Chapter 6. Ocean Systems

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Executive Summary

[to be developed after ZOD]

6.1. Water Property Changes, including Temperature and Ocean Acidification

6.1.1. Present Day Observations and Projections

A primary role of the world's ocean in the global climate system is related to its capacity to store heat. The ocean has absorbed ~90% of the total increase in the heat content of the world (Bindoff *et al*., 2007). Over the last 43 years warming has been strongest at the sea surface (>0.1 °C/decade) and at high latitudes. Warming decreases with depth, at 0.017 °C/decade observed at 700m (WG1 Ch. 3). The consequence of the warming is intensified thermal stratification of the upper ocean, associated with a shallowing of the mixed water layer depth and hence increased light exposure of the phytoplankton that inhabit the mixed layer zone. Coastal regions display large spatial variability in their temperature changes. For example, observations over 100 years in 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 increments in several inland seas also result 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 different changes in salinity, from increases in salinity in evaporation-dominated subtropical gyres to freshening in precipitation-dominated regions, e.g. at high latitude. Warming and freshening cause a weakening of the formation of intermediate waters at high latitude and of the formation of abyssal waters in polar regions (WG1 Ch. 3). Reduced vertical mixing of stratified waters and the weakened lateral import of aerated waters from high latitudes into the deep in turn have the potential to reduce the oxygenation of mid water layers and the deep oceans. Human activity supplies excess nutrients and pollutants via river inflow and by precipitation, thereby exacerbating ocean hypoxia in the pelagic, on continental shelves and in coastal areas. The oceans serve as a large natural sink of anthropogenic CO_2, which in turn leads to ocean acidification (WG1 Ch. 3, 6). All global scale modelling experiments to date provide further evidence 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; Gruber, 2011) and suggest climate change impacts on ocean ecosystems (Brierley and Kingsford, 2009). Long established multidisciplinary time-series sites detect change in the biota and/or ecosystems shifts, and report comprehensive background physical, chemical and biological data to support attribution of changes to their causes including anthropogenic climate change (Gille, 2002; Dore *et al.*, 2009).

Changes in large-scale ocean mixing related to the ocean oscillation systems (Figure 6-1) cause changes in currents and the distribution of water masses, affecting primary producers, fish and invertebrates in surface to mid-water depths, through physical displacement but also through changes in environmental conditions. Among them, temperature governs the occurrence, diversity, development, reproduction, behaviour and phenology of marine organisms (Edwards and Richardson, 2004; Beaugrand *et al.*, 2009; Brierley and Kingsford, 2009). In the North Atlantic, approximately half the temperature variance 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). However, global warming likely 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 forcing. Furthermore, 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 covaried 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).

[INSERT FIGURE 6-1 HERE
Figure 6-1: Spatial distribution of inter-annual temperature variability during the 1911 to 2010 period. Extended sea surface temperature data (ERSST) are available as 2°x 2° boxed time series from the National Climatic Data Center (http://www.ncdc.noaa.gov/ersst/). Each series was annualized, detrended and standardized before the computation of spectral density (as a proxy for temperature variability). The lower panel shows the accumulated spectral density values for each of the 8036 valid boxes of the World Ocean (no land, no ice, latitudes between 60°S and 70°N). Each map corresponds to one of the peaks in the series, identified by a letter. The number below each letter corresponds to the centered period value (years). Color scales are arbitrary, indicating maximum (red) and minimum (light blue) spectral density values for each frequency window. A general pattern reveals lower frequency variability (a) occurs mostly in polar regions, the interdecadal (10 to 20 years; b,c,d) at mid latitudes, and the strong peaks at higher frequencies (f,h) in the tropics. However, there are also important differences between maps suggesting the participation of different mechanisms. For example, the two peaks typically associated to the ENSO variability (f and h) exhibit strong differences, with the low frequency component (5.6 years) present in the north and south Pacific and the Indian ocean, while the high frequency (3.5 years) is concentrated in the eastern tropical Pacific.]

Next to physical changes, the ocean's physicochemistry is also altered. At present the ocean absorbs 25% of the CO_2 emitted by human activity. Hydrographic surveys quantify this sink from atmospheric O_2/N_2 ratio measurements as 2.3±0.6 PgC/y for 2008, after 2.0±0.6 PgC/y for the period1993-2003. This matches the estimate of 2.3±0.6 PgC/y resulting from various models. The carbon sink is beneficial for reducing climate change, however, causes the process of ocean acidification (OA), which is the increase in acidity, i.e. hydrogen ion (H^+) concentration in seawater, measured as pH. Anthropogenic OA has started with industrial revolution and is projected to reach all oceanic regions, surface and deep oceans. OA has already led to detectable changes in surface ocean pCO_2 (given in μatm, 10^{-6} of atmospheric pressure, or the mole fraction in ppm (10^{-6}) of CO_2 in the humidified gas mixture used for equilibration) and increased acidity (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 most likely "business as usual" scenario. This change occurs on top of natural pH variability. The pH of the present day pelagic ocean varies by approximately an order of magnitude 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. OA involves 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 quantify the oversaturation of calcium carbonates in seawater (Ω is the ratio of products of in situ concentrations of calcium, Ca^{2+}, and CO_3^{2-} over the solubility products (SP) K^*_{SP} of $CaCO_3$ in aragonite or calcite, different mineralogical forms of carbonate at *in situ* temperature, salinity and pressure; $\Omega = [Ca^{2+}][CO_3^{2-}]/K^*_{SP}$). Calcite or aragonite are important components of shells or skeletons in many marine organisms. Ω is smaller for aragonite than calcite at a given carbonate ion concentration which results in aragonite being more soluble in acidified seawater. In parallel with the variabilities in pH and in other carbonate system parameters, 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). Distribution maps of aragonite saturation (Figure 6-2) produced by an ocean carbon model (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. Increasing atmospheric and surface ocean pCO_2 have already caused Ω to decrease to present levels of around 3 in tropical and lower than 1.5 in the polar oceans. 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 to elucidate the factors governing its variability (Dore *et al*., 2009). Disregard of the biotic feedbacks (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 6-2 HERE
Figure 6-2: 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. The CO_2 concentration in 2100 approximates around 850 ppm similar to RCP8.5 (Moss *et al*., 2010). 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).]

Scenarios of future atmospheric pCO_2 have been described by SRES and for several RCPs (representative concentration pathways), which include non-CO_2 green house gases and approximate very different atmospheric concentrations of CO_2 (Moss *et al*., 2010). RCP 2.6 follows increments to somewhat less than 500 ppm followed by a decrease, RCP 4.5 assumes stabilization at around 600 ppm, RCP 6.0 at around 800 ppm, and RCP 8.5 at more than 1200 ppm.

Large-scale fluctuations of ocean oxygen concentrations have occurred over deep 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 diurnal time scales (Grantham *et al*., 2004; Connolly *et al*., 2010). Anthropogenic "dead zones" characterized by long-lasting extreme hypoxia, largely constrain metazoan life (Diaz and Rosenberg, 2008). Oxygen minimum zones (OMZs) associated with hypoxia at O_2<0.5 ml/l (~22 μ mol/l) occupy nearly 30x10^6 km^2 (102x10^6 km^3) in the open ocean (Paulmier and Ruiz-Pino, 2009), including about 1,15x10^6 km^2 on bathyal continental margins (Helly and Levin, 2004) and 245,000 km^2 in coastal waters (Diaz and Rosenberg, 2008). Seasonal or permanent OMZs are 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). In areas where oxygen levels fall to very low levels, hydrogen sulphide is formed by bacterial activity. 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 in many regions is expected to show an increase of up to 70% by the end of the century (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 discharges, as well as the warming of the ocean, will enhance the vertical density stratification in some regions and hence reduce the ventilation of subsurface layers. On the other hand, a number of poorly ventilated regions 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 winter convection 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).

6.1.2. Historical and Palaeo- Oceanography and Biological Impacts

The fossil record has the potential to reveal biotic responses to past episodes of global warming, as well as changes in ocean stratification, nutrient distribution and pH. Fossils, however, preserve only a small part of original ecosystems, with a bias towards skeletal organisms from stable, low-energy aquatic environments. As well, care must be taken when identifying appropriate past analogues for future environmental changes. For example, for much of Earth history, atmospheric CO_2 was higher than any level predicted for the next century. That marine biotas, including calcified organisms, thrived through most of this history has been taken to suggest that marine ecosystems will not be impaired in a future warm, high CO_2 world. However, such comparisons are invalid because the environmental issues of the 21st century are issues of rate, not simply magnitude. Long-term, high CO_2 steady states of the past had a well regulated carbonate saturation state, whereas the current anthropogenic perturbation represents a transient event, at least for time scales relevant to coming centuries (Zeebe and Ridgwell, 2011).

Historical datasets of long-lived organisms and high resolution sediment cores covering the last 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, Pacific Decadal Oscillation [PDO] or the El Niño-Southern Oscillation [ENSO]) but also a recent warming of the surface ocean (WGI, Palaeoclimate, chapter 6.1.1.). Many examples highlight the influence of associated changes in environmental variables like temperature and food availability on organisms and ecosystems for example range expansions of plankton, diachrony in phenology of different components of the ecosystem and calcification changes of macrobenthos (Figure 6-3, Chapters 6.2, 6.3).

[INSERT FIGURE 6-3 HERE
Figure 6-3: Atmospheric CO_2 (bottom) and temperature (middle) changes with associated biotic changes (top) for (from left to right) the industrial era, the last glacial to Holocene transition and the Pliocene warm period. Intervals of largest environmental change are indicated with brown bars. CO_2 data is based on measurements at Mauna Loa (Keeling *et al.*, 2009), ice core records from Antarctica (Etheridge *et al.*, 1998; Monnin *et al.*, 2004) and proxy reconstructions (Seki *et al.*, 2010). Temperature data is based on proxy data and models (Wilson *et al.*, 2006, [tropical ocean]; Lea *et al.*, 2003, [Caribbean]; Lawrence *et al.*, 2009, [North Atlantic]) 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 coralline algae growth increment changes (Halfar *et al.*, 2011), coral calcification as a product of density and linear extension (De'ath *et al.*, 2009) and foraminiferal weight (Barker and Elderfield, 2002). Evolutionary turnover of coccolithophores is defined as the sum of first and last appearances per 10 kyrs (Gibbs *et al.*, 2005). Abundance data of planktic foraminifers (Field *et al.*, 2006, [St. Barbara Basin]; Thornalley *et al.*, 2011, [North Atlantic]; Dowsett *et al.*, 1988; Dowsett and Robinson, 2006, [North Atlantic]) indicates the temperature change and consequent range expansion or retraction in all three time intervals.]

Biotic changes have also accompanied larger scale climate changes associated with the growth and decay of continental ice sheets over the past three million years. Foraminifers, coccolithophores, diatoms, dinoflagellates and radiolarians all showed marked range expansion during the last glacial-interglacial transition with warm water species increasing their abundances in higher latitudes associated with the warming (CLIMAP Project Members, 1976; MARGO Project Members, 2009; Figure 6-3). The glacial interglacial transition is associated with an increase in atmospheric CO_2 of around ~0.02 μatm/year on average over the transition and hence significantly slower than the current increase by 1 μatm/year on average over the last 100 years. Consequently, the resultant pH change of 0.002 pH units per 100 years is small and low to be comparable to the ongoing anthropogenic perturbation of >0.1 pH unit per 100 years. Lower CO_2 levels during the glacial interval led to higher carbonate saturation and increased calcification in planktic foraminifers, with a shell weight increase of 40-50% (Barker and Elderfield, 2002); no significant extinction or originations in plankton are associated with the glacial-interglacial transition (Lourens *et al.*, 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, Ma=mega-annum, geological age), with temperatures +2.4 to +2.9°C warmer than today (Haywood *et al.*, 2009) and atmospheric CO_2 levels between 330-400 μatm (Pagani *et al.*, 2010; Seki *et al.*, 2010). The ecological reflection of the warmth includes a migration of tropical calcifying plankton species towards the poles (Dowsett, 2007); however, no increased extinction compared to background values has been associated with Pliocene warmth or early Pleistocene cooling for coccolithophores (Bown *et al.*, 2004; Figure 6-3), corals (Jackson and Johnson, 2000) or molluscs (Vermeij and Petuch, 1986).

