfactory and acoustic perceptions (Munday *et al*., 2009c; Munday *et al*., 2010, Simpson *et al*. 2011). The high neural sensitivity to mild hypercapnia seen in tropical reef fishes warrants wider study in species from other climate zones before general conclusions can be drawn (see below).

Reduced calcification and a weakening of calcified structures was seen in some echinoderms, molluscs and, possibly, crustaceans (Kurihara and Shirayama, 2004; Arnold *et al*., 2009; Comeau *et al*., 2009; Lischka *et al*., 2011). However, changes in calcification rates as determined experimentally vary largely between species. Some of them even 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 these phenomena for fitness are unclear.

A preliminary assessment of fragmented information on species sensitivities available in the present literature suggests that, on average, echinoderms, the molluscan bivalves and gastropods as well as corals begin to respond negatively at lower CO_2 levels than crustaceans or cephalopods, a sensitivity pattern resembling one observed during the Permian evolutionary crisis (Knoll *et al*., 2007; Knoll and Fischer, 2011; Figure 6-9B). The picture for fishes is less clear. Studies analysing the sensitivity of animal species to OA during their whole life cycle or during critical transition phases (e.g. fertilization, gastrulation, metamorphosis, moulting) are scarce. In sensitive species from various phyla, specific early life stages appear most critical [Clemmesen *et al*., to come]. As delays occur in crucial processes like development of vulnerable larvae, enhanced mortalities are expected due to their extended predator exposure at ecosystem level. 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 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). Negative impact was found to accumulate from larvae to juveniles and during 4 months acclimation from adults to larvae in a sea urchin. 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. Imbalances between influenced processes may arise under OA. For example, some coral fish larvae were reported to remain undisturbed or even grow larger under elevated CO_2 tensions (Munday *et al*., 2009b; Munday *et al*., 2011b). However, the resulting fitness benefits are eliminated by behavioural disturbances, which would make them equally sensitive as the other taxa (Figure 6-9B, Munday *et al*., 2010; Ferrari *et al*., 2011, Devine *et al*. 2012, Domenici *et al*. 2012). A potential role of acid-base disturbances in these effects requires further study. It remains to be explored whether and to what extent species can undergo adaptation to progressive ocean acidification over generations.

Acidification studies at the demographic/metapopulation level for animals are presently limited to studies at natural analogues (CO_2 vents; Kroeker *et al*., 2011, Fabricius *et al*., 2011) which indicate decreased diversity, biomass and trophic complexity of benthic marine communities and can to some extent but not fully provide the picture to be expected for the future ocean (6.3.). The mechanisms discussed here may be involved and would explain the loss of sensitive species and possibly, changes in species interactions due to differental sentivities.

It should be noted that all processes affected by CO_2 are acutely responding to temperature and, as they are influencing whole organism performance, also link to thermal tolerance (Figure 6-7). Conversely, temperature extremes operative through hypoxemia and hypercapnia cause enhanced CO_2 accumulation in body fluids and thereby, associated CO_2 effects. Such interactions are characterizing or at last involved in the synergistic effects of ocean warming, acidification and hypoxia. At species level, limits are species-specific leading to differential responses at ecosystem level in similar ways as depicted in Figure 6-7. Importantly and with *high confidence*, the individual response and compensatory capacity depends on where in its thermal window the animal experiences exposure to elevated CO_2 levels. At temperatures below the thermal optimum, warming will be beneficial for resistance due to the stimulation of physiological processes; compensation of the CO_2 induced disturbance of growth and calcification during warming has in fact been observed (Brennand *et al*., 2010; Findlay *et al*., 2010; Walther *et al*., 2011). In contrast, sensitivity to CO_2 is exacerbated at higher than optimum temperatures, when elevated CO_2 levels enforce the lowering of performance during warming (Walther *et al*., 2009; Munday *et al*., 2009a). Enhanced CO_2 sensitivity at thermal extremes may represent a unifying principle (6.2.2.1., Figure 6-7) with consequences for biogeography (range contractions) and species interactions (6.3.6.). As a mechanism, heat exposure may involve endogenous CO_2 accumulation in macro-organisms such that CO_2 effects may develop even without ocean acidification, but also exacerbating phenomena that typically develop under OA. At the limits of the thermal window and, thus, of thermal acclimatization capacity, the capacity of an animal to acclimatize to elevated $p\mathrm{CO_2}$ levels may also be reduced and vice versa.

The climate zone plays a role in CO_2 sensitivity due to differences in temperature and its variability which shape energy turnover and functional capacities. The rise in energy demand and functional adaptations in Northern hemisphere species (Pörtner, 2006) may improve resistance to warming and OA. In contrast, Southern hemisphere species, especially in Antarctica, have specialized on a narrow temperature range and may display enhanced sensitivity to current warming trends and OA due to the reduction in energy expenditure and functional capacities associated with stenothermy. High levels of aerobic scope and energy turnover are seen in sub-Arctic eurytherms compared to their warm-temperate con-specifics. Mechanism-based knowledge suggests with *medium confidence* that these cold-eurythermal animals possess a higher capacity in acid-base regulation and are less sensitive to handle respiratory CO_2 accumulation and anaerobic disturbances of body fluid pH than polar stenotherms or even warm temperate species (6.2.2.1., 6.2.2.4.1.). This differentiation may involve local adaptation from within species genetic variability, which then also influences sensitivity to ocean acidification. A potentially higher CO_2 sensitivity was suggested for tropical coral reef fishes than for species from temperate regions (Pörtner *et al*., 2011). Polar calcifiers with low rates of metabolism, which are exposed to high CO_2 solubility and lowered aragonite and calcite saturation levels, also appear more sensitive to ocean acidification scenarios (Orr *et al*., 2005). Animals from more stable polar waters or the deep sea (crustaceans, Pane and Barry, 2007; bivalves, [Stark *et al.,* to come] are poorly able to compensate for the extracellular acidosis and may result more sensitive than temperate species. Fitness-related functions like growth, development and reproduction are highly slowed in the cold, especially in the most cold-adapted marine ectotherms, Antarctic fish and invertebrates (Stanwell-Smith and Peck, 1998; Pörtner, 2006). At present, it remains unknown whether CO_2 effects or their compensation may take longer to develop in polar species, due to extended acclimatization periods. It is also unclear whether adaptation to elevated CO_2 concentrations has occurred during evolution and supports resilience (the long-term compensation for initial effects including the re-establishment of original performance and fitness levels) in species endemic to cold waters, which experience higher CO_2 levels due to high solubility. Those from oxygen minimum zones, or marine sediments, also characterized by high CO_2 concentrations, may also be pre-adapted, possibly including reduced reliance on the strength of calcified structures (Clark *et al*., 2009; Walther *et al*., 2011; Maas *et al*., 2012). The rate of evolutionary adaption in macroorganisms is constrained by their long generation times but is enhanced by phenotypic variability among larvae.

With *high confidence* selected animal species are affected by OA directly via uptake of accumulating CO_2 or indirectly via sensitivity of their prey organisms. Variable, species-specific responses have been reported under the effects of hypercapnia (Figure 6-9B). *Evidence* and *confidence* are *medium* that within ecosystems and phyla, higher sensitivities to OA are associated with low metabolic rates and functional capacities of marine animal species. Data correlating effects with different degrees of extracellular acidosis would be needed for a comprehensive picture of CO_2 effects and of the putative central role of acid-base regulation in various compartments. With *medium evidence* and *medium confidence*, enhanced resistance to OA in marine invertebrates and fishes implies avoiding permanent CO_2 induced metabolic depression at tissue and organism levels or other means of sustaining a balanced energy budget. Comparisons across phyla also suggest with *medium evidence* as well as *medium agreement* and *confidence* that sensitivity to progressive OA is low and resilience high in more active marine animals with a high capacity to regulate ion and acid-base status. With *high confidence*, CO_2 or hypoxia elicit strategies of passive tolerance but bring the organism earlier to its limits of functional capacity and thus reduce the capacity to tolerate thermal extremes (6.2.2.4.3). Phenotypic variability among larvae differs between species and may provide the basis for differential but rapid evolution of adaptive traits over (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*., 2011).

6.2.2.4.4. Mechanisms shaping sensitivities of reef-building corals to climate change

Warm water coral reef ecosystems are biodiverse marine ecosystems housing over one million species in less than 1 % of the ocean (Reaka-Kudla, 1997). Reef-building corals form an endosymbiotic relationship with dinoflagellates from the genus *Symbiodinium*, which is central to their ability to build the prominent carbonate structures that define many tropical coastlines. *Symbiodinium* provides the coral host with abundant energy in the form of organic carbon from their photosynthetic activities (Pernice *et al*., 2012; Trench, 1979). In return, *Symbiodinium* has access to inorganic nutrients which are otherwise in short supply in the clear waters of tropical oceans (Muscatine and Porter, 1977; Muscatine and D'elia, 1978). The physiological advantages inherent in this intimate relationship enabled reef-building corals to establish the carbonate frameworks of coral reefs which otherwise form habitat for fish and other organisms (Wilson *et al*., 2010) and provide coastal protection against the force of ocean waves. These features of coral reefs are important to the food, resources and income of hundreds of millions of people across the tropics (WGII Box 5.3).

Sudden changes in light, temperature and salinity will trigger the breakdown of the symbiosis between corals and dinoflagellates, leading to a sudden loss of color as the brown dinoflagellates move out of the tissues of coral (‘bleaching’). While individual examples of coral bleaching date back well over 100 years (Yonge and Nichols, 1931), reports of mass coral bleaching only appear in the scientific literature from 1979 onwards (Glynn, 1991; Hoegh-Guldberg, 1999). Mass coral bleaching and mortality events affect thousands of square kilometres of coral reefs almost simultaneously, coinciding with slightly warmer than average sea temperatures. In rare instances, mass coral bleaching can also be triggered by anomalously cold conditions (Saxby *et al*., 2003; Hoegh-Guldberg *et al*., 2005). Experimental studies confirmed that small changes in sea temperature (1-3 °C) will cause the disintegration of the coral-dinoflagellate endosymbiosis (Glynn and D’croz, 1990; Hoegh-Guldberg and Smith, 1989), due to the disruption via damage to excitation processing within the light harvesting reaction centres of dinoflagellate photosynthesis. This is probably a consequence of direct damage to CO_2 fixation and Ribulose Bisphosphate carboxylase (Rubisco, Jones *et al*., 1998) and/or direct damage to photosystem II (PSII) of the symbionts (Warner, 1999). As the ability of process excitation is reduced, the energy from absorbed photons is transferred to molecular oxygen producing reactive oxygen species (ROS) such as superoxide. These oxygen radicals denature proteins and may lead to the disintegration of the symbiosis. The physiological consequences of mass coral bleaching result in starvation, disease and death across large areas of coral reefs. For example, in the warm conditions of 1997/1998, many reefs experienced levels of bleaching mortality of up to 95 % of their corals following mass coral bleaching events in some areas, with an estimated 16 % of corals being removed in 1997/98 alone (Wilkinson, 1998). Other events followed (e.g. Caribbean; Eakin *et al*., 2010) with devastating consequences for corals and the reef and its coverage with live corals.

There is a strong relationship between mass coral bleaching and mortality and relatively small increases in sea temperature. This has been demonstrated in the laboratory (Glynn and Dcroz, 1990; Hoegh-Guldberg and Smith, 1989) and has been confirmed by extensive field evidence detected by satellites that shows a strong correlation between sea surface temperature anomalies (+1-2 °C of the long-term summer maximum) and mass coral bleaching and mortality (Goreau and Hayes, 1994; Strong *et al*., 1997, 2011). The relationship is strong enough to enable accurate projections of where and when coral reefs will probably bleach (Strong *et al*., 1997). The latter is provided as a public service by NOAA through its Coral Reef Watch satellite bleaching alert system (Strong *et al*., 2011). The relationship between temperature and mass coral bleaching mortality has underpinned projections of how coral reefs might change as tropical sea temperatures increase. In this case, most projections predict that coral bleaching and mortality will develop with increasing frequency and severity until they occur on an annual basis by mid to late this century (Hoegh-Guldberg, 1999; Donner *et al*., 2005, 2007). There is *limited evidence* and *low agreement* that corals can rapidly adapt to the unprecedented changes in sea temperature (Hoegh-Guldberg *et al*., 2007, Hoegh-Guldberg, 2009). The rapid decreases in the abundance of reef-building corals throughout the world (1-2 % per year; Riegl, 2002; Bruno and Selig, 2007; Carpenter et al., 2008) make it hard to argue that corals are adequately adapting to the rapid changes in ocean temperature.

Some studies have focused on the differences in heat tolerance of different genera of corals (Hoegh-Guldberg and Salvat, 1995; Loya *et al*., 2001), while others have focused on differences between genetic clades of *Symbiodinium* (Baker, 2001, 2004; Jones *et al*., 2008; Ulstrup and Van Oppen, 2003). There is *limited evidence* and *low agreement* to support the hypothesis that the entire thermal tolerance of reef-building corals resides solely within their intracellular symbionts. Evidence that reef-building corals can change their thermal tolerance by swapping their *Symbiodinium* for more tolerant varieties is restricted to a few studies which are complicated by the possibility that changes involve acclimatization phenomena (Howells *et al*., 2012). Extensive co-evolution has occurred between corals and their intracellular symbionts (Bongaerts *et al*., 2010, Hoegh-Guldberg, 2002; LaJeunesse, 2001, 2005; Sampayo *et al*., 2008; Stat *et al*., 2006) which makes the *de novo* appearance of more thermally tolerant symbioses and especially their establishment at large scales extremely questionable. It is important to note that the survival of a coral species on future coral reefs is a necessary but not sufficient condition to conclude that coral reefs in their entirety and their ecosystem services will persist under rapid anthropogenic climate change. This point has been lost in many studies that have confused the survival of individual coral species with the persistence of complex coral dominated reefs (Baker, 2010; Baker *et al*., 2004; Maynard *et al*., 2008). Given the broad distribution of corals across the planet, it appears conceivable that corals will survive at low levels of abundance but coral reef ecosystems that provide coastal protection, fisheries habitat and other resources may not be sustainable (Box 30.8.2). Over the next decades the changing reef will see climate dependent species replacements, according to species specific sensitivities and a wide heterogeneity of responses (Pandolfi *et al*., 2011).

Reef-building corals also face physiological challenges from ocean acidification. Most studies on corals have focused on calcification (6.2.2.1., Kleypas et al., 1999). While there is variability in the response of different coral genera, there is *robust* experimental *evidence* that the calcification rate of corals is reduced with increasing ocean acidification (Hoegh-Guldberg *et al*., 2011; Kleypas and Langdon, 2006; Langdon and Atkinson, 2005; Leclercq *et al*., 2002), despite their capacity to maintain higher than ambient pH values at calcification sites (6.2.2.1.). Nutrient availability to symbionts may improve resistance to decreases in calcification under OA. Together with the observation that females may sacrifice calcification more than males due to tradeoffs with reproduction (Holcomb *et al.,* 2010, 2012) and that heterotrophic feeding may support resilience (Edmunds, 2011) this emphasizes the energy dependence of calcification and associated acid-base regulation. Investigations of coral reefs growing in and around natural CO_2 seeps reveals coral communities that have much lower growth, calcification and biodiversity (Fabricius *et al*., 2011). In this case, there are significant impacts of high CO_2 without the accompanying temperature stress, a situation that is echoed by coral communities growing under naturally high CO_2 in locations such as the tropical Eastern Pacific (Manzello *et al*., 2008). These studies reveal reefs shifting from the net accretion of calcium carbonate to a net state of erosion, depending on ambient CO_2 levels. Studies that investigate the impacts of both high CO_2 and temperature are rare (Anthony *et al*., 2008). Dove *et al*. [to come] studied reef-building coral communities growing in long-term mesocosm experiments that simulated both the temperature and carbonate chemistry changes expected under B2 and A1FI AR4 climate scenarios with realistic simulation of diurnal and seasonal variability patterns. The impact of these conditions led to decalcification of the coral reef community in summer under both scenarios, principally driven by nocturnal decalcification, and the loss of symbionts and corals but not of primary productivity then sustained by other photosynthetic organisms (cyanobacteria, algae). These findings suggest that temperature acted synergistically with the impacts of perturbed sea water chemistry, reducing calcification but also increasing sensitivity to other impacts such as the loss of symbionts (6.2.2.1., 6.3.6.1.). It is also clear that we are at an early stage of understanding the mechanisms of ocean acidification impacts on reef-building corals. In this respect, corals exposed to elevated CO_2 and temperature show a wide variety of changes to gene expression involving biochemical pathways associated with the deposition of calcium carbonate and skeleton formation (Kaniewska *et al*., 2012).

Conclusions on the potential climate sensitivity of cold water corals build on few available, in some respect preliminary ecophysiological studies and are therefore fraught with *low confidence*. Dodds *et al*. (2007) showed that *Lophelia pertusa* responded to a 3°C increase in temperature very sensibly, with a three-fold increase in metabolic rate. As acclimation has not been investigated, such response implies with high uncertainty, that these are stenothermal organisms (cf. Pörtner, 2006) sensitive to future warming. Only three studies provided proof for resilience of *L. pertusa* to OA. 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 at pH reductions by 0.1 units led to calcification rates being maintained over six months (Form and Riebesell, 2011). Recent data by McCulloch *et al*. (2012) are in line with an upregulation of pH and carbonate saturation values at calcification sites. Such mechanism may provide resilience of cold water corals to ocean acidification via high ion transport capacity or low leakiness across compartmental borders. More detailed studies are lacking as well as studies of performance and bio-erosion under the combined effects of ocean warming and acidification.

6.2.2.4.5. Sensitivities of air-breathing marine vertebrates to climate change

Sea turtles are ectothermic organisms, meaning that their physiology, phenology and reproductive biology (e.g. sex determination and hatching success) are influenced by ambient temperature to similar degrees as in other ectotherms. However, together with other vertebrate air breathers (mammals, birds) they are more independent from the special drivers of climate change in the oceans as ocean acidification and hypoxia would have minimal direct influences on these creatures. Their capacity to dive and forage in hypoxic or hypercapnic areas is not influenced by the degree of hypoxia and hypercapnia in the sea water, but rather depends on their capacity to breathhold dive to depth and use their body oxygen stores as scuba tanks over extended but limited periods of time. In contrast to turtles, birds and mammals are endotherms and thereby maintain body (core) temperatures more or less constant. This enables some of them to cover the widest ambient temperature ranges possible and support some of the largest migration ranges on earth. Nonetheless, constraints on thermal tolerance and associated distribution limits are imposed by various degrees of insulation of the body core which allows them (penguins, whales, larger seals) to forage in permanently cold waters. In light of the framework outlined under 6.2.2.1., their larger independence from physical and chemical drivers in the oceans would make air-breathing vertebrates 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 food availability (6.3). If habitat structure (e.g. sea ice for polar bears or walrusses) no longer offers retreats or ambush this will enhance the energetic cost of life due to lack of hides or enhanced foraging costs. If food items are only found in thermally restricted areas or move to large depths this may lead mammals and birds to be constrained to certain distribution ranges or to reach their physiological dive limits (McIntyre *et al.*, 2011).

Sea turtles

While temperature may exert a direct influence on sea turtle populations confounding factors such as population recoveries as a result of conservation efforts (Hays *et al.*, 2004; Dutton *et al.*, 2005) and, in the opposite way, population declines due to illegal poaching, over-exploitation and habitat loss (coastal squeezing and sea level rise; Mazaris *et al.,* 2009a; Fish *et al.,* 2009) have played an important role in defining the status of sea turtle species around the world. The expected general pattern is that, as global warming continues, nest sex ratios may be skewed towards a predominantly female output, higher egg and hatchling mortality (Fuentes *et al.,* 2009), earlier onset of nesting, decreasing nesting populations (Chaloupka *et al.,* 2008) and shifts in dietary breadths (Hawkes *et al.,* 2009). Investigations of the repercussion on the abundance and long-term dynamics of sea turtle populations are currently developing.

There is evidence, however, that turtles may not be as vulnerable to warming temperatures as first anticipated. Some nesting beaches have persisted with strong female biases over a few decades or even longer (Broderick *et al.*, 2000; Godfrey *et al.*, 1999; Hays *et al.*, 2003; Marcovaldi *et al.*, 1997) and there is no evidence to date that a low production of male hatchlings has resulted in a low reproductive success within populations (Poloczanska *et al.,* 2009). Moreover, the ability of males to fertilize the eggs of many females and for females to store sperm and fertilize many clutches may ameliorate the effects of climate change on the viability of sea turtle populations (Hays *et al.,* 2010).

Poleward distribution shifts consistent with recent warming have been recorded in almost all marine groups, however, Braun-McNeill *et al.* (2008) suggest that SST alone does not control the distribution of cheloniid sea turtles. Instead, the relationship between SST fields and the presence of sea turtles at nesting or foraging areas may be non-linear and tend to vary by region. In fact, the number of loggerheads (*Caretta caretta*) captured off the northeast USA, declined when water temperatures exceeded 21°C (Gardner *et al.,* 2008). The presence or absence of sea turtles in a given region, may be better explained by the temporal unavailability of food resources or strong thermoclines restricting their bottom foraging abilities (Braun-McNeill *et al.,* 2008).

In general, increases in SST have caused an earlier onset of nesting in loggerheads turtles, e.g. in Florida (Pike *et al.*, 2006; Weishampel *et al.*, 2004) or the Mediterranean (Mazaris *et al.,* 2008) and interannual variations in nesting activity are also correlated to environmental variability. Warming SST conditions at foraging grounds may influence the reproductive phenology of loggerheads in the Mediterranean and the eastern Pacific by lowering food availability and the abundance of nesting loggerhead turtles (Chaloupka *et al.,* 2008; Mazaris *et al.,* 2009 b). A decreasing number of nesters during positive SST episodes is also apparent for populations of Pacific green turtles (*Chelonia mydas*; Balazs and Chaloupka, 2004), the Pacific leatherback (*Dermochelys coriacea*; Saba *et al.*, 2007) and the hawksbills (*Eretmochelys imbricata*) at the Seychelles (Broderick *et al.*, 2001). On decadal time scales, climate fluctuations in the North Pacific (Pacific Decadal Oscillation) and in the Northwest Atlantic (Atlantic Multidecadal Oscillation) appear to affect recruitment success, with subsequent effects on nesting abundance of loggerheads and nesters populations of hawksbills in the Southern Gulf of Mexico, probably via food availability (Van Houtan and Halley, 2011). A considerable reduction in hatching success (by nest flooding) has been observed for the loggerhead and green turtle in Florida as a consequence of increasing incidence of extreme weather events in nesting areas (Van Houtan and Bass, 2007). Chelonians capable of changing developmental habitats under unfavorable conditions, like the leatherback turtle (*Dermochelys coriacea*; Fish and Drews, 2009; Hawkes *et al.*, 2009) will be less impacted than hawksbill turtles which show high fidelity to nesting and foraging sites (Cuevas *et al.*, 2008).

Sea birds

Seabird range modifications probably caused by climate change were recorded in polar areas and in the temperate zone of the North Atlantic (Grémillet and Boulinier, 2009). Northern-temperate species have shifted their breeding and non-breeding ranges to higher latitudes (Robinson *et al.,* 2005; La Sorte and Jetz, 2010). Range expansion or population growth are also reported in the Southern hemisphere, (e.g. Dunlop 2001, Bunce *et al.,* 2002) suggesting that some seabird species are extending their ranges southward, while high-latitude, cool-water species are extending their breeding seasons (Chambers *et al.,* 2005). Accordingly, warming trends in the Western Antarctic Peninsula have led to increased numbers and a southward expansion of Chinstrap Penguins (*Pygoscelis antarctica*) (Fraser *et al.*, 1992), however, followed by a decline probably due to decreasing food availability (Trivelpiece *et al.*, 2011). In contrast, for some species adapted to the high polar cold, large increases in air and sea temperatures and extensive melting of ice shelves have been related to low adult survival, habitat loss and the concomitant population reductions of the Adélie Penguin (*Pygoscelis adeliae*), Emperor Penguin (*Aptenodytes forsteri*), Snow (*Pagodroma nivea*) and Blue Petrels (*Halobaena caerulea*; Durant *et al.,* 2004). 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).

As global temperatures rise, many bird species are breeding earlier (Sydeman and Bograd, 2009). Nevertheless, there is no clear agreement regarding the causality of such relationship (Heath *et al.,* 2009) or whether those changes solely reflect long-term increases in ocean temperatures, a combination of human-induced climate change and natural variations or other synergistic, confounding 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). For example, laying dates of the Black-legged kittiwake (*Rissa tridactyla*) and common guillemot (*Uria aalge*) have become later over the past two decades in the North Sea as a result of positive SST trends, possibly related to prey availability (Visser and Both, 2005). In the Barents and North Sea, most species of seabirds have suffered a higher than usual proportion of years of breeding failure in the last decade (e.g Atlantic puffins, *Fratercula arctica*, Black-legged kittiwakes and the razorbill, *Alca torda*; Frederiksen *et al.,* 2004; Sandvik *et al.,* 2005), a period characterized by anomalously high SSTs. The causative links of such relationship are not well understood (Hyrenbach and Veit, 2003; Heath *et al.,* 2009).

Most of these changes in range shifts and phenology involve trophic relationships. The rationale is that climate change asymmetrically affects the different developmental habitats and seasonal cycles of both seabirds and food resources, creating a mismatch in the predator-prey system (Parmesan 2006). For example, as winter temperatures have increased, the Sanderling and the Ringed Plover began to winter at high quality feeding grounds in the East Coast of Britain (Robinson *et al.,* 2005). During the 1990s, a reduction in nestling growth rates of the Arctic Brunnich's guillemot coincided with a change in its diet composition as the Arctic cod (*Boreogadus saida*), its main prey, was progressively replaced by the Capelin (*Ammodytes spp.*). In turn, this switch was accompanied by a diminishing summer ice cover (Gaston *et al.,* 2005). Climatic influences on the distribution of Antarctic seabirds are presumably also mediated through the availability or abundance of prey (Croxall *et al.,* 2002; Trivelpiece *et al.*, 2011). Foraging performance of wandering albatrosses (*Diomedea exulans*) was improved by shortened foraging trips due to a more favorable wind regime between the 70ies and 2008, leading to higher reproductive success (Weimerskirch *et al.*, 2012).

Seabirds with narrow geographic domains and limited phenotypic plasticity are expected to be more susceptible to environmental perturbations caused by climate change (Chambers *et al.,* 2005; Grémillet and Boulinier, 2009); even leading to the extirpation of local populations (e.g. in case of the Galápagos penguin *Spheniscus mendiculus*, Vargas *et al*., 2007; and the marbled murrelet *Brachyramphus marmoratus*, Becker *et al*., 2007).

Marine mammals

Range shifts in marine mammals may also represent indirect effects of climate change on their prey distribution and abundance, or impacts on specific habitats. Colder water (prey) species will shift towards the poles followed by their mammalian predators (Simmonds and Isaac, 2007) and warmer water prey species will expand or shift their ranges. There is evidence suggesting that expected patterns may already be occurring (e.g. in case of the Pacific White-sided dolphin, *Lagenorhynchus obliquidens*, which decreased in abundance at its southern distribution limit (Gulf of California) and increased on the West coast of Canada, however, without an evident range shift of its food resources (Salvadeo *et al.,* 2010). MacLeod *et al.,* (2005) suggested that warming of local waters led to changes in the cetacean community of Northwest Scotland, with a range contraction and decline in occurrence of cold water species (White-beaked dolphin, *Lagenorhynchus albirostris*; Long-finned pilot whale, *Globicephala melas*; Northern bottlenose whale, *Hyperoodon ampullatus*) and range expansions of species restricted to warm waters (Commom dolphin, *Delphinus delphis*; Striped dolphin, *Stenella coeruleoalba*). Over the last decade, there also has been a redistribution of Harbour porpoises (*Phocoena phocoena*) in the North Sea with noticeable increases in density in the southern region.

A northward shift in the distribution of different whale species as indicated by shifted sightings in the California Current system (CCS), is suggested for sperm whale (*Physeter macrocephalus*), the Gray whale (*Eschrictius robustus*) and its use of northern-more breeding lagoons, and the Fin whale (*Balaenoptera physalus*) ranging around the Aleutian Islands, where the species has not been seen since the 1970s (Springer et al., 1999; Calambokidis et al., 2009; Moore and Barlow, 2011).

As in birds, vulnerability is high for those marine mammals with narrow geographic ranges and high habitat dependence. Illustrative examples are that of the critically endangered vaquita (*Phocoena sinus*) endemic to the Northern Gulf of California, which cannot move north because there is a land barrier or those of the polar bear (*Ursus maritimus*; Laidre *et al.,* 2008, Rode *et al.,* 2010) and the walrus (*Odobenus rosmarus*) that depend on sea ice as a platform for hunting, resting and giving birth. Negative effects of ice loss on polar bears have been documented for a couple of populations in the Baffin Bay and Davis Strait (Rode *et al.,* 2012). Potential effects of Arctic warming on marine mammals have been discussed in terms of decreased areal ice cover, but the most immediate effects may result from changes in the distribution of ice and snow. For instance, earlier snowmelts may prematurely destroy subnivean lairs of Ringed seal (*Phoca hispida*) pups subjecting them to adverse weather and increased predation. Decreasing sea ice cover in summer may decrease the Pacific walruses' access to food and increase their exposure to polar bear predation (Kelly, 2001). Narwhales (*Monodon monoceros*) are strictly polar specialists and have suffered major mortality events (Simmonds and Isaac 2007) attributable to a strong and increasing trend in winter sea ice concentrations along Baffin Bay and Davis Straight during the 1979-1996 period, causing the closure of leads and cracks in the ice that narwhales use to breath. Such trends in ice formation and the decline in narwhale abundance are also inferred as regional impacts of climate change (Laidre and Heide-Jørgensen, 2005). In contrast, sasonal migrants and some ice-associated species in the Arctic (Fin whale; Minke whale, *Balaenoptera acutorostrata*; Humpback whale, *Balaenoptera novaeangliae*; Gray whale; Killer whale, *Orcinus orca* 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).

Similarly to what is observed in seabirds, the effects of climate change on geographic distribution, phenology and migration timing of marine mammals are frequently coupled with alterations in the predator-prey dynamics. During the past two decades, the northward expansion of sperm whales along the Baja California Peninsula and Gulf of California coincided with the range shift of a dominant prey item of this species, the jumbo squid (*Dosidicus gigas*). The range shifts observed in Fin whales and the reestablishment of the Blue whale's (*Balaenoptera musculus*) migration circuit to pre-whaling conditions, have been explained in part to changes in prey availability driven by oceanographic (cold) regime shifts (Calambokidis *et al.,* 2009; Salvadeo *et al*., 2011). For polar bears, access to prey such as ringed seals have been disrupted by earlier breakup and later formation of sea ice in some areas of the eastern Canadian Arctic. Lusseau *et al.,* (2004) found that the group size of common Orcas in this same region and bottlenose dolphins (*Tusiops truncatus*) in Scotland, varied in relation to large scale decadal ocean climate variation, perhaps as an adaptation to a changing prey composition. Antarctic seals may benefit from the melting of sea ice and the influx of glacial melt water stabilizing the upper water column. The coastal surface water becomes fresher and warmer, encouraging primary and secondary production nearshore (Sun *et al.,* 2004). These authors proposed that during cold periods sea-ice extent would increase, providing fewer areas of open water for predators to feed.

Conclusions

Recent analyses of long-term data sets indicate with *robust evidence* and *high confidence* that some species of seabirds, marine mammals and sea turtles are already responding to the anomalous ocean climate of the 20th century, (Hughes, 2000). However, generalizations are still difficult to establish because in some instances there is, at best, *limited* and contrasting *evidence* or *low agreement* concerning the causal effects of climate change on the life history and population dynamics of marine tetrapods (Chambers *et al.,* 2009; Robinson *et al.,* 2005). In other cases the available information indicates consistent trends over time and space and has *high confidence* with respect to impacts of climate change (Barbraud and Weimerskirch, 2006; Visser and Both, 2005, Trivelpiece *et al*., 2011). Overall, *evidence* and *confidence levels* for direct, univocal attribution to climate drivers in general are *low*. Conversely, *confidence* is *high* that effects are mostly mediated through climate dependent changes in habitat structure and food availability, especially in mammals and birds.

6.2.2.5. Conclusions

A comprehensive understanding of mechanisms responding to climate related environmental factors at ecosystem, whole organism, tissue, cell and molecular levels of biological organization provides 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. 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. With *medium confidence* some species will be tolerant to OA, however, their capacity to acclimatize remains unidentified and the mechanisms setting limits to acclimation or adaptation capacity are presently unknown, not only for OA but also for temperature and hypoxia.

For animals there is *high confidence* that the species-specific capacity for performance and associated energy turnover shape sensitivity to environmental change. Excess food availability and sustained feeding capacity allow exploiting the full scope for performance. Sensitivity is highest at the highest complexity levels, organism and ecosystem. Polar ectotherms are confined to their cold-water environments and are the organisms most sensitive to warming, with no room to escape to cooler waters. Ecosystems in polar areas, especially in Antarctica are thus prone to lose some of their endemic species due to strong warming trends that impact highly specialized cold-stenothermal endemic fauna, with no possibility for that fauna to escape to colder regions. Although *confidence* in such projections is *high* when building on mechanism-based knowledge, formal loss of an Antarctic species has not been recorded. Some tropical species such as corals and ecosystems such as coral reefs also live close to their upper thermal limits and respond sensitively to thermal extremes and synergistic stressors like OA (6.3.2., 6.3.4.).

Climate change not only involves the concomitant change of various stressors, but also their synergistic or antagonistic effects (6.3.6.). In animals these integrated effects can be assessed through the OCLTT concept (Figure 6-7) while such theoretical framework to assess impacts of environmental drivers is not yet available for other organisms. The effects of various biotic and abiotic stressors on temperature dependent energy allocation and performance co-define the dynamic limits of the thermal niche of a species (Pörtner *et al*., 2010) and, in consequence, its biogeographical range (cf. Neuheimer *et al*., 2011). thermal challenges at the borders 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*). The synergistic effects of stressors at organism level cause relative changes in the performance of interacting species and lead to shifts in species interactions and food webs (*limited evidence*, *low confidence*).

6.3. From Understanding Biological Field Observations to Projections

This section will analyse how the various physical and chemical forces identified (6.1.1.) shape biological responses, largely in the field, considering the insight gained from studying the effective mechanisms (6.2.2.). Extrapolations from mechanistic knowledge and empirical observations support qualitative projections of future change. Modeling approaches and the resulting global projections are discussed under 6.5.