Understanding future oceans requires that we analyze moments in the past when environmental change occurred at rates comparable to today's. Perhaps the best analogue is the Paleocene-Eocene thermal maximum (PETM), 55 million years ago, though model simulations for the future show higher rates of environmental change at the surface than during the PETM (Ridgwell and Schmidt, 2010). 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 (Ridgwell and Schmidt, 2010) and a reduction in surface ocean aragonite saturation from $\Omega=3$ to $\Omega=2$ or even 1.5. Rapid global warming drove migration of warm-water planktic taxa towards higher latitudes. 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 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 (~50%, Thomas, 2007) and a major change in ichnofossils indicates turnover and replacements in the macrobenthic community (Rodríguez-Tovar *et al.*, 2011). However, 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 (6.3.2.) makes the attribution of a cause of this extinction difficult, though similar synergies are expected for the future (6.1.1). In contrast to sediment dwellers, ostracods do not show any significant turnover (Webb *et al.*, 2009). On the shelves, calcareous red algae and corals declined markedly and were replaced by larger benthic foraminifers (Scheibner and Speijer, 2008) suggesting that the combination of warming and acidification had a major impact on reef builders despite the smaller rates of change compared to the future.

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 recognisable 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 (normalised sum of originations and extinctions) of the marine fossilised plankton (an average of 30% for planktic 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. 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 true ecosystem collapse in the oceans, we need to expand into the deep historical record of the past five hundred million years. 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 million years ago fits the biological predictions of global change induced by rapid influx of 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 Myrs long reef gap. The scale of end-Permian biological collapse was greater than any predictions for coming centuries, but it underscores the vulnerability of marine life to environmental perturbation as well as the heterogeneous nature of responses among organisms of differing anatomy, physiology and ecology.

We can deduce from the geological record that the rate and magnitude of modern ocean acidification and warming appears to be unparalleled in Earth history highlighting the magnitude and scale of the current environmental change. As these smaller events in the geological history led to compositional changes in faunas and floras and in some cased to extinction, the geological record puts constraints on possible changes in ecosystems and their services in the future (6.4).

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

6.2.1. Ocean Characteristics

The ocean covers 71% of Earth's surface to an average depth of 3,800 m and contains more than 95% of the habitable space for life. Approximately one-half of total annual planetary production of organic matter derives from the marine environment (Field *et al*., 1998). Marine photosynthesis is supported by taxonomically diverse microscopic phytoplankton. Phytoplankton carbon production is coupled to the downward flux of particulate matter, and respiration links atmospheric carbon dioxide to the much larger reservoir of dissolved inorganic carbon in the deep sea (38.100 PgC versus <700 PgC in DIC in surface ocean). These processes comprise the biological carbon pump, which is variable in time and space over the global ocean.

Ecological processes in the oceans have been studied for more than a century, yet many features including photosynthesis, respiration, and carbon storage are grossly undersampled. Many oceanic regions even have never been sampled and in those regions studied most extensively, for example the North Atlantic Ocean, temporal variability is poorly understood as, in general, long-term ecological studies in the open sea are rare.

Physical and chemical variables shape ecosystems distinguished by their modes of energy capture and transfer to organisms in the food web, as well as community succession that optimize material transfer and cycling. The ocean is simply too large for direct observation and assessments of most relevant properties and processes at global scale so models are essential. The definition of a minimal set of functional subunits (ecosystems with a unique set of habitat conditions and controls) 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." This 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.

6.2.1.1. Life in the Sea, Foodwebs

All living organisms on Earth can be placed into one of three main phylogenic categories: archaea, bacteria or eukarya. Viruses have no means for independent metabolism or self-reproduction so are not technically part of the pool of marine life even though they play an otherwise important role in population dynamics and evolution. Archaea and bacteria are exclusively single-celled and microscopic. They share many characteristics including the fact that they contain no intracellular organelles (sometimes referred to collectively as 'prokaryotes' to distinguish them from the eukaryotes), but also have many key distinguishing characteristics as well. Most eukarya are also single-celled and microscopic, but this group also includes all of the more familiar macroscopic marine plants, invertebrates and vertebrates. Therefore the term 'microbe' is not very informative other than to make a statement about physical size. Typically a threshold of approximately 100 micrometers is used as the upper size limit for microorganisms. Although they are invisible and easy to overlook, marine microbes are the dominant contributors to biomass, metabolism (production/respiration) and biodiversity in all marine ecosystems.

Classification of marine life can use any of a number of different criteria including phylogenetic (evolutionary), biogeographical or trophic (feeding) relationships. For many ecological studies, it is desirable to classify organisms in terms of their metabolic characteristics. Traditionally, marine organisms were considered to be either autotrophic or heterotrophic depending upon whether their survival was dependent upon preformed organic matter (i.e., heterotrophic) or not. This led to the commonly used terms bacteria, phytoplankton/plants and animals (including zooplankton, invertebrates, fish and marine mammals). However, it is now apparent that microbes have much more complex modes of metabolism and that many 'bacteria' are more 'plant-like' than 'animal-like.' Indeed the two most abundant groups of marine phytoplankton, *Synechococcus* and *Procholorcoccus*, are actually bacteria not algae, a term reserved for the eukaryotic phytoplankton. Because the flow of carbon and energy in the sea is a fundamental consideration in ecology and oceanography, we need a more accurate assessment of metabolism. Explicit assignments can be made 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 carbon dioxide (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 lifestyles including those with mixed or hybrid metabolisms are also possible and, at least for microorganisms, may be the most common pathways 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).]

In marine food chains carbon and energy are systematically transferred from tiny phytoplankton to large predators, each step of the transformation being a trophic or feeding level. Because there is a significant loss of energy with each transformation, the number of trophic levels in a given ecosystem determines the overall efficiency of transfer to the top level. In marine ecosystems, large fish such as tuna are at the top of the trophic pyramid. Ecosystems that select for large phytoplankton and short (at most 3-4 trophic levels) food chains (e.g., coastal upwelling systems) support the largest and most productive fisheries in the global ocean. If upwelling ceased, the entire trophic structure would be altered and fish production would be greatly impacted. In reality, most marine ecosystems contain species that consume food at more than one trophic level, and have young that feed on different diets than the adults. This leads to a complex, often stabilizing structure known as a food web where carbon and energy flows can 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 certainty, though, decreased photosynthesis rates will lead to a reduction in the amount of energy dissipated through the food web and a decrease in the biomass of top level predators, including fish.

6.2.1.2. Major Pelagic Biomes and Ecosystems

An ocean biome is a time- and space-variable habitat, controlled by a complex interaction of physical processes. Both short- (seasonal) and long-term (millennia) variations in habitat characteristics select for the proliferation of diverse plant, animal, and microbial communities. Physical forcing controls nutrient input, subsequent growth of phytoplankton and the composition and efficiency of the food web. Physical attributes can be used to predict biogeochemical processes including carbon cycle dynamics. Two well established physical-biological coupling paradigms in marine plankton ecology are (1) Sverdrup's critical depth model describing the interactions of relationships between stratification, nutrients, light, and primary production (Sverdrup, 1953) and (2) Margalef's "mandala" describing the relationships between turbulence, nutrient delivery, and phytoplankton species succession (Margalef, 1978; Figure 6-4).

[INSERT FIGURE 6-4 HERE
Figure 6-4: Climate impacts on phytoplankton succession. Margalef's Mandala (Margalef, 1978; Margalef *et al.*, 1979) with additions on harmful algal blooms (Cullen *et al.*, 2007) described in a simplified framework of how the phytoplankton community structure changes in relationship to turbulence and nutrients, factors which have a strong

influence on phytoplankton reproduction and competitiveness. This model provides no quantitative predictions, but it is generally consistent with observation, experimentation, and theory (Kiørboe, 1993). As these factors are expected to vary with 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.]

Carbon fixation in the pelagic marine environment is controlled by light, inorganic nutrients (carbon dioxide, nitrate, phosphate), vertical mixing and temperature dependent stability of the upper portion of the water column, referred to as the mixed-layer depth (MLD). MLD establishes the mean position of the phytoplankton in the light field and thereby controls the rate of photosynthesis under nutrient replete growth conditions. 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.

Division of the ocean into discrete functional units would support tracking time-dependent changes in key processes and carbon inventories. Odum (1971) defined a biome as “the largest community unit which is convenient to recognize.” Longhurst (1998) defined four major ocean biomes: (1) *Westerlies*, where MLD is forced by local winds and heating, (2) *Trades*, where MLD is forced by geostrophic adjustment on ocean basin scale and remote winds, (3) *Polar*, where MLD is influenced by ice formation and ablation, and (4) *Coastal*, where MLD is forced by a variety of local processes. Using archived NOAA-NODC data sets Longhurst (1998) further subdivided these 4 major ocean biomes in each major ocean basin into a total of 51 provinces based on a comprehensive assessment of satellite-derived ocean colour data, global climatologies of temperature-derived MLD, Brunt- Vaisälä frequency analysis of density profiles along both zonal and meridional oceanographic sections, Rossby internal radius of deformation, photic zone depth based on light field and chlorophyll concentrations, and surface nutrient climatologies (Figure 6-5). In addition to pelagic provinces there are innumerable coastal habitats to consider, as well as marginal and inland seas. Near-shore habitats tend to be smaller and more well-defined functional units, and more variable in time and space than those in the pelagic realm. These ecosystems as well as inland and marginal seas need to be assessed on a region-specific basis (Ch. 30) when considering the role of the ocean as a whole. For the most accurate baseline data and global assessment of the state of the ocean and its sensitivity to change, it would be desirable to have long-term observatories in each of these pelagic provinces and in up to 100 or more key coastal and inland habitats. However, absent this comprehensive measurement program we need an alternate plan for a contemporary assessment. A number of distinguishing characteristics (Table 6-2) 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, and 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 FIGURE 6-5 HERE
Figure 6-5: Productivity in 51 distinct global ocean biogeographical provinces as represented by a grid of thin black lines (after Longhurst, 1998), overlaid with an annual composite plot of ocean colour, i.e. a proxy for phytoplankton stocks in the upper ocean) from the NASA/Orbimage SeaWiFs satellite. These provinces or biomes span several orders of magnitude in phytoplankton stocks from < 0.1 mg m^{-3} in the low latitude oligotrophic regions (denoted by purple and blue) to 1-10 mg m^{-3} in coastal upwelling regions in Eastern boundary currents (denoted by red).]

[INSERT TABLE 6-2 HERE
Table 6-2: Physical, chemical, and biological characteristics of major ocean ecosystems.]

6.2.1.3. Benthic Habitats and Ecosystems

The benthos includes all organisms, which live closely above, on or in the marine sediment. 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. They are classified by their size (mega-, macro-, meio-, microbenthos), their mode of energy supply (auto-, mixo-, heterotrophic) 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, for example, subtidal sand, deep-sea clay, anoxic-sulphidic mudflat, cold and warm water coral reefs, mangroves, saltmarshes or hydrothermal vents. Benthic habitats have also been classified based on total benthic organism biomass.

UNESCO (2009) used geophysical and environmental characteristics of benthic and pelagic environments to identify homogeneous regions of similar habitat and associated biological community characteristics. Benthic habitats are also spatially complex with steep chemical gradients and small-scale heterogeneity in physical and chemical characteristics. This leads to non-random distributions of plants, animals and microbes, and makes it very difficult to reliably sample, map, classify or scale any limited observations on the benthic ecosystem as a whole (UNESCO, 2009). Structuring criteria used are depths, depth range, seamounts and ridges, and surrounding sea floors. Communities are structured according to hard and sediment substrates as well as hydrographic eddies and flows. Further distinctions are regional, encompassing lower Bathyal provinces, Abyssal provinces, Hadal provinces, where hydrothermal vent provinces occur mostly at ocean ridges.

Benthic communities differ in their functional characteristics and demand for energy input, partly depending on the prevailing climate regime (6.2.2.). Jahnke (1996) proposed the use of sedimentary oxygen flux estimates as a means to classify benthic habitats. Because organic matter does not generally accumulate in deep sea sediments, total sedimentary oxygen demand for metabolism correlates with the rain rate of organic matter.

Benthic ecosystems are inherently intertwined with the pelagic realm. Therefore, benthic organisms and communities will be directly and indirectly affected by climate change. Benthic habitats, even those that exist in permanently dark regions of the deep sea, are connected to surface sunlit habitats by the gravitational settling of photosynthetically derived organic matter (Pfannkuche and Lochte, 1993). 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 and other microorganisms abound in all benthic habitats and 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).

Many benthic ecosystems are characterized by a high productivity (see coastal chapter) 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).

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

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 observed changes to relevant factors and processes often remains uncertain. Environmental variables influence various levels of biological organisation, molecule to whole organism and ecosystem. Changes in community composition and species interactions often build on organismal effects elicited by physical forcing (Pörtner and Farrell, 2008; Ottersen *et al.*, 2010). Knowledge on how these various levels are intertwined is a major prerequisite for more reliable predictions on the future of marine ecosystems. Previous efforts were successful in attributing field-observed ecosystem change or elements thereof to temperature or hypoxia effects. In contrast, attribution of on-going ecosystem change or elements thereof to anthropogenic ocean acidification has not (yet) been made compellingly. All factors exert specific effects, and may act synergistically or antagonistically with others. Temperature and hypoxia effects are accelerated through oscillations between seasonal or even diurnal extremes. In contrast, OA develops progressively, but adds CO_2 to pre-existing CO_2 levels. These may be elevated or variable as in oxygen deficient sediments and water layers, including upwelling systems (Feely *et al.*, 2008).

6.2.2.1. Microbes and Phytoplankton

The ocean contributes about half of global net primary production, largely due to photosynthesis by marine microorganisms (Field *et al.*, 1998). Microorganisms including phytoplankton, bacteria, archaea, protozoa and viruses are also responsible for nutrient cycling and, overall, net ecosystem productivity. 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 substrates 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 modelling. A wide range of environmental triggers, including temperature, light climate, pH and nutrient supply (see below), were identified which cause the distribution of 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).

6.2.2.1.1. Temperature – physiology and thermal tolerance

A warming ocean may stimulate the metabolic rates of microbes (Eppley, 1972) and also 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. Modelling studies point to the pivotal biogeochemical role that temperature sensitivity could play in ocean ecosystems by changing the composition of microbial foodwebs, and advocate a better understanding of such sensitivities (Taucher and Oschlies, 2011). There is evidence that heterotrophic bacteria are more responsive to warming than phytoplankton and hence there may be a non-linear ecological response to warming, i.e. greater stimulation of bacterial rate processes relative to that for phytoplankton, within upper ocean foodwebs (Riebesell *et al.*, 2009). There is some evidence to support the model projections. For example, coccolithophores in the NE Atlantic, displayed no change in physiological rates with higher temperatures (Feng *et al.*, 2009). Ocean time-series data, such as the Continuous Plankton Recorder survey also 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).

6.2.2.1.2. Irradiance – incident and underwater

All climate change modelling 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 thinner shallower surface mixed layer in which they will encounter higher mean irradiances. The physiological response of phytoplankton to higher irradiances (photo-acclimation) relies upon acclimation of cellular chlorophyll (Falkowski and Raven, 1997), which is however constrained by unidentified limits to its plasticity (Falkowski and Raven, 1997). Long-established oceanic time-series indicate, however, that the only pronounced changes to phytoplankton processes related to irradiance globally have resulted from reduced sea-ice cover rather than from shallower mixed layers. This is again illustrated by the finding of unchanged phenology of the diatom spring bloom in the North Sea (6.2.2.1.1.). In contrast, an intensified growing season, due to reduced sea-ice cover may increase productivity (based on a time-series of satellite ocean colour and a primary productivity algorithm) in Arctic waters by up to 27.5 Tg C yr^{-1} (mean) since 2003 (Arrigo *et al*., 2010). 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 increases in these properties to the S of 63°S. Montes-Hugo *et al*. (2009) 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.

6.2.2.1.3. Stratification – nutrients and trace element supply

All climate change modelling experiments to date also predict increased density stratification of the upper ocean (Sarmiento *et al*., 1998), which reduces vertical nutrient and/or trace metal supply into surface waters and hence leads to reduced primary productivity (Boyd and Abraham, 2001). Data from satellite archives of ocean colour (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 reduced 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). Polovina *et al*. (2008) reported 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, likely due to a warming ocean. 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, putatively characterised by higher levels of carbon dioxide, and lower concentrations of nutrients and trace metals (Boyd *et al*., 2010) microorganisms (including bacteria and archaea) may thrive which are capable to convert the relatively inert nitrogen gas (N_2) into biologically available ammonia (referred to as N_2 fixing microorganisms).

6.2.2.1.4. Ocean acidification: CO_2 and pH shifts

Physiological effects of ocean acidification may differ between phytoplankton groups (Dore *et al*., 2009). Whether higher carbon dioxide concentrations lead to fertilization of phytoplankton processes may depend on how they acquire carbon (i.e. presence or not 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*) had CCM's (Tortell *et al*., 2008a). OA may have the greatest potential effect on calcifying phytoplankton species – the coccolithophores. High carbon dioxide treatments of several species led to initial evidence for misshapen calcite liths (Riebesell *et al*., 2000). CO_2 was identified as the parameter of the carbonate system, which causes both aberrant morphogenesis in the coccolith *Calcidiscus leptoporus* and, at levels higher than 1500 μatm, aggregation of cells (Langer and Bode, 2011). Recent manipulation studies on various coccolithophores have revealed species specific (in *Calcidiscus leptoporus, Coccolithus pelagicus*, Langer *et al*., 2006) and strain-specific (in *Emiliana huxleyi*, Langer *et al*., 2009) responses of calcification to OA. Hence, responses to OA may vary considerably between species and even populations.

6.2.2.1.5. *Bacterial life in hypoxia and anoxia: formation of oxygen minimum zones (OMZ)*

Whereas most marine organisms have an absolute requirement for dissolved oxygen to sustain metabolism, many bacteria can live, indeed thrive, in the total absence of free oxygen. Marine bacteria survive in the absence of oxygen by one of two major biochemical strategies, the use of alternate terminal acceptors for electrons and anaerobic respiration, or the use of oxidizable organic substrate both as a source and a sink for electrons (fermentation). Both anaerobic metabolism and fermentation yield less energy per mole of substrate than aerobic (oxygen-based) metabolism: in the case of fermentation the yields are generally an order of magnitude less. However, both metabolic strategies allow a broad range of marine bacteria to live permanently in habitats that are completely devoid of free of oxygen.

At depleted oxygen concentrations bacteria capable of using alternate electron acceptors are selected for and multiply, mostly those using the most energetically favourable alternate form, nitrate. When nitrate concentrations are depleted, other less favourable 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 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 $p\mathrm{CO}_2$. OMZs are therefore a consequence of high nutrient loading or restricted water movement, or both. In effect, 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 thermohaline circulation becomes more sluggish (6.3.2.).

Since many end products of anaerobic respiration are highly reduced (ammonia, reduced iron/manganese, sulphide, methane) and contain biologically useful potential energy, other specialized bacteria can oxidize them when oxygen is introduced or when the reduced compounds migrate to interfaces surrounding the OMZs. This establishes new ecological niches where chemolithoautotrophic bacteria can fix carbon dioxide in the absence of light using the potential energy in one or more of the reduced inorganic compounds that were generated during anaerobic metabolism. It also creates an ‘oxygen debt’ within the OMZ that serves to remove any excess free oxygen that may be introduced thereby preserving the OMZ as a bacterial reactor.

6.2.2.2. Macrophytes

Although marine macrophytes (macroalgae and seagrasses) 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 play an important trophic role for many suspension feeders, detritivores and herbivores. Moreover, they provide habitat structure and protection for macrofauna and their offspring. Additionally, macrophytes are important in industry for the production of food and phycocolloides.

6.2.2.2.1. Macrophytes and temperature

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). 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). Temperature acclimatization 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 requires further study.

6.2.2.2.2. Macrophytes under ocean acidification

Most seagrasses appear limited by the availability of CO_2. Their rate of primary production, shoot density, reproductive output and/or below-ground biomass generally respond positively to elevated pCO_2; effects were identified 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 these habitats 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 calcification remains highly impacted beyond species-specific limits of pCO_2 (Anthony *et al.*, 2008; Ries *et al.*, 2009). 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. In general, the recruitment rate and growth of crustose coralline algae are severely inhibited and carbonate dissolution stimulated, especially under combined scenarios of warming and elevated pCO_2 (Kuffner *et al.*, 2007), at about 700 μatm in an experimental study (Martin and Gattuso, 2009).

6.2.2.3. Animals

The distribution, abundance and population dynamics of marine fishes and invertebrates follow climate change and variability according to climatic indices (6.1.2.). However, a detailed understanding of contributing factors and drivers is frequently lacking. Climate change affects individual organisms, populations and communities as well as species interactions and the food web. Empirical and mechanistic studies have identified unifying principles defining sensitivity at various levels of biological organisation, which should improve certainty in the projection of future change (Pörtner, 2002a; Somero, 2011).

6.2.2.3.1. Performance and fitness in various climates

Marine ecosystem changes attributed to climate change (Hoegh-Guldberg and Bruno, 2010) have mostly been related to temperature, with temperature extremes rather than means as mediators of effects (Easterling *et al.*, 2000; Grebmeier *et al.*, 2006; Pörtner and Knust, 2007; Wethey *et al.*, 2011). Temperature dependent fitness indicators like growth, exercise capacity or reproductive output delineate the window of temperature dependent performance and its limitation. For water breathing animals the concept of oxygen and capacity limited thermal tolerance (OCLTT) provides access to the mechanistic underpinning of such changes, by integrating findings at various, molecular to whole organism and ecosystem levels of biological organisation (Pörtner, 2001; 2002a). This overarching concept explains the shape of thermal performance curves (also called reaction norms; Huey and Kingsolver, 1989; Deutsch *et al.*, 2008; Angilletta, 2009) and the temperature range they cover in relation to the climate regime (Figure 6-6). Functional capacities of tissues and the whole organism together with oxygen availability for aerobic energy turnover define the level of performance capacity and its sensitivity to temperature change. Such thermal specialization results from the need to minimize energy turnover, which in turn causes an earlier loss in performance capacity at extreme temperatures, transition to time limited tolerance and unfavourable shifts in energy allocation and thereby, a narrowing of thermal windows (Pörtner *et al.*, 2010). Such a narrowing also results with increasing body size when oxygen supply limitations are exacerbated causing heat tolerance limits to fall (Pörtner *et al.*, 2008). Conversely, these principles contribute to explaining the overall reduction of body sizes observed in warming aquatic communities (Daufresne *et al.*, 2009). Finally, a reduction in growth, activity and abundance of fish and invertebrate populations results near biogeographical limits (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) lead to shifts of biogeographical ranges to high latitudes (Graham and Harrod, 2009). At an ecosystem level, OCLTT related performance shifts are also projected to underlie changing interactions of species with differential thermal sensitivities, as well as changing phenologies, the seasonal timing of biological processes (Pörtner and Farrell, 2008). As a result, mismatch with available prey organisms may become critical, again causing losses in abundance or local extinction implicating a biogeographical shift (Figure 6-6; Beaugrand, 2009). The OCLTT concept also integrates the (limited) capacity of molecular to organismal mechanisms to shift thermal windows. This occurs short-term through acclimatization of the individual and long-term through evolutionary adaptation over generations (Pörtner *et al.*, 2008; Eliason *et al.*, 2011) involving adjustments in enzyme quantities, their functional properties and the fluidity of membranes. Palaeo-studies have successfully adopted these principles 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). Overall, the OCLTT concept provides an integrative understanding of climate sensitivity in marine animals. Certainty is enhanced when explaining organism level specialization and sensitivity to climate. However, while thermal performance curves may be unifying between organisms (6.2.2.1., 6.2.2.2.; Chevin *et al.*, 2010), their mechanistic underpinning likely differs and has not been systematically explored in microbes and plants. Furthermore, such principles require integration into ecosystem level approaches.

[INSERT FIGURE 6-6 HERE
Figure 6-6: Mechanisms linking organism to ecosystem response (A) Concept of oxygen and capacity limited thermal tolerance (OCLTT) characterizing the specialization of animals on limited thermal windows set by (aerobic) performance capacity (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. Pejus temperatures (T_p) indicate limits to long-term tolerance, critical temperatures (T_c) the borders of short-term passive tolerance and transition to anaerobic metabolism (after Pörtner and Farrell, 2008, and Pörtner, 2010). 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. 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) (A, C). Applicability of such reaction norms to other organisms (phytoplankton, macroalgae, bacteria) is likely. Temperature-dependent performance forms the basis of shifts in phenologies, namely the seasonal timing of biological processes, of changes in species co-existence ranges and interactions as well as in biogeography during climate warming (D). Here, the black line surrounding the polygon limits 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 (modified after Beaugrand, 2009).]