6.3.1. Contrasting Observations and Projections on Primary Production

Continued economic use of the ocean under climatic change depends on the maintenance of primary productivity and the transfer of this energy to higher trophic levels of the foodweb. There is supporting observational confirmation (*high agreement, medium evidence*) for a significant alteration of NPP when the environmental controls are altered due to natural perturbations, e.g. volcanic eruptions and enhanced iron supply in High Nitrate Low chlorophyll waters of the NE Pacific (Hamme *et al*., 2010). Similarly, climate variability can drive pronounced changes in primary productivity, with *medium evidence* and *medium confidence* (Chavez *et al*., 2011), such as during the El Niño to La Niña transition in Equatorial Pacific, when enhanced nutrient and trace element supply are observed (Chavez *et al*., 1999).

By the analysis of Behrenfeld *et al*. (2006) using SeaWiFs satellite data, there has been a prolonged and sustained NPP decrease of 190 Tg C per year since 1999 - an annual reduction of approximately 0.4 % of total global NPP. These changes are traceable to the expansion of permanently stratified, tropical regions (WGII, Ch. 3) and are therefore climate sensitive. Increased frequency of or transition to permanent El Niño favorable conditions in a warmer future world (Wara *et al*., 2005) and further expansion of the subtropical ocean gyres (Polovina *et al*., 2008), are predicted to lead to lower global ocean NPP. Other more recent regional studies, based on a regionally validated NPP algorithm in tandem with remotely sensed archives of ocean color, point to increased NPP in the Arctic Ocean (Arrigo and van Dijken, 2011). There have also been reports of altered NPP, based on analysis of trends from > decade-long time-series of directly measured ocean productivity (i.e. *in situ* incubations using the radiotracer ^{14}C-bicarbonate) for two low latitude open ocean sites (Saba *et al*., 2010). In contrast to the trends reported for the low latitude ocean by Behrenfeld *et al*. (2006), Saba *et al*.'s analysis revealed an increase (2 % yr^{-1}) in NPP over the period 1988 to 2007.

The analysis of Saba *et al*. (2010), for trends at the long-established open ocean time-series sites in the Subtropical North Pacific Gyre (HOT, Hawaii Ocean Time-series, 22°45'N, 158°W) and Subtropical NW Atlantic Gyre (BATS, Bermuda Atlantic Time Series, 31°40'N, 64°10'W), linked trends of increased NPP at each of these sites to a climate variability signature (North Pacific Gyre Oscillation). Similar temporal trends in NPP have recently been reported at near-shore time series sites such as Monterey Bay (California) and La Coruña in NW Spain (Figure 6-10). The opposite trends for rates of NPP in recent decades in the low latitude ocean reported by Behrenfeld *et al*. (2006) and Saba *et al*. (2010) may be due to either methodological issues (i.e. means of validation of satellite-derived chlorophyll concentrations, 6.2.2.2.) and/or the extent to which discrete sites are broadly representative of the surrounding oceanic provinces, respectively (Saba *et al*., 2010).

[INSERT FIGURE 6-10 HERE
Figure 6-10: Time-series of water column integrated primary production (PP) anomalies for time-series sites: 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). Integrated PP and Chl anomalies were calculated by integrating over the

water column, then interpolating, smoothing and differencing. For PP, the 1992–1993 and 1997–1998 El Niño signals are less apparent, except perhaps at La Coruña and Monterey Bay, but all the sites except Cariaco seem to show positive (pink) PP anomalies after 2000.]

The oceans provide half of global NPP annually (Field *et al.*, 1998) and thus much attention has focussed on whether climate change will alter global NPP and whether there is evidence for alteration of rates of NPP. Research into this topic has relied heavily upon the application of satellite-derived estimates of chlorophyll in conjunction with algorithms to convert chlorophyll to NPP. The reported trends for much of the low latitude ocean using this method differ considerably from those few sites at which sufficiently long time-series of more robust direct estimates of NPP have been obtained. There is *medium confidence* based on *limited evidence* from these relatively few offshore time series sites that there has been a small but significant increase in NPP over the last two decades, but this increase may be linked more closely to shifts in climate variability than to climate change. At high latitudes, there is *medium confidence* based on *limited evidence* from satellite images that an increase in the number of sea-ice free days is resulting in higher rates of NPP.

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 (6.2.2.1.) or via additional changes in the physical environment, for example through changing degrees of stratification. Species responses to temperature depend on location, the respective climate regime and, potentially, local adaptation (6.2.2.1.). The diverse degrees of species shifts at the same location in the marine realm emphasize that thermal window widths and associated thermal sensitivities are species specific (Perry *et al.*, 2005), in line with their differentiation according to mode of life, phylogeny and associated metabolic capacities (6.2.2.1.).

6.3.2.1. Species Abundance, Biogeography and Diversity

6.3.2.1.1. Pelagic examples

Long-term observations (6.1.3.) encompassing the whole pelagic North East 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). Warm water copepods expanded their range by 10° North since 1960 (Beaugrand *et al.*, 2009), with attendant diachrony in phenology and mismatch between 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 the warming trend 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 (6.2.2.2.; 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.

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 (Philippart *et al.*, 2011). 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; Figure 6-11), with a parallel retreat of colder water plankton to the north (Beaugrand *et al.*, 2002; Bonnet *et al.*, 2005; Lindley and Daykin, 2005; Richardson *et al.*, 2006). For comparison, terrestrial shifts occur by 6 km per decade according to meta-analyses of individual species responses (Parmesan and Yohe, 2003) to 16.9 km per decade shift in northern range boundaries according to a meta-analysis using means across taxa groups, but with a high diversity of range shifts among species (Chen *et al.*, 2011). Altitudinal shifts in terrestrial environments resemble shifts to cooler depths in marine environments (Burrows *et al.*, 2011).

Any displacement of zooplankton in response to temperature anomalies is not uniform across oceanic regions or taxa (Johns *et al.*, 2001; Johns *et al.*, 2003; Mackas and Beaugrand, 2010; McGinty *et al.*, 2011). For example, between 1960 and 2000 the northwest Atlantic saw an increase in the abundance of a number of arctic boreal plankton species, notably copepods like *Calanus hyperboreus* (Krøyer), *Calanus glacialis* (Jaschnov) and the dinoflagelate *Ceratium arcticum*, and a southerly shift of the copepod *C. hyperboreus* (Johns *et al.*, 2001), linked to the strengthening of the colder Labrador Current as far south as Georges Bank.

[INSERT FIGURE 6-11 HERE
Figure 6-11: A. Long-term changes in the ecosystem state based on 5 biological parameters (phytoplankton color index, mean size of calanoids, mean calanoid diversity, an index of change in plankton composition and cod recruitment). B. Long-term changes in the multiscale temporal 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).]

Warming in the North Atlantic, between temperate and polar latitudes, was paralleled by a reduction in the average body lengths of about 100 copepod species, from 3-4 mm to 2-3 mm. The changes support expectations according to temperature related trends in body size (6.2.2.4). Warming also led to an increase in species richness among copepods and in the dinoflagellate genus *Ceratium* (Beaugrand *et al.*, 2010). Warming and decreasing annual variability in SST was associated with lower diversity, smaller size and reduced abundance of diatoms (Beaugrand *et al.*, 2010), which are major contributors to carbon export (Armbrust, 2009). There is *low confidence* that outbreak frequencies of jellyfish aggregations are following the rising SST (Mills, 2001; Purcell, 2005; Purcell and Decker, 2005).

The ecosystem shift observed in North Sea plankton in the late 1980s involved an increase in phytoplankton and changes in the species composition and abundance among holozooplankton (animals that are planktonic for their entire lifecycle). Increases in the frequency of jellyfish in the plankton and of decapods and detritivores in the benthos were paralleled by an increase in the abundance of decapod and echinoderm larvae, but a decrease in bivalve larvae (Reid *et al.*, 2001; Kirby and Beaugrand, 2009; Kirby *et al.*, 2009; Lindley *et al.*, 2010). This North Sea regime shift (a regime shift is a relatively sudden change between contrasting persistent states of a system; de Young *et al.*, 2008) was paralleled by an increase in variance which was related to the northward propagation of a Critical Thermal Boundary (CTB) found at 9-10°C beyond which such ecosystem shifts set in (Beaugrand *et al.*, 2008). The CTB reflects the boundary region between the temperate and the polar biome. Passing the CTB led to pronounced variance in phytoplankton measured from SeaWIFS, 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 (*Gadus morhua*) at large scales of the North Atlantic Ocean (Beaugrand *et al.*, 2010). These patterns also extend to the Southern North Sea with some modifications. They were associated with elevated salinities and average warming by 1.6°C to higher temperatures both in summer and winter between 1962 and 2007, expanding the time window for growth of microalgae and possibly causing the significant increase observed in the numbers of large diatoms (Wiltshire *et al.*, 2010).

These studies also revealed that marine ecosystems of the North Atlantic are not equally sensitive to climate warming. Regions of high vulnerability exist as areas where mild warming can trigger rapid and substantial ecosystem shifts. These findings offer a way to anticipate future shifts in the North Atlantic sector. Recent findings indicate another occurrence of a regime shift in the Bay of Biscay, the Celtic and the North Seas in the mid to the end 1990s (Luczak *et al.*, 2011). 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 a stepwise warming in the mid 1990s. A further shift discovered at the end of the 1990s in the North Sea (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.

Both benthic and pelagic fish species also display latitudinal movements, in parallel to the large-scale biogeographical shifts observed in the phyto- and zooplankton of the North East Atlantic (Quero *et al.*, 1998; Brander *et al.*, 2003; Perry *et al.*, 2005). 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 during the timeframe from 1977 to 2001 in the North Sea, with winter warming being effective for Atlantic cod (Perry *et al.*, 2005, 6.2.2.). In the Northwest Arctic winter and spring warming were effective for Atlantic salmon (Friedland and Todd, 2012). Further examples include pelagic sardines and anchovies extending into the North Sea in the early to mid 1990s, in response to intensified NAO and AMO, after about 40 years of absence (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). Warming also caused shifts of North Sea cold water fish assemblages to larger depths of occurrence between 1980 and 2004 (Dulvy *et al.*, 2008). Again, the cooling and freshening of the north-west Atlantic has had the opposite effect, with capelin and their predator, Atlantic cod shifting further south, beginning in the late 1980ies (Rose and O'Driscoll, 2002).

Further examples exist in other ocean regions. In the northeast Pacific there has also been a general increase in the frequency of southern species moving northward with El Niño associated warming events in the late 50ies, early 80ies and late 90ies and, with a general interdecadal climatic regime shift in the California Current beginning in the late 70ies (McGowan *et al.*, 1998). Migratory sockeye salmon *Oncorhynchus nerka* and other salmonids entering freshwater streams for spawning may not suffer from a warmer ocean but rather from excessive warming of the rivers (Eliason *et al.*, 2011). Northward range extensions of pelagic fish species related to warming have been reported for the Northern Bering Sea region in 2002 to 2004 (Grebmeier *et al.*, 2006, WGII, Ch. 28). Blooms of coccolithophores (*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 shallowing mixed layer depths, higher PAR and low zooplankton grazing (Merico *et al.*, 2004). A southward movement of was also detected for coccolithophores in the Southern Ocean in the 2000s (Cubillos *et al.,* 2007).

In the Southwest Atlantic sector and the Bellingshausen Sea a historical analysis of the distribution of Antarctic macrozooplankton between 1925 and 1951 also 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*). A further 1°C warming was projected to cause subpolar species expanding into high latitudes and Antarctic species retreating to constricted ranges (Mackey *et al.*, 2012).

6.3.2.1.2. Responses of ocean benthos

Limited information is available on the response of ocean benthos to climate change. Overall, the consequences of global warming at the level of benthic communities are complex but recent evidence indicates, with *high confidence*, the relatedness to the mechanistic basis outlined in Figure 6-7. Responses of intertidal organisms to warming are shaped by exposures to temperature extremes and will be dealt with by WGII, Ch. 5. The distribution of sublittoral benthos appears to respond more slowly to warming than that of plankton, fish and intertidal organisms, but immigration and proliferation of species from warmer waters has been observed in selected areas like the British channel (Hinz *et al.*, 2011) or the North Sea coastal area (Reise and van Beusekom, 2008). NAO-driven variability in growth rate has been documented for the Atlantic quahog, *Arctica islandica* from Iceland (Schöne *et al.*, 2005), the coralline alga *Clathromorphum compactum* off Newfoundland (Halfar *et al.*, 2011) and the bivalve *Clinocardium ciliatum* in the Barents Sea (combined NAO and ACRI; Carroll *et al.*, 2011). A role for temperature has yet to be unequivocally demonstrated. 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 (6.2.2.1., Pörtner and Knust, 2007). Benthic invasion of warm water species included the Pacific oyster (*Crassostrea gigas*) (Wiltshire *et al.*, 2010).

Some changes as in the Southern North Sea are also attributed to a reduced frequency of storm events or cold temperatures in winter, conversely, an increase in species numbers between 1980 and 2005 may be due to rising SSTs (Junker *et al.*, 2012).

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 (Lough, 2008; De'ath *et al.*, 2009). These changes have been attributed to both temperature and carbonate saturation state (Cooper *et al.*, 2008), although *evidence* is more *robust* for an attribution of present changes to the warming trend (WGII, Ch. 5, Crosschapter coral box). Waming also comes with poleward shifts in coral distribution (Precht and Aronson, 2004; Yamano *et al.*, 2011).-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). These findings indicate various environmental influences and limited specialization of reef ecosystem structure on the prevailing climate regimes, but also possibilities for various pathways of change in species composition in response to a future climate. Temperature also shapes the geographic distribution of macroalgae (van den Hoek, 1982). A strong poleward shift of the kelp *Laminaria hyperborea* is evident along European coasts (Müller *et al.*, 2009, 2011) and also in algal shifts along both sides of the Australia continent (Wernberg *et al.*, 2011). Similar shifts are documented e.g. in Japan (Kirihara *et al.*, 2006) and are expected in the cold temperate region off South America. Latitudinal distribution of Antarctic algae may remain mostly unchanged until the end of this century because expected temperatures (2080–2099 mean SSTs) according to Scenario B1 (SRESA1B) emission scenario remain within the thermal range identified for selected species, however, this conclusion is fraught with *low confidence* due to limited data (Müller *et al.*, 2011). Modeling results suggest that North Atlantic polar to cold temperate species will extend their distribution into the High Arctic and retreat along the north-eastern Atlantic coastline (6.5.). 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).

Similarly, new diseases typically have emerged through temperature-related range shifts of known pathogens (Harvell *et al.*, 1999). For example, pathogens detrimental to oysters have spread from the mid-Atlantic states into New England (Harvell *et al.*, 1999). Compared to terrestrial systems, marine epidemics can spread at two to ten times faster rates (McCallum *et al.*, 2003).

6.3.2.2. Community Reponses – Species Phenologies and Interactions

6.3.2.2.1. Pelagic examples

Since the 1600s, high catches of the Japanese sardine (*Sardinops melanostictus*) have occurred in association with a southeasterly shift and intensification of the Aleutian Low and a positive mode of the PDO (Yasuda *et al.*, 1999). The climate-induced regime shift from sardines (*Sardinops melanostictus*) to competing anchovies (*Engraulis japonicus*) occuring during the 1990s in the Japanese Sea is clearly attributable, with *high confidence*, to temperature change. With food preferences of the competing species being similar (Li *et al.*, 1992), the differential thermal response for anchovies and sardines (Takasuka *et al.*, 2007; Takasuka *et al.*, 2008, 6.2.2.1., 6.2.2.4.) may shape their competition, indicating with *medium evidence* and *agreement*, and *medium confidence* that warming directly favors the anchovies and harms the sardines. In the Southern ocean, the 50% loss in krill abundance between 1926 and 2003 (Atkinson *et al.*, 2004) came with an increase in salp biomass. If warming reduces the extent and duration of sea-ice cover, survival of larval krill and adult recruitment are impaired (Hays *et al.*, 2005). 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 (Beaugrand *et al.*, 2003). This shift was thereafter shown to be largely caused by temperature (Helaouët and Beaugrand, 2007). Statistical analysis of a time series for four commercial fish species and their zooplankton prey in the Norwegian and Barents Seas also showed with *high confidence* that climate shapes population growth rates through a complexity of 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, primary producers (microalgae), primary, secondary and tertiary consumers (zooplankton, fish and jellyfish) and benthic detritivores (echinoderms and bivalves) species interactions 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; 6.3.6.).

6.3.2.2.2. Ocean benthos

According to results by Schiel *et al*. (2004) 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). Another study focused on various intertidal sites along a west to east cline of Vancouver island and Olympic Peninsula (WA) which are thermally impacted to different degrees. Observations along this cline together with a comparison of two sampling periods in 1957/58 and 2007/8 showed that the response to temperature leads to shifts in vertical zonation and even to local extinctions. 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). Changes in competitiveness are also involved in the following examples: In cold-temperate to polar transition areas – assuming a moderate global warming scenario B1 (SRESA1B) with temperature shifts between -1.5 and 4°C depending on the region and the season - foliose and leathery perennial algae will probably be replaced by turf species (Müller *et al*., 2011), which inhibit a reestablishment of canopy forming macroalgae (Airoldi, 1998). In tropical seas, turf algae can rapidly colonize thermally damaged corals (Fricke *et al*., 2011), depending on the extent to which coralline red algae, which are the most important substrate for coral recruitment, suffer from ocean acidification (Hoegh-Guldberg *et al*., 2007). Long-term observations and experimental research have identified, with *high confidence* and building on *robust evidence*, shallow-water reef-building corals and their ecosystems at low latitudes as one of the marine ecosystems most sensitive to climate change and experiencing large scale mortalities due to bleaching (Veron *et al*., 2009). With *high confidence* the deterioration of coral reef ecosystems and associated reduction in coral cover due to bleaching has already started and the risk of it continuing unabated is especially high. Recovery may take thousands, if not millions of years (Veron 2008). In general, such shifts may with *medium evidence* and *medium confidence* originate from species-specific climatic niches and associated changes in species interactions in space and time (competitiveness, predation), which then accelerate and drive species distributions, abundances and species richness (6.2.2.1., 6.2.2.4., cf. Figure 6-7).

6.3.2.3. Conclusions

Overall, there is *very high confidence* that temperature has a key role in directly affecting marine organisms and their biogeography as well as community structure in the context of climate change, as has been elaborated in key examples from pelagic and benthic systems. With *very high confidence* and building on *robust evidence*, shallow-water reef-building corals and their ecosystems at low latitudes are among the marine ecosystems most affected by climate change and especially associated warming. However, in many cases other factors change concomitantly, such that quantification of the fraction of ecosystem change attributable to temperature has not always been possible.

6.3.3. Effects of Hypoxic Events and Expansion of Oxygen Minimum Zones

Hypoxic or anoxic conditions in both water and sediments strongly impact marine biota (6.2.2.). Depth levels corresponding to oxygen concentrations of about 9 μmoles kg^{-1} (~0.2 ml L^{-1}) form an interface where vertically migrating organisms concentrate in abundances that may be higher than in the upper productive layers of the ocean. These high concentrations of meso- and macroplankton play an important role in trophic relations in mesopelagic ecosystems. These areas are unique foraging grounds for mesopelagic planktivorous fauna, especially myctophids (lanternfish), which are expected to become more important for fishery in the future (Pierre *et al.*, 2005; Kadilnikov and Myskov, 2007). Exacerbated oxygen 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). A major effect of expanding OMZs is the compression of habitat for intolerant taxa relying on high oxygen concentrations such as billfishes and other pelagic fishes with a high oxygen demand (Prince and Goodyear, 2006; Prince *et al.*, 2011, Stramma *et al.*, 2012, cf. 6.2.2.), lobsters and crabs (Chan *et al.*, 2008) and groundfishes (McClatchie *et al.*, 2010). Affected species may experience enhanced capture by fisheries (Prince and Goodyear, 2006; Prince *et al.*, 2010) or may abandon the area, otherwise mass mortality may occur. Expanding OMZs and coastal hypoxia may support range expansions or population growth in hypoxia-tolerant taxa such as anaerobic bacteria, gelatinous zooplankton (medusae, ctenophores) and selected fishes (gobies, hake), or possibly of selected cephalopods like the Humboldt squid along the East-Pacific coast although the drivers for the expansion of the squid have not yet been clearly identified (Gilly *et al.*, 2006; Zeidberg and Robinson, 2007; Bazzino *et al.*, 2010). A lower overall level of biodiversity is expected (Levin, 2003; Levin *et al.*, 2009; Ekau *et al.*, 2010; Gooday *et al.*, 2010).

Upwelling events associated with exposures to hypoxic or corrosive deep water can be accompanied (*high confidence*) by strong ecosystem responses, such as a reduction in biomass of fish and invertebrate fauna (Keller *et al.*, 2010), near complete mortality of benthic invertebrates and increases in sulphide-oxidizing bacterial mats (Chan *et al.*, 2008). These events have also been blamed for the sporadic massive mortalities of highly valuable fish resources (i.e. abalone) occurring on the west coast of the Baja California Peninsula during the last 5 years. Shifts in upwelling activity with climate change coincide with the apparent increase in the frequency of massive submarine gas eruptions of methane (CH_4) and hydrogen sulphide gas (H_2S) off southwestern Africa (Weeks *et al.*, 2002). These eruptions have been attributed to the enhanced formation and sinking of phytoplankton biomass and the accumulation of non-oxidized organic matter on the hypoxic to anoxic sea floor (Bakun *et al.*, 2010). They have been blamed for extensive mortalities of coastal fish and invertebrates (Bakun and Weeks, 2004) and reductions in fishing productivity, particularly of the Cape hake (*Merluccius capensis*), which forms the basis of Namibia's most valuable fishery (Hamukuaya *et al.*, 1998).

The large and synchronous fluctuations of alternating sardine and anchovy abundances observed during the last century in eastern (Humboldt, Benguela, California) and western (Japan) boundary currents (Lluch-Belda *et al.*, 1989; 1992; Schwartzlose *et al.*, 1999) have been typically related to changes in temperature (6.3.2.; Chavez *et al.*, 2003; Tourre *et al.*, 2007), food availability and prey size spectra (van der Lingen *et al.*, 2006). Off Peru, however, the region with the largest fishery of small pelagics on Earth, recent analyses of a comprehensive oceanographic data set have documented that the dissolved oxygen concentrations also play a key role in determining their distribution and abundance and help explaining the alternating pattern through differential responses of these species: During the 1960s to early 1970s and the 1990s to 2000s, when the anchovy dominated over the sardine in the southeast Pacific, the oxygen concentration was lower and the oxycline was shallower than during the sardine period in the late 1970s and 1980s. This is consistent with the observations that 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 will occur in both benthic and pelagic ecosystems (Ekau *et al.*, 2010), with undetermined population-level consequences. 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.*, 2009; Stramma *et al.*, 2010). In a worldwide spread of communities of anoxic "black sediments", some groups of organisms such as Ciliata, Turbellaria, Gnathostomulida, Nematoda, Oligochaeta live at the thin oxic-anoxic interface and many of these have adaptations allow them to utilize chemosynthetic production.

6.3.3.1. Interaction with Other Drivers

Marginalization of calcifiers is observed in OMZs, where CO_2 levels parallel those of hypoxia (Levin, 2003). Furthermore, significant correlations between H_2S concentrations and climate change indicators such as the sea surface temperature and sea level pressure at the interannual and interdecadal scales have been documented for the open part of the Black Sea (Daskalov, 2003; Faschuk, 2011). Climate associated processes via changes in circulation patterns, biological productivity and associated vertical fluxes of organic matter may change the parameters of anoxic and oxygen minimum zones and of zones poisoned by hydrogen sulphide (their extent and location, O_2 and H_2S concentrations) and thus influence corresponding pelagic and bottom fauna distributions, trophic relations, energy flows and productivity (Figure 6-12). Even hypoxia-tolerant species like the Humboldt squid (*Dosidicus gigas*) may only tolerate transient exposure to such conditions and be driven into shallowing oxygenated waters by expanding oxygen minima when repaying oxygen debt (Rosa and Seibel, 2008).

[INSERT FIGURE 6-12 HERE
Figure 6-12: Diagram schematizing the principal mechanisms underlying the formation of hypoxic conditions and their biological background and consequences along continental margins (modified from Levin *et al.* 2009; Levin and Sibuet, 2012).]

6.3.3.2. Microbial Denitrification Under Hypoxia

With enhanced variability and expansion of OMZs both denitrification and annamox will become more important as processes leading to the loss of fixed N_2 and so, with *medium confidence*, will limit oceanic primary productivity. Foraminifera are widespread and abundant in OMZs, so OMZ expansion may promote further denitrification (N_2 production) in marine sediments via protists (6.2.2.2). Spread of large sulphur bacteria (*Thioploca* and *Thiomargarita*) on the seafloor within expanding OMZs may contribute to N loss via sequestration and reduction of nitrate and release of NH_4^+ at depth in the sediment - which then stimulates anaerobic ammonium oxidation.

There is now recognition that estimates of N flux have traditionally been highly underestimated and that water column denitrification and N_2 fixation are spatially and temporally variable (*limited evidence, low confidence*). Thus climate effects on these processes are *unlikely* to operate uniformly (Brandes *et al.*, 2007) and any attempt to project effects is premature and fraught with *low confidence*.

6.3.3.3. Conclusions

There is *low confidence* on how climate change might impact nitrogen cycling in OMZs. There is *limited evidence* and *medium confidence* that the expansion of OMZs 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 (Auel *et al.*, 2005; Ekau *et al.*, 2010). Effects of OMZ expansion will with *high confidence* propagate along the food chain and thereby affect fish stocks and top predators (Stramma *et al.*, 2010). If oxygen levels decline/OMZs expand further, there is *high confidence* that on a time scale of weeks, a community change toward hypoxia-tolerant fauna will occur in midwater. There is *high confidence* that with progressive hypoxia the diversity of macroorganisms will change and, under extreme hypoxia finally, higher marine organisms will disappear and heterotrophic microorganisms will dominate.

6.3.4. Anthropogenic Ocean Acidification – Effects in Warming and Hypoxic Oceans

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 (6.2.2.1, 6.2.2.4). 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 contributions of OA to climate-induced alterations have not yet been clearly established, partly because on-going OA as well as OA research are still early in the process and because the concomitant trends of warming, oxygen depletion and OA in the paleo-record (6.1.2.) and in on-going change make it difficult to attribute changes exclusively to OA. Similar to today, OA paleo-events were characterized by warming and enhanced stratification of the oceans and, consequently, a stronger deoxygenation of deeper waters (Thomas, 2007; Gattuso *et al.*, 2011). The PETM (55 Ma) provides useful information for plankton and benthic foraminifera and the Permian Triassic (251 Ma) for marine animal phyla (6.1.2., 6.2.2.4.). However, present day OA develops more than 10 times faster than comparable paleo-events (Ridgwell and Schmidt, 2010). Furthermore, ocean physicochemical conditions prior to each of those paleo-events was very different from the present situation.

6.3.4.1. Bacterial Communities and Nutrient Cycles

Field experiments in several locations in the tropical Atlantic and Pacific oceans 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 will occur on a time scale from 30 (SRES scenario A1FI) to 60 years (scenario B2) and will correspond to a rise in atmospheric CO_2 concentration by approximately 100 μatm (6.1.1.). 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, these short term experiments cannot account for changes in population numbers that might occur over longer periods. For example, lower per cell nitrification rates reported following short-term pH perturbation experiments could lead to changes in cell abundance (either decreases or increases in cell number) further decreasing or restoring, respectively, the total volumetic rate of nitrification. If the proposed decrease in rate leads to an accumulation of the rate limiting substrate, ammonium, then the nitrifier population might also be expected to change over time to utilize the excess, rate-limiting substrate. If the rate of nitrification does decrease under enhanced OA, this would lead to a lower production of oceanic nitrous oxide and counter the effects of suboxic water expansion. It is currently unknown whether this will occur.

Overall, however, 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. Assessments include: (1) cellular elemental stoichiometry (C-N-P ratios), (2) rates of CO_2 and N_2 fixation, (3) rates of nitrification and (4) changes in the proportion of dissolved to particulate photosynthate carbon production and the implied efficiency of the biological carbon pump (6.3.4.2.). While effects have been observed in the laboratory and in coastal mesocosm studies (Weinbauer *et al.*, 2011) or the field experiments described above, 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). 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 such that projections of future changes are not yet possible.

6.3.4.2. Phyto- and Zooplankton Communities

While there is *robust evidence* and *high confidence* for 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. In terrestrial systems, rising atmospheric CO_2 concentrations are reported to enhance productivity due to "CO_2 fertilization" (Fung *et al.*, 1997; Cao and Woodward, 1998). In marine systems, phytoplankton physiological rates and growth might also benefit from "fertilization" by CO_2 (Rost *et al.*, 2008; Hutchins *et al.*, 2009). For natural phytoplankton assemblages there is *limited evidence* and *medium confidence* to date that NPP is stimulated during experiments in which CO_2 concentrations are increased (Riebesell *et al.*, 2008;

Tortell *et al*., 2008b). A number of laboratory studies observed enhanced rates of photosynthesis under elevated CO_2, e.g. for the coccolithophore *Emiliania huxleyi* (e.g. Riebesell *et al*., 2000; Rost *et al*., 2003; Leonardos and Geider, 2005) or the diazotrophic cyanobacterium *Trichodesmium* (e.g. Barcelos e Ramos *et al*., 2007; Hutchins *et al*., 2007; Kranz *et al*., 2010). In the latter species, elevated CO_2 levels also result in higher cell division rates, altered nutrient utilization (C:N and C:P ratios) and enhanced rates of N_2 fixation (e.g. Hutchins *et al*., 2009; Kranz *et al*., 2011; Gattuso *et al*., 2011). Among cyanobacteria, cell division was increased (by ~25%) as was photosynthetic rate (by ~15%) in *Synechococcus* spp., while *Prochlorococcus* spp. remained unaffected at 750 μatm CO_2 (Fu *et al*., 2007).

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-stimulation of primary production rates for Southern Ocean diatom-dominated assemblages (Tortell *et al*., 2008b). For dinoflagellates, relatively little is know with regard to their sensitivity to elevated CO_2 as most studies exposed them to high pH (Hansen *et al*., 2007). In *Prorocentrum minimum*, however, carbon fixation rates were enhanced at 750 μatm CO_2 while growth remained unaffected (Fu *et al*., 2008). The above examples highlight the difficulties in projecting the effects of 'CO_2 enrichment' from species-specific responses. Furthermore, 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). Species- or taxa-specific differences in CO_2 responses can often be linked to the capacity and energetic costs of their CO_2 concentrating mechanisms (CCM; Giordano *et al*., 2005; Kranz *et al*., 2011). As responses to elevated CO_2 may influence the competitive abilities of species, implications for the natural phytoplankton communities may be larger than indicated from results obtained in laboratory of individual species. In other words, small differences in CO_2 sensitivity may lead to pronounced shifts in the dominance of species (Tortell *et al*., 2008b, Beaufort *et al*., 2011).

There is *medium evidence* and *low confidence* that CO_2 induced OA will cause some planktonic organisms having exoskeletons that are insufficiently calcified for sustained structural support and protection. In coccolithophores, however, uncertainty remains as the function(s) of calcification are yet not known, i.e. consequences of lowered calcification are difficult to be estimated (e.g.,Trimborn *et al*., 2007; Rost *et al*., 2008), and the responses to OA are highly variable. Reductions, increases and unchanged shell structure or calcification rate have been documented under end-of-century CO_2 conditions (i.e. year 2100, see below) in different coccolithophore species (Riebesell *et al*., 2000; Zondervan *et al*., 2001; Langer *et al*., 2006; Iglesias-Rodriguez *et al*., 2008). Manipulation studies on various coccolithophores then revealed species-specificity for the OA response in *Calcidiscus leptoporus* and *Coccolithus pelagicus* (Langer *et al*., 2006) and strain-specificity (strains are genetically distinct populations, including those "evolved" and adapted under laboratory conditions) for calcification in *Emiliana huxleyi* (Langer *et al*., 2009; Hoppe et al. 2011; Langer *et al*., 2011). Results obtained in bloom-forming *Emiliania huxleyi* and *Gephyrocapsa oceanica* suggest decreased calcification rates (-25% to -66%) under elevated P_{CO_2} values (i..e. 560 to 840 μatm; Riebesell *et al*., 2000; Zondervan *et al*., 2001; Zondervan *et al*., 2002; Sciandra *et al*., 2003; Delille *et al*., 2005; Engel *et al*., 2005). In contrast, Langer *et al*. (2006) found calcification unchanged in *Coccolithus pelagicus* (now *C. braarudii*) between 150 to 915 μatm. Iglesias-Rodriguez *et al*. (2008) found a doubling of cell-specific calcification for *E. huxleyi* brought from 300 to 750 μatm, paralleled by an increasing mean cell size and coccolith mass. By using the same strain as well as different types of CO_2 manipulation (TA or DIC), Hoppe *et al*. (2011) have tested these seemingly contradictory results and found reduced rates of calcification under elevated CO_2 levels.

Predictions of OA impacts on phytoplankton may additionally become complicated by synergistic effects with other environmental factors (Boyd, 2011). For example, when jointly considering irradiance and CO_2 effects, under low light, there is a strong OA-effect on calcification and a beneficial OA-effect on photosynthesis. Under high light, these effects become very small (Rokitta and Rost, 2012). Furthermore, coccolithophores are a diverse group with more than 500 extant species (Young *et al*., 2005), so as for other algal groups it may be difficult to scale the results of monospecific culture experiments to the response of the whole group. Thus, there may be merit in using studies, such as mesocosms in which the different responses of coccolithophore species and strains may be averaged out across a diverse population. Due to the complexity in response patterns, an up-scaling of effects of calcification in coccolithophores cannot be straightforward. For example, a shift to cooler temperatures from low to high latitudes implies higher solubilities of CO_2, thereby putatively hampering calcification. The shift from 'overcalcified' to weakly 'calcified' coccolithophores *Emiliania huxleyi* with higher latitudes may, however, not reflect effects on cellular calcification rates but a temperature-related shift in ecotype dominance (Cubillos *et al*., 2007, 6.3.2.).

Moreover, quantification of the calcite mass of dominant coccolithophores in the present ocean and over the last 40 kyr revealed patterns of decreasing calcification with increasing $P\text{CO}_2$, 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 that are characterised by low pH, a finding which highlights the complexity of assemblage-level responses.

For zooplankton, there is *medium confidence* that pteropods (planktonic molluscs with aragonite shells) at high latitudes (e.g. Subarctic Pacific and Southern Ocean) will reduce their calcification during OA until the end of the century (6.1.1., Orr *et al*., 2005; Comeau *et al*., 2009; Comeau *et al*., 2010; Lischka *et al*., 2011). This may have severe impact on Sub-Arctic and Antarctic populations and ecosystems as pteropods can reach high biomass and form an integral part of the foodweb as grazers and as prey for fishes like pink salmon (Bathmann *et al*., 1991; Armstrong *et al*., 2005; Hunt *et al*., 2008). Planktonic calcifiers with calcite tests, like foraminifera, may be affected later by enhanced dissolution than pteropods, since calcite is less soluble than aragonite (Feely *et al*., 2004). Decreasing calcification and shell weight were elicited in planktonic foraminifera exposed to elevated CO_2 (Bijma *et al*., 1999; Russell *et al*., 2004; Lombard *et al*., 2010) and was also evident from a comparison of modern foraminifera and those preserved in the sediments (i.e. 50 kyr) in the Southern Ocean (Moy *et al*., 2009). The similarity with patterns observed during the water chemistry changes associated with glacial interglacial cycles (Barker and Elderfield, 2002; Figure 6-4) makes projections of future reductions in net calcification in foraminifera highly certain (*high confidence*). Food quality may be affected by OA, however, this aspect has been scarcely studied (*limited evidence*). In one study, elevated CO_2 significantly changed fatty acid composition and levels in a diatom, *Thalassiosira pseudonana*, which led to apparent constraints on growth and reproduction of the copepod *Acartia tonsa* (Rossol *et al*., 2012). Otherwise, *confidence* is *high* that direct effects of OA on copepods will be small, possibly except for synergistic detrimental interaction with temperature at the edges of their biogeographical range (6.2.2.)

6.3.4.3. Macrophytes and Macrofauna at Ecosystem Level

Extrapolations from laboratory studies of affected mechanisms (6.2.2.3., 6.2.2.4.) suggest that most seagrasses and non-calcifying algae respond to OA by increasing production, growth and recruitment, while calcifying algae experience reduced productivity. The wide range of responses among macrofaunal calcifiers (e.g. Ries *et al*., 2009) suggests diverse ecosystem level consequences. 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., Table 6-3). Observations at volcanic CO_2 vents in a naturally acidified Mediterranean coastal site (e.g. at Ischia, Hall-Spencer *et al*., 2008) as compared to control sites at the same ambient temperatures suggest differential OA effects on non-calcifying and calcifying algae and animals, with non-calcifiers increasingly outcompeting calcifiers towards a mean pH of 7.8. The finding of predominantly calcitic bryozoans persisting in lower pH conditions than coralline algae which have more soluble high calcite skeletons reflects differential sensitivities among calcifiers (Martin *et al*., 2008). Major shifts between calcifiers and toward non-calcareous macroalgae also occurred between pH 8.1 and 7.7 at CO_2 seeps on reefs off Papua New Guinea, associated with decreased calcification rates in the corals (Fabricius *et al*., 2011) and confirming experimental findings of enhanced competitiveness of macroalgae over corals under elevated CO_2 tensions up to 1140 μatm (Diaz-Pulido *et al*., 2011). However, with high pH variability at natural sites, lower pH values than indicated by the average change may have been effective (Hall-Spencer *et al*., 2008; Porzio *et al*., 2011). Conversely, recolonization of the seep areas by larvae from neighbouring areas with normal pH or during periods of high pH may prevent long-term consequences of low pH that would develop otherwise as during OA scenarios. Overall, these findings indicate with *medium confidence* that long-term limits to acclimatization capacity exist in some marine calcifiers (Hall-Spencer *et al*., 2008). Findings in mesocosms during 30 d exposures of benthic marine communities from British Channel habitats are generally in line with these extrapolations. Communities diversity was reduced in response to falling pH, shifting from a community dominated by the biomass of calcareous organisms to one dominated by non-calcareous organisms around pH 7.8, with loss of calcareous individuals and species down to pH 7.2 and a switch from net calcification to net dissolution around pH 7.4 (Ωcalcite = 0.78, Ωaragonite = 0.5) [Christen *et al.,* 2012 to come]. Such findings and thresholds cannot be generalized for all benthic habitats. Sensitivity thresholds will with *high confidence* shift to lower CO_2 concentrations and toward alkaline pH once hypoxia or warming to beyond the thermal optimum exacerbate the effects of CO_2 (6.2.2.1., 6.2.2.4.). With *limited evidence* and, thus *medium confidence*, such extrapolation indicates that CO_2 effects on communities are probably exacerbated by warming at the warm edges of the biogeographical ranges and vice versa. Such conditions may already prevail for warm water coral reefs (Veron *et al*., 2009). For cold-water corals experimental and observational findings suggest, with *limited evidence* and thus, *low confidence*, some resilience to OA (6.2.2.4.4.).

It remains to be explored further whether organisms and ecosystems characterized by fluctuating or permanently elevated CO_2 levels (6.1.1.), like stratified fjords, upwelling areas, oxygen minimum zones or the intertidal may have evolved a higher resistance to further, anthropogenic increases in CO_2 levels than organism con-specifics or congeners and their ecosystems in environments with permanently low CO_2 levels. As a projection with *medium confidence* 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., Miller *et al*., 2009; Denman *et al*., 2011).

6.3.4.4. Conclusions

Overall, *confidence* is *high* that ocean acidification is occurring at unprecedented rates and, together with warming, hypoxia and salinity changes, will affect marine ecosystems for centuries. The severity of effects will depend on applicable RCP emission scenarios and maximum CO_2 levels reached, but effects cannot be quantified or allocated to any scenario at present. Detection, attribution and projection of OA effects (via accumulating CO_2) at ecosystem level are limited by the nature and duration of existing laboratory studies on individual species or life stages (6.2.2, Table 6-3) and the diversity of responses observed in various groups of organisms and communities in mesocosms. Thresholds beyond which effects will set in can be quantified only with *low confidence*. Observations and experiments support some overarching trends with *medium confidence*, like projections of reduced competitiveness of calcifiers, or of enhanced primary production in some species. At present it is impossible to predict the potential impact of OA on broad-scale ecosystem functions, including sustenance of marine biodiversity. Projections of ecosystem level effects of OA thus remain qualitative at best and are fraught with *low confidence*.

Confidence 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 some calcifying coralline algae. *Confidence* is *low* that it will cause a stimulation of phytoplankton primary production overall in the oceans and is *medium* for the net stimulation of nitrogen fixation by phytoplankton. Both would have biogeochemical implications at global scale. 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 and impact food webs and higher trophic levels.

Attribution of biological responses to OA in a climate change context is complicated by the observation that water temperature, salinity, oxygenation often change concomitantly (6.1.1.). Building on mechanistic knowledge enhances *confidence* from *low* to *medium* in the projection that OA within future scenarios may cause a narrowing of thermal windows and biogeographical ranges of animals (6.2.2.1.). Accordingly, *confidence* is *high* that synergistic effects of temperature with other stressors like OA are contributing to the on-going loss of cover with live corals on coral reefs at low latitudes. These principles remain largely unexplored in virtually all other organisms such that the respective consequences for fitness, abundance, distribution and species interactions cannot be projected. *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. With *medium confidence* synergistic effects of warming and OA will constrain many more species at the warm ends of their distribution ranges, and constraints will be even stronger through synergisms of warming, OA and hypoxia.

6.3.5. ***Secondary Drivers: Biotic Interactions***

Impacts of climate change on marine populations include alterations of ecosystems structure and functioning. The wide spectrum of potential forms and magnitudes of population responses to the different environmental stressors is underlying ecosystem restructuring, with obvious consequences for individuals that include changes in predation, competition and food availability. Also, some species (so-called ecosystem-engineers) strongly shape the physical and chemical characteristics of their habitats and thereby change environmental parameters as a basis for specific communities dependent on these actvities.

6.3.5.1. Community Structure and Food Webs

Changes in NPP affect organisms at higher trophic level and food web structure (Figure 6-13; Utne-Palm *et al.*, 2010) as well as in fisheries yields (Parsons and Lear, 2001; Brown *et al.*, 2010, Cheung *et al.*, 2010). Short- and long-term (Kirby and Beaugrand, 2009) shifts in dominant trophic pathways have been documented for a variety of marine ecosystems (Moloney *et al.*, 2011). Some of these may be reversible, but other ecosystems have not reverted to their previous states over time (Jarre and Shannon, 2010). For example, the changes in the oceanic and cryospheric conditions of the Southern Ocean (Parkinson, 2002; King *et al.*, 2003; Meredith and King, 2005; Turner *et al.*, 2005) have been accompanied by decreases in the abundance of key zooplankton species, such as the Antarctic krill *Euphausia superba* (Atkinson *et al.*, 2004). In parallel, abundances of various top predators, including birds, have shown both increases and decreases in different regions (Fraser *et al.*, 1992; Ainley *et al.*, 2003; Fraser and Hofmann, 2003; Clarke *et al.*, 2007; Ducklow *et al.*, 2007; Jenouvrier *et al.*, 2009; Moloney *et al.*, 2011; 6.3.6.4.).

[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) A coupled pelagic and benthic foodweb that 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. (B) 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 *high confidence* that climate change will affect biodiversity (Sala and Knowlton, 2006; Cheung *et al.*, 2009) and community reassembly in time and space (Parmesan and Mattews, 2006; Parmesan *et al.*, 2011). Species dominance changes (Occhipinti-Ambrogi, 2007), for example, could occur when species may gain predominance and increase abundance from fitness benefits due to temperature change (6.2.2.1.) 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 (Simpson *et al.*, 2011, Harley, 2011). 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 Mattews, 2006; Luczak *et al.*, 2011).

Many expected impacts of climate change on marine food webs resemble those caused by other factors such as fishing, pollution, eutrophication and associated hypoxia (6.3.2.) as well as habitat change (Brander, 2007), leading to concern that unambiguous attribution to climate as a proximate or ultimate cause remains difficult (Parmesan *et al.*, 2011). Conversely, these other anthropogenic factors can affect ecosystem responses to climate change. Fishing truncates the age structure of populations making them more dependent on annual recruitment (Perry *et al.*, 2010; Botsford *et al.*, 2011) and reducing their ability to buffer environmental fluctuations (Planque *et al.*, 2010). Both adult and larval fish show greater variability in population abundance exploited than unexploited populations (Hsieh *et al.*, 2006; Hsieh *et al.*, 2008).

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 between 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).

In conclusion, there is *medium confidence* that climate change will alter marine community structures and foodwebs. However, there is *low confidence* in the quantitative projections of such changes (for further discussion see 6.5.).

6.3.5.2. Biogenic Habitats

To date the most intensively studied benthic ecosystem engineers are tropical corals and this body of knowledge illustrates that the twin impacts of ocean warming and acidification can have a variety of deleterious effects on the structure of the biogenic habitat from increased coral bleaching and impeded calcification rates to increased rates of coral disease (6.2.2.4.4.; Veron *et al*., 2009; Veron, 2011). There have been far fewer studies of other benthic ecosystem engineering groups but it is important to note their significance in providing structural habitat and supporting locally high biodiversity. A tremendous variety of marine benthic species form biogenic reefs, including calcified algae, bryozoans, bivalve molluscs, sponges, corals and tube-forming serpulid polychaete worms (Wood, 1999). Deep-water coral reefs or deep-water sponge grounds form an important structural habitat in the deep sea. Cold-water corals form elaborate, biodiversity-rich habitats in cold, deep waters at continental shelf, slope and seamount settings. Individual cold-water coral reefs on the continental shelf may persist for thousands of years with their growth and demise intimately linked with glacial-interglacial history and the reconfiguration of water masses (Wienberg *et al*., 2009; Wienberg *et al*., 2010; Frank *et al*., 2011). Sponge grounds range from the giant glass sponge reefs off British Columbia (only otherwise known from Jurassic fossils) to dense sponge aggregations of Antarctica (Hogg *et al*., 2010). Habitats like these rely on productivity in surface waters, making them vulnerable to any alteration in local productivity patterns and food flux associated with climate change. In coastal waters, vulnerability to increased precipitation may be an issue, increasing mortality of e.g. oyster beds may affect habitat structure during reduced salinity exposures (Levinton *et al*., 2011).

Stable temperatures and low aragonite saturation states might make especially deep-water scleractinian corals vulnerable to ocean warming and acidification, as they form their skeletons from aragonite, without the help of autotrophic symbionts. Virtually all reef-forming, deep-water scleractinian corals are found in waters currently saturated with respect to aragonite, possibly reflecting its overriding importance in controlling the occurrence of cold-water corals (Davies *et al*., 2008; Tittensor *et al*., 2009). Following projections of shallowing depths of the aragonite saturation horizon (Orr *et al*., 2005) only ~30% of these locations will remain in fully saturated sea water within the next century (Guinotte *et al*., 2006). However, these considerations contrast recent findings of substantial resilience of cold-water corals to OA (Roberts *et al*., 2009; 6.2.2.4.4.).

Burrowing infauna (e.g. fishes like gobies and snake blennies, *Lumpenus lumpretaeformis*, mud shrimps and echiurids) of marine sediments also generate habitat for themselves and other organisms. These organisms are subject to the general temperature trends in their environments and follow biogeographical shifts (Perry *et al*., 2005), but may be protected more than other benthos from environmental extremes in surface waters. However, they are exposed to hypoxia and hypercapnic waters in their ventilated burrows (Atkinson *et al*., 1987), with as yet unexplored consequences for their range of thermal tolerance. Food availability and temperature interact to affect the burrowing activity of infauna. For burrowing infauna lowered bioturbation rates result (the reworking and mixing of sediment particles and solutes by fauna) leading to steepened sediment oxygen and pH gradients with the potential to alter abundances of other infaunal invertebrates, microbial communities and their functioning (Przeslawski *et al*., 2009) today as also seen in the paleo-record (6.1.2.). *Confidence* is *high* that the development of extreme long lasting hypoxia in bottom waters will cause the emergence of mobile infauna and detrimentally affect macrofauna overall (Riedel *et al*., 2008; Haselmair *et al*., 2010).

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*.

6.3.6. Concurrent Community Responses to Multiple Drivers

The alteration of environmental stressors is projected to take place concurrently, and such alteration can affect many oceanic processes, from the organismal physiology to the areal extent and geographical boundaries of biogeographical regions confounding the attribution of altered biological trends, from individuals to ecosystems, to climate change (Parmesan *et al*., 2011). Figure 6-14 provides an attempt to categorize these multiple influences on marine biota – including temperature, carbon dioxide, dissolved oxygen 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 where two or more stressors have either synergistic or antagonistic effects. Effects range from direct impacts of ocean warming on organismal physiology (Pörtner and Knust, 2007), to complex large-scale synergistic influences such as on both coccolithophore calcite production and abundances due to increasing carbon dioxide concentrations and warming (Feng *et al*., 2009).

[INSERT FIGURE 6-14 HERE
Figure 6-14: A schematic highlighting the potential interactions between modes of forcing (anthropogenic and natural) on different levels of biological organisation. These interactions, from simple to complex, are illustrated with published examples and each is assigned a circle the size of which is the level of *confidence* in the findings of the study, ranging from *low* for modeling studies such as (10; Griffith *et al*., 2011) to *high* for lab physiological studies placed into context of field data (1; Pörtner and Knust, 2007). Circles with "?" define the bounds on our understanding of the relationship between forcing and its effect on organisational level. 1 denotes the effects of a single driver - warming on alteration of organismal physiology and field abundance (Pörtner and Knust, 2007); 2 the synergistic effects of multiple drivers - warming and increased [CO_2] on coccolithophore calcification (Feng *et al*., 2009); 3 the effects of multiple drivers on larval fish (Perry *et al*., 2010; Runge *et al*., 2010); 4 a single driver - altered pH and the different responses of coccolithophore species (Langer *et al*., 2006); 5 differential responses of cyanobacterial groups to multiple drivers - warming and increased [CO_2] (Fu *et al*., 2007); 6 Altered maturation age and growth rate due to fishing (Fairweather *et al*., 2006; Hseih *et al*., 2006); 7 differential effect of multiple drivers, light and temperature, on copepods versus diatoms (Lewandowska and Sommer, 2010); 8 the effect of fishing on ecosystem structure (Frank *et al*., 2005); 9 the interplay of fishing pressure and climate change on ecosystems (Kirby *et al*., 2009); 10 the interplay of ocean acidification and fishing pressure on benthic communities (Griffith *et al*., 2011); 11 detailed time-series observations on warming and the alteration of zooplankton biomes (Beaugrand *et al*., 2009). (TO BE DEVELOPED FURTHER AFTER FOD)]

6.3.6.1. Synergistic versus Antagonistic Effects

A recent metaanalysis of 171 experimental studies that exposed marine systems to two or more stressors identified cumulative effects in individual studies that were either additive (26%), synergistic (36%), or antagonistic (38%) (Crain *et al*., 2008). In the surface ocean, there are many examples of microbes and phytoplankton being simultaneously limited by more than one environmental factor, for example cobalt and iron (Saito *et al*., 2002; Bertrand *et al*., 2007), or iron and irradiance (Boyd *et al*., 2010). There is *medium confidence* based on *medium evidence* of both synergistic and antagonistic effects of multiple drivers on ocean biota shipboard and/or laboratory manipulation experiments (Boyd *et al*., 2010). The interplay of such simultaneous or co-limitation with the projected concurrent alteration of multiple environmental factors may result in synergisms (i.e. amplification of environmental effects) or antagonisms (i.e. diminution of environmental effects) for upper ocean organisms (Folt *et al*., 1999; Gruber, 2011). As the combination of environmental factors that co-limit microbes/phytoplankton varies 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), predicting how climate change will impact these biogeochemically important groups is currently limited (Boyd *et al*., 2010).

At the ocean basin scale, modeling experiments provide the most reliable suite of projections to date (Gruber, 2011). For different phytoplankton groups, concurrent experimental manipulations of up to three environmental properties have revealed a range of responses from no significant change to synergistic and/or antagonistic effects. For example, under the identical high CO_2 and warming conditions, the photo-physiology of the cyanobacterium *Synechococcus* was synergistically enhanced, whereas another cyanobacterial group *Prochlorococus* showed no physiological change (Fu *et al*., 2007). Such different responses to environmental forcing may result in floristic shifts in the phytoplankton in a changing climate with the potential to restructure predator-prey interactions within ecosystems (Figure 6-14). Modeling of large scale interactive environmental effects have so far mainly pointed to synergistic effects, such as the interplay between reduced ocean pH, de-oxygenation and/or warming. An example is the predicted effect of OA on altering the characteristics of sinking particles (C:N ratio and/or reduced calcite content and slower sinking) and the knock-on effects on increased water column oxygen demand (Gruber, 2011).

For more complex organisms, climate change effects also involve synergisms and antagonisms of both abiotic and biotic factors. Moderate warming below the thermal optimum may improve performance and resistance to other stressors like CO_2 (6.2.2.1.). However, when organisms were brought closer to their heat tolerance limits under projected CO_2 partial pressures heat sensitivity was enhanced 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). Warming thus loses its beneficial effects once it occurs above the thermal optimum. Here, CO_2 not only constrains acute tolerance to thermal extremes but may also act by constraining the capacity to shift tolerance limits via acclimatization and associated gene expression [Lucassen *et al.,* to come]. The resulting narrowing of the thermal niche (Walther *et al*., 2009) leads to qualitative projections of shrinking biogeographical ranges and changing phenologies and competitive or trophic species interactions with a medium level of certainty (Figure 6-7). Furthermore, adaptation to present climate zones and variability may co-define species sensitivity to temperature, hypoxia or OA (6.2.2.). The effect of synergistic or antagonistic effects of various drivers at the level of animal communities remains largely unexplored. This includes the role of light versus temperature in shaping phenologies and species interactions, for example during latitudinal shifts in distribution (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 PEQD (Pacific Equatorial Divergence Province), linked to the associated aggregation of macrozooplankton and micronekton, may have contributed to the net eastward shift of skipjack tuna stocks between 1985 and 2010 (Lehodey *et al*., 2011).

6.3.6.2. Ocean Upwelling

Eastern boundary upwelling systems cover 1% of the ocean surface area but are estimated to account for 11% of new production (Monteiro, 2010) and around half of the world's commercial fish catches (Merrett and Haedrich, 1997). Thus, understanding whether upwelling and a changing climate will impact the resident biota in a synergistic or antagonistic manner is highly relevant for projections of climate change impacts on these areas and the resulting impact on humans dependent on this protein source. Upwelling in a changing climate will have both beneficial and detrimental effects. The upwelling of waters that are hypoxic and more acidic will affect marine biota and ecosystem structure of the upper ocean. 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.

There is *robust* observational (Schwing and Mendelssohn, 1997; Demarcq, 2009) and modeling *evidence* (Bograd and Lynn, 2003; Snyder *et al*., 2003; Di Lorenzo *et al*., 2005) of increased alongshore upwelling favored by winds over recent decades, as a putative consequence of global warming (Bakun, 1990). Upwelling regions sit closer to thresholds for hypoxia and acidification where shifts in ecosystem states may occur. For example, changes in sea surface temperature in the California Current System have been clearly 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*., 2009; Zwolinski and Demer, 2012, 6.3.3.). However, the relationship between upwelling activity and sea surface temperature is not significant. 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. The effect of climate change on upwelling systems through stronger winds, altered current patterns or enhanced OA remains unclear (Chavez and Messie, 2009).

6.3.7. Summary and Conclusions

Anthropogenic warming, oxygen depletion and acidification add progressively to pre-existing levels of temperature, hypoxia and CO_2 (6.1.1.). Considering mechanistic knowledge (6.2.2.) and observations (6.3.) supports attribution to climate change with *medium to high confidence* of impacts like: (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) increased propensity for change, including increased 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 (*medium evidence*; *medium confidence*) (e.g. Pörtner and Knust, 2007; Diaz and Rosenberg, 2008). This may also be the case for effects of anthropogenic OA (*low evidence*, *low confidence*), as indicated by the detrimental effects of upwelling hypercapnic waters on oyster cultures in the Northeast-Pacific (Barton *et al.*, 2012). Except for the attribution of detected climate change effects to temperature, clear attribution to one of the other drivers is only possible in a few cases.

Robust evidence from various ocean regions demonstrates with *high confidence* that temperature governs the geography, diversity, development, reproduction, behaviour and phenology of marine organisms (Edwards and Richardson, 2004; Beaugrand *et al.*, 2009; Brierley and Kingsford, 2009) as well as the composition of communities and the seasonal timing of relevant processes (phenology) (6.2.2.1.). Accordingly, hydro-climatic variability, with a contributing role of the warming trend, causes large-scale biogeographical changes, abundance and community structure of marine species (Richardson, 2008). In light of the underlying unifying physiological principles und a large number of similar observations, this conclusion has *very high confidence*.

With *medium evidence* and *high confidence*, warming causes changing community composition, associated with reduced body body size (6.2.2.4) and increased diversity in some groups. Individual examples show, with *robust evidence* and *high confidence*, the specialization of animal species on the regional climate regimes and, conversely, their immediate sensitivity to change. Such principles may also shape species interactions (*low evidence, medium confidence*). Due to differential species responses to temperature, species interactions across tropic levels can be modified through trophic amplification (*medium evidence*, *high confidence*).

Changes in local and regional species richness as well as community composition result from latitudinal range shifts, depth distribution and possibly species extinctions and the associated structure and functional properties of ecosystems, such as productivity, energy flows and invasion resistance (*medium evidence*, *high confidence*). (Stachowicz *et al.*, 2002; Duffy, 2003). Fish communities studied in temperate zones display increments in species richness resulting from latitudinal shifts (*robust evidence, high confidence*) (Perry *et al.*, 2005; Hiddink and ter Hofstede, 2008). Similar phenomena in sedentary organisms and benthic macroalgae (e.g. of the Mediterranean, Bianchi, 2007) are complicated by the influence of local dynamics and topographic features (islands, channels, coastal lagoons) on biogeographic boundaries (Poloczanska *et al.*, 2011).

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 seasonal upwelling of hypercapnic deep waters in the Arabian Sea (de Moel *et al.*, 2009) (*robust evidence, medium confidence*). An eight year trend for (variable) pH to 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 (*low evidence, medium confidence*) (Wootton *et al.*, 2008). Declines in calcification reported in corals (De'ath *et al.*, 2009) were elicited by thermal extremes and associated productivity losses, but may include an as yet unclear contribution by OA. A later study also found species-specific declines in calcification correlated with average annual sea surface temperature but at different temperature ranges characterizing the respective reef (Carricart-Ganivet *et al.*, 2012) (*medium evidence, medium confidence*).

The full scope of large-scale ecosystem shifts remains difficult to understand and anticipate (deYoung *et al*., 2008), due to the multitude and complexity of factors and processes involved. With *low evidence*, *medium agreement* and thus *medium confidence* community reassembly might involve the mixing of ecosystems and strongly alter their trophodynamics through trophic cascades (Cury *et al*., 2003; Parmesan and Mattews, 2006; Luczak *et al*., 2011). Trophic amplification may then drive an ecosystem towards a new dynamic regime. Non-linearities that can operate within an ecosystem make the understanding and projection of marine ecosystem trajectories under climate warming more difficult. Such 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, global climatic including temperature change on top of climate variability may contribute to such shifts, with *low evidence, medium agreement* and thus*, medium confidence* (Beaugrand *et al*., 2008; 6.2.2.). With *limited evidence*, but *high agreement* and thus *medium confidence* climate change can strongly interact with further top down human interferences like fisheries or other forms of harvesting which then accelerate such changes.

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

6.4.1. Ecosystem Services

Human societies benefit from multiple resources and processes supplied by natural ecosystems, collectively called ecosystem services and commonly classified as provisioning, regulating, cultural and supporting (MEA 2005). Provisioning services include the products people obtain from ecosystems, such as food, fuel and biochemical and genetic resources. Regulating services include benefits like carbon storage, water purification and climate regulation. Cultural services include benefits to humans like recreational and spiritual opportunities or aesthetic enjoyment. Supporting services include processes like 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 generally 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. Similarly, the biogeography and diversity of marine biota affect provisioning services (e.g., fisheries), supporting services (e.g., habitat creation, food supply from photosynthesis), cultural services (e.g. tourism opportunities), and regulating services (e.g. maintenance of marine food webs). Assessing ecosystem services and their capacity for future change requires accounting for the multiple and sometimes overlapping roles of marine ecosystem components in contributing to human well-being.

Simply quantifying marine ecosystem services can be a challenge. Goods and services that are bought and sold in markets such as fisheries and raw materials production can be valued directly from market prices and quantities. To estimate the benefits from ecosystem services that do not have a market, a range of methods to capture these non-market values have been developed, Generally, these non-market valuation methods involve a three-step process (Barbier *et al*., 2011). First, the changes in ecosystem structure, function, or processes that alter a service are characterized. Next, the changes that influence ecosystem services must be traced back to human communities. Finally, the resulting changes in human well-being must be assessed. This final step has usually been performed using economic methods that assign a monetary value to an ecosystem service. For services without a market, indirect valuation methods such as avoided cost, replacement cost, factor income, travel costs, hedonic pricing, or contingent valuation (often applied to regulating, cultural and supporting services) are used (Farber *et al*., 2002). However, such an approach for capturing non-market ecosystem services has been criticized for insufficiently valuing some types of ecosystem services, particularly cultural and supporting services. Ecosystem assessments, which engage stakeholders in an iterative evaluative approach to combine formal and informal knowledge collected by both natural and social scientists, represent more complete ways to quantify ecosystem services (Ash *et al*., 2010).

Forecasting possible climate-change-mediated shifts in marine ecosystem services and assessing their effects on human communities is particularly difficult. Some of the challenge comes from the difficulty of measuring and assessing the services themselves in ways that are comparable among ecosystem service categories. But some of the challenge is related to the difficulty of predicting how human communities will adapt to changing marine ecosystem benefits. 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. Future adjustments will range from making adaptive changes to long-established industries, such as commercially valuable fisheries, to exploring the potential of new technologies, such as geoengineering methods designed to help mitigate rising global temperatures and carbon dioxide concentrations. Planning for the future, however, requires gaining a better understanding of how marine systems will change and affect human communities.

6.4.1.1. Provisioning Services

6.4.1.1.1. Food from the sea

Biomass production from the oceans that contributes to direct or indirect consumption by humans depends on primary and secondary productivity (Cheung *et al.* 2008; Jennings *et al.* 2008; Chassot *et al.* 2010). Fisheries catch statistics provides an estimation of historical and current level of food production from the sea. It is estimated that seafood currently provides over 1.5 billion people with almost 20 percent of their average per capita intake of animal protein and up to over 90% in some regions (Bell *et al.*, 2009; Garcia and Rosenberg 2010). Of the 142 million tonnes produced in 2008 by capture fisheries and aquaculture, over 80% was used for human consumption, providing the highest per capita supply ever (17kg). After decades of rapid fisheries expansion (Swartz *et al.* 2010), World marine capture fisheries catches stabilized in the mid-1990s at between 75 and 85 million tonnes (Pauly *et al.*, 2002; FAO, 2010). This is probably an underestimate of the actual fisheries production from the ocean because of illegal and unreported catches (Pauly *et al.,* 2002; Agnew *et al.,* 2009). It is estimated that primary production appropriated by current global fisheries is 17–112% higher than that appropriated by sustainable fisheries (Chassot *et al.,* 2010). Theoretically, changes in primary production and other ocean conditions as a result of climate change and/or variability will affect global capture fisheries production (Brander, 2007; Cheung *et al.,* 2010), however, attempts to quantify such linkages are considered variable and uncertain (Brander, 2007; Brown *et al*., 2010). Robust linkages between climate variability and fisheries production particularly for some ecosystems such as upwelling have been observed and established. However, there is *limited evidence* that attributes observed changes in fisheries production to climate change.

Total aquaculture production in 2008 was approximately 52.5 million tonnes or 37% of world total fish production, mostly concentrated in coastal areas and comprising primarily molluscs and crustaceans. During the early 2000s this industry reported growth rates around 12% a year, but the growth rate has recently decreased to nearly 7% because of many factors, including the limited availability of suitable new culture sites in Asia and Pacific countries, where aquaculture was more heavily developed. In regions such as Africa and Latin America, aquaculture is considered to be a development opportunity and a strong need. However, for aquaculture to provide long-term sustainable animal protein production, it is vital for regional aquaculture industries to be both ecologically and economically sustainable and to include provisions for dealing with challenges that might arise due to climate change.

There is *robust evidence* of the interplay between non-climatic anthropogenic drivers and climate change (see Figure 6-14) and how they may have significant effects on a wide range of ocean processes and ecosystem services, including marine fisheries. For example, there is *high confidence* that over-exploitation of fisheries is having a top-down effect on ecosystems. There is *medium confidence* (*high agreement* but *limited evidence*) that the top-down effects of overfishing will concurrently be encountering climate change-mediated alteration of their environment, leading to unpredictable non-linear outcomes. The production of food from the sea is already highly constrained by intensive fishing, contaminants and habitat disruptions (Garcia and Rosenberg, 2010). Climate change is imposing an additional stress on these systems (Perry *et al*., 2010). It will affect fishing communities directly by changing the productivity and availability of fish species and indirectly by altering migration patterns of people to coasts and by impacting coastal infrastructures (Daw *et al*., 2009; Sumaila *et al*. 2011).

There is thus *high confidence* that resilience of marine ecosystems to climate change will be reduced by the actions of other sectors (Hughes *et al*., 2003; Worm *et al*., 2006). The demographic effects of fishing, for instance, alters the age structures of fished species, their potential productivity (Planque *et al*., 2010), their behavioural complexity (Petitgas *et al*., 2006) and can alter their genetic diversity. In turn these can all substantially alter a species' capacity to buffer changes in climate variability (Fromentin and Fonteneau, 2001; Hilborn *et al*., 2003; Ottersen *et al*., 2006).

These processes can extend to the adaptive capacity of entire marine communities, if there has been differential exploitation or impacts on community components, which have altered ecosystem complexity, make-up or turnover rates (Balvanera *et al*., 2006; Planque *et al*., 2010).

6.4.1.1.2. Changes in food from the sea: Effects on human communities

Allison *et al*. (2009) estimated the vulnerability of 132 national economies to the potential impacts of climate change, as represented by changes in surface air temperatures projected for 2050 under the A1F1 (high dependence on fossil fuels, rapid economic growth, continued population growth) and B2 (moderate population and economic growth) scenarios. The countries most vulnerable to climate-induced changes in fisheries were in Africa, northwestern South America and Asia, but because of lack of sufficient data, the study excluded 60 small islands that are vulnerable. Eleven of the twelve most vulnerable nations were the same for both climate change scenarios. Among high latitude countries, only the Russian Federation was ranked as highly vulnerable, owing to the importance of fishing to the economy, high exposure to predicted climate change and relatively low adaptive capacity (Allison *et al*., 2009). The study noted that the majority of countries whose fisheries are most vulnerable to climate change's impacts are very poor, and their inhabitants depend on fishing for 27% of their dietary protein, compared with 13% elsewhere (Allison *et al*., 2009). The study concluded that, whereas the detailed impacts of climate change on regional marine production systems are uncertain, these changes may have a negative overall impact on food security for those nations which mostly depend on fisheries and have limited capacities to adapt to the changes (Allison *et al*., 2009).

In a similar study, Cooley *et al.,* (in press) assessed the vulnerability of nations worldwide to losses of mollusk harvests from OA, based on present patterns of nutritional and economic dependence on mollusks and model forecasts of the decrease in sea water carbonate saturation state. Results showed that countries with high dependence on mollusks, low adaptive capacity, rapidly growing populations, or rapidly approaching the sea water chemical change could fare worst (Cooley *et al.,* in press). This includes many low-latitude and small island developing nations, which are often the same nations expected to be very vulnerable to climate change (Allison *et al.,* 2009). These studies clearly show that stressors such as rising temperature and OA will independently affect some of the same human communities in negative ways, and they also suggest that overlapping stressors could act synergistically to intensify each other.

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). Losses in developing countries are projected to range from US$7 to US$ 19 billion, whereas losses in developed countries are projected to range from US$2 to US$8 billion (with slight gains possible for Europe; Sumaila and Cheung, 2010). Losses in dockside revenue just from OA-related shellfish harvest decreases in the United States have been estimated at $17-40 billion over the next fifty years (Cooley and Doney, 2009). Globally, the extent of ecosystem shifts will be dictated by the degree and frequency of perturbation, sensitivity of the system components and timescales of recovery, which will depend on the adaptive capabilities of constituent species (Dollar and Tribble, 1993) and the flexibility of system structures, responses (Elmqvist *et al*., 2003) and other factors (Planque *et al*., 2011a). The specific implications for industries such as fisheries are still poorly known, as *confidence* in future predictions 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).