6.2.2.3.2. Hypoxia effects at various temperatures, sulphide tolerance

Expanding oxygen minimum zones (OMZ) and enhanced formation of anoxic dead zones (6.3.2.) represent the decreasing oxygenation of the world's oceans and emphasize the need to understand hypoxia sensitivity of marine organisms. The OCLLT concept allows adding further stressors towards an understanding of their synergistic ecosystem effects. It predicts that hypoxia, i.e. oxygen partial pressure ($P\text{O}_2$) in the water falling below air saturation, reduces the tolerance to temperature extremes. In other words, hypoxia supports an earlier onset of thermal stress, especially in warm oceans where oxygen solubility per unit of $P\mathrm{O}_2$ is less (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). Exposure to hypoxia constrains aerobic performance. Compensation by hypoxia acclimation leads to improved oxygen supply capacity in relation to demand, for example by enhancing blood pigment content or reducing energy demand. Heat tolerance is enhanced by hypoxia acclimation (Burleson and Silva, 2011).

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, defined as the $P\mathrm{O}_2$ at which an organism switches from aerobic to anaerobic energy production (Pörtner and Grieshaber, 1993). The P_c is specific for each life stage of a species and increases with growing body size (Pörtner, 2002b; Ekau *et al*., 2010; Seibel, 2011). It is found at higher values than those characterizing the thermodynamic limits to oxygen dependent metabolism (Brewer and Peltzer, 2009). The P_c varies dynamically with temperature, food consumption, oxygen demand and environmental stressors. On average, more active animals with high oxygen demands are the most sensitive to permanent hypoxia, for example fishes, crustaceans and muscular cephalopods. However, specialists adapted to hypoxia are also found in these groups (Childress and Seibel, 1998; Richards *et al*., 2009; Seibel, 2011).

Transient exposures to extreme hypoxia, e.g. when migrating into OMZ (Seibel, 2011), or even to anoxia are sustained by time-limited depression of metabolic rate as during periods of arrest (diapause; Auel *et al*., 2005). Time-limited exploitation of efficient anaerobic metabolic pathways (Grieshaber *et al*., 1994) may also occur at hypoxia below the P_c, complemented by mechanisms providing tolerance to elevated sulphide levels (Grieshaber and Völkel, 1998) or to oxidative stress (Lesser, 2006). 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).

In contrast, permanent life in the OMZ and associated hypoxia is only possible above P_c and relies on fully aerobic metabolism. Species are favoured 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). Cold temperature plays a key role in supporting 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. 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, hypoxia induced extinctions spare the specialists and cause a loss in biodiversity (Vaquer-Sunyer and Duarte, 2008).

[INSERT FIGURE 6-7 HERE
Figure 6-7: (OPTIONAL, TO BE DEVELOPED AFTER ZOD) Ranges of oxygen concentrations (and temperatures) covered by various groups of organisms (archaea to animals), reflecting a narrowing of life options with rising levels of organisational complexity.]

6.2.2.3.3. *Ocean acidification in various climates*

The mechanisms and processes responding 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). Meta-analyses indicate that among affected processes, the rate of calcification is most sensitive (Hendriks *et al*., 2010). However, changes in calcification rates vary largely between species, with some species enhancing calcification in the range of $p\mathrm{CO}_2$ up to 1000 μatm (Ries *et al*., 2009). Reduced calcification causes a weakening of calcified structures in some echinoderms, molluscs and, possibly, crustaceans (Kurihara and Shirayama, 2004; Arnold *et al*., 2009; Comeau *et al*., 2009; Lischka *et al*., 2011). In contrast, enhanced calcification yields stronger cuttlebones or otoliths in juvenile cuttlefish (cephalopods) and fishes (Gutowska *et al*., 2008; Checkley Jr *et al*., 2009; Munday *et al*., 2011a) with unclear effects on fitness. Enhanced calcification in brittle stars was paralleled by the degradation of muscle tissue (Wood *et al*., 2008), indicating an imbalance in energy budget.

Animal species exposed to OA scenarios showed variable responses, with either decrements in energy turnover elicited by reduced protein synthesis and growth (Langenbuch *et al*., 2006; Pörtner, 2008) or increments in energy turnover. The latter can increase resilience (Parker *et al*., 2011), or indicate excessive cost and imbalances, as in brittle stars (Wood *et al*., 2008). Conversely, observed CO_2 induced stimulation of growth (cf. Gooding *et al*., 2009; Munday *et al*., 2009b; Dupont *et al*., 2010) might involve enhanced energy efficiency. Further effects likely causing reduced fitness comprise depressed immune functions (Bibby *et al*., 2008) or reductions in the maturation of sexual glands (Kurihara *et al*., 2011), 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 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 disorientation (Munday *et al*., 2009c; Munday *et al*., 2010). Unrestrained food availability may support fitness and stress resistance (Gooding *et al*., 2009).

Meta-analyses have not been able to resolve for the diversity of species-specific responses (within and between phyla) or the existence of bottle-neck processes or life stages (Hendriks and Duarte, 2010; Hendriks *et al*., 2010). The development of an overarching concept comprehending CO_2 action and levels of sensitivity has not progressed as far as for temperature. Central elements of an existing concept (Figure 6-8) comprise CO_2 induced shifts in acid-base status of body fluid compartments and the capacity of acid-base regulation to withstand such shifts. Available evidence shows an unequivocal role for lowered blood pH in eliciting metabolic depression in muscle (Reipschläger and Pörtner, 1996; Vezzoli *et al*., 2004) or liver (hepatocytes; Langenbuch and Pörtner, 2003) of vertebrates and invertebrates. Reduced energy turnover involves reduced ion exchange (Pörtner *et al*., 2000) and 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; Kurihara *et al*., 2011) and, thereby, causes slower growth (Michaelidis *et al*., 2005). Processes also affected through these mechanisms may include gonad maturation (Kurihara *et al*., 2011), egg fertilisation (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) or the immune response (Boyd and Burnett, 1999) and exercise performance (Pörtner, 2002b). Compensation of acid-base disturbances by stimulated ion exchange and associated base accumulation likely maintains performance capacity but may cause over-compensated calcification rates (see above). The metabolic cost involved in compensation may balance metabolic depression in some tissues and turn into metabolic stimulation. This may be beneficial for resistance or detrimental once imbalances between functions arise (Wood *et al*., 2008; Beniash *et al*., 2010; Thomsen and Melzner, 2010; Parker *et al*., 2011).

[INSERT FIGURE 6-8 HERE

Figure 6-8: (A) Unifying physiological principles characterizing the responses of a schematized marine water breathing animal (dashed blue line) sensitive to ocean acidification (OA), mediated via entry of CO_2 (black arrows) 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). In less sensitive species, pH compensation would occur extracellularly and/or 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). (B) % fraction of studied molluscan, echinoderm, crustacean and fish species affected negatively, positively or not at all by various levels of elevated ambient CO_2. Effects considered include those on various life stages and processes reflecting changes in physiological performance (oxygen consumption, aerobic scope, calcification, growth, immune response, maintenance of acid-base balance, fertilization rate, sperm motility, developmental time, production of viable offspring, morphology). Behavioural effects have not been widely studied and thus not considered in this comparative analysis. Also, 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 (Literature base in online supplementary material).]

While enhanced resistance implies avoiding CO$_2$ induced metabolic depression at tissue and organism levels (Pörtner *et al*., 2004; Thomsen and Melzner, 2010) the unifying validity of this hypothesis remains to be established. Mechanisms supporting resilience (and likely the resulting performance and fitness levels) are subject to acclimatization when exposed to elevated CO$_2$ partial pressures. Proteins involved in ion and acid-base regulation undergo gene expression changes as seen in echinoderm larvae (Martin *et al*., 2011), or in fishes exposed medium-term (up to six weeks) to elevated CO$_2$ levels (Deigweiher *et al*., 2008). 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.

A preliminary assessment of fragmented information on species sensitivities available in the present literature suggests that, on average, echinoderms and the molluscan bivalves and gastropods begin to respond negatively at lower CO$_2$ levels than crustaceans, cephalopods or fishes, a sensitivity pattern resembling one observed during the Permian evolutionary crisis (Knoll *et al*., 2007; Knoll and Fischer, 2011; Figure 6-8). 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. Negative impact was found to accumulate from adults to larvae and from larvae to juveniles of a sea urchin (Dorey *et al*., 2011). Moulting success into the final larval stage was reduced in a crab (Walther *et al*., 2010). In an oyster species, however, enhanced resilience was carried over to offspring when parents were pre-exposed to elevated CO$_2$ levels (Parker *et al*., 2011). Imbalances between influenced processes may arise. 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 (Munday *et al*., 2010). It remains to be explored whether and to what extent species can undergo adaptation to progressive ocean acidification over generations.

Comparisons across phyla suggest with medium certainty that sensitivity to progressive OA is low in more active marine animals with sophisticated regulation of body functions like ion and acid-base status, especially fishes and cephalopods, and also crustaceans including copepods (Ishimatsu *et al*., 2008; Melzner *et al*., 2009; Ishimatsu and Dissanayake, 2010; Pörtner *et al*., 2011). Within ecosystems and phyla, higher sensitivities to OA may therefore be associated with low metabolic rates and functional capacities.

Climate zone and variability also shape energy turnover and functional capacities (cf. Pörtner, 2006), likely co-defining resistance. Polar calcifiers and cold-water corals (Maier *et al*., 2009), which display low rates of metabolism and are exposed to high CO$_2$ solubility and lowered aragonite and calcite saturation levels, appear more sensitive to ocean acidification scenarios (Orr *et al*., 2005) but may have evolved some resilience (cf. 6.3.5.2.). Animals from cold polar waters or the deep sea (crustaceans, Pane and Barry, 2007; bivalves, Stark *et al.,* to come) in fact are poorly able to compensate for the extracellular acidosis. However, fitness-related functions like growth, development and reproduction are highly delayed in the cold, especially the most cold adapted marine ectotherms, Antarctic fish and invertebrates (Stanwell-Smith and Peck, 1998; Pörtner, 2006). At present, it remains uncertain whether CO$_2$ effects or their compensation may take longer to develop, due to extended acclimatization periods. It is also uncertain whether adaptation to elevated CO$_2$ solubility has occurred during evolution and supports resilience in species endemic to cold waters and further areas characterized by high CO$_2$ concentrations, possibly including reduced reliance on the strength of calcified structures (Clark *et al*., 2009; Lamare *et al*., 2011; Walther *et al*., 2011).

CO$_2$ accumulation coincides with hypoxia in OMZs and other oxygen deficient habitats and with water column depth everywhere in the ocean. These changes also combine with the warming trend. In some cases, compensation for the CO$_2$ induced disturbance of growth and calcification can benefit from warming (Brennand *et al*., 2010; Findlay *et al*., 2010; Walther *et al*., 2011). This can easily be explained if CO$_2$ exposure has occurred at temperatures below the thermal optimum. Stimulation of physiological processes by warming may then enhance

CO_2 resistance, possibly supported by enhanced energy efficiency and linked to enhanced feeding (Gooding *et al.*, 2009). In contrast, sensitivity to CO_2 may be exacerbated at higher than optimum temperatures, when warming under elevated CO_2 levels results in lowered performance and resistance to heat (6.3.6.). A potentially higher CO_2 sensitivity was suggested for tropical coral reef fishes than for species from temperate regions (Pörtner *et al.*, 2011).

6.2.2.4. Conclusions

A comprehensive understanding of mechanisms responding to climate related environmental factors at ecosystem, whole organism, tissue, cell and molecular levels of biological organisation provides a solid foundation for more reliable interpretation and projection of climate change effects on ocean biology. The responses of various levels of biological organisation are intertwined with progressively rising sensitivities at increasing complexity levels (Pörtner, 2002a). Therefore, 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 far from complete for many organism groups.