Further uncertainties remain for specific regions and timelines, but a growing number of studies, and experience based on other sources of anthropogenic impacts on marine systems, indicate that there is *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*., in press). Analyses of survey data have identified migration of fish stocks to higher latitudes driven by climate in the last 25 years (Perry *et al*., 2005). Further migrations due to climate change may result in stocks straddling economic zones, perturbing existing international fisheries agreements and causing excessive exploitation (Hannesson, 2007; Sumaila *et al*., 2011). A number of studies do however argue that there might be a beneficial effect of warming for fisheries productivity in, for instance, the North Atlantic (Arnason, 2007; Stenevik and Sundby, 2007; Cheung *et al.* 2010). Similarly, a number of studies suggests that there is a potential eastward displacement of tuna stocks in the Pacific Ocean (Lehodey, 2000; Lehodey *et al.,* 2010, 2011), with differential positive and negative consequences for island economies (McIlgorm, 2010). However, increasing stock fluctuations with resulting management and socioeconomic challenges are also apparent, although modeling 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). Using the IS92a global warming scenario and the Global Commons economic scenario, Merino *et al.* (2010) projected that small pelagic fish biomass (such as sardines, anchovies), exploitation, catches of small pelagic fish and market trade volumes of fishmeal and fish oils in 2080 would be similar to present conditions. In contrast, using the World Markets scenario, which involves open and competitive trade, they predicted reductions of about 50% in small pelagic fish biomass, exploitation, fishery catches and market trade by 2080 compared with present conditions (Merino *et al*., 2010).

Preliminary modeling studies (Cheung *et al*., 2010; Fulton, 2011) find a decline in the predicted potential catch in the tropics (6.5), where countries depend on fisheries for the economy and food security (27% of the dietary protein is from fish, compared to 13% in less vulnerable countries). Such countries result highly vulnerable to predicted impacts, also because they possess limited societal capacity to adapt to potential impacts or opportunities (Allison *et al*., 2009). This will be further compounded if increases in the frequency and severity of extreme events (e.g. floods or storms) effect the citizenry 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).

In summary, there is *high agreement and robust evidence* that the impacts of climate change will be significant for the production of food from marine ecosystems and human food security. Marine ecosystems are already under stress and food production from wild capture fisheries may have peaked. The impacts of climate change will occur in addition to these existing stressors, with the potential for significant negative effects in particular to developing nations in tropical regions (declining fish biodiversity, shifts of species distributions polewards, declining fisheries catch potentials, national economies vulnerable to fluctuations in fisheries supplies). It appears to be that the more northerly (and developed) nations may benefit from climate change, at least initially. There is still not enough evidence on the long-term consequences of climate change for capture fisheries production. Such evidence will also depend on what happens to marine primary production, the projections for which at present are highly variable.

6.4.1.1.3. Other provisioning services

Currently, the largest energy industry operating in the ocean is the extraction of oil and gas supplying fossil fuels. As oil deposits are depleted, the industry is progressively moving towards deeper waters, which potentially exposes moored developments to greater storm hazards (see WG II, ch. 30) (Considine *et al*., 2004). Extraction of kinetic energy from ocean currents, winds and waves (Fraenkel, 2002; Henderson *et al*., 2003)(see IPCC SRREN) has only been tested in pilot forms on tidal streams (Douglas *et al*., 2008), but estimates based on present conditions may need to be revised in the future if energy availability from ocean currents and waves changes locally due to a changing climate, which could modify ocean currents and wind action (IPCC SRREN). Mining activities for gas hydrates from seeps, phosphates from oxygen minimum zones, precious metals from manganese nodules and hydrothermal vent-associated seafloor massive sulfides and rare earth elements from abyssal muds, also show promise for providing additional provisioning services. Future development of any type of energy- or resource-extraction platform involving near-surface structures, like oil and gas platforms or kinetic energy rotors, should consider that potential changes in ocean dynamics due to climate change could influence their efficiency and security. Plans should incorporate heavy engineering where appropriate to guard against the possibility of stronger forces acting in the near-surface zone in the future owing to climate change.

Opportunities for new marine industries may arise as systems change into the future. In other fledgling industries, marine biodiversity holds future or option value for industries such as marine pharmaceuticals, biologically inspired technologies and biomonitoring of pollution. Although a diverse range of phyla have been investigated (Hunt and Vincent, 2006), there is no current appraisal of the status of these industries and of any key species or phyla that could be used as a platform to explore how climate change might alter these industries in the future. Future 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 discovery of genetic resources from marine species useful in the pharmaceutical, aquaculture and agriculture and other industries (Arrieta *et al*., 2010), leading to a loss of option value from marine ecosystems.

6.4.1.2. Regulating Services

6.4.1.2.1. Climate regulation and feedbacks

Climate regulation refers to the balance and maintenance of the chemical composition of the atmosphere and oceans by marine organisms and chemical and physical processes (Beaumont *et al*., 2007). Ice core records reveal that for the last 800 kyr, atmospheric carbon dioxide has been no lower than 170 μatm and no higher than 276 μatm (Siegenthaler *et al*., 2005; Lüthi *et al*., 2008). Even over time scales of several millions of years, proxy data suggest maximum CO_2 concentrations of 400 μatm (Pagani *et al*., 2010; Seki *et al*., 2010). This relatively stable envelope of carbon dioxide concentrations is due to the interplay between ocean-atmosphere exchange, carbon storage on land, the exchange of carbon between surface and deep ocean via the biological and inorganic pumps and over longer time scales, the dissolution of marine carbonates and weathering of rocks on land (Sigman and Boyle, 2000).

The ability of the biota to continue regulating climate can be altered due to a changing climate. Marine biota play a key role in regulatory mechanisms (Reid *et al*., 2009) that include the balance between photosynthesis and respiration (Johnson *et al*., 2010), the biological pump (soft tissue and bio-minerals, Volk and Hoffert, 1985; carbonate chemistry, Feely *et al*., 2008; N fixation and denitrification, Falkowski, 1997), the modulation of other 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). There is high confidence that the effect of climate change on the biota will alter the magnitude of many, if not all of these processes. The strongest evidence that such processes may be dramatically altered comes from both the geological record and contemporary time-series records that detail how climate variability or natural perturbations affect marine biota.

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). The coccolithophores in coastal waters underwent a floristic shift to organisms flourishing in higher productivity waters, similar to the contemporary *Gephyrocapsa*, an important DMS producer (Gibbs *et al*., 2006). In contrast, the open ocean coccolithophore flora was dominated by warm-adapted and low-nutrient-adapted species. Decreases in carbon isotopic gradients between surface and deep waters at the onset of the PETM are interpreted to be a result of increased stratification, reduced nutrient supply and a less efficient biological pump (Zachos *et al*., 2003). Interestingly, the benthic foraminiferal fauna suggest that there was no reduction in export production reaching the deep ocean, suggesting better organic carbon preservation due to lower oxygen 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.).

Phytoplankton can have significant feedbacks on atmospheric CO_2 and other atmospheric gases. For example, increased N_2 fixation rates during glacial periods have been suggested as a result of increased airborne dust (containing the required trace element iron) supply to the open ocean (Falkowski, 1997). Dust and trace metal input to the Southern Ocean might have driven an increase in carbon fixation by phytoplankton, though with high regional variability. Specifically, *confidence* is *high* that diatoms have been less abundant during glacial periods in polar waters while in the subantarctic region, diatom export production was much increased (Mortlock *et al*., 1991). High export production has been estimated to have drawn down atmospheric CO_2 by up to 40 μatm (Watson *et al*., 2000) which may have been aided by an increased alkalinity pump associated with higher export of heavier foraminiferal shells (Barker and Elderfield, 2002). Large scale (> 10,000 km^2) natural perturbation of the ocean also reveals how rapidly feedbacks can take place. In 2009, nutrients added by volcanic ash from an eruption in Alaska stimulated a large diatom bloom and hence enhanced productivity but caused little increase in the sequestration of atmospheric CO_2 (Hamme *et al.*, 2010).

Long time-series records detail how climate variability or natural perturbations affect marine biota and their feedback on climate. For example, there is *medium confidence* that increases in phytoplankton biomass detected in a long time series from 1986 until present may be a response to warming (driven by both climate variability and change) in the North Sea and west of the British Isles, whereas south of Iceland, phytoplankton biomass decreased over this period (Beaugrand and Reid, 2003) highlighting the regional differences and hence the difficulty in global up-scaling of these processes and their effects on climate. Other multi-decadal ocean time-series – such as HOT and BATS – have revealed feedbacks linked to climate variability such as NAO and ENSO, resulting in an increase in the N_2 fixation rate in response to altered mixed layer depth, iron input and/or changes in underwater irradiance climate (Karl *et al.*, 1995; Karl *et al.*, 1997; Bates and Hansell, 2004), though internal oscillations in the community structure of N_2 fixers have alternatively been used to explain this variability (Karl, 2002; Monteiro and Follows, 2009). A new generation of 'self assembling' ecosystem models suggest that the biome of N_2 fixers is not directly controlled by temperature and light, but is restricted to ocean regions with low fixed nitrogen and sufficient dissolved iron and phosphate concentrations. Hence changes in nutrient distribution are likely to influence N_2 fixation (Monteiro *et al.*, 2011). The environmental changes during ENSO cycles in the equatorial Pacific are associated with shifts in phytoplankton groups. The 1997 and 2006 El Niños were characterised by a decrease in *Synechococcus* density and an increase in nanophytoplankton and low chlorophyll concentrations. The 1998 La Niña led to an increase in diatom dominance and increases in NPP due to enhanced upwelling (Masotti *et al.*, 2011).

Modeling simulations provide our most powerful tool for exploring the role of marine biota in regulating climate (Boyd and Doney, 2002; Hashioka and Yamanaka, 2007). Climate change may decrease global ocean NPP by > 10% (i.e. 5% of global NPP, Field *et al.*, 1998) under a high emission scenario (SRES A2), with projected increases in NPP at high latitudes being more than offset by predicted decreases at low latitudes (Bopp *et al.*, 2002, *low confidence*, 6.5.1.). Such changes in NPP are predicted to lead to a decrease in the export of biogenic carbon to the deep ocean (Bopp *et al.*, 2002) as a positive feedback on climate change. For quantifying the importance of changing pelagic carbonate production on the ability of the oceans to sequester CO_2 a few global models have so far been applied. Additional quantities between 5.9 and 18 PgC of anthropogenic CO_2 are taken up by the ocean by the year 2100, as a negative feedback on climate change (Heinze, 2004; Gehlen *et al.*, 2007; Ridgwell and Hargreaves, 2007). Models that use a large ensemble of differing experimental findings, which explicitly take into account the broad range of calcification responses observed in laboratory manipulation studies, give projections of a mean CO_2 uptake of 17.2 PgC (Ridgwell and Hargreaves, 2007, WGI Chapter 6). Each of these modeling investigations into the sign and magnitude of specific oceanic feedbacks need to be synthesised, such that the cumulative effect of such feedbacks can be estimated (Boyd and Doney, 2002). However, such a synthesis would not take into account the potential interplay between feedbacks (Riebesell *et al.*, 2009).

In many cases, the effect of a changing climate on some potentially important feedbacks such as the ocean's biological pump cannot be reliably modeled, as many of the factors controlling the functioning of this pump are poorly understood (Figure 6-15). For example, any significant changes to NPP may also alter the magnitude of biogenic carbon that is sequestered into the deep ocean and hence be a feedback on climate. Other illustrative examples of factors that are thought to drive the biological pump and that might be altered by climate change include a shift from diatoms (major exporters of carbon to depth) to coccolithophores (Cermeño *et al.*, 2008), leading to a reduction in the strength of the carbon pump. Such a floristic shift might be exacerbated by the processing of organic carbon through smaller-sized zooplankton and thus its enhanced dissipation through more complex food webs (Li *et al.*, 2004).

[INSERT FIGURE 6-15 HERE
Figure 6-15: A schematic representation of the ocean's biological pump, an important conduit for carbon sequestration. Processes involved (Table 6-4) may each be altered by climate change. In a changing climate it is difficult to predict how the pump might be altered and hence whether it would represent a positive or negative feedback to climate change. Factors reported to be altered by a changing climate include: A, changes to 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, change 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). Figure 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 6-15). 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 the extent of the knowledge platform needed to provide *high agreement* / *robust evidence* of these biogeochemical ramifications. TEP, DOM and POM denote Transparent Exopolymer Particle, Dissolved Organic Matter and Particulate Organic Matter, respectively.]

In conclusion, *robust evidence* from many studies in the geological past points to significant effects that marine biotic feedbacks, such as on ocean productivity (Martinez-Garcia *et al.*, 2011), particle export (Murray *et al.*, 2012) or N_2 fixation (Ren *et al.*, 2009) can have on global climate. There is *medium confidence* in *limited evidence* for effects of marine biotic feedbacks on global climate in the present day, as many such feedbacks are more localized, regional and transient (Boyd and Doney, 2002; Chavez *et al.*, 1999; Karl *et al.*, 1995) than those larger scale sustained events in the geological past. Thus, the ability to predict both the sign and magnitude of specific feedbacks to climate change with even a *medium* degree of *confidence* is presently at an early stage of development.

6.4.1.2.2. 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. The role of natural ocean structures and organisms in lessening the effects of natural hazards has been undervalued, although it can be quite significant. For example, a considerable buffering of the impact of tsunamis by coral reefs is suggested by observations (Fernando *et al.*, 2005) and modeling (Kunkel *et al.*, 2006). 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). Therefore, there is *high confidence* that anthropogenic impacts, 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. The role of OA on mangroves or wetlands has not been determined (Cooley *et al.* 2009, Cooley submitted), but human activities causing climate change and pollution negatively impact mangroves. Marshes and wetlands respond poorly to human perturbation, climate change, deoxygenation and pollution as well as overlapping stressors enhance each other (Cai *et al.*, 2011, Howarth *et al.*, 2011, Feely *et al.* 2010). Whether these single or overlapping stressors will also decrease the ability of mangroves, marshes and wetlands to protect coastal regions from storms is still to be determined.

6.4.1.3. Cultural Services

Cultural services are non-material benefits provided by ecosystems to people through spiritual, cognitive, aesthetic and recreational activities. Many of these services are often viewed as impossible to replace by any amount of technological innovation or economic activity. Cultural services relating to 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 quantify. Nevertheless, cultural services are often cited by coastal users as primary reasons to preserve the marine environment.

Leisure and recreation centered on the marine environment can contribute significant economic benefits in allied spending and create thousands of jobs. Not only does this include sales of fishing and access permits and sales or rental of recreational equipment, like fishing tackle, diving gear and boats, but this also includes indirect economic benefits earned by supporting businesses like the service industries that support tourism-rich communities. Marine biodiversity, an important component of other ecosystem services, is also a key piece of cultural ecosystem 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 tourism of reefs yield about US$ 9.6 billion (Cesar *et al.*, 2003). If degradation of cultural ecosystem services because of climate change occurs, coastal visitors will spend their recreational budgets on terrestrial attractions, which could significantly alter the well-being of many coastal communities and even some nations that depend on tourism for income. In some cases, 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. For example, marine and terrestrial mammals are widely harvested among Arctic communities for sustenance and cultural reasons. Traditional foods constitute a significant portion of Arctic communities' meals (Van Oostdam *et al.*, 2005). Inuit hunting in the Canadian Arctic is largely subsistence-based (Gombay, 2006). Sea ice is important for transportation of hunted animals, for example during caribou hunting. Changes in sea ice exposure have been linked to increased danger and decreased accessibility during the seasonal hunting of ringed seal and walrus (Laidler *et al.*, 2009). Some of the harvested animals are exchanged with other groups in reciprocal relationships related to sustenance, kinship and support (Nuttall, 1998). 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 way that high water quality and infrequent occurrences of harmful algal blooms keep real estate prices and shellfish landings high (Jin *et al.*, 2008). Changes in biogeochemistry, biodiversity, or sea level could harm communities that value the aesthetic benefits from wetlands, sandy beaches and aesthetically pleasant coastlines.

Heritage benefits, or the values 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 loss of biodiversity 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.

6.4.1.4. Supporting Services

Supporting services essentially form the foundation of all other ecosystem services. These services set up the systems that other services depend on and include things like atmospheric oxygen production, nutrient cycling and habitat creation. Although not able to be sold on an open market, their broad global importance means that their "value" adds up to more than that of all the above services combined. Furthermore, because they are so diverse in nature and scales, identifying and describing all supporting services in the marine environment is virtually impossible. However, considering 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 (6.3.5.2.). Changes in the conditions under which these ecosystem engineers produce biologically mediated habitat (Beaumont *et al.*, 2007) would directly affect the entire ecosystem, altering the biomass for fisheries, the biodiversity they sustain, the cultural and leisure values of these landscapes and their climate regulation capacity (6.3.5.2). In another example, warming-related changes in ocean stratification that affect nutrient cycling will broadly influence marine biogeochemical cycles, with the possibility of diverse results on marine biota that could ultimately affect human communities via specific provisioning, regulating, or cultural ecosystem services. These types of changes are very likely to occur due to climate change, but currently there is insufficient evidence to trace these linkages exactly.

The provision of open waterways for shipping is a specific supporting service that is very likely to change in specific, measurable ways in the next several decades. 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. Potential impacts of international shipping on climate and air pollution are a significant contribution to global climate change and health impacts through emission of greenhouse gases and other pollutants (Lauer *et al.*, 2009; Corbett *et al.*, 2010). Extreme events can disrupt these newly open routes (Becken, 2005). Furthermore, increased shipping in the Antarctic has been suggested to increase the number of non-indigenous species via invasion via the hulls of Southern Ocean vessels (Lewis *et al.*, 2004). Similar trends can be expected with increased shipping in the warming Arctic.

6.4.1.5. Conclusions

Human societies benefit from and depend on ecosystem services, including provisioning of food and other goods, climate and natural hazards regulation, cultural and supporting services. Projecting their climate-change-mediated shifts remains a challenge, partly because the intrinsic difficulties of assessing these services themselves. However, there is *robust evidence, high agreement* and *very high confidence* that climate change impacts the marine ecosystems and their 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 for significant negative effects in particular to developing nations in tropical regions. With *limited evidence* and *low confidence*, socio-economic consequences of OA may be felt (Cooley and Doney, 2009; Cooley *et al.*, 2011) and might be delimited once an OA threshold not to be surpassed is defined (Turley *et al.*, 2010). Marine ecosystems regulate climate through mechanisms such as the biological pump, the balance between photosynthesis and respiration and modulation of greenhouse gases with high warming potential. There is *high confidence* that the effect of climate change on the biota will alter the magnitude of many, if not all of these processes.

6.4.2. Management-Related Adaptations and Risks

6.4.2.1. Ecosystem Management

All of the potential ecological, social and economic shifts associated with 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). Ecosystem-based management (EBM), or the ecosystem approach (EA), is already being increasingly adopted around the world (FAO, 2003) to deal with the multitude of anthropogenic 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 widespread and *robust evidence* and *high agreement* that the effects of different human activities will undermine resilience to other impacts or attempts at mitigation and adaptation. For example, along coastal margins existing infrastructure (e.g. roads and settlements) may act as a barrier for landward migration of fringing ecosystems, such as salt marshes (Hughes, 2004). In other cases, consequences are more subtle. Recruitment variability, or reduced larval survival, as a result of shifting climate or OA may undermine fisheries management. For instance, climate change has already contributed to shifts in abundance of cod (Eero *et al.*, 2011), salmon (Miller and Munro, 2004) and herring (Sissener and Bjorndal, 2005) complicating management of those species. Modeling studies have suggested a potential for moderate to strong reduction in sustainable catch yields for some fish species (Kaplan *et al.*, 2010; Cheung *et al.*, 2011; Fulton, 2011) under the combined effects of OA (assuming a loss of shelled benthos as food), habitat degradation and altered water column properties (6.5).

Analyses of the North Sea regime shift in the 1980s indicate that there is a potential for early detection of ecosystem shifts (deYoung *et al.*, 2008). Quantification of the multivariate multiscale variance revealed that changes in ecosystem state were paralleled by an increase in variance. In this case, rising variance can thus provide an early warning to ecosystem managers of an impending regime shift (Carpenter and Brock, 2006). In general, there is an insufficient number of observations and an insufficient quantitative understanding of regime shifts, and until those needs are fulfilled, adaptive management will only be able to react based on short-term forecasts of the future, rather than based on any early conclusions that a shift has just or is on the verge of taking place. Periods of low variance in the ecosystem state alternate with periods of more pronounced variability (shifts). Overall, adaptation and management of risks build on successful detection and attribution; as these are early days, detection and attribution currently have priority as a precondition for successful adaptive fisheries management.

To date, increasing ecosystem resilience via the reduction in the magnitude of other human perturbations (e.g. fishing mortality in overexploited fisheries) is the principal feasible means of accounting for additional shifts in commercial fish stocks driven by climate change and variability (Brander, 2008). However, physical effects of climate change may act, under some circumstances, as an additional conservation pressure that cannot be mitigated by a reduction in the activities of extractive human sectors. As an example, a reduction in the accidental capture of turtles in fishing gear may not successfully protect the population if a significant number of nesting beaches are impacted by sea-level rise or storm surges (Fuentes *et al*., 2010; Fulton, 2011). Additional effects of climate change will complicate management regimes. Many of these kinds of challenges will not be evident until they have already begun to be expressed, and as a result it is still uncertain what exact form of fisheries management will be implemented and be successful in any location. For example, model predictions suggest there may be the potential for significant change in biodiversity in some locations (Danovaro *et al*., 2004; Cheung *et al*., 2009; Fulton, 2011) (section 6.5) and there are already well-documented shifts in species distributions (ICES, 2008; Last *et al*., 2011), which are presenting direct challenges to the objectives of spatial management, which has become 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).

6.4.2.2. Effects of Geoengineering Approaches

The vast size of the ocean with its enormous buffering capacity for both heat and CO_2 has long attracted attention for possible active intervention or geoengineering as a way of ameliorating climate change. The earliest suggestion was by Marchetti (1977) who advocated direct injection of CO_2 beneath the Mediterranean outflow waters. It was recognized that some 85% of all atmospheric CO_2 emissions will eventually be transferred from air to sea (Caldeira *et al*., 2005) and that direct CO_2 sequestration (termed CDR – carbon dioxide removal by Shepherd *et al*. (2009) could avoid much of the atmospheric heat trapping. This CDR approach and now many others (including the SRM approach (Solar Radiation Management (Shepherd *et al*., 2009), for active ocean manipulation or disposal (see Table 6-5) are currently being initially evaluated and given preliminary rankings on criteria such as efficacy, safety and cost (Boyd, 2008). Many of these SRM schemes predate OA concerns and would do little to solve that problem (Shepherd *et al*., 2009). All have very large associated environmental footprints, with some actually requiring purposeful alteration of ocean ecosystems for implementation (Boyd, 2009). These footprints themselves arouse concern and there are substantial legal and practical barriers associated with chemical disposal in its various forms (Shepherd *et al*., 2009). To date, there have been no published reports or evidence from any commercial trials or pilot studies of any ocean geoengineering method (Boyd, 2008). Note that mesoscale open ocean iron enrichment studies (see Boyd *et al*., 2007) are not geoengineering studies, but do provide valuable insights into some of the unanticipated side effects of such medium scale (1000 km^2) ocean manipulation. There has been a recent initial comparative assessment of how ecosystems will be altered (some purposefully, such as by CRD methods including ocean fertilization, others inadvertently, such as by SRM) by different geoengineering methods versus how they will be altered by ongoing climate change (Russell *et al*., 2012).

[INSERT TABLE 6-5 HERE
Table 6-5: Challenges for the oceans that will arise from the employment of a range of geoengineering methods (SRM, solar radiation management, CDR, carbon dioxide removal).]

Solar radiation management (SRM) techniques rely upon causing increased albedo, for example via stratospheric sulphur injection (Crutzen, 2006). SRM is fraught with the shortcoming that atmospheric CO_2 release and OA are left unabated unless SRM is combined with CO_2 emission reductions. Carbon dioxide removal 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 6-5). CO_2 injection would directly expose deep-sea organisms to elevated CO_2 levels (hypercapnia) and associated acidification (Caldeira *et al.*, 2005). After purposefully altering upper ocean ecosystems, ocean fertilization would do the same indirectly via the greater net export of organic material to the deep ocean and its coupled decomposition, thereby, causing CO_2 accumulation. The addition of alkalinity appears more benign but involves large-scale mining activities and their consequences on land. 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 release of the greenhouse gas N_2O. Enhanced NPP by ocean fertilization would add more carbon to the base of food webs (de Baar *et al.*, 2005).

Most prominently, however, the sustained formation, export and oxidative catabolism of organic material in a fertilized ocean region causes enhanced oxygen demand and deep-water oxygen depletion as confirmed by modeling experiments (Sarmiento *et al.*, 2010). On global scales, oxygen levels are permanently and significantly below air saturation in wide ocean areas, indicating that physical oxygen supply by ventilation and circulation to the oceans as a whole is limited and insufficient to fully match oxygen demand (Frölicher *et al.*, 2009). Various degrees of hypoxia result in many areas and exert specific and synergistic effects on ecosystems (6.2.2., 6.3.2., 6.3.6.). The ongoing decline in ocean oxygenation and expansion of hypoxic areas (6.1.1.) therefore reflects a shift from the steady state equilibrium of biological oxygen demand and physical supply (Frölicher *et al.*, 2009) to enhanced demand or reduced supply or both. This unequivocally indicates that oxygen demand enhanced by sustained fertilization will exacerbate hypoxia further and support the expansion of oxygen deficient areas in the ocean. Effects on ocean biology and especially, higher organisms, specifically fish and invertebrates depend on the degree of hypoxia reached and its synergistic effects with other stressors (6.2.2., 6.3.2., 6.3.6.). The temporal and spatial extent of hypoxia expansion requires exploration. From this point of view, direct injection of CO_2 into the ocean and, especially, its localized disposal (deep-sea lake option) appear more benign than the binding and wide spread deep-ocean release of the same amount of CO_2 via ocean fertilization (Pörtner *et al.*, 2005). The concomitant reduction of the warming trend would alleviate the synergistic effects of temperature with hypoxia and hypercapnia. Since these factors act as synergistic stressors, however, delicate balancing of the trade-offs between the alleviation of warming stress on ecosystems and the exacerbation of ocean hypercapnia and hypoxia (the latter in case of ocean fertilization) would be required upon implementation of injection and fertilization techniques.

6.4.2.3. Health Issues

6.4.2.3.1. Harmful algal blooms

Harmful algal blooms (HABs) are mostly a natural phenomenon having occurred throughout recorded history (Dale *et al.*, 2006). Biogeographical range extensions caused by regional climate change may have increased the regional presence of HABs (Edwards *et al.*, 2006), which are considered a major threat to the functioning of near-shore ecosystems. The opportunistic range expansion of HABs can be explained by increasing temperature, nutrient fluctuations in upwelling areas, eutrophication in coastal areas and enhanced surface stratification, which all have species specific responses. For example, the progressive freshening of the Labrador Sea region caused by increased melting associated with an increased stability of the water-column has resulted in shifts in seasonal cycles and blooms of dinoflagellates (Johns *et al.*, 2001). Similarly, both increased HABs in the North Sea and coccolithophore blooms in the Barents Sea are associated with negative salinity anomalies, warmer temperatures and increased stratification (Smyth *et al.*, 2004; Edwards *et al.*, 2006). Thus, an increase of haline stratification in regions susceptible to fresh-water inputs could act as an important environmental stimulus for bloom formation. 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). There may be a potential for OA to 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* and *low confidence* how global climate change will impact HABs. However, because of the potential impacts of HABs in human health and different ecosystem services, human societies should be preparing for significant range extensions and increases in biotoxin problems, particularly through adequate monitoring (Hallegraeff, 2010).

6.4.2.3.2. Pathogen proliferation

There has been considerable debate about the influence of climate change on pathogens in the ocean. On the one hand, there have been reports of climate change driving changes in pathogen species (Hoegh-Guldberg and Bruno, 2010). Lafferty (2009) cites a number of case studies (e.g. Dobson, 2009) in which a wide range of factors, including climate variability, could be the drivers behind many of the observed trends in pathogens. He suggested that projecting a higher incidence of infectious diseases in the future is a simplistic view.

One of the most comprehensive studies of climate impacts on infectious disease is that of the waterborne bacterium, *Vibrio cholera*, the causative agent of cholera. Cholera is a human diarrheal disease that has re-emerged in a number of tropical and subtropical regions in the past few decades even in areas where it was thought to have been eradicated. *V. cholera* is a marine bacterium that associates with a number of marine plants and animals, especially chitin-containing zooplankton. The growth of *V. cholera* on chitinous exoskeletons provides an environmental reservoir that facilitates persistence of the pathogen in the marine environment during inter-epidemic periods (Vezzulli *et al.*, 2010). Therefore, long-term survival in the absence of human infection is highly probable. Variability in climate can affect the marine host species, which in turn can diminish or amplify the levels of the pathogen in coastal marine environments. In regions where cholera is endemic (e.g, India, Bangladesh, Latin America), disease outbreaks have been observed to correlate with elevated sea water temperature and zooplankton blooms (Lobitz *et al.*, 2000; Lipp *et al.*, 2002). Based on the results of an 18-year climate record for Bangladesh, Pascual *et al.* (2000) have reported an interannual component of the 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). Continued warming of coastal tropical habitats, excessive nutrient loading leading to phytoplankton and zooplankton blooms and sea water inundation due to sea level rise are all predicted to exacerbate the global threat of cholera (*limited evidence, low confidence*).

Another health issue that has been related to climate change is ciguatera, a disease occurring when people eat fish that has bioaccumulated ciguatoxins due to exposure to the epiphytic dinoflagellate *Gambierdiscus* sp. Based on historical records, significant correlations have been reported between fish poisoning levels and sea surface temperature in South Pacific nations (Hales *et al.*, 1999); however, more recent analyses suggest that the relation is non linear, and that there is a thermal window for ciguatera to prevail (Llewellyn, 2010), which complicates the simple extrapolation of temperature-ciguatera rates relation to climate change scenarios.

6.4.2.4. Interaction between Climatic and Non-Climatic Drivers

Changes to the environment mediated by anthropogenic enhancement of the ozone hole over the Southern Ocean have increased windiness over the Southern Ocean and hence reduced its ability to sequester anthropogenic CO_2 from atmospheric emissions. An upward trend in the Southern Annular Mode (SAM, also called Antarctic Oscillation, AAO) since the 1970s has resulted in a stronger South Pacific gyre forced by intensification of the wind stress curl arasing from southwards shift in circumpolar westerly winds (Cai, 2006). This change in wind stress curl causes a spin-up of the entire southern mid-latitude ocean circulation including a southward strengtening of the East Australian Current (Cai, 2006). The cause of the trend is contentious but partly attributable to ozone depletion in the last few decades (Cai *et al.*, 2005, Cai and Cowan, 2007). While the overall contribution of increasing atmospheric CO_2 to the observed SAM trend is uncertain, climate models predict an upward SAM trend in response to increasing CO_2 (Cai *et al.*, 2005). This increased windiness associated with anthropogenic alteration of the ozone hole, has so far been implicated in decreased oceanic carbon dioxide storage (Le Quéré *et al.*, 2007) and deepening of the surface mixed layer depth (Sallee *et al.*, 2010). Again, there is *low confidence* concerning the nature of the interplay between increased windiness and the on-going effects of climate change, and the outcome for the biota is highly uncertain.

6.4.2.5. Conclusions

There is *high confidence* that the already challenging task of managing ocean, 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 to increase the ecosystems resilience to climate variability and change. Active ocean manipulation strategies to amend climate change might prove detrimental for different aspects of the ecosystems, such as augmented exposure of deep water organisms to elevated CO_2 and acidification due to artificial injection, which highlights the need for further research. There is strong interest in elucidating the potential changes of different human health issues related to ingestion of marine organisms that have bioaccumulated toxins, or direct exposure to toxic organisms and pathogens; however, *evidence is still insufficient and confidence low* on how harmful algal blooms and 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). These models incorporate the influences of ocean physics and chemistry on marine biota focusing on different spatial and temporal scales. Models range from empirical approaches to mechanistic models describing population/species responses and/or trophic interactions in marine ecosystems, including nutrient flows and feedbacks among primary producers, consumers and decomposers 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 Chapter 6). Also, models that focus on population and species level responses to environmental changes have been applied to a wide range of taxonomic groups, from invertebrates, fishes to marine mammals, globally and for many regions. Common classes of such models include population dynamic models and species distribution models. Moreover, there is a growing number of applications of “end-to-end” 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). A variety of such “end-to-end” models are being applied in many regions (e.g., Brown *et al*., 2010; Fulton *et al*., 2011; Kishi *et al*., 2011), for hindcast simulations of fish stocks (Collie *et al*., 2009; Link *et al*., 2009; Fennel, 2010), to link biogeochemical dynamics to mid- and high trophic levels (Libralato and Solidoro, 2009; Maury, 2009; Kishi *et al*., 2011) and to address spatio-temporal variability in competition and predation across all trophic levels (Brown *et al*., 2010; Travers and Shin, 2010). Results indicate some skill in these “end-to-end” models in reproducing the timing of events and the magnitudes of state variables (Link *et al*., 2009). However, numerous technical (Travers *et al*., 2009; Shin *et al*., 2010) and other challenges remain. Overall, the above models are currently useful for developing qualitative scenarios of 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 predictions from these models have *low confidence* (Rose *et al*., 2010; Hannah *et al.,* 2010; Stock *et al*., 2011).

6.5.1. Ocean Primary Production

Global ocean net primary productivity (i.e., NPP) is projected to change with climate, with large variations in the magnitude and direction of projected changes between coupled carbon cycle-climate models and empirical approaches (Figure 6-16). Bopp *et al*. (2002) predicted that climate change (based on a range of IPCC scenarios) may decrease global ocean NPP by > 10% (i.e. 5% of global NPP; Field *et al*., 1998), with projected increases in NPP at high latitudes (of up to 10%) being more than offset by predicted decreases at low latitudes (20%). Projections from four different fully-coupled (physics, biogeochemistry and plankton groups) global Earth System Models (WGI Ch. 6) show a reduction in global mean NPP of 2 to 13% by 2100 relative to 1860 under the high emission SRES A2 scenario (Steinacher *et al*., 2010). This is by contrast with recent projected changes using empirical methods that project a slight increase in global NPP (Sarmiento *et al*., 2004). Regionally, the Earth System Models project a decrease in NPP in the North Atlantic, the 'subpolar gyre marginal sea ice' biome in the Northern Hemisphere (decrease of 33 – 39 %), the tropics and the permanently stratified oceans at mid-latitude due to the reduced input of macro-nutrients into the euphotic zone. These decreases in NPP are mainly driven by the projected reduction in the area of the biome associated with reduced mixed layer depth, increased stratification and slowed circulation causing a decrease in macronutrient supply. In contrast, the models project increases in NPP in Northern and Southern Hemisphere 'subpolar gyre' biomes where an alleviation of light and/or temperature limitation leads to an increase in NPP, with little change in the areal extent of these biomes.