6.3. Detection and Attribution from Organism to Ecosystem Level: Individual and Interactive Effects of Stressors

It is virtually certain that marine ecosystems respond to climate change, with examples found in all of the world's oceans. Beyond the study of mechanisms in experimental studies (6.2.2.) field and mesocosm observations contribute to identify sensitivities of ecosystems to climate related factors at the levels of organisms, populations and communities. Relevant abiotic factors involved in causing climate change impacts on marine ecosystems include rising temperature means and extremes (Hoegh-Guldberg and Bruno, 2010) and ocean acidification due to CO_2 enrichment from the atmosphere (Caldeira and Wickett, 2005; Orr *et al.*, 2005). Warming, stratification, wind driven upwelling and eutrophication cause the expansion of hypoxic or anoxic zones (Diaz and Rosenberg, 2008; Stramma *et al.*, 2008; Keeling *et al.*, 2010; Stramma *et al.*, 2010b), paralleled by an accumulation of CO_2 from the oxidation of organic material (Pelejero *et al.*, 2010) and, at extreme hypoxia, of ammonia and hydrogen sulphide (Gray *et al.*, 2002; Kump *et al.*, 2005; Chan *et al.*, 2008; Levin *et al.*, 2009). Nutrient quantities available from e.g. nutrient-rich deep waters directly dictate phytoplankton growth, plankton size and community and food web structures. Warming of the surface layers enhances stratification, especially during summers, but also during particularly warm winters, thereby limiting nutrient provision to spring phytoplankton blooms. Conversely, light availability to phytoplankton will increase due to shoaling of the upper mixed layer (Sarmiento *et al.*, 1998). Warming gyres and projections of enhanced stratification at low to mid latitudes may lead to a reduction in nutrient availability with presently unclear consequences for primary production (Polovina *et al.*, 2008; Doney, 2010). Ice melt or an excess of precipitation over evaporation cause salinity reductions (Jacobs and Giulivi, 2010; Vélez-Belchí *et al.*, 2010) and, thereby, enhanced stratification as well as an exacerbation of ocean acidification (Steinacher *et al.*, 2009; Denman *et al.*, 2011). Presently observed climate-induced changes in marine ecosystems (Hoegh-Guldberg and Bruno, 2010) support projections of impacts like: (i) changes in 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 frequency of events, (vi) changes in connectivity among populations and habitats, and (vii) increased propensity for change, including increased frequency and severity of waterborne diseases.

Climate change not only involves the concomitant change of various stressors, but also their synergistic or antagonistic effects. In animals these integrated effects become accessible through the OCLTT concept (Figure 6-7) while such insight is not yet available for other organisms. In animals, hypoxia or CO_2 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 (6.2.2.3.3). Furthermore, it is conceivable that at the limits of the thermal window and, thus, of thermal acclimatization capacity, the capacity of an animal to acclimatize to elevated pCO_2 levels is also reduced, and vice versa. 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, would influence its biogeographical range (cf. Neuheimer *et al.*, 2011).

6.3.1. Temperature Mediated System Changes

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) (6.2.2.3.1.). Temperature exerts direct effects on ecosystems via organism responses leading to changing biogeography and interactions and indirect effects by changing the physical environment further, for example through modulating the degree of stratification.

6.3.1.1. Species Abundance, Biogeography, and Diversity: A Pelagic Example in the North East Atlantic

Identifying the climate signal in on-going change ideally builds on long-term observations of biological phenomena in relation to climate variability. A study geographically encompassing the whole North East Atlantic over a 50 year period showed 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° since the 1960s (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 likely favoured growth and the observed increase in phytoplankton biomass, whereas a decrease in nutrient supply likely prevented growth in warmer regions and caused a decrease in biomass (Richardson and Schoeman, 2004). Overall, 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). This conclusion is drawn with high confidence.

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 (Beaugrand *et al*., 2009; Figure 6-9). A parallel retreat of colder water plankton occurred to the north (Beaugrand *et al*., 2002; Bonnet *et al*., 2005; Lindley and Daykin, 2005; Richardson *et al*., 2006). For comparison, terrestrial shifts have an average of 6 km per decade (Parmesan and Yohe, 2003). In the northeast Pacific there has also been a general increase in the frequency of southern species moving northward (McGowan *et al*., 1998). However, 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, 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 6-9 HERE
Figure 6-9: A. Long-term changes in the state of the ecosystem calculated by applying a principle component analysis (PCA) on 5 biological parameters (phytoplankton colour index: correlation r with first principal component: 0.91; mean size of calanoids: r=0.84; mean calanoid diversity (Gini index): 0.82; plankton change index: 0.76; cod recruitment: -0.69). B. Long-term changes in ecosystem variability (in red) from a multiscale multivariate non-parametric quantification of the variance. The light gray rectangle shows the unstable period (1980-1989). C. Observed mean annual sea surface temperature in the North Sea during 1960-1981. D. Observed mean annual sea surface temperature in the North Sea during 1988-2005. 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 maximum values are rarely superior to 1

because they are averages based on every 2-month and both daylight and dark periods. Many species are not found near the surface during the daylight period (e.g. *Pleuromamma robusta*) while some overwinter in deeper water (e.g. *Calanus finmarchicus*). After Beaugrand *et al.* (2008) and Beaugrand *et al.* (2009).]

Following temperature related trends in body size (6.2.2.3) warming in the North Atlantic caused a reduction in the average body lengths of about one hundred copepod species between temperate and polar oceans, from 3-4 mm to 2-3 mm, but an increase in species richness of both copepods and the dinoflagellate genus *Ceratium* (Beaugrand *et al.*, 2010). Decreasing annual variability in SST likely reduce the diversity and abundance of diatoms, major contributors to carbon export (Sarmiento *et al.*, 2004; Bopp *et al.*, 2005; Hashioka and Yamanaka, 2007). There is medium confidence that outbreak frequencies of jellyfish aggregations are following the rising SST (Mills, 2001; Purcell, 2005; Purcell and Decker, 2005).

The ecosystem shift in North Sea plankton includes an increase in phytoplankton, a change in the composition and abundance of holozooplankton (animals which are planktic 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). The North Sea regime shift in the 1980s 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 across which ecosystem shifts set in. CTB reflects the boundary 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, a reduction in the mean size of calanoids and a decrease in the probability of occurrence of Atlantic cod (*Gadus morhua*) at large scales of the North Atlantic Ocean. The study 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 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 probability of occurrence of both sardine and anchovies and of the endangered seabird Balearic shearwater (*Puffinus mauretanicus*) 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.*, submitted) had the same magnitude as the shift in 1980s and impacted about 40% of phytoplankton and zooplankton species.

6.3.1.2. Further Evidence-Based Examples and Projections

Further examples corroborate these principles. Latitudinal movements of fish species, both benthic and pelagic paralleled the large-scale biogeographical shifts observed in the plankton (Quero *et al.*, 1998; Brander *et al.*, 2003; Perry *et al.*, 2005), with likely unifying mechanisms in operation (6.2.2.). Similar to plankton, northward range extensions or redistributions in fishes were largest along the European Continental shelf and attributed to regional warming. Examples include pelagic sardines and anchovies extending into the North Sea in response to intensified NAO and AMO, after about 40 years of absence (Alheit *et al.*, 2011). Red mullet and bass extend to western Norway, and Mediterranean and north-west African species to the south coast of Portugal (Brander *et al.*, 2003; Beare *et al.*, 2004; Genner *et al.*, 2004). Again, the cooling and freshening of the north-west Atlantic has had the opposite effect, with some groundfish species expanding further south (Rose and O'Driscoll, 2002). Warming also caused shifts to larger depths of occurrence (Dulvy *et al.*, 2008). Sockeye salmon *Oncorhynchus nerka* and other salmonids entering freshwater streams for spawning migrations 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 (Grebmeier *et al.*, 2006). Similarly, new diseases typically have emerged through 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).

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. Regions highly influenced by river runoff and experiencing increased precipitation will see a shift from marine to more brackish and even freshwater species. Semi-enclosed systems tend to lose their endemic species, and the associated niches may be filled by invasive species, either from nearby systems or artificially introduced.

Limited information is available on the response of ocean benthos to climate change. 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 needs to be unequivocally demonstrated. Studies of tropical environments document growth reductions in *Porites* and other corals over the last two decades, a change unprecedented in preceding centuries (Lough, 2008; De'ath *et al.*, 2009). These changes have tentatively been linked to temperature and carbonate saturation state (Cooper *et al.*, 2008), although causality cannot, as yet, be established for complex systems such as the Great Barrier Reef (Chapter 5).

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.*, 2011). Similar shifts are documented e.g. in Japan (Kirihara *et al.*, 2006) and are expected in the cold temperate region of South America. Latitudinal distribution of Antarctic algae may remain mostly unchanged until the end of this century because expected temperatures remain within the thermal range identified for selected species, however, this conclusion is fraught with high uncertainty due to limited data (Müller *et al.*, 2011). Modelling 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. 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). Studies of algal heat tolerance limits showed these are firmly set to 30-33 °C 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 likely to suffer irreparable effects from short-term/episodic changes only after exposure to temperatures of 40 to 45 °C (Campbell *et al.*, 2006).

The ecological consequences of global warming on phytobenthos are difficult to predict. Significant community-wide changes in abundance and composition were detected among 150 species of algae and invertebrates after a long-term warming by 3.5 °C at a power station in temperate California (Schiel *et al.*, 2004), or in the Californian intertidal after warming by 0.79-1.26 °C within 60 years (Sagarin *et al.*, 1999). 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 are likely to 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 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).

Climate change and direct human interventions, including overfishing, chemical pollution, habitat destruction and introduction of non-native species, affect the composition of marine communities (Carlton, 2000). The introduction of non-indigenous species, when supported by climate induced alterations of competitive species interactions, may provoke the displacement of ecotypes and shifts in ecosystem functioning (Occhipinti-Ambrogi, 2007). In the Mediterranean Sea a significant rate of introduction (Coll *et al.*, 2009; Costello *et al.*, 2010) is accompanied by wide spreading of introduced species (Occhipinti-Ambrogi, 2007).

Changes in local and regional species richness 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 (Stachowicz *et al.*, 2002; Duffy, 2003). Even where marine ecosystems are strongly influenced by many other factors, such as nutrient enrichment and overfishing, at least fractions of those changes are likely attributable to recent climate change (Philippart *et al*., 2011). Fish communities studied in temperate zones display increments in species richness resulting from latitudinal shifts (Perry *et al*., 2005; Hiddink and ter Hofstede, 2008). Similar phenomena in sedentary organisms and benthic macroalgae (Bianchi, 2007) are complicated by the influence of local dynamics and topographic features (islands, channels, coastal lagoons) on biogeographic boundaries (Poloczanska *et al*., 2011).

6.3.1.3. Species Phenologies and Interactions

Altered phenology and biogeography of individual species will trigger community reassembly in time and space (Parmesan and Mattews, 2006) with shifting species composition and predominance. At southern distribution boundaries local abundance likely 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 (6.2.2.3.1.).

Since 1600, 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*) in the Japanese Sea is clearly attributable to 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). 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. Warming reduces the extent and duration of sea-ice cover, impairing survival of larval krill and adult recruitment (Hays *et al*., 2005). Both warming and the decreasing spatial extension of krill habitat benefits the salp (Pakhomov, 2004) and likely also governs the on-going reductions in Adelie and chinstrap penguin populations (Trivelpiece *et al*., 2011). Climate effects on Atlantic cod (*Gadus morhua*) populations in the Eastern North Atlantic reflect direct effects of warming on both, the Atlantic cod and the putative copepod prey species of juvenile cod. Backed by the OCLTT concept findings suggest highest sensitivities of egg and larval stages and adult spawners of Atlantic cod to moderate warming (Pörtner *et al*., 2008). Accordingly, winter warming has been identified to drive the northward shift in the distribution of North Sea cod (Perry *et al*., 2005). At the same time, however, the regime shift in the North Sea, from the larger copepod *Calanus finmarchicus* to smaller ones including *C. helgolandicus* represents an unfavourable shift to smaller food particles for juvenile cod, 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 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).

Modeling studies building on bioclimate envelopes (limited windows of environmental factors supporting existence of a species) use ambient variables at known species locations to project future existence and geographical ranges of a species. Results suggested that climate change under SRES A1B, B1, and "commit" scenarios for the period 2005 to 2050 will result in a global extinction rate of marine species by 3% of the initial species richness (Cheung *et al*., 2009). Predicted extinction rates would result highest in the tropics (4%) and sub-polar biomes (7%). These models also predict shifts in biogeography, with approximately 80% of these shifts poleward, and with the distribution of pelagic species shifting more than that of demersal species. When the mechanistic principles of climate effects (6.2.2.) and trends of ocean oxygen content, acidity, and phytoplankton community structure were keyed into the picture (Cheung *et al.*, 2011), their estimates of biomass of fishes and invertebrates were reduced by 20 to 40% below earlier results (Cheung *et al.*, 2009; Cheung *et al.*, 2010). The certainty of such projections will depend on the certainty of projected physical and biogeochemical conditions, on cross-calibration with observational studies and the precision with which mechanisms and stressors can be weighted for each of the species involved. Uncertainty depends on simplified modeling assumptions, for example, that adaptation to changing conditions may not occur. So far, there have been reports on climate-induced changes in species abundances but not on climate-induced extinctions in the oceans.

6.3.1.4. Conclusions

Overall, the key role of temperature in directly affecting marine organisms and their biogeography in the context of climate change is highly certain as has been elaborated in key examples. However, in many cases other factors change concomitantly, such that identification of the fraction of ecosystem change attributable to temperature has not always been possible. The full scope of mechanisms causing 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. Nonlinearity that can operate within an ecosystem also makes the 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 (Beaugrand *et al.*, 2008; 6.2.2.). Climate change can strongly interact with the top down human interference like harvesting which then accelerates such regime shift. There is medium confidence that the responses of various plankton functional groups, dinoflagellates, copepods or diatoms 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; 6.3.1.1., 6.3.6.). Community reassembly might involve the mixing of ecosystems and strongly alter the trophodynamics of marine ecosystems 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.

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

The distribution of dissolved oxygen in the world ocean is a result of gas solubility and exchange at the air-sea interface, ocean circulation and mixing, and the net balance between gross primary production and respiration. Oxygen concentrations range from greater than 500 μmoles kg^{-1} in productive nutrient rich Antarctic waters (up to 140% saturation relative to equilibrium with the atmosphere; Carrillo *et al.*, 2004) to zero in coastal sediments rich in organic matter and permanently anoxic regions such as the Black Sea and the Cariaco Basin. Because oxygen solubility is determined by temperature and salinity, polar waters have much higher concentrations of oxygen than tropical waters at 100% air saturation. Most of the respiration (oxygen consumption) in the ocean is attributable to bacteria that respire dissolved organic matter (DOM). Once a parcel of seawater is isolated from gas exchange at the surface, oxygen can be added only by net photosynthesis, a process usually restricted to the upper 50 m of the water column, or by lateral import via ocean currents. At all greater depths, most of the ocean is hypoxic, i.e., the partial pressure of oxygen (pO_2) is less than 100% of air saturation. Oxidative metabolism occurs at rates that deplete oxygen faster than it is reintroduced (Rabalais *et al.*, 2009). The pO_2 reached depends on time since the water parcel was in contact with the atmosphere or depending on lateral import or mixing with oxygenated water. When oxygen levels fall below approximately 10 μmoles kg^{-1}, the ocean is said to be suboxic.

The degree of hypoxia is a major determinant in the distribution, abundance and survival of many marine organisms. Hypoxia in ambient water may be sensed early by animals, especially when combined with temperature extremes (6.2.2). Extremely hypoxic and anoxic regions excluding metazoans have been termed 'dead zones' although they are not devoid of bacterial life. The number of "dead zones" (6.1.1.) reflects the increasing deoxygenation of the oceans. A total of over 400 dead zones worldwide was reported for 2008, compared with 300 in the 1990s and 120 in the 1980s (Diaz and Rosenberg, 2008). Furthermore, expansion of midwater oxygen minimum zones has occurred over the past 50 years in tropical and subtropical waters of the world ocean where the rate of oxygen decrease was from 0.1 to over 0.3 μ mol/l per year (Stramma *et al.*, 2008; Stramma *et al.*, 2010a). In the California Current System in the Northeast Pacific, the rates of oxygen decrease ranged even up to 2.1 μmol/l per year, 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 μmol kg^{-1} decade^{-1} have been documented at mid water depths over much of the subarctic North Pacific (Keeling *et al.*, 2010).

Hypoxic or anoxic conditions in both water and sediments strongly impact marine biota. Depth levels corresponding to oxygen concentrations of about 0.2 ml/l (~9 μmol/l) 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 the most important target fish of 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 such as large billfishes (Prince and Goodyear, 2006; Prince *et al.*, 2011), 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 will lead to range expansions or population growth in hypoxia-tolerant taxa such as nitrate-utilizing sulphur bacteria, selected cephalopods (Gilly *et al.*, 2006) gelatinous zooplankton (medusae, ctinophores), and selected fishes (gobies, hake), with a lower overall level of biodiversity expected (Levin, 2003; Levin *et al.*, 2009; Ekau *et al.*, 2010; Gooday *et al.*, 2010).

There is now strong evidence that shelf hypoxia conditions, well documented for upwelling systems like Benguela and Humboldt (Helly and Levin, 2004; Monteiro *et al.*, 2008) are increasing in the California Current system. At the same time seasonal upwelling is linked to the advection of corrosive (low pH) deep water onto the continental shelf (Feely *et al.*, 2008). These events can be accompanied 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 (Micheli *et al.*, submitted, Saenz-Arroyo *et al.*, submitted). 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 poisonous 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).

In benthic ecosystems, the expansion of OMZs will with a high level of 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.*, 2010a). In a worldwide spread of communities of anoxic “black sediments”, some groups of organisms such as Ciliata, Turbellaria, Gnatostomulida, Nematoda, Oligochaeta live at the thin oxic-anoxic interface and have adaptations allowing them to utilize chemosynthetic production. Increased susceptibility of early life stages to hypoxia is likely in benthic and pelagic ecosystems (Pörtner and Farrell, 2008), with undetermined population-level consequences.

Hypoxia is extraordinarily interactive with changes in climate (warming, acidification) and human-induced stressors like eutrophication (Figure 6-10). 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). OMZs are characterized by CO_2 induced acidification and thereby put calcifying species at a disadvantage (6.3.3.3.). 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. 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 6-10 HERE
Figure 6-10: Diagram schematizing the principal mechanisms underlying the formation of hypoxic conditions along continental margins (modified from Levin *et al.* 2009; Levin and Sibuet, in prep., Ann. Rev. Mar. Sci.).
TO BE DEVELOPED AFTER ZOD]

Models suggest that (a) the spatial extent of hypoxia is highly sensitive to small changes in ocean oxygen content, especially at suboxic O_2 concentrations where anaerobic metabolisms (by bacteria) are dominant (Deutsch *et al.*, 2011) and (b) there will be a 50% increase in the ocean's suboxic water volume by the end of this century in response to the climate-driven changes in depth of the thermocline (Deutsch *et al.*, 2011) and to respiration of excess organic carbon formed at higher CO_2 levels (Oschlies *et al.*, 2008). Such an increase would have major implications for oxygen-sensitive nutrient recycling (denitrification, anaerobic ammonium oxidation), and, hence, for oceanic nutrient inventories. These processes account for half of the nitrogen removal from the ocean and lead to nutrient limitation of photosynthesis (Codispoti, 1989). Partially, or completely denitrified waters usually contain excess phosphate and iron and may select for the growth of nitrogen fixing bacteria and archaea especially when light is available for photosynthesis. This process helps to restore some of the fixed nitrogen that is lost through denitrification (Deutsch *et al.*, 2007).

Hypoxic waters ($O_2 < 60$ μM) presently occupy 7.6 x 10^{16} m^3 (5% of the ocean) while suboxic waters ($O_2 < 5$ μM) occupy only 4.5 x 10^{14} m^3 (0.1 %), mainly in the East Pacific (Karstensen *et al.*, 2008). A drop in oxygen by 2 μM in the surface ocean would result in a doubling of the suboxic water volume. These waters experience denitrification and are exported to other parts of the Pacific Basin, yielding N limitation of primary production. 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 complicated by decadal climate events.

Nitrogen cycling/biogeochemistry in the ocean is highly dependent on redox reactions carried out by microbes. Nitrous oxide (N_2O) is a very potent greenhouse gas. N_2O yields by denitrifiers are high where oxygen is low. Favourable conditions for N_2O production occur where suboxic waters develop at shallow depths, permitting periodic injection of O_2 (Codispoti, 2010). Expansion and shoaling of hypoxic and suboxic waters, combined with human nutrient inputs in shallow water are likely to increase N_2O production (Figure 6-10).

While most of the focus in the literature is on water column denitrification, one of the few eukaryotes found to carry out denitrification is the benthic foraminifera *Globobulimina pseudospinescens* (Risgaard-Petersen *et al.*, 2006). This genus is widespread and abundant in OMZs, so OMZ expansion may promote further denitrification (N_2 production) in marine sediments via protists. 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 to N_2O. At the same time that expanding suboxia is predicted to enhance N_2O production, ocean acidification is predicted to reduce nitrification rates of ammonium oxidizing bacteria and archaea by 3–44% within the next few decades (Beman *et al.*, 2011). This would lead to reduced production of oceanic nitrous oxide and could counter the effects of suboxic water expansion. Follow on effects may include a shift in the dominant form of N provided to phytoplankton (from NO_3^- to NH_4^+), favouring small photosynthetic taxa (Beman *et al.*, 2011). Many uncertainties exist and there is now recognition that water column denitrification and N_2 fixation are spatially and temporally variable and thus climate effects on these processes are unlikely to operate uniformly (Brandes *et al.*, 2007).

In conclusion, there is medium to high confidence that the incidence and extent of hypoxic events will increase from a global perspective, and this is especially likely in coastal and upwelling regions. An average decline in dissolved oxygen by 1-7% is predicted for the ocean interior over the next century (Keeling *et al*., 2010) associated with a progressive expansion of OMZs (Stramma *et al*., 2008; Stramma *et al*., 2010a). There is limited evidence and medium confidence that the expansion of OMZs is causing habitat loss to groundfishes 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). These effects will likely propagate along the food chain and thereby affect fish stocks and top predators (Stramma *et al*., 2010a). Depending on the oxygen levels reached, a community change toward hypoxia-adapted fauna would occur in midwater. With extreme hypoxia, species diversity would fall and, finally, higher marine organisms be replaced by heterotrophic microorganisms.

6.3.3. Attribution Ecosystems: Acidification of 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 field and the assessment of organism responses after acute exposure to elevated CO_2 levels (6.2.2.). 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 projections on longer timescales. Depending on the organisms studied and their generation time perturbation studies measure tolerance and acclimation, but rarely adaptation or natural selection. However, at ecosystem level contributions of OA to climate-induced alterations have not yet been clearly identified, partly because on-going OA as well as OA research are still early in the process and because of the concomitant trends of warming, oxygen depletion and OA in the palaeo-record (6.1.2.) and in on-going change.

Insight is complemented by observations in natural analogues or palaeo-studies. Examples include CO_2 venting areas as the one around Ischia (Hall-Spencer *et al*., 2008) or historical observations since the beginning of industrialisation. The Palaeocene–Eocene Thermal Maximum (PETM, 55 Ma) provided useful information for plankton and benthic foraminifera and the Permian Triassic (250 Ma) for general processes affecting marine animal phyla (6.1.2.). Similar to today, OA palaeo-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). However, present ocean acidification develops more than 10 times faster than comparable events in earth history (Ridgwell and Schmidt, 2010). Ocean physicochemistry prior to each of those palaeo-events was very different from the present situation. In conclusion, projections of ecosystem level effects of OA at present remain qualitative at best.

6.3.3.1. Marine Bacteria and Nutrient Cycles

Existing studies on the effect of ocean acidification on 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 carbon production and the implied efficiency of the biological carbon pump. Presently, there is no evidence 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 processes are likely affected by OA, some positively, others negatively. The potential of the microbial community to adapt to ocean acidification 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. A final assessment is not yet possible.