[INSERT FIGURE 6-16 HERE
Figure 6-16: 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 for the SRES A2 scenario for the period 2080 to 2099 relative to 1870 to 1889.]

It is concluded with *high confidence* that global NPP will change with increased greenhouse gas emission and global warming: In particular, there is *medium agreement and confidence* that primary production will decrease from present rates by 2100 under the SRES B1 and A2 scenarios, although there is *limited evidence* suggesting an increase in global NPP. There is *low confidence* for regional differences. The observed variability in projected future ocean primary production is due to differences in the responses of ocean physics to global warming, to differences in biology models and to differences in the simulation of micronutrient limitation (Steinacher *et al*., 2010). Most of the above projections on ocean biogeochemistry represent open ocean systems rather well, but coastal and shelf seas regions only poorly. Moreover, there is a large variation in estimates of the present-day magnitudes and the distribution of primary production in models and observation-based estimates (cf. 6.3.1.). The validation of future modeling, projections and improved model parameterisations require convergence of observational trends in NPP, from a range of independently-derived approaches from remote-sensing to ship-based rate measurements, and confirmation of the underlying mechanism(s) driving these trends in all oceanic provinces where altered rates of NPP, over decadal scales, have been reported.

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 6-17). Species distribution modeling (SDM) is a commonly used approach to project future changes in species distribution based on projected changes in climatic and other environmental conditions (Ready *et al*., 2010, Jones *et al*., 2012). Using a global scale SDM that has explicit representation of population dynamics and dispersal driven by changes in temperature, salinity, ocean current and sea ice extent, Cheung *et al*. (2009) project shifts in the distribution of 1066 species of exploited marine fishes and invertebrates in the world ocean of a median of around 50 km per decades (range limits) to higher latitude by 2050 relative to 2000 under the SRES A1B scenario. The rate of range shifts is projected to be three times higher for pelagic than for demersal fishes (Cheung *et al*., 2009). As a result, high latitude regions (the Arctic, Southern Ocean) are projected to have high rates of species invasions. In contrast, high rates of local extinction are projected for the tropic, sub-Arctic and semi-enclosed seas (e.g., Mediterranean Sea, Persian Gulf).

[INSERT FIGURE 6-17 HERE
Figure 6-17: Scenarios of the effects of climate change on the biogeography of marine fishes and invertebrates, their biology and fisheries catch potential. (A) The main hypotheses of climate change effects on marine fishes and invertebrates. (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*. submitted). The median rate of the rate shift observed from the 1970s to the 2000s in the North Sea and Bering Sea are indicated by the arrows. (C) Projected change in the maximum body size of 610 species of marine fishes from 2000 to 2050 under the SRES A2 scenario (Cheung *et al*. submitted). The values represent the average results from projections using outputs from the NOAA/GFDL ESM2.1 and IPSL-CM4-LOOP models. The white area is not occupied by the sample of species (D) Example of formulization of these hypotheses through a simulation model

to project 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).]

The global pattern of distribution shifts generally agrees with regional-scale projections driven by scenarios of temperature changes. Distributions of eight exploited fish species in the North Atlantic are projected to shift northward by 2090-2099 relative to 2000-2005 under both the SRES A2 and B2 scenarios (Lenoir *et al*. 2011). Long-term observations from the European Large Marine Ecosystems study (Philippart *et al*. 2011) confirm projections of the northward movement of species, converting polar into more temperate and temperate into subtropical systems. In the Northwest Atlantic, the distribution centre of Atlantic croaker (*Micropogonias undulatus*) along the east coast of the United States is projected to shift northward by 50–100 km by 2100 relative to the 2000s under both SRES A1B and B1 scenarios (Hare *et al*., 2010). In the Pacific Ocean, spawning habitat of bigeye tuna (*Thunnus obesus*) is projected to improve in the subtropical Pacific by 2100 relative to the 2000s under the SRES A2 scenario, while both spawning and feeding habitats improve in the eastern tropical Pacific regions (Lehodey *et al*., 2010). In the southern hemisphere, the core ranges of 14 species of tunas and billfishes in the east and west coast of Australia are projected to shift towards higher latitude (southward) and contract by 2100 relative to 1990-2000 using a statistical model driven by changes in sea surface temperature projected from an ensemble of 9 climate models with 25 scenarios for each species (Hobday, 2010). Similarly, distributions of 30 species of fishes and invertebrates around Western Australia are projected to shift their distribution at a median rate of around 19 km poleward and 9 m deeper per decade by 2055 relative to 2005 under the SRES A1B scenario (Cheung *et al*., 2012). The analysis also projects gradual ‘tropicalization’ (increased dominance of warm-water species) of the communities along the Western Australia coast.

For corals, all modeling approaches project high level of impacts of ocean warming on coral reefs through coral bleaching, although some of the main assumptions in these approaches need to be verified. Assuming a monthly SST threshold for coral bleaching and using projected future SSTs under the IS92a scenario, Hoegh-Guldberg (1999) projects that coral bleaching in French Polynesia, Jamaica, Rarotonga, Thailand and at three sites on the Great Barrier Reef would occur biannually within 20-40 years from 2000. Using a similar approach, Sheppard (2003) projects most of the 33 Indian Ocean coral reefs south of the equator would become extinct between 2010 and 2030, while extinction would occur later for corals north of the equator (Sheppard 2003). Moreover, Donner *et al*. (2005) project that most coral reefs of the tropics would exceed the bleaching thresholds by the 2050s. With consideration of possible adaptation and acclimatization by corals, it is expected that temperature would exceed bleaching thresholds at least biannually by 2020 or 2030 under the SRES A1B and B1 scenarios (Donner *et al*., 2007). In addition, using an empirical model on coral bleaching extent developed from historical data, McWilliams *et al*. (2005) predict a 35 % increase in the area of bleaching and a 42 % increase in the fraction of coral colonies bleached with an 0.1 °C increase in average SST in the Caribbean. These projections assume little adaptability to intensifying heat stress which needs to be further examined by field and experimental studies (6.2.2.4.). It also did not account for OA to which coral reefs appear particularly vulnerable (6.2.2.4.4.).

Projections are also available for selected groups of marine megafauna. Similar to the projected pattern of changes for fishes and invertebrates using SDM, 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). The population growth rate of Cassin’s auklet in the California Current ecosystem is projected to decline by 11 to 45 % by 2080-2099 relative to 1980-1999 driven by changes in temperature and upwelling intensity under a scenario in which mean annual SST at the Farallon Island increases by 1.97 °C (Wolf *et al*., 2010). Using SST as 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).

Overall, there is *high confidence* that the distribution and abundance of fishes, invertebrates, cetaceans and some marine megafauna will shift under most emission scenarios, with the projected rate and direction of range shift being consistent with observations in the last century (6.3.). More specifically, there is *high confidence* that the shift in distribution is generally poleward at large spatial scale and there is *medium confidence* that the distribution of demersal fishes and invertebrates shifts towards deeper water. These shifts are *likely* to result in changes in patterns of species richness. However, projections of future distribution for specific species and at fine spatial scale are more uncertain. There is *high agreement* between models that warming will have large impacts on coral reefs through bleaching. Some key assumptions are common across these analyses. Firstly, the confidence of the projections will depend on the confidence of projected physical and biogeochemical conditions (WG I). Secondly, predicted distributions of the studied species are based on potential distributions or niches, which may be different from the presently realized niches. Moreover, potential adaptive and evolutionary responses by the organisms are not considered in these models. So far, there have been reports on climate-induced changes in species abundances but not on climate-induced extinctions in the oceans. As a note of precaution, models assuming uniform climatic envelopes for species may underestimate extinction risk of individual populations if strong local adaptation has occurred and caused specialization of populations on local climate regimes. Trophic interactions are not considered in most SDMs. Furthermore, these projections are affected by the uncertainty of outputs from climate or earth system models. These uncertainties and assumptions may affect the fine-scale projections of changes in species distributions and abundance [Cheung *et al*., 2012].

6.5.3. Ecosystems and Fisheries

One of the most direct impacts of climate change on marine ecosystem services is through fisheries (6.4., WGII Ch. 7). Globally, Cheung *et al*. (2010) suggests that climate change may lead to large-scale redistribution of global catch potential (from 1066 exploited fishes and invertebrates), with an average of 30–70 % increase in yield of high-latitude regions (>50° N in the northern hemisphere), but a drop of up to 40% in the tropics by 2055 relative to 2005 under the SRES A1B scenario (Figure 6-17). This highlights the high vulnerability of national economies of tropical coastal countries through fisheries impacts to climate change (Allison *et al*., 2009, 6.4.). More specifically, a modeling study that assesses the effects of climate change on tuna fishery in the south Pacific projects an increase in catch for 2035 relative to 1980-2000 for skipjack and bigeye tuna under the SRES B1 and A2 scenario (Lehodey *et al*., 2011), However, skipjack tuna catch is projected to decrease for 2100 under the A2 scenario, while bigyeye tuna catch is projected to decrease under both A2 and B1 scenarios for 2100. Regionally, catches in the western Pacific is projected to decrease while those in the eastern Pacific will increase (Lehodey *et al*., 2011). In the North Atlantic region, Cheung *et al*. (2011) incorporates the potential impacts of OA, low oxygen and changes in size-structure of phytoplankton resulting from greenhouse gas emission under the same emission scenario to project maximum catch potential in the North Atlantic by 2050 relative to 2000 (using outputs from GFDL ESM2.1). The results suggest that these additional factors are expected to reduce catch potential, turning some regions to a loss that were expected to gain in catch potential from warming. However, such projections admittedly are sensitive to the assumed level of biological sensitivity of the modeled organisms to OA (section 6.3.4). Moreover, Cheung *et al*. (submitted) applies the same model but with consideration of warming and changes in oxygen content as main climate drivers to project future changes in maximum body size and other life history characteristics of 610 exploited demersal marine fishes globally. Maximum body weights at community level are projected to decrease by about 20% across ocean basins under the SRES A2 scenario, with approximately equal contribution from general poleward movements of the smaller, warmer water species and the reduction in maximum body size at population level from organisms' ecophysiological responses (Figure 6-17). The decrease in maximum body size may reduce yield-per-recruit and, thus, potential catch.

Responses to climate change may become more complicated when species interactions and multiple stressors are considered. Responses of exploited marine species and their fisheries may interact with other human stressors such as overfishing. Using a statistical ecosystem model and an ensemble of multiple climate model outputs, Lindegren *et al*. (2010) project that the Baltic cod is expected to have a high extinction risk (>95%) by the mid-2060s with warming (+3.5 °C of SST), decreasing salinity (- 4.8 psu) and a mean historical fishing mortality level (1974 to 2004). Under the scenario in which fishing is reduced to the recommended precautionary reference levels, projected extinction may be postponed to the 2080s (Lindegren *et al*., 2010). Clark *et al*. (2003) used projections of future North Sea surface temperatures and estimated the potential impact of climate change on the reproductive capacity of the cod stock. Output from the model suggested that a relatively modest level of climate change (+0.005 °C yr^{-1}), resulted in a more rapid decline in fish biomass and juvenile recruitment. In a re-analysis by Kell *et al*. (2005), the authors modeled the effect of introducing a cod recovery plan. The overall cod productivity was impacted, and spawning stock biomass (SSB) was predicted to be considerably less than would have been the case assuming no temperature increase. Models representing marine ecosystems around Australia suggest that the biomass of plankton, pelagic invertebrates and pelagic fish biomass are projected to increase while demersal fish biomass is expected to decline in all regions by 2050 relative to 2010 under the SRES A2 scenario (Fulton, 2011). The increase in biomass of pelagic systems is largely due to their better adaptive capacity to the changing environmental and ecosystem conditions relative to the demersal groups. However, the direction of changes in some specific groups such as invertebrates and top predators differ between regions. Overall, the projected multi-species maximum sustainable yields are 27 % lower for the Great Barrier Reef and 12 % lower for SE Australia (Fulton, 2011).

Model projections suggest that the interplay of such top-down ecological effects with bottom-up chemical and physical controls on the environment may increase the susceptibility of certain communities to both a changing environment and altered ecosystem. Using the model specific for SE Australia, Griffith *et al.* (2011) show that OA and fishing may have additive, synergistic and antagonistic effects, depending on the biological groups and the intensity of the stressors. In the South Pacific region, vulnerability of foodwebs in different biogeochemical provinces to projected changes in water temperature, mixed layer depth, upwelling, solar and ultraviolet radiation, dissolved oxygen and OA were assessed (Le Borgne *et al.*, 2011). Such assessment projects that foodwebs in these provinces have low to moderate vulnerability for 2035 and moderate to high vulnerability for 2100 under the SRES B1 and A2 scenarios (Le Borgne *et al.*, 2011). Moreover, using a trophodynamic ecosystem model that assesses the projected reduction in phytoplankton on the marine foodweb in the Warm Pool province (10°N – 15°S and 110°E – 165°E) of the South Pacific region, biomass of zooplankton, micronekton and large pelagic fishes are projected to decrease by 2035 and 2100 relative to 2000-2100 under the SRES B1 and A2 scenario (Le Borgne *et al.*, 2011). The decreases are largest (>15 %) for mesopelagic and bathypelagic micronekton and skipjack tuna. Using five ecosystem models representing the major marine ecosystems along the NE Pacific coast, Ainsworth *et al.* (2011) show that fisheries landings decline in response to cumulative effects of changes in ocean biogeochemistry under the SRES A1B scenario, with possible synergistic effects when multiple factors are considered. Our current understanding of how different modes of forcing, either individually or together, alter biological organizations, from physiology to biomes, is rudimentary (i.e., *medium agreement, limited evidence*) for many of these interactions (Figure 6-14). 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 (Hunt Jr and McKinnell, 2006). Such insights would improve model projections.

Although the numerical projections of future changes in fisheries under climate and ocean changes are considered to have *low confidence* because of the various levels of structural and parameter uncertainties of the models, there is *high confidence* that changes in primary productivity and temperature will lead to large scale changes in fisheries production and that tropical fisheries are highly vulnerable to climate change impacts. There is *medium confidence* from quantitative projection that multiple stressors, including warming, OA, de-oxygenation and other human impacts, will interact with each other, exacerbating the expected impacts from single stressors. Each modeling approach has various assumptions and uncertainties, including those from the biological and ecological components in the impact assessment model and the physical and chemical components of the Earth System Models (Stock *et al.*, 2011). Given these model assumptions and uncertainties, interpretation of these model projections should focus on qualitative trends instead of the detailed numerical projections. Moreover, such interpretation highlights the need to consider multiple stressors in projecting changes in ecosystems and the services they provide.

6.5.4. Conclusions

Overall, there is *high agreement* on the projections of large-scale changes in species distribution and abundance and *medium agreement* on projections of ocean productivity and fisheries catch. It is concluded with *high confidence* that global primary production will change and there is *medium agreement* between models that it will decrease by 2100 relative to now under the SRES A1 and A2 scenarios. Also, there is *high confidence* that distributions for fishes, invertebrates, cetaceans and some marine megafauna will shift further under most emission scenarios, with the projected rate and direction of range shift being consistent with observations in the last century. More specifically, there is *high confidence* that the shift in distribution is generally poleward at large spatial scale and with *medium confidence* on projected distribution shift of fishes and invertebrates towards deeper water, leading to shifts in patterns of species richness and community structure (*high confidence*). Moreover, there is *high confidence* that changes in primary productivity, ocean conditions and species distributions will lead to large scale changes in fisheries production. There is *medium confidence* that multiple stressors, including warming, ocean acidification, de-oxygenation and other human impacts, may interact with each other, exacerbating the expected impacts from a single stressor. However, there is *low confidence* on fine-scale quantitative projections for the above changes because of model uncertainties.

Models that integrate climate and ocean changes with biological responses and interactions with human activities, at present, have led to some general agreement on possible species and food web responses to climate change. Population dynamic models and species distribution models demonstrate some skills in assessing impacts of climate change on species abundance, distribution and composition (Stock *et al*., 2011; Jones *et al.,* 2012). However, these models do not include a range of biological processes such as trophic interactions and evolutionary adaptation that affect responses of biota to physical and chemical changes in the ocean. Some ecosystem models that incorporate ocean physics and chemistry, trophic interactions between low and high trophic levels, and human activities are available. However, these ecosystem models currently have limited capability to predict impacts (Overland *et al*., 2010), particularly over long time scales (Fulton, 2011), because of intricate linkages in food webs (Brown *et al*., 2010), non-linear relationships between variables, and the inherent abilities of living organisms to adapt and evolve (Kirby and Beaugrand, 2009; Murawski *et al*., 2010; Moloney *et al*., 2011). Further progress in forecasting future biological responses and food web scenarios, beyond the range of current data, requires improved data acquisition and management in conjunction with approaches to address focused questions. This assessment indicates that the principle links between different levels of biological organization and especially between organism specialization and functional characteristics (6.2.2.) and ecosystem have not sufficiently been considered in these analyses. Better representation of these processes in these models enhances certainty and confidence in modeled projections of future change.

6.6. Conclusions and Key Uncertainties

This section provides an overview of the chapter with respect to the levels of evidence and the resulting confidence in the detection and projection of climate change effects on ocean systems, as well as the levels of confidence in attributing these effects to the respective forcings (Figure 6-18).

[INSERT FIGURE 6-18 HERE
Figure 6-18: Overview of the levels of confidence in detection (black letters), in both detection and projection (blue) as well as in projection only (red letters) of climate change effects on ocean systems, in relation to the levels of confidence in attributing these effects to the respective climate forcings. Areas where firm and detailed knowledge on climate change impacts is currently lacking have been condensed into rather broad categories in order not to overpopulate the figure (e.g. **BG**, Biogeochemical Processes). If a process is marked by blue letters, the levels of confidence are the same for both detection and projection in relation to that for attribution. Note that the term attribution is not only used in the context of detections but, in some cases, also for projections. Experiments (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 processes. (TO BE DEVELOPED FURTHER AFTER FOD, E.G. FOR THE DISTINCTION BETWEEN BROAD CATEGORIES AND SPECIFIC EXAMPLES IN TWO SUBFIGURES)]

6.6.1. Drivers of Change and their Effects

Present day observations and the information from the geological past display similarities with respect to environmental changes and their ecological consequences in the ocean. Warm times with high atmospheric CO_2 are evident in the geological past (Figure 6-18, **GR**, *high confidence* in detection). Thus, the geological record provides *robust evidence* of alterations of both multiple ocean properties and ecosystems, which are comparable (*medium confidence*) in terms of sign and combination of properties, to present and projected climate change. While a number of past events share characteristics of future climate change, the present and predicted rate of anthropogenic CO_2

input and hence resulting ocean acidification is unprecedented in the last 300 Ma (*robust evidence, high agreement and confidence*, 6.1.2). However, there are few studies that identified a response to recent ocean acidification trends in the field. Decreases in shell weight have been detected in foraminifera in the field (*medium evidence*, *agreement* and *confidence*) and attributed to ocean acidification effects (**OAE**, *medium evidence* and *confidence*). Furthermore, attribution is supported by *robust* experimental *evidence* showing that species from many phylogenetic groups display diverse sensitivities to OA effects and will develop species specific responses (*high agreement* and *confidence*). Harmful effects were seen among some corals at low latitudes, some echinoderms, bivalves and gastropods or crustose algae, but also in some crustaceans and tropical fishes. Detection of such effects at ecosystem level has not been possible to date, but projections from these studies and observations at natural analogues indicate a shift in community composition to more active animals and from calcifiers to non-calcifiers in all organism groups ((*high agreement* and *confidence* in both projection and attribution, 6.3.4.3.; 6.2.2.4.).

In the oceans hypoxic zones (**HypZ**) with oxygen levels below 60 μmoles kg^{-1} expand due to enhanced stratification and microbial respiration (*high agreement* and *confidence*) and will continue to do so, due to climate induced warming trends (*high confidence*, 6.1.1.). Some bacteria can still grow aerobically and most efficiently at even nanomolar oxygen concentrations, causing formation of an 'oxygen minimum zone' (OMZs), which is also characterized by elevated $p\mathrm{CO}_2$ (*high confidence*). Expanding OMZs are therefore a consequence of high nutrient loading or restricted water movement, or both. Similarly, marine sedimentary habitats have OMZs below shoaling sediment horizons due to limited penetration and movement of dissolved oxygen. Expanding OMZs have also been detected in coastal waters and sediments downstream of regions of high inorganic nutrient or organic matter loading (6.1.1., 6.2.2.2.). Expanding hypoxia exerts strong local and regional effects on the biota (**HE**, *high agreement, high confidence*), causing a shift of community composition over to hypoxia tolerant species commonly observed in OMZs, excluding the calcifiers and benefiting the microbes (6.2.2.4.2., 6.3.3.), trends which will, with *very high confidence*, be exacerbated in the future. Such shifts are associated with a reduction in biodiversity and the loss of high activity life forms in those areas (*robust evidence, high agreement* and *confidence*). Furthermore, vertical expansion of OMZs has led to compression of oxygenated water layers as a habitat for, e.g., pelagic billfishes with a high oxygen demand. These effects are attributable to an anthropogenic exacerbation of hypoxia regimes (*high confidence*).

Present variability in oceanographic conditions are linked to large fluctuations in the structure of marine ecosystems and in fish stocks (*robust evidence, high agreement*, *very high confidence*), with a key role for temperature effects (**TE**) and change in current regimes as drivers (*robust evidence, very high confidence*. Long term observations show shifts in phenology, abundance, migration patterns, reduction in body size and largely poleward shifts in biogeographical distribution (20 to 200 km per decade) of zooplankton and fish (6.3.2.). Many biological changes detected in ocean ecosystems are attributed to ongoing anthropogenic warming (*very high confidence*). These effects are *likely* to continue with progressive warming in the 21st century, with implications for decreasing fisheries catch potential (**FCP**) in low to mid latitude areas and increasing FCP at high latitudes, resulting from species displacements and changes in primary production under the SRES A1B and B2 scenarios (*high confidence*, 6.5.2.; 6.5.3.). In particular, many polar organisms (**PO**) are unable to migrate or will be unable to acclimate or adapt to rising temperatures on relevant time scales (*high agreement*, *very high confidence*), contributing to the projection of high species turnover in polar areas (*high confidence*, 6.2.2.4.1., 6.5.2.).

In general, climate change may involve the combination of temperature effects with those of other climate related drivers (progressive ocean acidification, expanding hypoxia zones, freshening, organism shifts resulting in changing food availability, changes in habitat structure, e.g. loss of sea ice, further human interference, e.g. eutrophication). Synergistic amplification (**SE** – Synergistic Effects) of warming effects may occur in the future, due to expanding hypoxia zones and ocean acidification trends but such synergisms have been discussed but not yet been clearly identified (detected) in the field (*low confidence*). Attribution to such synergisms and their projected impact is supported by experimental studies, especially in maroorganisms (*high confidence*), and, such effects will be exacerbated in the future (*medium confidence*). Climate change can strongly interact with further top down human interferences like fishing or other forms of harvesting which then accelerate and amplify climate induced changes (*medium evidence, high confidence*, 6.2.2.1., 6.3.6.).

6.6.2. Microbial Responses and Biogeochemical Consequences

For microbial species and associated processes, a coherent picture covering various levels of biological organisation, from gene to ecosystem is needed but not available. Therefore, there is conflicting evidence, *low agreement* and *confidence* in our present knowledge of alteration of microbial effects (**ME**). *Confidence* in attributing such effects and the resulting processes to climate change including ocean acidification is equally *low*, albeit some experimental evidence from lab and coastal mesocosms indicates changes in individual processes such as the N cycle (6.2.2.2., *low confidence*). As a general constraint in detection and attribution for microbial (pro- and eukaryote) processes one or several unifying concepts (**MC**) comprehensively explaining the effects of climate drivers on each major group of marine microbes (e.g., bacteria, archaea and protists) are lacking (6.2.2.1.): While various physiological mechanisms and processes are known to respond to changes in irradiance, nutrient supply, temperature, CO_2 or hypoxia in microbes (6.2.2.2.), the knowledge base on how these processes may be altered does not (yet) support an integrated whole organism understanding of climate impacts on individual species (and their strains) and in turn on communities, reflecting *medium evidence,* but *low agreement* and *confidence* in detecting related effects in the field and attributing them to climate change. This limits the *confidence* to *low* in attributing detected changes to larger scale influences of climate change and also in projecting them to the future (6.3.1.).

Based on empirical observations the trends in net primary production (NPP) recently reported for much of the low latitude ocean using satellite observations differ considerably from those few sites at which sufficiently long time-series of more robust direct estimates of NPP have been obtained (6.3.1.). There is *medium confidence* based on *limited evidence* from these relatively few offshore time series sites that there has been a small but significant increase in global NPP (**gNPP**) over the last two decades, but *confidence* is *low* that this increase may be linked to climate change. At high latitudes, there is *medium confidence* based on *limited evidence* from satellite images that an increase in the number of sea-ice free days is resulting in higher rates of **hNPP** (attributable to climate change with *high confidence*, 6.3.1.). Such trends are projected to be strengthened with further warming and there is *medium agreement* between models that global NPP will decrease by 2100 relative to now under the SRES A1 and A2 scenarios, however, such trends cannot presently be quantified with sufficient accuracy and projections are fraught with *low confidence* (6.5.1.).

Other biogeochemical processes (**BG**) identified as potentially responsive to climate change including ocean acidification comprise carbon sequestration and export production, calcification, and respiration with the result of water oxygen depletion and acidification (see **HypZ**). With *medium evidence*, *low agreement* and *low confidence* in detecting and attributing microbial organismal responses to climate change, effects on N cycling may occur (6.2.2.2.). Overall, *confidence* is *low* in that shifts in biogeochemical pathways such as oxygen 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 (6.3.3.2., 6.3.4.1., 6.3.6.1.).

6.6.3. Macroorganism Responses and their Implications

Temperature effects reflect the specialization of, especially higher life forms on limited ambient temperature ranges. Temperature has strong effects on macroorganisms (**MAE**), especially marine animal species, with attribution being confirmed through applicability of the OCLTT concept (**OCLTT**: oxygen and capacity limited thermal tolerance) which integrates findings across levels of biological organisation, molecule to ecosystem (6.2.2.1., *robust evidence, high agreement* and *high confidence*). The concept supports a comprehensive cause and effect understanding of climate change effects on marine animal species, as observed in the field and thereby lends support to projections of temperature effects (**TE**) in the future (6.3.2., *robust evidence, high agreement* and *very high confidence*). There is *medium evidence* for the suitability of this concept to integrate the synergistic effects (**SE**) of multiple drivers, such as ocean acidification and hypoxia, into a comprehensive whole organism picture of climate related constraints (6.2.2.5., 6.3.6.1.).

Among fishes examples reflecting the direct effects of temperature include the shifting geographical distribution of Atlantic cod (**AC**, 6.3.2.1., *robust evidence*, *high confidence* in detection, *medium confidence* in attribution), falling abundance of eelpout in the Wadden Sea (**EWS**, 6.2.2.1., 6.3.2.1., 6.3.7., *robust evidence*, *medium confidence* in detection, *high confidence* in attribution), the collapse of spawning migration of Pacific salmon during warm years in the Fraser River of BC (**PS**, 6.3.2.1., *robust evidence*, *high confidence* in detection, *high confidence* in attribution), the temperature related patterns of growth in banded morwong around New Zealand (**BW**, *medium evidence*, *high confidence* in detection, *medium confidence* in attribution) and the shifts from sardines to anchovies in the Japanese Sea (**SAJ**, 6.2.2.4.1., 6.3.2.2., *robust evidence*, *medium confidence* in detection, *medium confidence* in attribution). Fish communities studied in temperate and high latitude zones display increments in species richness (**FSR – Fish Species Richness**) resulting from warming (and other related changes such as retreat in sea ice) and the induced latitudinal shifts (6.3.7., 6.5.2., *high confidence* in detection, *medium confidence* in attribution). Such temperature driven latitudinal shifts of macro-organisms (**MAE**) are projected to continue (*very high confidence*) in the 21st century under all IPCC emission scenarios, being attributable to progressive warming (6.2.2.4.1., 6.3.2.1., 6.3.5.1., 6.3.7., 6.4.1.1., 6.5.2., *very high confidence*).

The shift in the distribution of fish species as for Atlantic cod in the North Sea, detected together with a regime shift and regional changes in plankton phenology (**PP**, *medium confidence*) that came with changes in food composition and availability are *with medium confidence* attributed to climate change (6.3.2.1.). As a consequence, the changing fish catch potential for e.g. cod in the Southern North Sea (*high confidence*, **FCP**) is, with *high confidence,* partly attributable to climate change and to maintained fishing pressure (6.5.3.). Further effects attributed, with *high confidence* to climate change include alterations in abundance (**AB**) of e.g. corals, fishes or intertidal species detected with *high confidence* when organisms are exposed to increasing extreme temperatures. Such trends will with *high confidence*, be exacerbated during future warming (6.5.2.).

Among marine mammals and birds (**MAB**) there is *robust evidence* and *high confidence* in the detection of changing individual phenomena in some species of seabirds (reduced abundance, species shifts), marine mammals (ditto) and sea turtles (changing sex ratio) and equally *high confidence* in their attribution to the changing climate. However, as a general pattern, *evidence* is *limited* and *confidence low* for direct, univocal attribution to climate drivers (except for the thermally driven sex ratio in turtles). As a reason, effects are mostly mediated through climate dependent changes in habitat structure, in the availability and phenology of prey organisms, or in foraging efficiency, especially in mammals (polar bear, walrusses) and birds (pinguins, albatrosses), such that differential sensitivities result between species (*high confidence*). Overall, there is *medium confidence* in detection but *high confidence* in attribution to climate change. Such trends will with *high confidence*, be exacerbated during future warming (6.2.2.4.5.).

Over the last three decades, several species of shallow water reef-building warm water corals (**RWC**) have with *very high confidence* displayed increased bleaching and decreased calcification, and thereby, with *very high confidence* responded negatively to the ongoing warming trend and the associated rise in extreme temperature events and amplitudes (6.2.2.4.4.). Such trends will with *very high confidence*, be exacerbated during future warming, with some amelioration by latitudinal shifts and evolutionary adaptation (6.3.2.1., *medium evidence*, *low confidence*). The patterns seen may involve an increasing influence of ocean acidification, confirmed by *medium evidence* for 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 number of long term ecological time series in the ocean basins being limited and thus from insufficient sampling in various ocean regions such as the subantarctic and polar Southern Ocean. Furthermore, due to the complexity of climate change effects in the oceans and the methodological challenges involved in studying those effects, experimental and field research is usually being carried out and biased by different foci according to the interests and expertise of the research teams involved. Research foci have not been coordinated well enough. For example, one group may focus on selected effects in defined ecosystems and their dominant organisms (e.g. pelagic phytoplankton versus benthic animals). Another one may investigate individual species, genera and more rarely, phyla and organism kingdoms, the latter for the identification of unifying principles of effects within a kingdom. For the same reason, a third may address mechanistic (physiological) principles in one or, from a comparative point of view, various species and their populations. Finally, a fourth focus addresses changes in biogeochemical processes (e.g. nitrogen fixation, carbon export in the oceans) more than the sensitivities or effects on the organisms that cause such changes. According to each of the different foci progress has been made and hypotheses have been developed. However, these foci have not normally been linked and a coherent picture of climate change effects is thus not available. Each of these approaches is important but they are usually not well integrated and reductionist with respect to the level of organisation addressed, i.e. ecosystem, whole organism, tissue, cell or molecular. For example, upscaling from physiological studies on individual species to shifts in species interactions or foodwebs has not been successful to date. Processes investigated by the various biological disciplines also differ largely between organisms, like plants, animals, phytoplankton, and bacteria. The conceptual and mechanistic understanding of microbial functioning is more deficient than that of higher organisms. A unifying approach which, for example, addresses principles operative across organism kingdoms is lacking such that an integrated framework of climate sensitivity at ecosystem level cannot presently be developed. 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. Future experiments need to be inspired by the respective hypotheses developed from long-term field observations and from observations at natural or paleo-analogues.

Frequently Asked Questions

FAQ 6.1: Why is ocean life fundamental to the planet and how might climate change affect it? (place into 6.1., before 6.1.1.)

Oceans cover 70 % of the planet and marine ecosystems provide important services to humankind. Life they contain creates about half of the oxygen we breathe and also consume by the burning of fossil fuels. Oceans currently absorb ~25 % of the carbon dioxide emitted from the burning of fossil fuels each year. Fisheries and aquaculture provide on average 20 % of the animal protein to more than 1.5 billion people. The oceans sustain charismatic species and ecosystems valued in tourism and for recreation. The rich biodiversity of the oceans provides resources for innovative approaches like medical drug design or biomechanics. Ocean ecosystems also 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 warming temperatures, acidification of ocean chemistry, changed nutrient supply and expansion of low oxygen areas. These drivers, assessed in the chapter in the context of other marine forcings, pose risks for ocean life and may impair the ability of marine biota to perform these vitally important functions.

FAQ 6.2: What does the geological past teach us about future oceans and ecosystem responses to climate change? (place into 6.1.2.)

The geological record contains evidence for a variety of global environmental perturbations, including warming and ocean acidification, and how their cumulative effect causes ecosystem responses. Although similarities exist, no past event perfectly parallels future projections of ongoing climate change. This is a consequence of the unprecedented speed of current CO_2 accumulation in the atmosphere and ocean which is capable of driving a rate and magnitude of chemical changes potentially unparalleled in the last ~300 Ma of Earth history. This raises the possibility that we are entering an unknown territory regarding marine ecosystem change. If climate change is leading to extinction, it takes roughly 10 million years to achieve pre-extinction levels of biodiversity.

FAQ 6.3: Why do marine organisms rely on a sufficiently alkaline ocean? (place into 6.2.2.1.)