6.3.3.2. Phyto- and Zooplankton

There is strong evidence for systematic changes in plankton abundance and community structure over recent decades (6.1.2, 6.3.1), with most changes being caused by both the direct and indirect effects of warming, and driven in many cases by climate variability (Chavez *et al*., 2011). In terrestrial systems, rising atmospheric CO_2

concentrations are reported to enhance productivity due to “CO_2 fertilisation” (Fung *et al.*, 1997; Cao and Woodward, 1998). In marine systems, phytoplankton physiological rates and growth might also benefit from “fertilisation” by CO_2 (Rost *et al.*, 2008; Hutchins *et al.*, 2009). While there is relatively little evidence to date that net primary production (NPP) of natural phytoplankton assemblages 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 also result in higher cell division rates, altered nutrient utilisation (C:N and C:P ratios) and enhanced rates of N_2 fixation (e.g. Hutchins *et al.*, 2009; Kranz *et al.*, 2011). Increased cell division (by ~25%) and photosynthetic rates (by ~15%) have been shown 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 its 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 up-scaling 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 likely 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. Small differences in CO_2 sensitivity may lead to pronounced shifts in the dominance of species (Tortell *et al.*, 2008b).

CO_2 induced ocean acidification will likely result in 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, 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) and even in strains (genetically distinct populations) within a species (Langer *et al.*, 2009; Langer *et al.*, 2011). Results obtained in bloom-forming *Emiliania huxleyi* and *Gephyrocapsa oceanica* suggest decreased calcification rates (-25% to -66%) at $P\text{CO}_2$ values between 560 and 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 cell mass. 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 factors (Boyd, 2011). 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. 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 shift in ecotype dominance (Cubillos *et al.*, 2007). However, quantification of the calcite mass of dominant coccolithophores in the present ocean and over the last 40 kyr in fact yielded 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.

In contrast, there is medium confidence that pteropods (planktonic molluscs with aragonite shells) at high latitudes (e.g. Subarctic Pacific and Southern Ocean) reduce their calcification until the end of the century (Orr *et al*., 2005; Comeau *et al*., 2009; Comeau *et al*., 2010). 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 than pteropods, since calcite undersaturation occurs later than aragonite undersaturation (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). The similarity with patterns observed during the saturation changes associated with glacial interglacial cycles (Barker and Elderfield, 2002; Figure 6-3) makes projections of future reductions in calcification highly certain.

6.3.3.3. Macrophytes and Macrofauna

Among macrophytes, most species of seagrass and non-calcifying algae respond positively to OA by increasing production, growth and recruitment, while calcifying algae experience reduced productivity (6.2.2.). The picture is less uniform among macrofauna. Variable levels of sensitivity or resilience have been found across life stages and between as well as within phyla and even species populations, with one hypothesis indicating that sensitivity to progressive OA is low in more active marine animals with sophisticated regulation of body functions like ion and acid-base status (6.2.2.). In various 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). The wide range of responses among calcifiers (Ries *et al*., 2009) suggests diverse ecosystem level consequences. Observations at volcanic CO_2 vents in a naturally acidified Mediterranean coastal site (e.g. at Ischia, Hall-Spencer *et al*., 2008) do, however, 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. Major shift 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). 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 that long-term limits to acclimatization capacity exist in some marine calcifiers (Hall-Spencer *et al*., 2008). Concomitant warming or hypoxia would exacerbate the effect of CO_2 and lead to earlier thresholds, shifted toward alkaline pH. Marginalization of calcifiers is also observed in OMZs, where CO_2 levels parallel those of hypoxia (Levin, 2003). Some resilience was found in cold-water corals (6.2.2.). It remains to be explored whether organisms in habitats characterized by fluctuating or permanently elevated CO_2 levels, like stratified fjords, upwelling areas, oxygen minimum zones or the intertidal may have evolved a higher resistance to elevated CO_2 levels than their con-specifics or congeners in low CO_2 environments. Findings that enhanced resilience is carried over to offspring are scarce, as in the example of Sydney rock oysters (6.2.2.). Therefore, uncertainty also remains high whether and to what extent species can undergo adaptation to progressive ocean acidification over generations.

[INSERT TABLE 6-3 HERE
Table 6-3: Preliminary assessment of effects of ocean acidification on marine taxa, giving the number of laboratory and field studies, parameters and total number of species studied in the range from pCO_2 <650 to >10000 μatm. Parameters investigated in various 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. +: denotes that possibly more species or strains were studied, as only genus or family were specified; RCP 6.0: representative concentration pathway with projected atmospheric $pCO_2 \approx 850$ μatm in 2100; RCP 8.5: representative concentration pathway with projected atmospheric $pCO_2 > 1370$ μatm in 2100 (Moss *et al*., 2010). Note that certainty is limited by the short- to medium-term nature of various studies and the common lack of sensitivity estimates across generations, i.e. on evolutionary timescales. Certainty was estimated by considering the number of studies, the number of species studied and the level of agreement amongst studies. (Literature base to be complemented and as suppl. mat. online).]

6.3.3.4. Conclusions

Detection, attribution and projection of OA effects 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 habitats. While these observations support some overarching trends like reduced competitiveness of calcifiers, larger scale ecosystem level implications remain obscure. Attribution of biological responses to OA in a climate change context is complicated by the fact that water temperature, salinity, oxygenation often change concomitantly (6.1.2.). The diversity of sometimes contrasting responses becomes accessible once responding mechanisms are identified and understood. Therefore, studies integrating mechanistic knowledge (6.2.2.) and evolution over generations, as well as in various climate zones and biomes are needed. Experiments need to be inspired by long-term field observations and by observations at natural or palaeo-analogues.

Overall, the level of confidence is high that ocean acidification proceeds and will affect marine ecosystems for centuries. At present it is impossible to predict the potential impact of ocean acidification on broad-scale ecosystem functions, including sustenance of marine biodiversity. As a projection with a medium to high uncertainty reduced salinity 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 (Miller *et al.*, 2009; Denman *et al.*, 2011). Building on mechanistic knowledge enhances certainty in the projection that OA within future scenarios may cause a narrowing of thermal windows and biogeographical ranges of animals (6.2.2.) and will thereby exacerbate local effects of warming on ecosystems. Confidence is high that OA will stimulate primary production in macrophytes. Confidence is lower that it will cause a stimulation of primary production or 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. Socio-economic consequences may be felt (Cooley and Doney, 2009) and might be delimited once an ocean acidification threshold not to be surpassed is defined (Turley *et al.*, 2010).

6.3.4. Nutrient and Irradiance Controls on Primary Production

Sustenance of economic uses of the ocean under climatic change highly depends on the maintenance of primary productivity and its exploitation in intact foodwebs. There are multiple controls on Net Primary Production (NPP), some of which are long-established such as mean underwater light levels (Sverdrup, 1953), while others, 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 – will control NPP (Saito *et al.*, 2008). Many of these controlling factors are predicted, by coupled-ocean atmosphere modelling simulations, to be altered – directly or indirectly - by a changing climate (Doney, 2006; 6.2.2.). There is supporting observational confirmation for a significant alteration of NPP when the environmental controls are altered due to natural perturbations, i.e. 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 increases in primary productivity (Chavez *et al.*, 2011), such as during the El Nino to La Nina transition in Equatorial Pacific, when enhanced nutrient and trace element supply are observed (Chavez *et al.*, 1999).

Climate mediated changes in primary production across major oceanographic provinces over the period 1997 to 2006 have been reported by (Behrenfeld *et al.*, 2006). Such detection of altered primary productivity is based on an algorithm developed specifically for use in conjunction with remotely sensed ocean colour datasets 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) were 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, 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). 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 Nino/Southern Oscillation 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). By their analysis, since 1999 there has been a prolonged and sustained NPP decrease of 190 Tg C per year - an annual reduction of approximately 0.4% of total global NPP. These changes are traceable to the expansion of permanently stratified, tropical regions and are therefore climate sensitive. Increased frequency of or transition to permanent El Niño favourable 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 colour, point to increased NPP in the Arctic Ocean (Arrigo *et al.*, 2010). 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 ^{14}C radio-isotopes) 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 a slight increase (2% yr^{-1}) in NPP over the period 1988 to 2007.

Each of these studies provided mechanistic explanations for the reported trends in NPP. 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. For both specific regions and time-series sites within regions, other mechanisms to explain long-term climate-mediated trends in NPP have been invoked. For example, in the Arctic Ocean, Arrigo *et al.* (2010) proposed that an increased growing season for phytoplankton, due to reduced seasonal sea-ice cover, was the main explanation for increased NPP of up to 27.5 Tg C yr^{-1} (mean) since 2003. 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 other near-shore time series sites such as Monterey Bay (California) and Coruna in NW Spain (Figure 6-11). 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) and/or the extent to which discrete sites are broadly representative of the surrounding oceanic provinces, respectively (Saba *et al.*, 2010).

[INSERT FIGURE 6-11 HERE
Figure 6-11: 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.]

Some of these recently reported observational trends for climate-mediated alteration of rates of NPP support projections from modelling experiments which suggest that increased stratification of the surface ocean may decrease upward nutrient supply at low latitudes, but enhance the mean underwater light climate in high latitude regions, many of which have high (i.e. non-limiting for the rates of NPP) year-round concentrations of nutrients (NODC or Boyd *et al.*, 2007). For example, 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%). A recent inter-comparison of four coupled climate-carbon models of differing complexity (Steinacher *et al.*, 2010) supported the general trends reported in the projections by Bopp *et al.* (2002), and also showed general agreement between models (3 out of 4) for a projected increased in NPP rates in the Arctic under a

SRES A2 emission scenario relative to the pre-Anthropocene. The validation of future modelling, projections and improvement 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.

6.3.5. *Secondary Drivers: Biotic Interactions and Habitat Structuring by Ecosystem Engineers*

1 FIGURE ON FOODWEB EFFECTS TO BE DEVELOPED AFTER ZOD

Changes in species interactions and food webs are brought about by changes in ocean primary production and by direct influences of climate change on individuals and populations (6.2.2.), as well as complex indirect, and potentially non-linear and delayed impacts through the food web (Kirby and Beaugrand, 2009; Stock *et al.*, 2011). There is currently limited capability to predict these 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).

6.3.5.1. Species Interactions and Food Webs

Model projections suggest that climate-change mediated alteration of NPP will result in increased productivity at high latitudes and reduced productivity in the sub-tropical and tropical waters (Bopp *et al.*, 2002). Such potential alteration of NPP may cause changes in food web structure and at higher trophic levels (Utne-Palm *et al.*, 2010) and affect fisheries yields (Parsons and Lear, 2001; Brown *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 are 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 (Atkinson *et al.*, 2004). In parallel, abundances of various seabird species 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).

It is likely 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). 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 (6.2.2.4.) while others become less competitive or easier prey. Shifted geographical distribution, e.g. to higher latitude or larger depth cause changes in community composition and interactions. Reassembly 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.), and habitat change (Brander, 2007), making unambiguous attribution to climate as a proximate or ultimate cause difficult. Furthermore, these 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 population variability in 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).

End-to-end models incorporate the influences of ocean physics and chemistry into the total feeding interactions of marine ecosystems, including nutrient flows and feedbacks among primary producers, consumers, and decomposers over a range of time and space scales. These end-to-end models are useful to explore climate change effects through higher trophic levels (Rose *et al.*, 2010), and to test hypotheses about responses of food webs and ecosystems (Fulton *et al.*, 2011). A variety of such 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 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 and applicability in true forecasting mode is unlikely in the near future (Rose *et al.*, 2010; Hannah *et al.,* 2010.

In conclusion, end-to-end models at present function as dynamic repositories of data and knowledge (Fulton *et al.*, 2011). This has led to some general agreement on possible food web responses to climate change but demonstrated limited ability to narrow these down in specific ecosystems. Further progress in forecasting future food web scenarios, beyond the range of current data, requires improved data acquisition and management in conjunction with approaches to address focused questions.

6.3.5.2. Habitat Structuring, Benthic Ecosystem Engineers

Ecosystem engineers (sensu Jones *et al.*, 1994) 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 or their effects on local biogeochemistry.

To date the most intensively studied benthic ecosystem engineers are tropical corals (WGII, ch. 5) and this body of work illustrates that the twin impacts of ocean warming and acidification can have a variety of deleterious effects from increased coral bleaching and impeded calcification rates to increased rates of coral disease (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. For example, deep water coral reefs (see below) or deep-water sponge grounds form an important structural habitat in the deep sea. Sponge grounds reach 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 during reduced salinity exposures (Levinton *et al.*, 2011).