Many species of marine biota, ranging from microscopic plankton to shellfishes and coral reef builders are generically referred to as calcifiers, as they critically depend on using solid calcium carbonate ($CaCO_3$) as the principal construction material for their skeletons or shells. The different forms of solid calcium carbonate are called calcite and aragonite; aragonite is more soluble than calcite. Sea water has ample calcium ions dissolved but this substance needs to be transported across barriers to the sites where calcification occurs. Carbonate is not transported but formed where it is needed. In order to support the deposition of solid $CaCO_3$, the calcification site is made alkaline, meaning that pH is kept high, higher than in other parts of the body or in ambient sea water. Again, this occurs by transport of relevant substances, in this case proton ions (outward) or bicarbonate ions (inward), in a process called acid-base regulation. The organism uses energy to transport the relevant ions and to form and maintain ion and thereby pH gradients. However, the capability and energetic cost to do so are influenced by the

CO_2 concentrations of the ambient sea water as this CO_2 also penetrates the organisms. At low CO_2 levels, the sea water at the surface and above a certain depth is supersaturated with respect to $CaCO_3$. Similarly, low CO_2 levels lower the cost for organisms to reach high carbonate saturation levels at calcification sites as needed to cause the precipitation of $CaCO_3$. However, as the oceans and organisms are acidified by the anthropogenic accumulation of CO_2, the saturation levels of $CaCO_3$ fall in the water and at calcification sites. As saturation levels are lower in the water this favors the dissolving of carbonate shells on the water side unless they are protected from direct contact with sea water by a special coating (as is the case in mussels). In parallel, CO_2 accumulating inside the organism impedes acid-base regulation in the formation of alkaline fluids at calcification sites and thereby slows or even prevents calcificiation. However, CO_2 accumulating inside organisms causes further effects such that species not using calcified exoskeletons may also be affected by ocean acidification. Sensitivity is highest for all of them at extreme temperatures and thus, at the edges of their thermal windows. Ocean acidification affects sensitive organisms directly. If they have a strong capacity for acid-base regulation, they may result insensitive, but may still be affected indirectly via sensitivity of their prey organisms.

FAQ 6.4: Will climate change have different environmental effects on the ocean than on land? (place into 6.2.2.5.)

Although there are many similarities in the manner in which climate change will alter the land and ocean environments and ecosystems, for example through warming trends, there will also be fundamental departures. Such differences are primarily due to the physicochemical properties of the ocean, including ocean circulation and sea water chemistry. The warming of the ocean will have significant indirect effects on oceanic properties - for example by forming stable ocean layers separated by density and, thereby, altering the degree of communication between cold nutrient rich waters in the deep and warm nutrient poor waters at the surface. Increasing respiration by organisms in the mid-water layers of stratified oceans will cause further oxygen depletion (hypoxia) and CO_2 enrichment (hypercapnia) in expanding oxygen minimum zones, excluding large, more active fishes from permanent life in these areas. Specialized animals will sustain which economize the use of the little oxygen available, but the resulting communities are very different from those in well oxygenated waters. The additional, sustained absorption of large amounts of anthropogenic CO_2 from the atmosphere are also altering ocean chemistry - specifically by acidifying the ocean (making it less alkaline). While higher CO_2 will be found in both the atmosphere and the ocean, most animals in the ocean breathe water and have lower CO_2 levels in their blood than those on land and may therefore experience much stronger changes than those respiring air (turtles, mammals, birds) and on land. Thus, oceanic biota will have to adjust to a fundamentally different ocean environment and one that may be even more altered than that of the land.

FAQ 6.5: How will climate change impact marine ecosystems? (place into 6.3.7. or 6.5?)

There is general consensus among scientists that climate change significantly affects marine ecosystems and may have profound impacts on ocean biodiversity in the future. In the last century changes in species distributions, species richness and community structure have been attributed to ocean warming. The projected changes in physical and biogeochemical drivers, such as warming, acidification, hypoxia, nutrient supply and others like sea ice cover, will continue to affect marine biological communities, their abundance and distributions. Generally, climate change is expected to favor further poleward invasions of non- resident species. The associated migration patterns will be complex, but, under most climate change scenarios, a median shift or expansion of habitat range limits towards higher latitudes by tens of kilometres per decade can be foreseen for many species. As a result, marine communities in mid- to high- latitude regions are expected to become more like present-day tropical assemblages. Organisms that are more tolerant to direct effects of climate change may be affected indirectly through climate change restructuring the food webs. Species may be lost by local extinctions and especially in polar areas where warming does not allow them to retreat to cooler areas and such species may be lost altogether. Similarly, species in semi-enclosed seas such as the Wadden Sea and the Mediterranean Sea also face higher risk of local extinction because shifts in distribution in response to warming and other environmental changes are limited by the land-boundary (the Cul-de-Sac analogy). In the tropics, the loss of species that are sensitive to climate change including ocean acidification may lead to a decrease in species richness. In particular, the impacts of climate change on vulnerable biogenic habitats such as coral reefs are expected to affect the associated ecosystems. In response to climate change, alteration of the seasonal activity (phenology) of marine organisms, their biology and distribution will affect foodweb interactions such as grazing between species. Ocean primary production is also expected to change. Increasing temperature, nutrient fluctuations in upwelling areas, eutrophication may favor harmful algal blooms in coastal areas. 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). In addition, climate change is expected to interact, in a complex non-linear manner, with other human stressors such as overfishing and pollution, which potentially exacerbate the impacts on marine ecosystems. Overall, these changes will lead to large-scale shifts in the patterns of marine productivity, biodiversity, community and ecosystem structure. Together with other human activities climate change may also cause a redistribution of pathogens. For example, warming of coastal tropical habitats, excessive nutrient loading causing phytoplankton and zooplankton blooms and sea water inundation due to sea level rise are all predicted to exacerbate the global threat of cholera.

FAQ 6.6: Can we say how much of the changes we see nowadays is caused by climate change in relation to other human influences or natural variability? (place into 6.3.7.)

The ongoing changes in marine biological communities reflect the impacts of not only natural variability in climate and of climate change but also of other anthropogenic pressures such as overfishing, pollution, nutrient runoff and deposition, associated eutrophication and others. The interplay between these multiple drivers may have significant non-linear effects on a wide range of ecosystem processes. Model projections reveal that the manifestation of climate-induced alterations in marine ecosystems goes far beyond the range of natural variability. The resilience of marine ecosystems to climate-change mediated impacts is likely to be reduced by the individual and interactive effects of multiple drivers. 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. Effects of the various drivers may be additive but are often synergistic, i.e. the effect of each driver is amplified by the concomitant change of the other drivers. This prevents any quantification of how much of the change is caused by other human activities. Therefore the answer to this question is currently No.

FAQ 6.7: Can we predict climate change effects on marine ecosystems and how? (place into 6.5.3.)

Some insights can be obtained from extrapolating the present day trends from the existing long time series (i.e. decades) of data and from analysing past events of climate change. State-of-the-art ecosystem models are built on empirical observations and enable us to obtain estimates for some responses of marine biota to climate change as well as consequences for uses by human societies. Examples are the projected large scale shift in the distribution of commercially relevant fishes to high latitudes and the loss of catch potential for those fishes at their original sites. However, formulating well founded or detailed projections is a challenging task because of the large number of interactive feedbacks, never mind those we have yet to discover, that must be taken into account and the potential sources of error that must be dealt with. As a precondition, the 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 6.8: Will we have enough marine fish to catch, to meet human demand in the future? (place into 6.5.3.)

Overfishing and other non-climatic human stressors have already led to a decrease in fisheries yield and opportunities in many regions. In addition, both negative and positive effects of climate change on fisheries and aquaculture are envisaged. Based on the most recent model projections, global primary production is projected to decrease by 2 to 13% by 2100 relative to 1860 under the SRES A2 scenario. Since many of the fisheries stocks are fully to over-exploited, a decline in primary productivity is expected to further limit global fisheries production. According to most of the projected scenarios, climate change will lead to a large scale redistribution of the global fishery potential. The impacts manifested in catch rates, production, prices, fishing costs and profits will vary at regional scales. Some models forecast significant regional reductions of fish biomass and catches while catches may be increase in others, but such predictions are prone to large uncertainties. Generally, the net fishery catches are likely to increase at high latitudes, but are expected to drop significantly in the tropics. For example, a global simulation model projected a large-scale redistribution of global catch potential, with an average of 30–70% increase in high-latitude regions and a drop of up to 40% in the tropics by 2055 relative to 2000 under the SRES A1B scenario. Global potential catches may be further reduced, particularly for the shellfish fisheries, if the potential impacts of ocean acidification are realised. However, the level of sensitivity of most exploited species to climate change including ocean acidification is still uncertain. Some countries in the tropics are, therefore, particularly vulnerable, considering the relatively high degree of dependency of their economies and food security on fisheries.

The additional impacts of climate change will put additional pressures on long-term sustainable fisheries for current and future generations.

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Table 6-1: Variations in metabolism based on sources of energy, electrons and carbon according to Karl (2007).

Source of Energy[1]	**Source of Electrons**	**Source of Carbon**
Sunlight *photo-*	Inorganic *-litho-* Organic *-organo-*	CO_2 *-autotroph* Organic *-heterotroph*
Chemical *chemo-*	Inorganic *-litho-* Organic *-organo-*	CO_2 *-autotroph* Organic *-heterotroph*
Radioactive Decay *radio-*	Inorganic *-litho-* Organic *-organo-*	CO_2 *-autotroph* Organic *-heterotroph*

[1] A "mixotroph" is an organism that uses more than one source of energy, electrons or carbon

Table 6-2: Physical, chemical, and biological characteristics of major pelagic ecosystems[1].

	Size		**Stratification**			**Nutrient[2]**	
System	**Area (km^2x10^6)**	**%**	**Degree of**	**Duration**	**Productivity and Pattern**	**Level**	**Source**
Low-latitude gyre	164	52	Strong	Permanent	High, Continuous	Low	Eddy diffusion
Southern Ocean	77	25	Very weak, except strong when ice melts in summer	Seasonal	Moderate in summer only, Strongly seasonal	High	Mixing and upwelling
Equatorial upwelling	22	7	Strong stratification following vertical transport	Permanent	High, Continuous	High	Upwelling and 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] Adapted from Barber (2001) based on original analysis by McGowan (1974)
[2] Nitrate and phosphate

Table 6-3 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. +: 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). Note that *confidence* is limited by the short to medium-term nature of various studies and the common lack of sensitivity estimates across generations, on evolutionary timescales (Reference list added separately).

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*)
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*)
Coccolithophores	20	6	4+	800	Tolerant (*low*)	Vulnerable (*low*)
Dinoflagellates	5	4	3+	350-750*	Beneficial (*low*)	Beneficial (*low*)
Diatoms	9	5	7+	400-820*	Tolerant (*low*)	Tolerant (*low*)
Cyanobacteria	8	5	5+	370-1000*	Beneficial (*low*)	Beneficial (*low*)
Foraminifers	7	4	5	800	Tolerant (*low*)	Vulnerable (*low*)
Annelids	4	6	4+	2800	Tolerant (*medium*)	Tolerant (*medium*)
Molluscs	54	33	40+	600	Vulnerable (*low*)	Vulnerable (*high*)
Bryozoans	2	3	5+	2900	Tolerant (*medium*)	Tolerant (*medium*)
Corals	25	17	22+	560	Tolerant (*low*)	Tolerant (*medium*)
Crustaceans	33	27	37	700	Tolerant (*low*)	Tolerant (*medium*)
Echinoderms	33	29	29+	600	Tolerant (*medium*)	Vulnerable (*high*)
Fish	30	24	25	700	Vulnerable (*low*)	Vulnerable (*low*)

Table 6-4: A wide range of processes make up the ocean's biological pump (Figure 6-15). 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 the extent of the knowledge platform needed to provide high agreement / robust evidence of these biogeochemical ramifications. TEP, DOM and POM denote Transparent Exopolymer Particle, Dissolved Organic Matter and Particulate Organic Matter, respectively.

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)		DOM vs. POM – TEP (Riebesell *et al.*, 2007)	Elemental stoichiometry (Karl *et al.*, 2003)
TEP production (Engel *et al.*, 2004)	Zooplankton biomes (Beaugrand *et al.*, 2009)		Sinking rates/s/water viscosity (Lam and Bishop, 2008)	Remineralization rate – [O2]; hypoxia; nutrient resupply (Gruber, 2011)
Microzooplankton grazing rates (Rose *et al.*, 2009)			Ballasting - calcite (Klaas and Archer, 2002)	

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

Topic	**Brief Description**	**Challenge and Impact**	**References**
Solar radiation management techniques	Deflection of approximately 1.8 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. 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 a power plant, followed by injection of liquid CO_2 by pipeline or from a ship into the deep ocean. Technology only practical for power plants situated in coastal regions.	Will add to ocean acidification and create localized harm to marine life. CO_2 capture is expensive. 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. CO_2 capture costs from extracted gas are less than from post-combustion. 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 using addition of macronutrients to oceanic regions where they are depleted by direct or indirect (ocean pipes) addition	Much of the exported organic matter is remineralized at shallow depths creating local oxygen stress and shallow CO_2 enrichment, N_2O production. These effects are temporary and the effective retention time is short. Relatively low cost procedure. If sustained, reduced surface-ocean and increased deep-ocean acidification. O_2 loss in ocean interior.	de Baar *et al.*, 1995; de Baar *et al.*, 2005; Boyd *et al.*, 2007; Buesseler *et al.*, 2008; Law, 2008; Cao and Caldeira, 2010
Artifical upwelling	TO BE DEVELOPED AFTER ZOD		
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. Relatively low cost. Environmental impact issues related to discharge 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

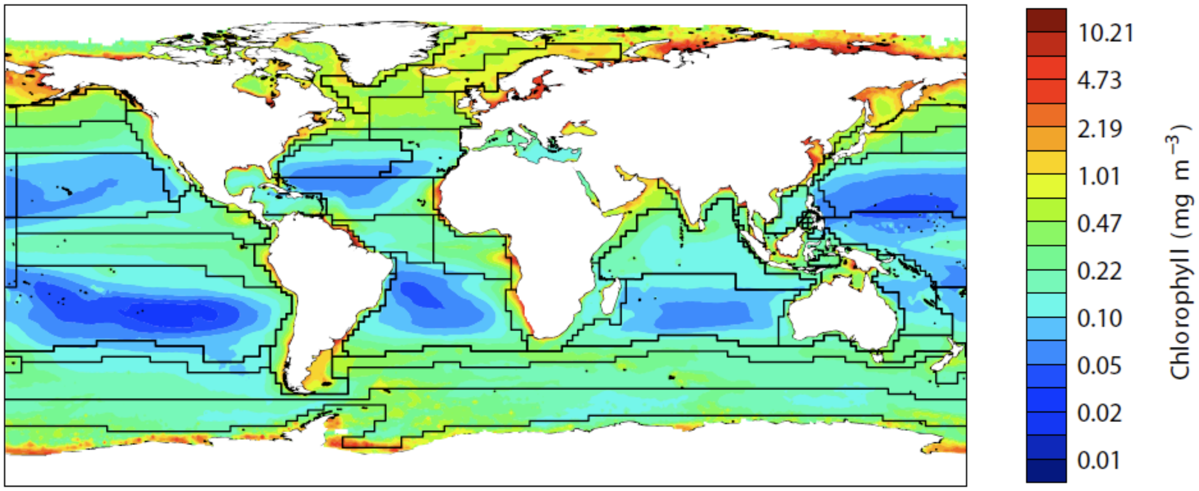


Figure 6-1: Productivity in 51 distinct global ocean biogeographical biomes as represented by a grid of thin black lines (after Longhurst, 1998), overlain with an average annual composite plot of chlorophyll *a* concentration, i.e., a proxy for phytoplankton stocks in the upper ocean, from the NASA/Orbimage 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).

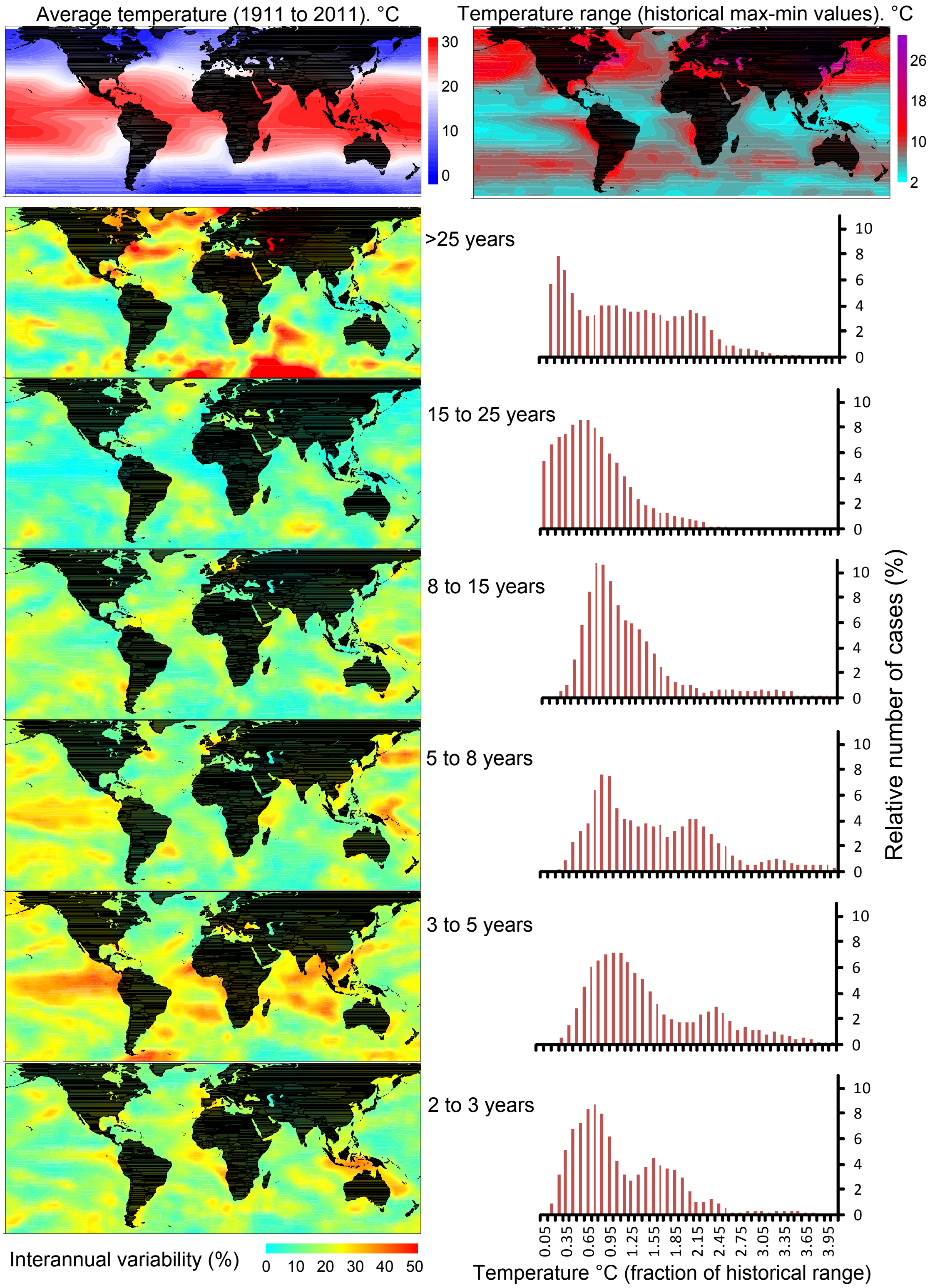

Average temperature (1911 to 2011). °C
30
20
10
0
Temperature range (historical max-min values). °C
26
18
10
2
>25 years
15 to 25 years
8 to 15 years
5 to 8 years
3 to 5 years
2 to 3 years
10
8
6
4
2
0
Relative number of cases (%)
Interannual variability (%)
0 10 20 30 40 50
0.05
0.35
0.65
0.95
1.25
1.55
1.85
2.15
2.45
2.75
3.05
3.35
3.65
3.95
Temperature °C (fraction of historical range)

Figure 6-2

Figure 6-2: Last Century sea surface temperature variability. The top left map shows the long term (1911 to 2011) sea surface temperature average. The top right map illustrates the temperature range calculated as the difference between the historical maximum and minimum values for each grid component. 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 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. Right hand histograms show 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).

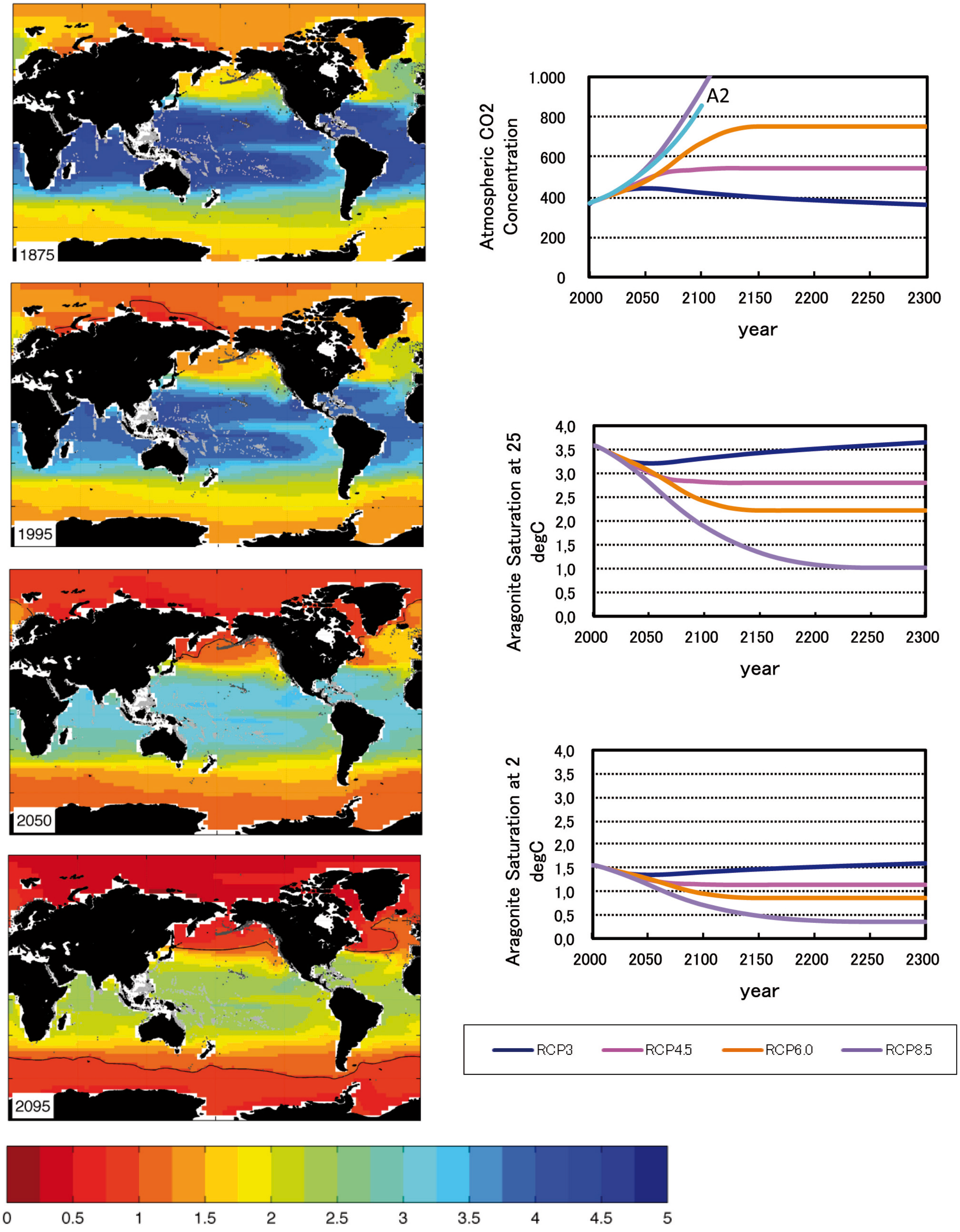
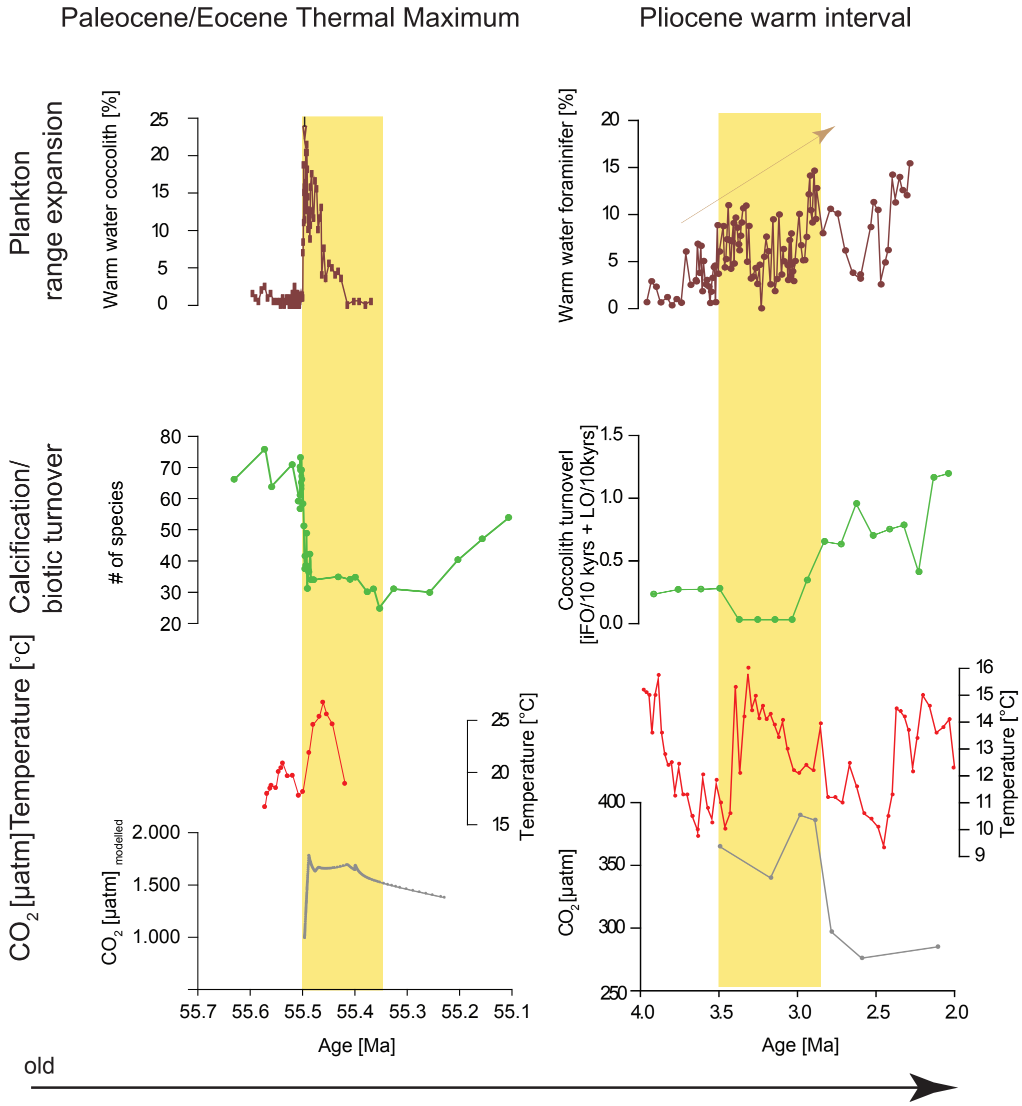

1875
1995
2050
2095
Atmospheric CO2 Concentration
1.000
800
600
400
200
0
A2
2000
2050
2100
2150
2200
2250
2300
year
Aragonite Saturation at 25 degC
4,0
3,5
3,0
2,5
2,0
1,5
1,0
0,5
0,0
year
Aragonite Saturation at 2 degC
year
RCP3
RCP4.5
RCP6.0
RCP8.5
0
0.5
1
1.5
2
2.5
3
3.5
4
4.5
5

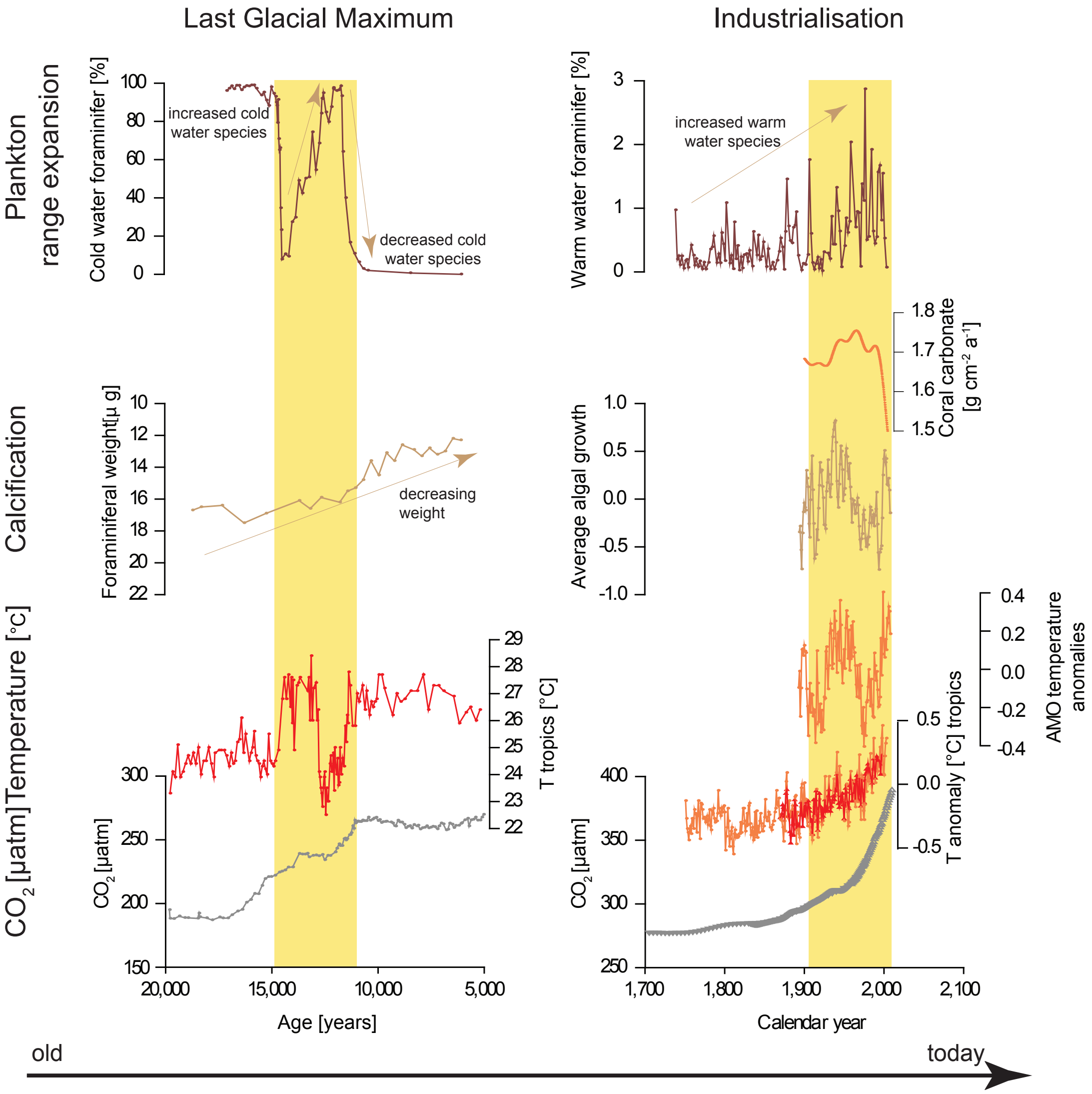
Figure 6-3

Figure 6-3: CCSM3-modeled decadal mean aragonite saturation (Ω) at the sea surface, around the years 1875, 1995, 2050, and 2095 following the SRES A2 emission scenario (left panel). The mean atmospheric CO_2 concentration in 2100 approximates around 850 μatm, somewhat below levels according to RCP 8.5 and mean aragonite saturation state at 2°C will drop to almost 0 by 2300 (Meinshausen *et al.*, 2011, right panels). Deep coral reefs are indicated by darker gray dots; shallow-water coral reefs are indicated with lighter gray dots. White areas indicate regions with no data (Feely *et al.*, 2009).



Panel A

Figure 6-4 A



Panel B

Figure 6-4 B

Figure 6-4: Atmospheric CO_2 (bottom, grey) and temperature (middle, red/orange) changes with associated biotic changes (top) for (panel A) the Palaeocene Eocene Thermal Maximum (PETM), the Pliocene warm period, and (panel B) the last glacial to Holocene transition and the industrial era. Intervals of largest environmental change are indicated with yellow bars. CO_2 data are based on measurements at Mauna Loa (Keeling *et al.*, 2005, modern), ice core records from Antarctica (Petit *et al.*, 1999; Monnin *et al.*, 2004, LGM), proxy reconstructions (Seki *et al.*, 2010, Pliocene) or represent model output (Ridgwell and Schmidt 2010, Zeebe *et al.* 2009, PETM). Temperature data are based on proxy data and models (Wilson *et al.*, 2006, [tropical ocean] modern; Lea *et al.*, 2003, [Caribbean], LGM; Lawrence *et al.*, 2009, [North Atlantic], Pliocene; Kennett and Stott, 1991 [Southern Ocean], PETM) representing the regional temperature changes in the surface ocean. For the recent anthropocene record, the Atlantic Multidecadal Oscillation is shown to highlight natural temperature fluctuations (Enfield *et al.*, 2001). Biotic responses include calcification, e.g. coralline algal growth increment changes (Halfar *et al.*, 2011), coral calcification as a product of density and linear extension (De'ath *et al.*, 2009) [modern] and foraminiferal weight (Barker and Elderfield, 2002), LGM. Evolutionary changes are indicated by turnover of coccolithophores defined as the sum of first and last appearances per 10 kyrs (Gibbs *et al.*, 2005, Pliocene) and extinction of benthic foraminifers (Thomas, 2003). Abundance data (top row) of planktonic foraminifers and coccolithophores (Field *et al.*, 2006, [St. Barbara Basin], modern; Thornalley *et al.*, 2011, [North Atlantic], LGM; Dowsett *et al.*, 1988; Dowsett and Robinson, 2006, [North Atlantic], Pliocene, Bralower, 2002 [Southern Ocean], PETM) indicate the temperature change and consequent range expansion or retraction in all four time intervals.

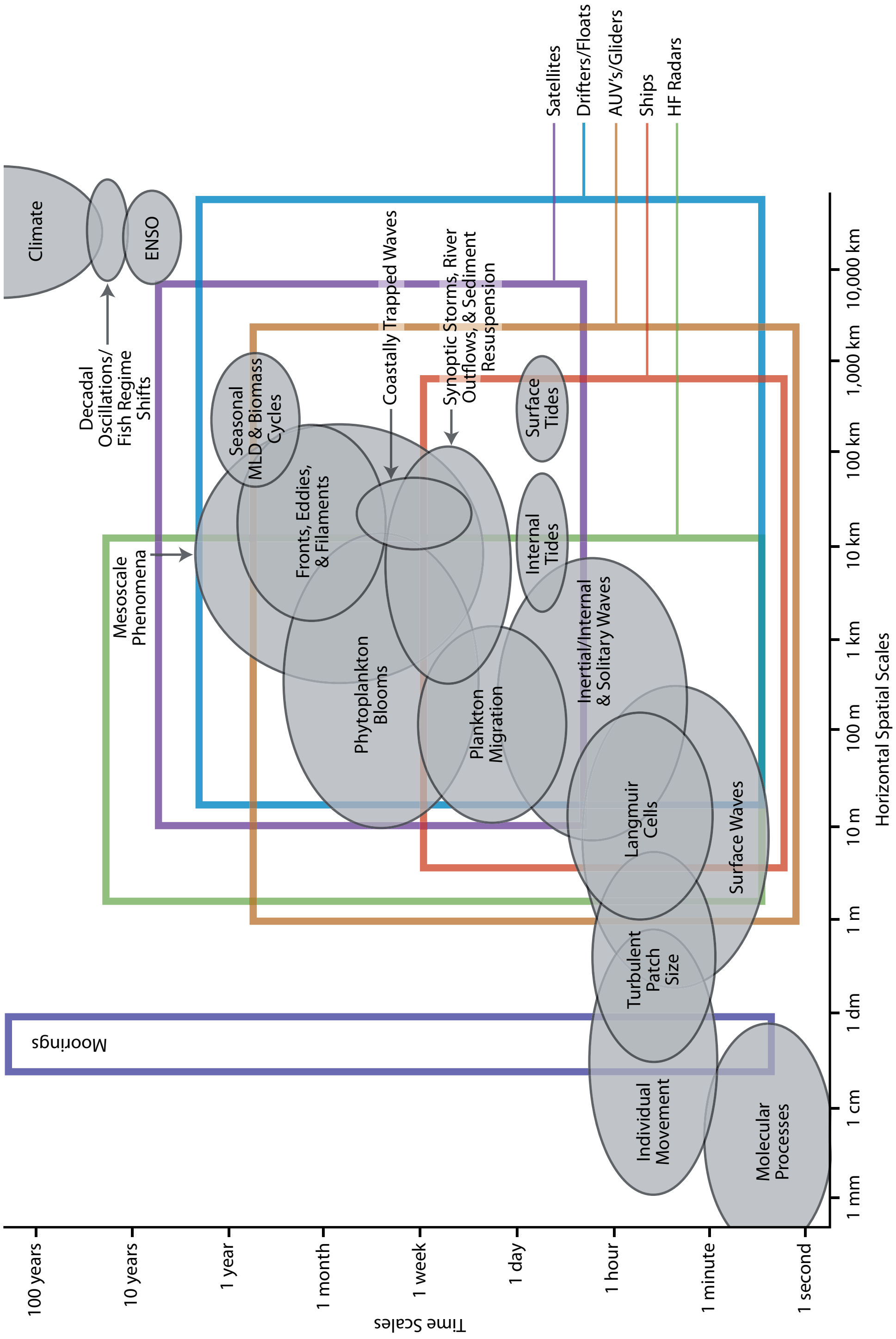


Figure 6-5: Multiple coupled temporal and spatial scales of variability in physical, physiological and ecological processes of interest in contemporary marine system research. Observations over broad time and space scales are necessary to separate natural variability from impacts due to human-induced 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. From Karl (2010), as modified from Dickey (1991). (TO BE DEVELOPED FURTHER AFTER FOD)

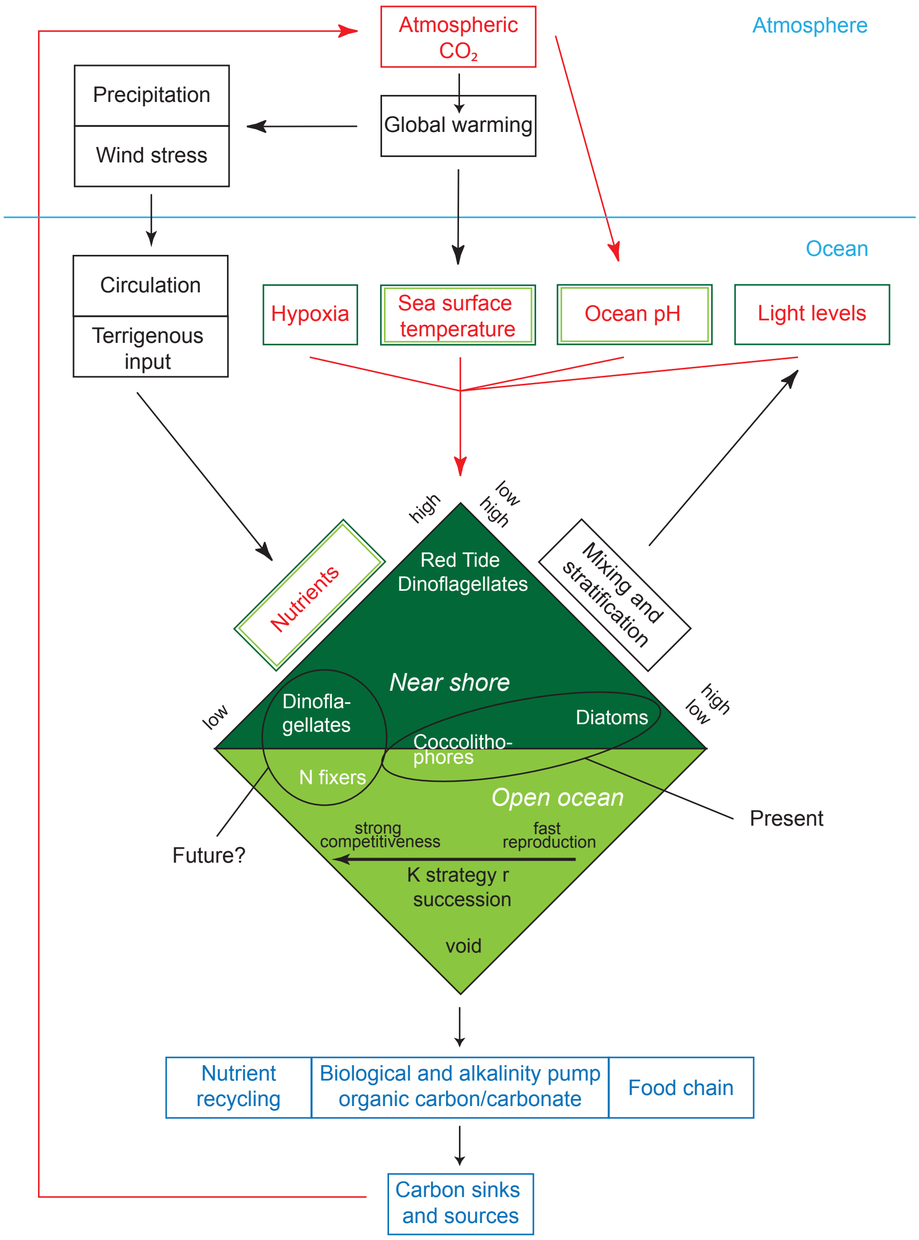


Figure 6-6: Climate impacts on phytoplankton succession. Margalef's "mandala" offers no quantitative predictions, but it is generally consistent with observation, experimentation and theory (Kiørboe, 1993). As turbulence and nutrient supply are expected to be altered by climate change, indirect climate factors (black), direct forcings (red) and possible feedback mechanisms (blue) on climate and marine ecosystems are highlighted. The arrows indicate the linkages between the processes. Predominantly coastal processes and organisms are indicated in dark green, while processes dominating the open ocean are indicated in light green. Future projections of climate-mediated phytoplankton succession presently rely upon a knowledge base that has *low confidence* and highly depends on regional patterns of change. As an example and based on the mandala, a phytoplankton community that is presently dominated by diatoms and coccolithophores (ellipsoid on the right) may in the future be mainly composed of dinoflagellates and nitrogen fixers (circle on the left) if nutrient supply decreases and stratification intensifies. Conversely, Hinder *et al*. (2012) described a recent decline in dinoflagellates compared to diatoms in the northeast Atlantic and North Sea, associated with warming, increased summer windiness and thus, turbulence (see 6.3.1.)

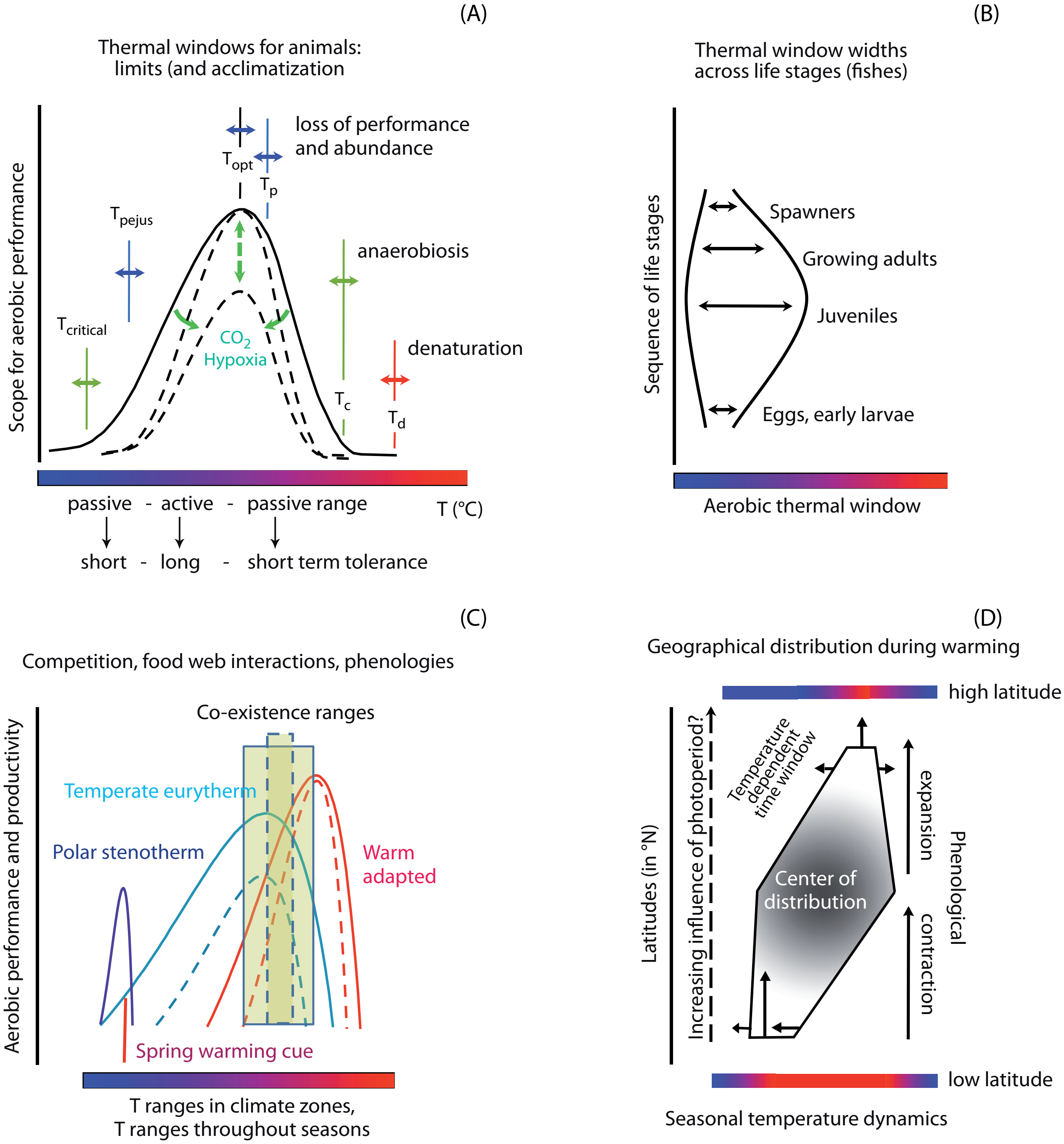

(A)
Thermal windows for animals: limits (and acclimatization)
Scope for aerobic performance
loss of performance and abundance
T_{opt}
T_p
T_{pejus}
anaerobiosis
$T_{critical}$
CO_2 Hypoxia
denaturation
T_c
T_d
passive - active - passive range
T (°C)
short - long - short term tolerance
(B)
Thermal window 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, generalizing from the principles identified in animals (after Pörtner and Farrell, 2008; Pörtner, 2001, 2002a, 2010). Wider applicability of such reaction norms to bacteria, phytoplankton, macrophytes requires exploration. (A) Concept of oxygen and capacity limited thermal tolerance (OCLTT) characterizing the specialization of animals on limited thermal windows set by (aerobic) performance (shaping fitness, growth, specific dynamic action (SDA), exercise, behaviours, immune capacity, reproduction) and, as a consequence, the why, how, when and where of climate sensitivity. Optimum temperatures (T_{opt}) indicate performance maxima, pejus temperatures (T_p) indicate limits to long-term tolerance, critical temperatures (T_c) quantify the borders of short-term passive tolerance and the transition to anaerobic metabolism. Denaturation temperatures (T_d) indicate the onset of cell damage. (B) Thermal specialization and response is dynamic between individual life stages in animals. (C) Performance curves of polar, temperate and tropical animal species reflect evolutionary adaptation to the respective climate zones. The effect of additional stressors and species interactions can be understood through dynamic changes in performance capacity and thermal limits (dashed curves), causing feedbacks on higher-level processes (phenology, interactions). Temperature-dependent performance forms the basis of shifts in phenologies, namely the seasonal timing of biological processes, of changes in thermal ranges of species co-existence and interactions (competition, predator-prey). (D) Shifts in biogeography result during climate warming (modified after Beaugrand, 2009). Here, the black line surrounding the polygon delineates the range in space and time, the level of grey denotes abundance. Thermal specialization causes species to display maximum productivity in spring toward southern distribution limits, wide seasonal coverage in the centre and a maximum in late summer in the North. The impact of photoperiod increases with latitude (dashed arrow). During climate warming, the southern time window shifts and contracts while the northern one dilates (direction and magnitude of shift indicated by arrows), until control by other factors like water column characteristics or photoperiod may overrule temperature control in some species (e.g. diatoms), above the polar circle causing contraction of spatial distribution in the north.

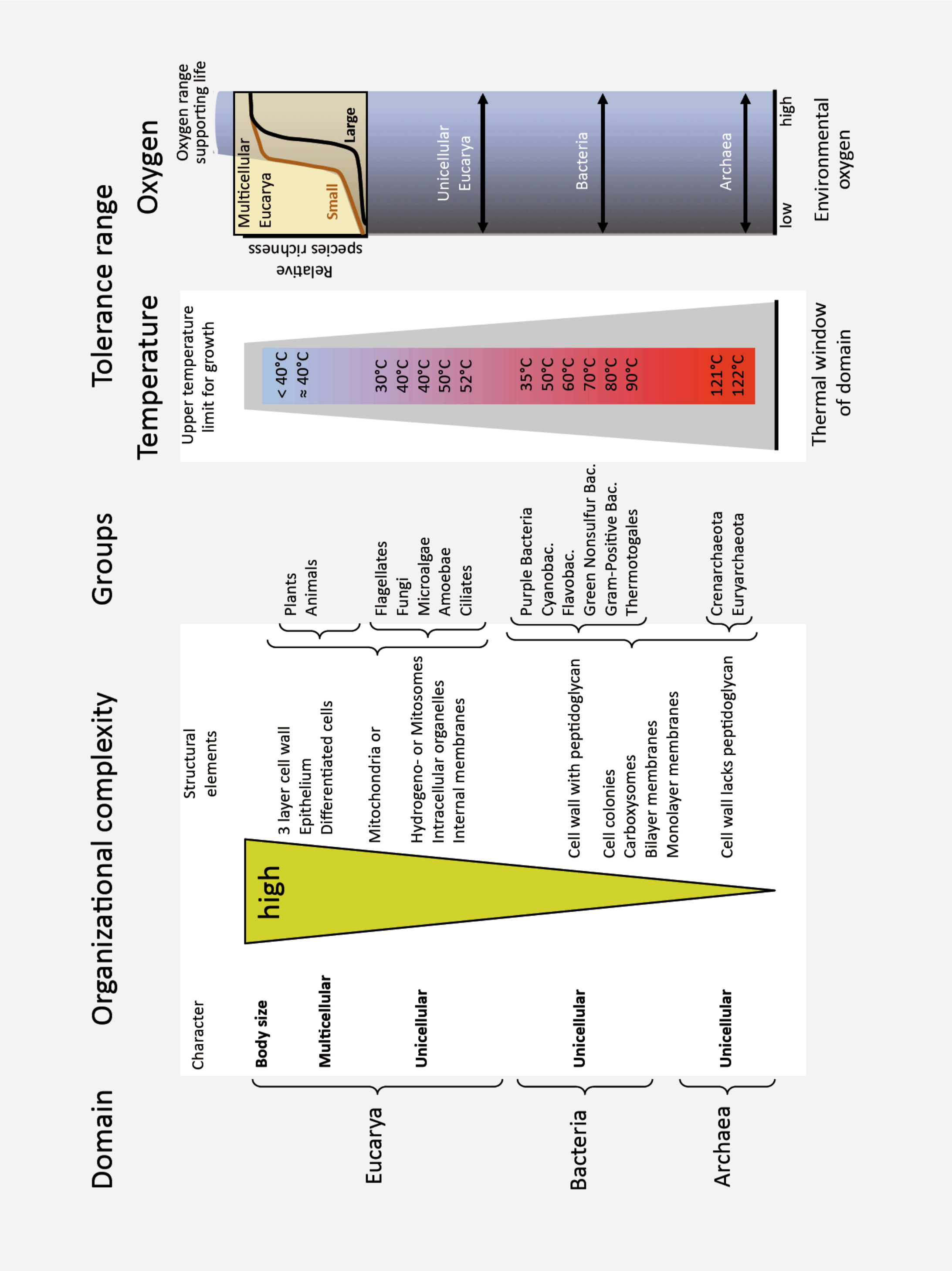

Domain
Eucarya
Bacteria
Archaea
Organizational complexity
Character
Body size
Multicellular
Unicellular
Unicellular
Unicellular
high
Structural elements
3 layer cell wall
Epithelium
Differentiated cells
Mitochondria or
Hydrogeno- or Mitosomes
Intracellular organelles
Internal membranes
Cell wall with peptidoglycan
Cell colonies
Carboxysomes
Bilayer membranes
Monolayer membranes
Cell wall lacks peptidoglycan
Groups
Plants
Animals
Flagellates
Fungi
Microalgae
Amoebae
Ciliates
Purple Bacteria
Cyanobac.
Flavobac.
Green Nonsulfur Bac.
Gram-Positive Bac.
Thermotogales
Crenarchaeota
Euryarchaeota
Tolerance range
Temperature
Upper temperature limit for growth
< 40°C
≈ 40°C
30°C
40°C
40°C
50°C
52°C
35°C
50°C
60°C
70°C
80°C
90°C
121°C
122°C
Thermal window of domain
Oxygen
Oxygen range supporting life
Relative species richness
Multicellular Eucarya
Small
Large
Unicellular Eucarya
Bacteria
Archaea
low
high
Environmental oxygen

Figure 6-8

Figure 6-8: Ranges of temperatures and oxygen concentrations covered by various domains and groups of free living marine organisms (archaea to animals), reflecting a narrowing of environmental regimes tolerated with rising levels of organizational complexity and increasing body size ([Storch and Pörtner, to come], extending from Pörtner, 2002a,b). High organizational complexity enables an increase in body size, at the expense of decreasing hypoxia and heat tolerance (reflected in falling upper temperature limits of detected growth). Anoxic habitats can be conquered by small multicellular Eucarya (3 known species at < 0.5 mm body size, with about 10,000 differentiated cells, Danovaro *et al*., 2010) and unicellular Eucarya, by means of special adaptations, e.g. using less complex hydrogenosomes or mitosomes instead of mitochondria in energy metabolism. Domains and groups are modified after Woese *et al*. (1990). In the domain Bacteria, the group Thermotogales is most tolerant to temperature. It comprises obligate anaerobes and displays less complex structures indicated by a single layer lipid membrane. In the various domains, most heat tolerant representatives are as follows: **Eucarya**: Animals *Alvinella pompejana* (Chevaldonnè *et al.,* 2000) and *Paraalvinella sulfincola* (Girguis & Lee, 2006); Plants *Cymnodocera rotundata, C. serrulata* and *Halodule uninervis* (Campbell *et al.,* 2006); Flagellate *Heterocapsa circularisquama* (Yamaguchi *et al.,* 1997); Fungus *Varicosporina ramulosa* (Boyd and Kohlmeyer,1982); Microalga *Chlorella pyrenoidosa (Eppley, 1972*); Amoeba *Marinamoeba thermophila* (Jonckheere *et al.,* 2009); Ciliate *Trimyema minutum* (Baumgartner *et al.,* 2002); **Bacteria**: Purple Bacteria *Rhodovulum iodosum* sp. Nov. (Straub *et al.,* 1999); Cyanobacterium *Halomicronema excentricum* (Abed *et al.,* 2002); Flavobacterium *Thermonema rossianum* (Tenreiro *et al.,* 1997); Green Nonsulfur Bacterium *Chloroflexus aurantacus* (Madigan 2003); Gram-Positive Bacterium *Thermaerobacter marianensis* (Takai *et al.,* 1999); Thermotogales *Thermotoga maritima* (Huber *et al.,* 1986); **Archaea**: Crenarchaeota *Pyrolobus fumarii* (Kashefi & Lovely (2003); Euryarchaeota *Metanopyrus kandleri* Strain 116 (Takai *et al.,* 2008). Highest exposure temperatures at 122°C of growing species were found under high hydrostatic pressure. Black arrows denote the wide range of oxygen tolerances in unicellular Archae, Bacteria and Eucarya. Species richness of animals (upper right graph) increases with oxygen levels and reflects the higher hypoxia tolerance in small compared to large individuals/taxa (6.2.2.4., 6.3.3.).
(TO BE DEVELOPED FURTHER AFTER FOD).

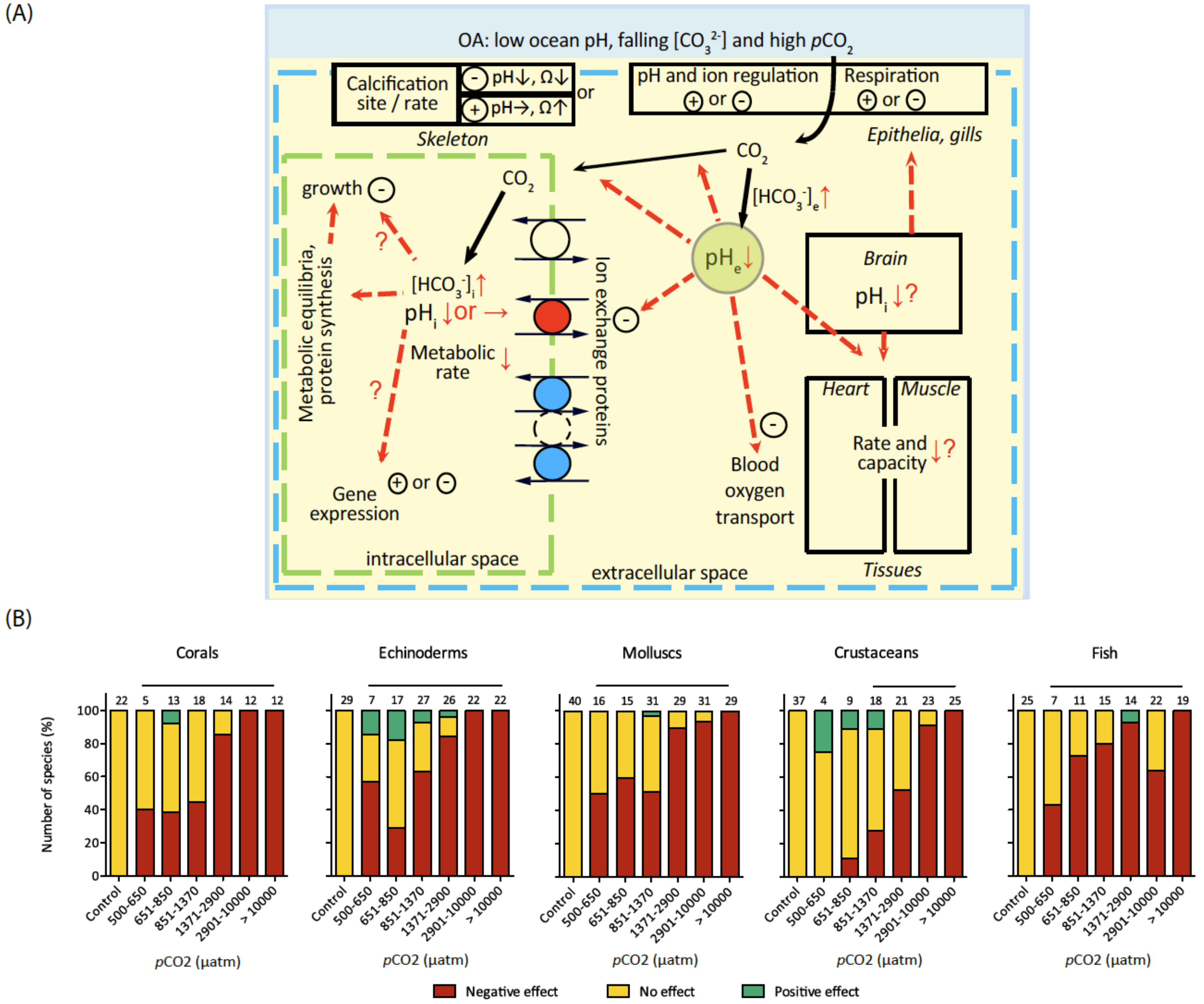

(A)
OA: low ocean pH, falling [CO_3^{2-}] and high pCO_2
Calcification site / rate
- pH↓, Ω↓
or
+ pH→, Ω↑
Skeleton
pH and ion regulation
+ or -
Respiration
+ or -
Epithelia, gills
CO_2
[HCO_3^-]$_e$↑
pH_e↓
Brain
pH_i↓?
Heart
Muscle
Rate and capacity ↓?
Tissues
Blood oxygen transport
-
Ion exchange proteins
-
CO_2
growth -
?
Metabolic equilibria, protein synthesis
[HCO_3^-]$_i$↑
pH_i ↓or →
Metabolic rate ↓
?
Gene expression
+ or -
intracellular space
extracellular space
(B)
Corals
Echinoderms
Molluscs
Crustaceans
Fish
Number of species (%)
100
80
60
40
20
0
Corals: 22 5 13 18 14 12 12
Echinoderms: 29 7 17 27 26 22 22
Molluscs: 40 16 15 31 29 31 29
Crustaceans: 37 4 9 18 21 23 25
Fish: 25 7 11 15 14 22 19
Control
500-650
651-850
851-1370
1371-2900
2901-10000
> 10000
pCO2 (µatm)
Negative effect
No effect
Positive effect

Figure 6-9

Figure 6-9: (A) Unifying physiological principles characterizing the responses of a schematized marine water breathing animal (dashed blue line) to elevated partial pressures of CO_2. Effects are permanent if the animal is sensitive to ocean acidification (OA) or transient during acute CO_2 exposure if sensitivity is low. Effects are mediated via entry of CO_2 (black arrows) into the body, resulting in a permanent drop in extracellular pH and its putative effects (red dashed arrows) on various tissues (boxes surrounded by solid black lines) and their processes, including calcification as well as performance and fitness of the whole organism (simplified and updated from Pörtner, 2008). Sensitivity is reduced with efficient extracellular pH compensation and/or pH compensation in each of the compartments exerting specific functions including calcification. Variability of responses according to the capacity of compensating mechanisms is indicated by + (stimulation) or – (depression). Many of these elements are similar across organism kingdoms but the link to performance-related processes has only been tested for animals. (B) % fraction of studied scleractinian coral, echinoderm, molluscan, crustacean and fish species affected negatively, positively or not at all by various levels of elevated ambient CO_2 (6.1.1.). Effects considered include those on various life stages and processes reflecting changes in physiological performance (oxygen consumption, aerobic scope, behaviours and scope for behaviours, calcification, growth, immune response, maintenance of acid-base balance, gene expression, fertilization rate, sperm motility, developmental time, production of viable offspring, morphology). Note that not all life stages, parameters and ranges of CO_2 partial pressures were studied in all species. Two assumptions were made to partially compensate for missing data within CO_2 ranges: 1) Species with negative effects at low pCO_2 will remain negatively affected at high pCO_2. 2) If a species is positively or not affected at both low and high pCO_2, it will show the same effect at intermediate pCO_2. Note that it was not possible to derive the response of each species for each CO_2 category, such that variable species numbers (on top of columns) result in each category. Bars above columns represent frequency distributions significantly different from the control treatment (Fisher's exact test, $p < 0.05$; (Literature base added separately; from [Wittmann and Pörtner, to come]).

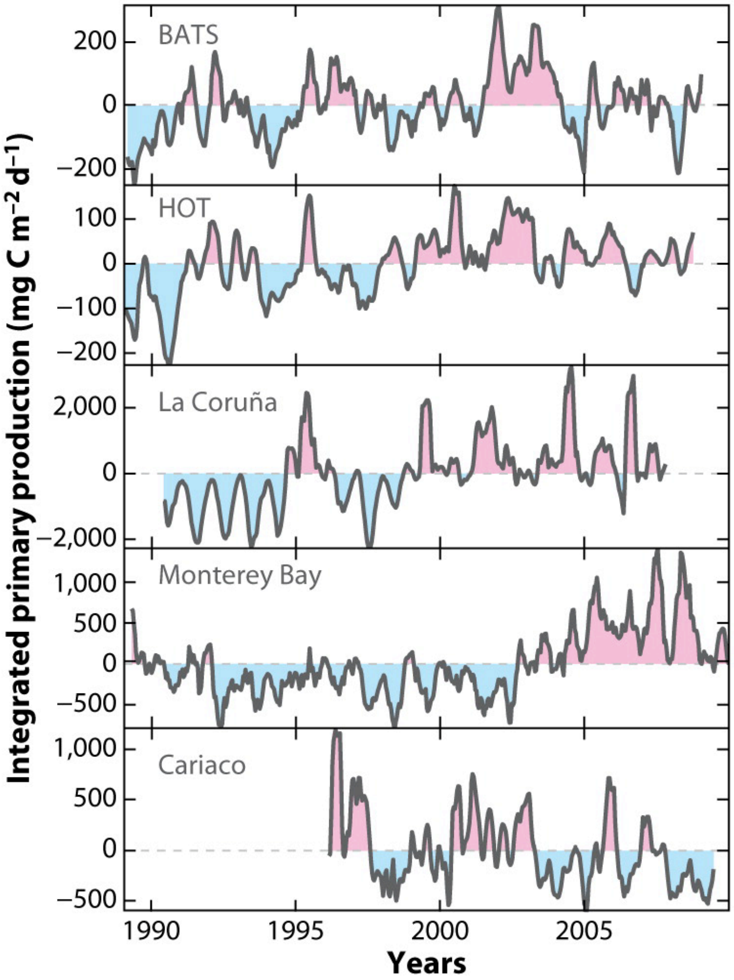


Figure 6-10: Time-series of water column integrated primary production (PP) anomalies for time-series sites: Northwestern Spain, La Coruña (43° 25.2 N, 8° 26.4 E); HOT (22° 45 N, 158°W); BATS (31° 50 N, 64° 10 W); Monterey Bay, Central California Current (37°N, 122°W); Cariaco Basin, Venezuela (10°30 N, 64°40 W) reproduced from Chavez *et al*. (2011). Integrated PP and Chl anomalies were calculated by integrating over the water column, then interpolating, smoothing, and differencing. For PP, the 1992–1993 and 1997–1998 El Niño signals are less apparent, except perhaps at La Coruña and Monterey Bay, but all the sites except Cariaco seem to show positive (pink) PP anomalies after 2000.

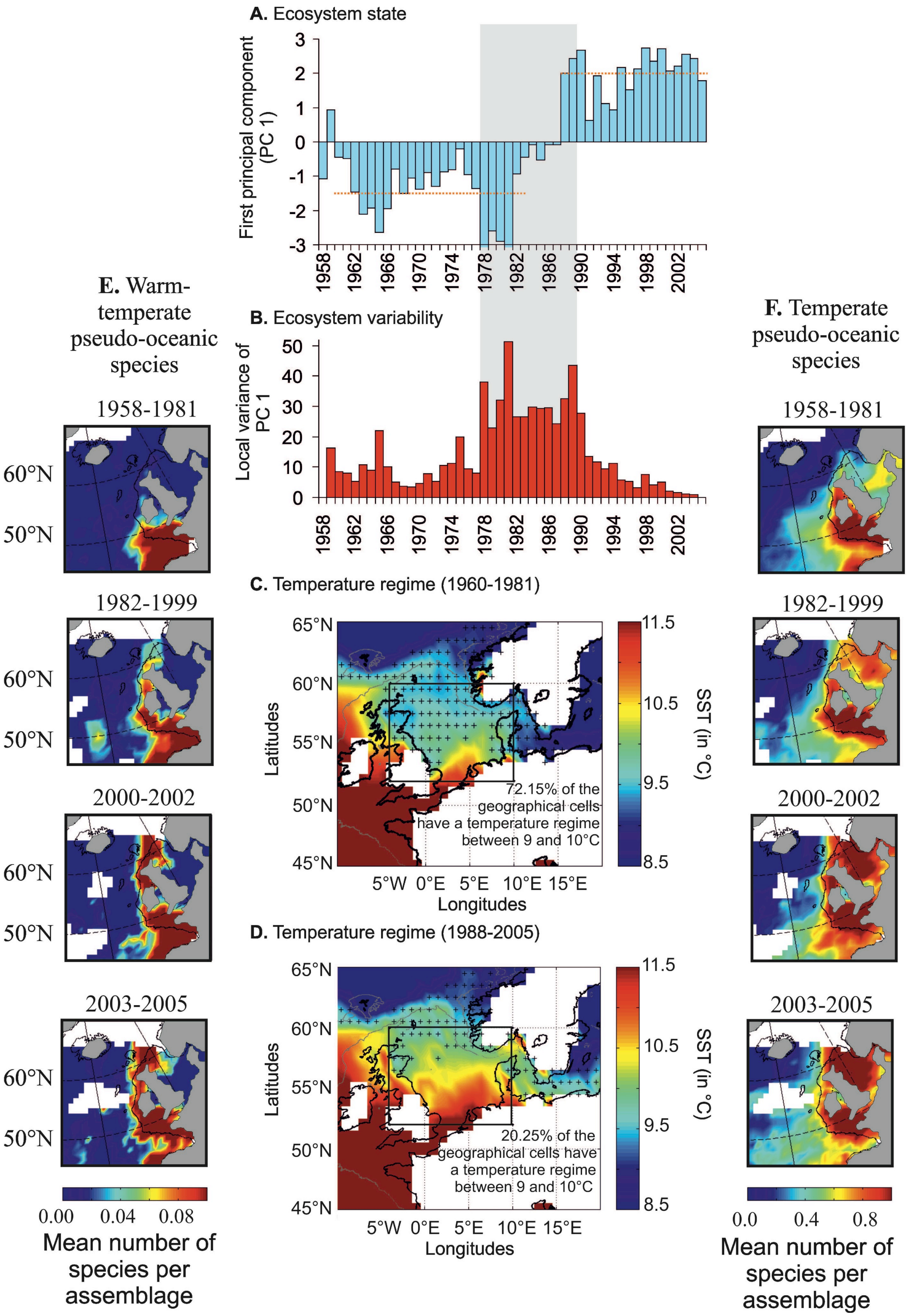

A. Ecosystem state
First principal component (PC 1)
3
2
1
0
-1
-2
-3
1958
1962
1966
1970
1974
1978
1982
1986
1990
1994
1998
2002
B. Ecosystem variability
Local variance of PC 1
50
40
30
20
10
0
C. Temperature regime (1960-1981)
65°N
60°N
55°N
50°N
45°N
Latitudes
5°W 0°E 5°E 10°E 15°E
Longitudes
72.15% 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
Mean number of species per assemblage

Figure 6-11

Figure 6-11: A. Long-term changes in the ecosystem state based on 5 biological parameters (phytoplankton color index, mean size of calanoids, mean calanoid diversity, an index of change in plankton composition and cod recruitment). B. Long-term changes in the multiscale temporal 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).

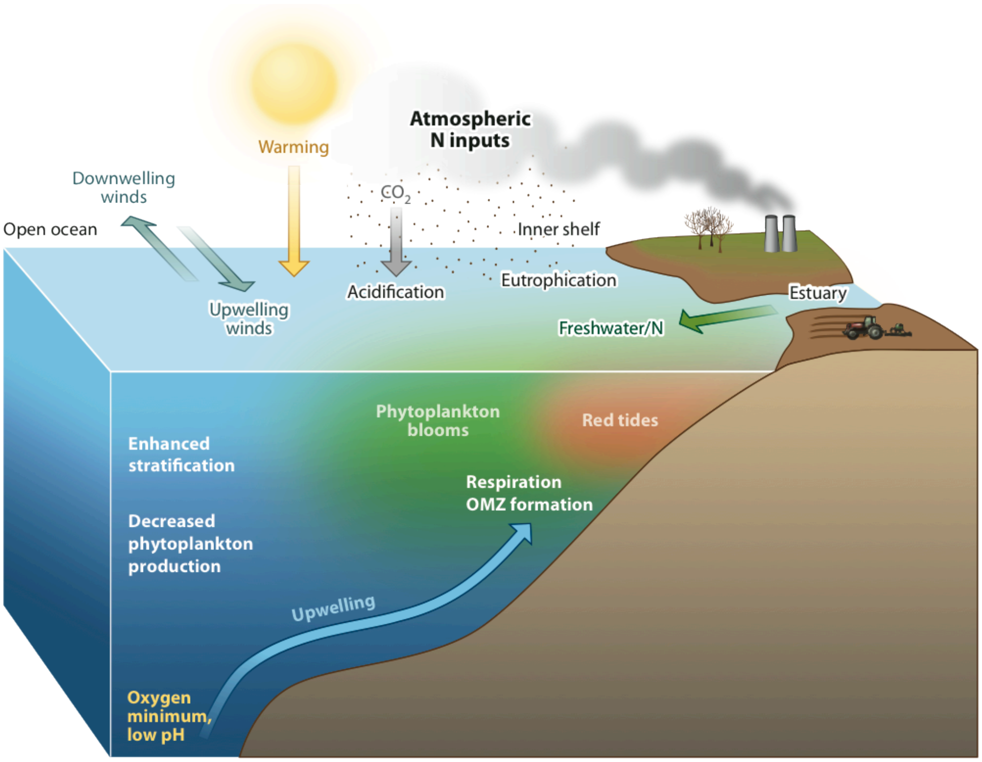
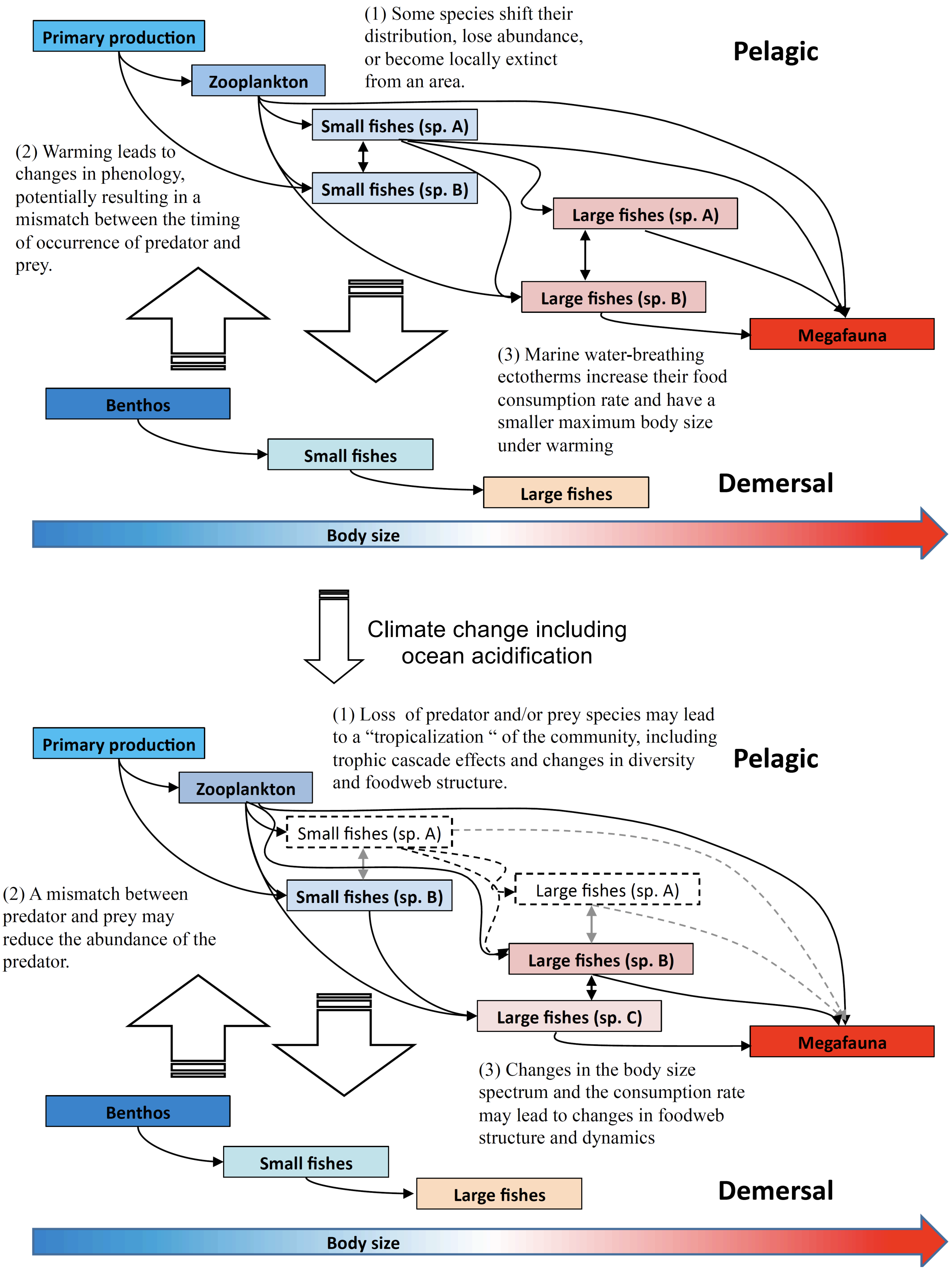


Figure 6-12: Diagram schematizing the principal mechanisms underlying the formation of hypoxic conditions and their biological background and consequences along continental margins (modified from Levin *et al.*, 2009; Levin and Sibuet, 2012).



(1) Some species shift their distribution, lose abundance, or become locally extinct from an area.

(2) Warming leads to changes in phenology, potentially resulting in a mismatch between the timing of occurrence of predator and prey.

(3) Marine water-breathing ectotherms increase their food consumption rate and have a smaller maximum body size under warming

(1) Loss of predator and/or prey species may lead to a "tropicalization " of the community, including trophic cascade effects and changes in diversity and foodweb structure.

(2) A mismatch between predator and prey may reduce the abundance of the predator.

(3) Changes in the body size spectrum and the consumption rate may lead to changes in foodweb structure and dynamics

Figure 6-13

Figure 6-13: Schematic diagram of a marine foodweb and the expected responses to climate change including ocean acidification: (A) A coupled pelagic and benthic foodweb that 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. (B) 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.

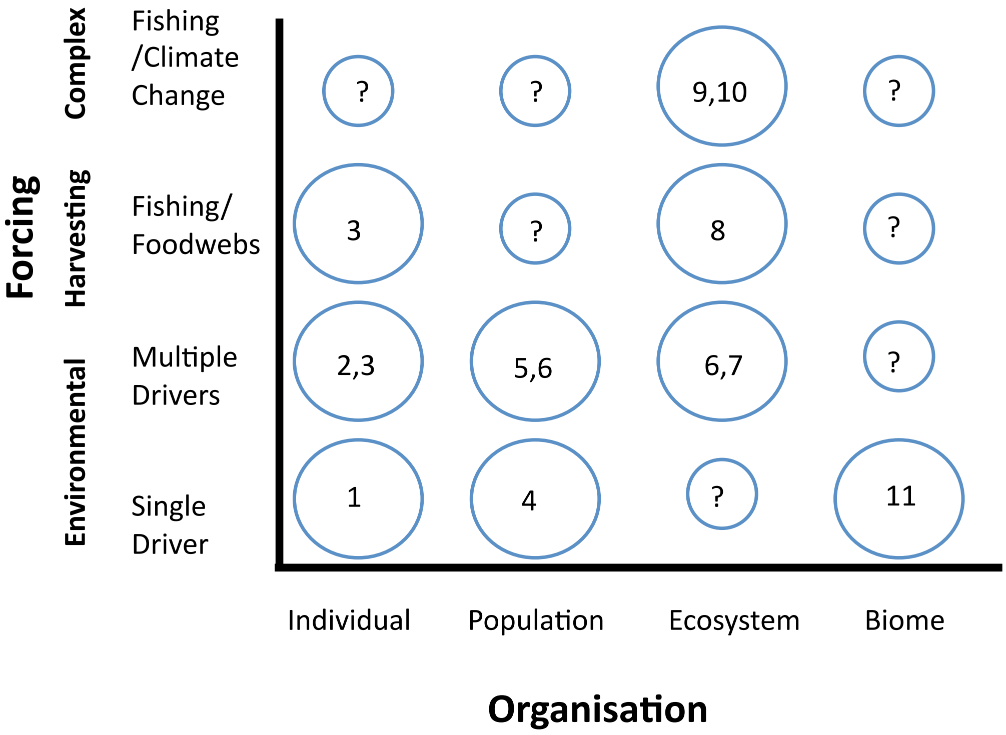


Figure 6-14: A schematic highlighting the potential interactions between modes of forcing (anthropogenic and natural) on different levels of biological organisation. These interactions, from simple to complex, are illustrated with published examples and each is assigned a circle the size of which is the level of *confidence* in the findings of the study, ranging from *low* for modeling studies such as (10; Griffith *et al.*, 2011) to *high* for lab physiological studies placed into context of field data (1; Pörtner and Knust, 2007). Circles with "?" define the bounds on our understanding of the relationship between forcing and its effect on organisational level. 1 denotes the effects of a single driver - warming on alteration of organismal physiology and field abundance (Pörtner and Knust, 2007); 2 the synergistic effects of multiple drivers - warming and increased [CO_2] on coccolithophore calcification (Feng *et al.*, 2009); 3 the effects of multiple drivers on larval fish (Perry *et al.*, 2010; Runge *et al.*, 2010); 4 a single driver - altered pH and the different responses of coccolithophore species (Langer *et al.*, 2006); 5 differential responses of cyanobacterial groups to multiple drivers - warming and increased [CO_2] (Fu *et al.*, 2007); 6 Altered maturation age and growth rate due to fishing (Fairweather *et al.*, 2006; Hseih *et al.*, 2006); 7 differential effect of multiple drivers, light and temperature, on copepods versus diatoms (Lewandowska and Sommer, 2010); 8 the effect of fishing on ecosystem structure (Frank *et al.*, 2005); 9 the interplay of fishing pressure and climate change on ecosystems (Kirby *et al.*, 2009); 10 the interplay of ocean acidification and fishing pressure on benthic communities (Griffith *et al.*, 2011); 11 detailed time-series observations on warming and the alteration of zooplankton biomes (Beaugrand *et al.*, 2009). (TO BE DEVELOPED FURTHER AFTER FOD)

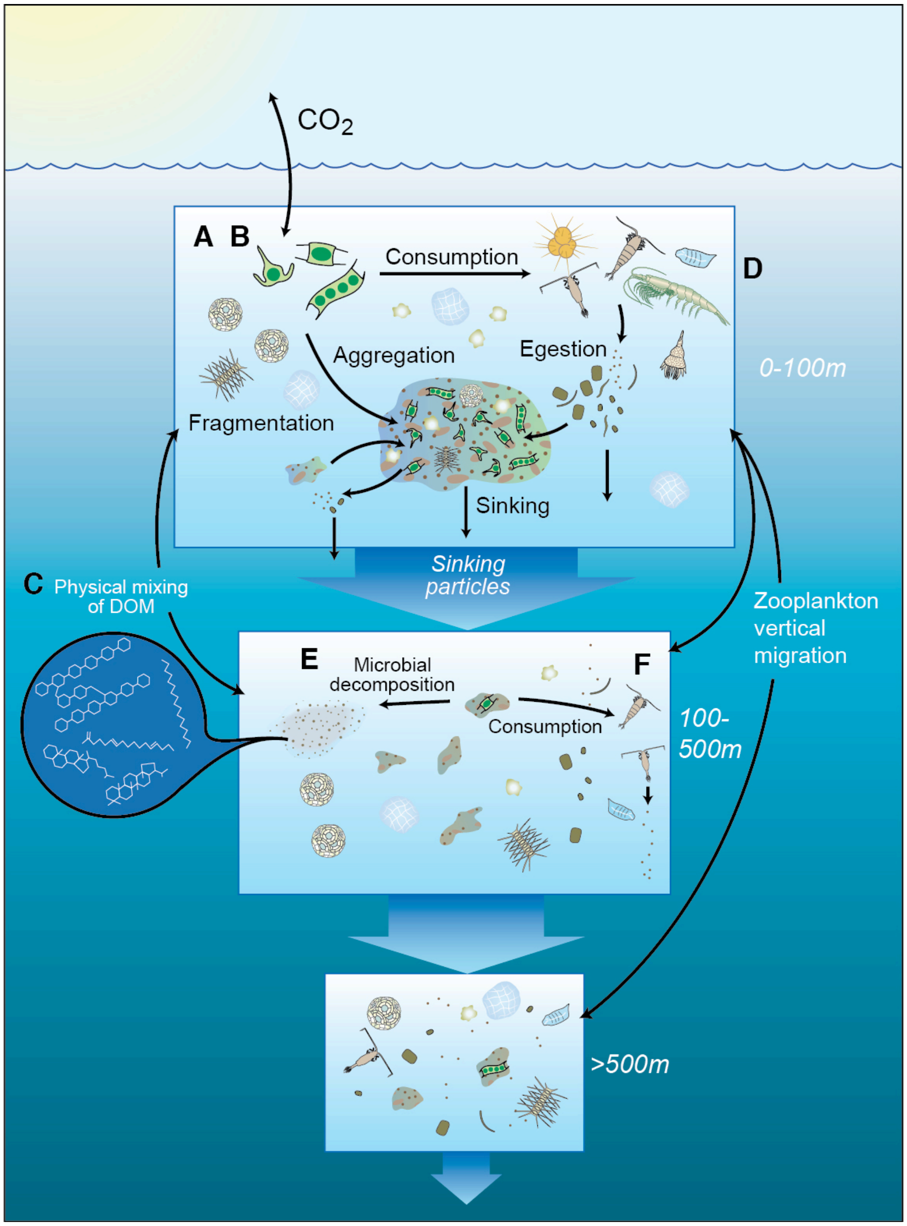


Figure 6-15: A schematic representation of the ocean's biological pump, an important conduit for carbon sequestration. Processes involved (Table 6-4) may each be altered by climate change. In a changing climate it is difficult to predict how the pump might be altered and hence whether it would represent a positive or negative feedback to climate change. Factors reported to be altered by a changing climate include: A, changes to 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, change 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). Figure modified from Buesseler *et al.* (2008) by J. Cook (WHOI).

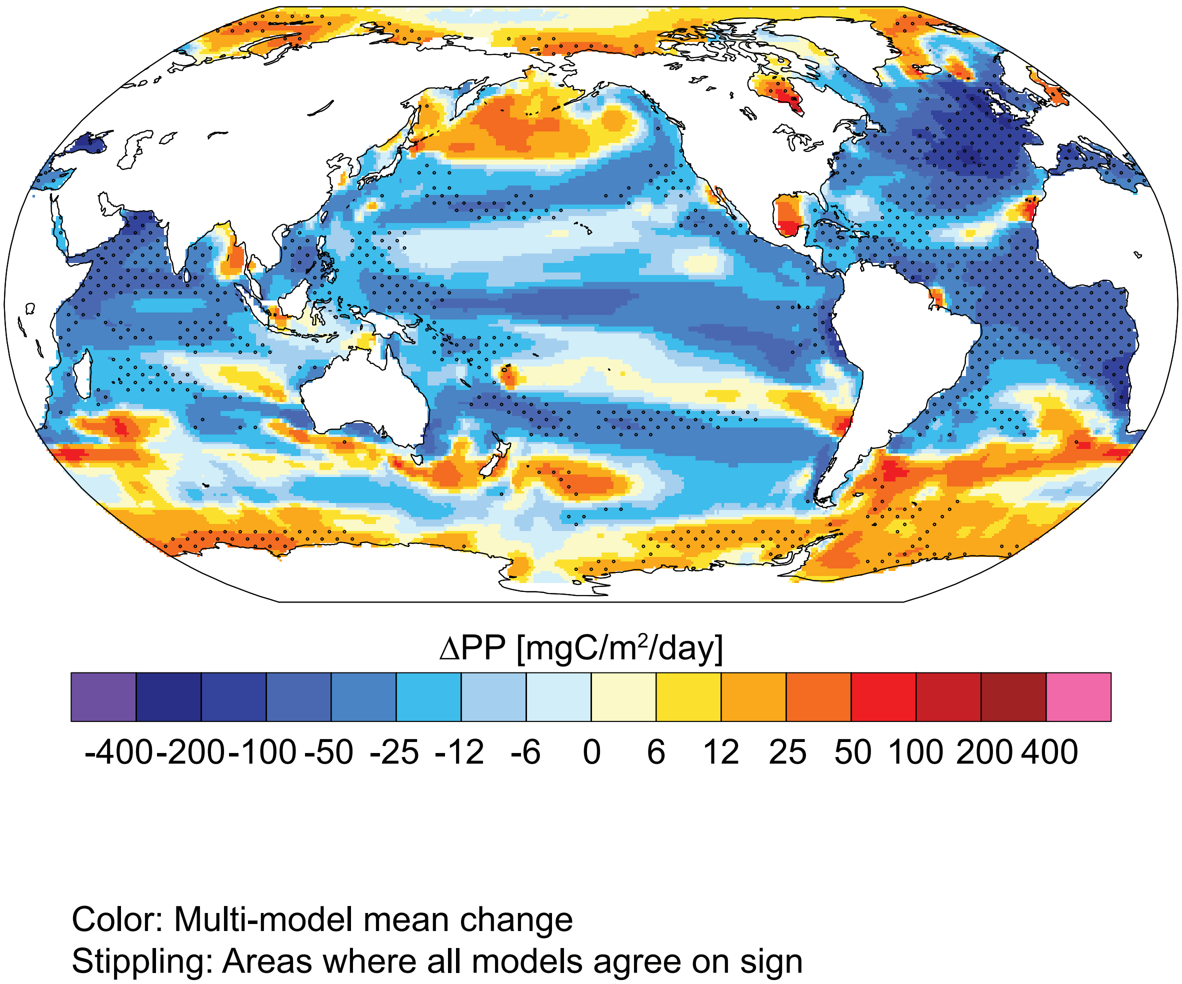


Figure 6-16: Multi-model mean changes of projected vertically-integrated net primary production (small and large phytoplankton). To indicate consistency in the sign of change, regions are stippled where all four models agree on the sign of change. Changes are annual means for the SRES A2 scenario for the period 2080 to 2099 relative to 1870 to 1889, after Steinacher *et al*. (2010).

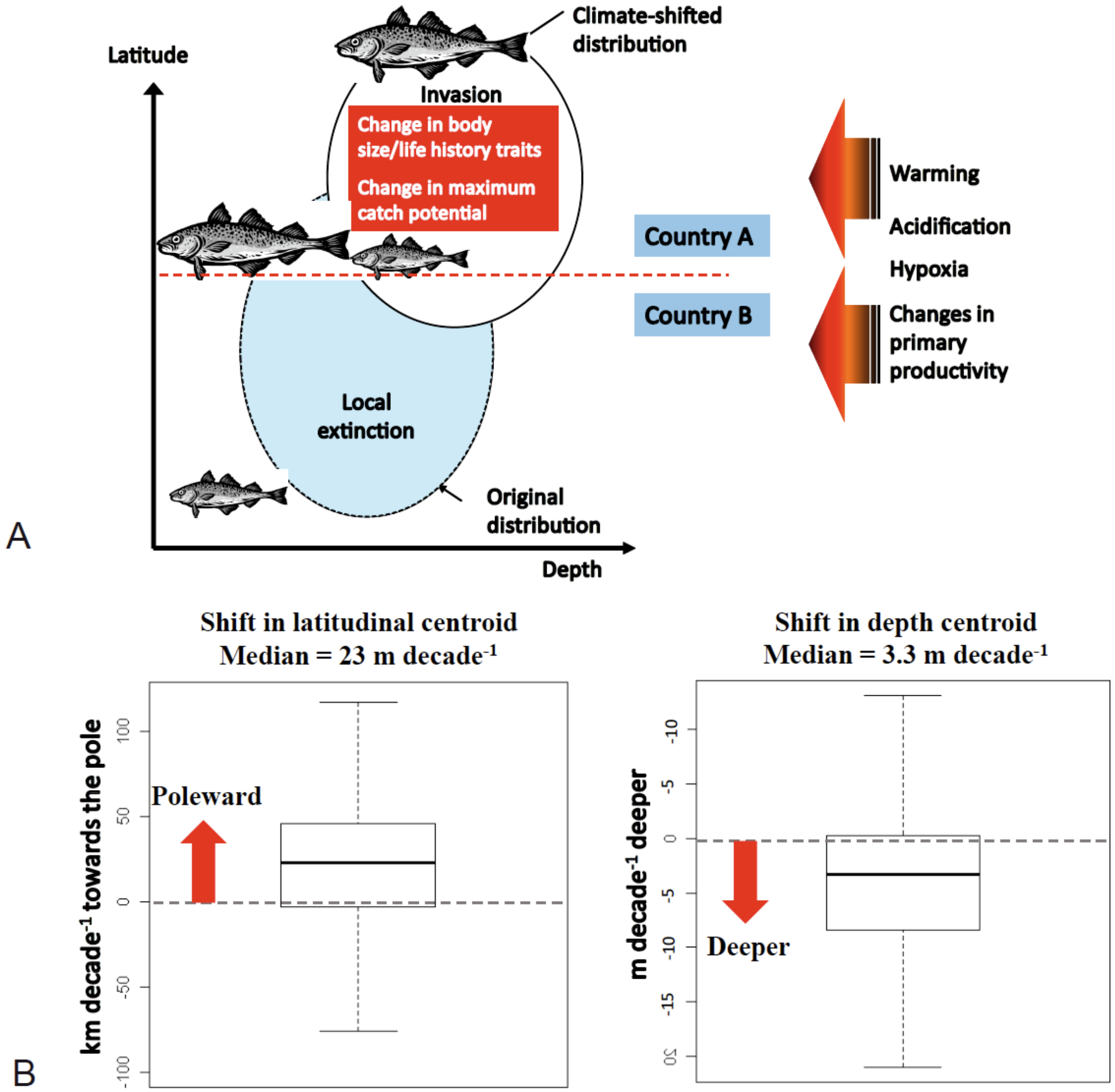


Figure 6-17 A, B

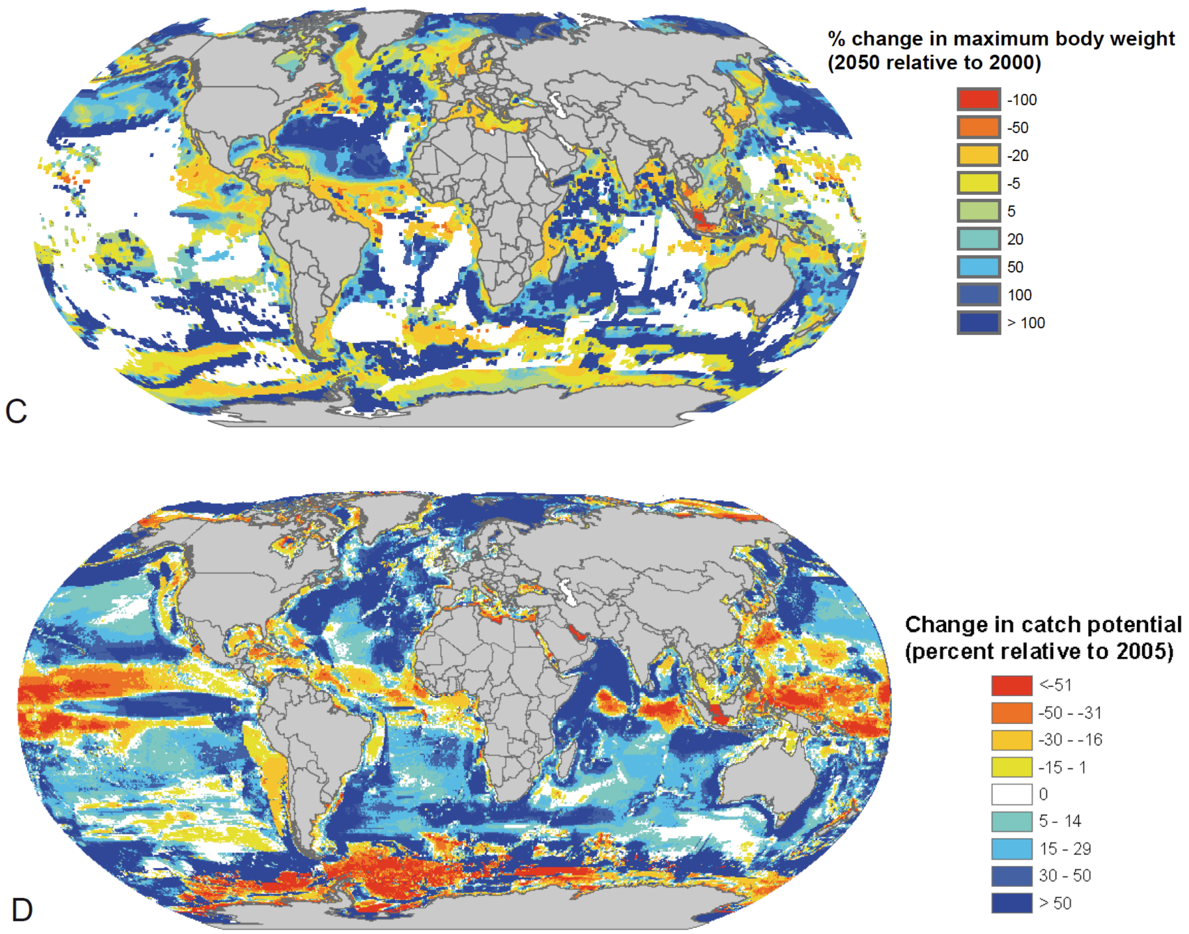
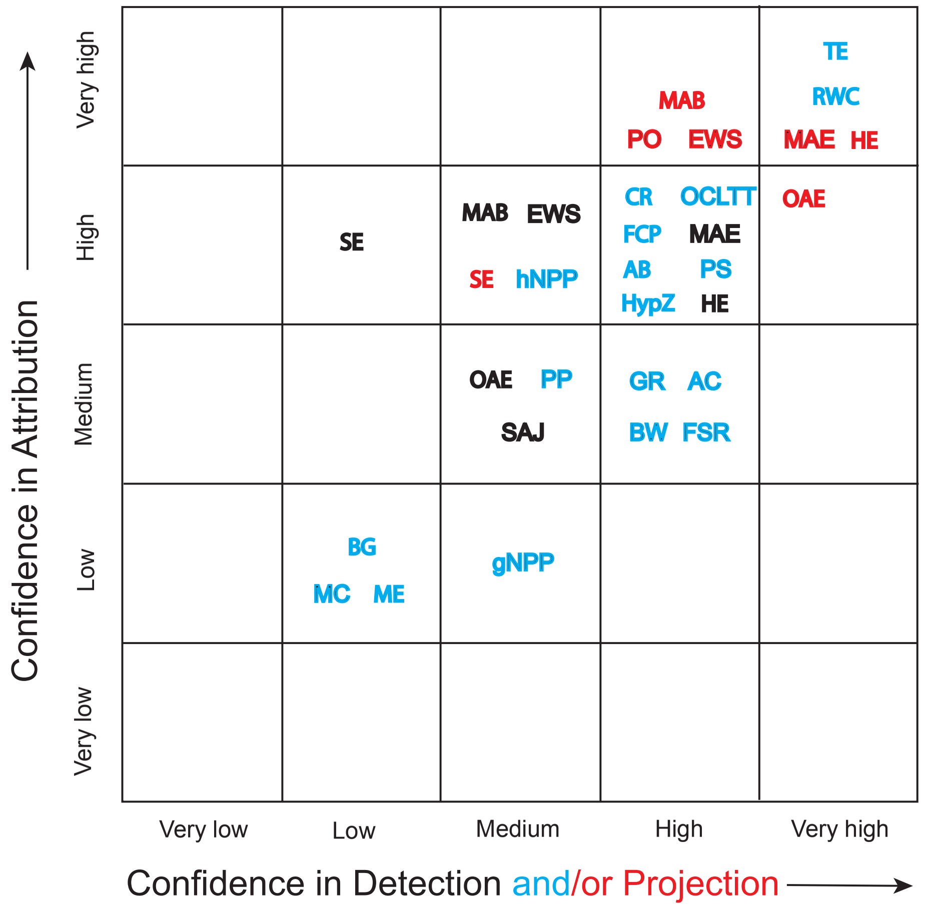


Figure 6-17 C, D

Figure 6-17: Scenarios of the effects of climate change on the biogeography of marine fishes and invertebrates, their biology and fisheries catch potential. (A) The main hypotheses of climate change effects on marine fishes and invertebrates. (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.*, submitted). The median rate of the rate shift observed from the 1970s to the 2000s in the North Sea and Bering Sea are indicated by the arrows. (C) Projected change in the maximum body size of 610 species of marine fishes from 2000 to 2050 under the SRES A2 scenario (Cheung *et al.*, submitted). The values represent the average results from projections using outputs from the NOAA/GFDL ESM2.1 and IPSL-CM4-LOOP models. The white area is not occupied by the sample of species (D) Example of formulization of these hypotheses through a simulation model to project 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).



AB,	Abundance
AC,	Atlantic Cod
BG,	Biogeochemical Processes
BW,	Banded Morwong
CR,	Community Response
EWS,	Eelpout, Wadden Sea
FCP,	Fish Catch Potential
FSR,	Fish Species Richness
gNPP,	global Net Primary Production
GR,	observations in the Geological Record
HE,	Hypoxia Effects
HypZ,	Hypoxic Zones
hNPP,	high latitude Net Primary Production
MAB,	Marine Air Breathers
MAE,	Macroorganism Effects
MC,	Microbial Concepts
ME,	Microbial Effects
OAE,	Ocean Acidifciation Effects
OCLTT,	Oxygen and Capacity Limited Thermal Tolerance
PO,	Polar Organisms affected
PP,	Plankton Phenology
PS,	Pacific Salmon
RWC,	Reef-building warm water corals
SAJ,	Sardine and Anchovies Japan Sea
SE,	Synergistic Effects
TE,	Temperature effects

Figure 6-18: Overview of the levels of confidence in detection (black letters), in both detection and projection (blue) as well as in projection only (red letters) of climate change effects on ocean systems, in relation to the levels of confidence in attributing these effects to the respective climate forcings. Areas where firm and detailed knowledge on climate change impacts is currently lacking have been condensed into rather broad categories in order not to overpopulate the figure (e.g. **BG**, Biogeochemical Processes). If a process is marked by blue letters, the levels of confidence are the same for both detection and projection in relation to that for attribution. Note that the term attribution is not only used in the context of detections but, in some cases, also for projections. Experiments (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 processes.]
[TO BE DEVELOPED FURTHER AFTER FOD, E.G., FOR THE DISTINCTION BETWEEN BROAD CATEGORIES AND SPECIFIC EXAMPLES IN TWO SUBFIGURES]