A tremendous variety of marine benthic species including calcified algae, bryozoans, bivalve molluscs, sponges, corals and even in rare instances tube-forming serpulid polychaete worms (Wood, 1999) form biogenic reefs. Effects of global climate change have been studied most intensively on shallow, tropical coral ecosystems (ch. 5) and more recently, on deep-water cold-water coral ecosystems (Roberts *et al.*, 2009). 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). Stable temperatures and low aragonite saturation states make especially scleractinian corals vulnerable to ocean warming and acidification, as they form their skeletons from aragonite. Virtually all reef-forming, deep-water scleractinian corals are found in waters currently saturated with respect to aragonite, 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 seawater within the next century (Guinotte *et al.*, 2006).

Preliminary conclusions on climate sensitivity of cold water corals result from the few available ecophysiological studies. 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 two studies provided evidence 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). More detailed studies are lacking as well as studies of performance and bio-erosion under the combined effects of ocean warming and acidification.

Studies of community changes near volcanic CO$_2$ vents have shown subtle changes along natural pH gradients with some organisms such as the predominantly calcitic bryozoans persisting in lower pH conditions than coralline algae which have more soluble high magnesium calcite skeletons (Martin *et al.*, 2008). In analogy, we may anticipate shifts in ecological composition associated with ocean warming and acidification but the magnitude and nature of such shifts remain highly uncertain.

Burrowing infauna (e.g. fishes like snake blennies, *Lumpenus lumpretaeformis*) of marine sediments 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 are likely 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 burrowing activity of infauna. Severe stress as projected from increased temperature, hypoxia and ocean acidification likely cause reduced performance and increasing mortality (6.2.2.), both of which result in lowered bioturbation rates (the reworking and mixing of sediment particles and solutes by fauna), 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 palaeo record (6.1.2.). Overall, the development of extreme long lasting hypoxia in bottom waters will detrimentally affect infauna first. As the number of available studies is scarce, uncertainty is high with respect to projecting any more specific climate change effects.

6.3.6. Concurrent Responses to Multiple Stressors

TABLE ON CLIMATE VARIABILITY EXAMPLES, WIDTH OF THEM, SEASONALITY AND THE PRESENT AND PROJECTED ANTHROPOGENIC IMPACT TO BE DEVELOPED AFTER ZOD

6.3.6.1. Interactive Effects of Stressors – from Organisms to Ocean Provinces

Projections from modelling experiments into how the environmental properties of the ocean will be altered by climate change all point to the changes of multiple properties – including temperature, carbon dioxide, dissolved oxygen and nutrient concentrations - that influence marine biota (e.g. Sarmiento *et al.*, 1998; Matear and Hirst, 1999; Boyd and Doney, 2002; Ekau *et al.*, 2010). These predicted changes to multiple environmental stressors will confound the attribution of altered biological trends, from individuals to ecosystems, to climate change (Parmesan *et al.*, 2011). 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 (Figure 6-12), for example copepod distribution in the NE Atlantic (Beaugrand *et al.*, 2009). The stressors can act individually, or interactively where two or more stressors have either synergistic or antagonistic effects on ocean biota. Examples range from direct effects, such as ocean warming and its effect on organismal physiology (Pörtner and Knust, 2007), to complex large-scale synergistic effects such as changes in both coccolithophore calcite production and abundance due to increasing carbon dioxide concentrations and warming (Feng *et al.*, 2009; Figure 6-12).

[INSERT FIGURE 6-12 HERE
Figure 6-12: A schematic highlighting the potential interactions between modes of anthropogenic forcing on different levels of biological organisation. These interactions, from simple to complex, are illustrated with published examples and each is assigned a circle to indicate our degree of confidence in the findings of the study, ranging from low for modelling studies such as (8; Griffith *et al.*, 2011) to large for lab physiological studies placed into context of field data (1; Pörtner and Knust, 2007). The space populated by the circles points to the extent of our understanding of this relationship between forcing and its effect on organisational level. 1 denotes the effects of a single stressor - warming on alteration of organismal physiology and field abundance (Pörtner and Knust, 2007); 2 the synergistic effects of multiple stressors - warming and increased [CO_2] on coccolithophore calcification (Feng *et al.*, 2009); 3 a single stressor - altered pH and the different responses of coccolithophore species (Langer *et al.*, 2006); 4 differential responses of cyanobacterial groups to multiple stressors - warming and increased [CO_2] (Fu *et al.*, 2007); 5 differential effect of multiple stressors, light and temperature, on copepods versus diatoms (Lewandowska and Sommer, 2010); 6 the effect of fishing on ecosystem structure (Frank *et al.*, 2005); 7 the interplay of fishing pressure and climate change on ecosystems (Kirby *et al.*, 2009); 8 the interplay of ocean acidification and fishing pressure on benthic communities (Griffith *et al.*, 2011); 9 detailed time-series observations on warming and the alteration of zooplankton biomes (Beaugrand *et al.*, 2009). TO BE DEVELOPED FURTHER AFTER ZOD]

6.3.6.2. Co-Limitation of Organisms by Multiple Factors

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). 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 versus diatoms, predicting how climate change will impact these biogeochemically important groups is currently limited (Boyd *et al.*, 2010).

6.3.6.3. Synergistic versus Antagonistic Effects

Most of the evidence for synergistic versus antagonistic effects of multiple stressors comes from shipboard and/or laboratory manipulation experiments (Boyd *et al.*, 2010), whereas, at the ocean basin scale, modelling 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 same 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 6-12). Modelling 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 ocean acidification 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.). 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 6-6). Furthermore, adaptation to present climate zones and variability may co-define species sensitivity to temperature, hypoxia or OA. High temperature variability and the associated functional adaptations and rise in metabolic expenditures (Pörtner, 2006) may improve resistance of Northern hemisphere species to temperature and OA. In contrast, Southern hemisphere species may display enhanced sensitivity due to reduced energy expenditure and functional capacities.

6.3.6.4. Interplay of Ecosystem and Environmental Effects

The impact of alteration of ecosystem top-down effects, for example due to marine harvesting changing ecosystem structure will also alter the forcing on a range of levels of biological organisation. The interplay of such top-down ecological effects with bottom-up environmental forcing may enhance the susceptibility of certain communities to both, a changing environment and altered ecosystem. For example, Griffith *et al.* (2011) modelled the joint effects of fishing pressure and ocean acidification on benthic communities around Australia, and reported that sustained fishing pressure enhanced the effects of ocean acidification in their model simulations. Our current understanding of how different modes of forcing, either individually or together, alter biological organisations, from physiology to biomes, is rudimentary for much of these interactions (Figure 6-12).

6.3.6.5. Ocean Upwelling

Upwelling is a process that clearly illustrates how the combined effects of various environmental factors play an interactive role on the biota. For example, upwelling brings waters with a cluster of altered environmental properties (Boyd *et al*., 2010) to the surface ocean, with altered temperature, nutrient, oxygen and carbonate chemistry as is evident in eastern boundary currents such as off the Western seaboard of the USA (Feely *et al*., 2008). 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 (Steinacher *et al*., 2010), upwelling of both nutrients and trace elements may become increasingly important in maintaining upper ocean nutrient and trace metal inventories. As 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), understanding whether they 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.

There is observational (Schwing and Mendelssohn, 1997; Demarcq, 2009) and modelling evidence (Bograd and Lynn, 2003; Snyder *et al*., 2003; Di Lorenzo *et al*., 2005) of increased alongshore upwelling favoured by winds over recent decades, as a putative consequence of global warming (Bakun, 1990). For the California Current System changes in sea surface temperature have been clearly linked to shifts in faunal composition and fisheries regimes (Lluch-Belda *et al*., 2001; Lluch-Belda *et al*., 2003). 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), however, the effect of climate change on upwelling systems through stronger winds, altered current patterns or enhanced ocean acidification remains unclear (Chavez and Messie, 2009). For the California Current,System, changes in sea surface temperature have been clearly linked to shifts in faunal composition and fisheries regimes (Lluch-Belda *et al*., 2001; Lluch-Belda *et al*., 2003).

6.4. Interactions between Ecosystems and Human Activities: Adaptation Benefits and Threats

6.4.1. Ecosystem Services

Human societies benefit from multiple resources and processes supplied by natural ecosystems, collectively called services and commonly classified as provisioning, regulating, cultural, and supporting (EMA reference). Impacts of climate change on marine ecosystems will impact the services they provide; however, for some of them the evaluation of the magnitude of those impacts and the projection of future scenarios remains a challenge. Provisioning services include the products people obtain from ecosystems, such as food, fuel, and biochemical and genetic resources. They are easier to quantify, because they can be associated to a monetary value. Regulating services, which include climate regulation, are not properly represented in the marketplace because they occur over vast areas and are connected to a range of other services. The task is even harder for the cultural (aesthetic, recreational, educational) and supporting services (those supporting the existence of all other ecosystems), because they cannot be represented in the market.

6.4.1.1. Provisioning Services

6.4.1.1.1. Food from the sea

Food production from the oceans depends on the primary and secondary productivity of marine areas and how they respond to climate change, with current estimates being highly variable and uncertain (Brander, 2007; Brown *et al*., 2010). The best way we have to estimate the food production potential from the sea is to use fisheries catch statistics. As summarized by Garcia and Rosenberg (2010) from a number of sources, seafood provides over 1.5 billion people with almost 20 percent of their average per capita intake of animal protein. Of the 144 million tons produced in 2006 by capture fisheries and aquaculture, over 75% was used for direct human consumption and the remainder was used as fish meal for indirect human consumption via aquaculture and cattle, pig, and poultry farming.

There is growing evidence of the potential interplay between non-climatic anthropogenic stressors and climate change (see Figure 6-12), and how they may have potentially significant effects on a wide range of ocean processes. For example, over-exploitation of fisheries will have a top-down effect on ecosystems which may concurrently be encountering climate-change mediated alteration of their environment, leading to highly uncertain 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).

The resilience of marine ecosystems to climate impacts is thus likely 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), 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 and adapt to climate change (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 has altered ecosystem complexity, make-up or turnover rates (Balvanera *et al*., 2006; Planque *et al*., 2010).

Projections based on bioclimate envelope approach models (6.3.1.3.), combined with spatially explicit projections of primary production changes (and assuming no change in the trophic level(s) on which a species feeds) have been used to estimate the global pattern of food availability (i.e. annual maximum fisheries catch potential) under high and low climate change scenarios (Cheung *et al*., 2010). Globally, a relatively small change in maximum catch potential (±1%) is projected to 2055, with changes resulting from the high emissions scenario being about 1.6 times the changes under the low emissions scenario (Cheung *et al*., 2010). Results were less optimistic with catch potential in the Northeast Atlantic falling by 20 to 30% relative to these earlier simulations once models included projected changes in ocean biogeochemistry and by another 10% with changes in phytoplankton community structure considered (Cheung *et al.*, 2011; 6.3.1.). With low confidence levels these studies project considerable change for the spatial distribution of this food availability potential. Deep ocean regions are projected to increase their maximum catch potential from 10% to 20% (over 50% in northern high latitude regions), whereas continental shelf regions are projected to develop a decrease on average from 4% to 5%.

The economic and social consequences of this food availability changes is further influenced by the coping capacity of human societies (6.4.2).

6.4.1.1.2. Other provisioning services

Energy availability from ocean currents and waves may change locally with climate change due to warming, changing ocean currents and wind action (IPCC SRREN). The ocean environment has revealed highly valuable biochemical resources, used for diverse of goods and services, such as pharmaceuticals, personal care and cosmetics, biologically inspired technologies, and biomonitoring (i.e., the biological monitoring of pollution). The lost of biodiversity would be detrimental for these provisional services (6.3.5.1). Reductions in sea ice in the Arctic likely allows to establish new trade passages such as the North West Passage thereby raising the possibility of economically viable trans-Arctic shipping as well as increasing access to regional resources supporting natural resource extraction and tourism. 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). 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.

6.4.1.2. 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 kyrs atmospheric carbon dioxide has been no lower than 170 ppmv and no higher than 276 ppmv (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 ppmv (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 gas exchange between surface and deep ocean via the biological and inorganic pumps and over longer time scales, the dissolution of marine carbonate and weathering of rocks on land (Sigman and Boyle, 2000).

The ability of the biota to continue regulating climate will probably be altered due to a changing climate. Marine biota play a key role in regulatory mechanisms 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 GHG's with high warming potential such as N_2O (Jin and Gruber, 2003; Law, 2008), and other climatically reactive gases such as dimethylsulphide (Vogt *et al.*, 2008). 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, increased weathering and hydrological cycle and hence run off on 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 exhibited 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 and low nutrient-adapted species. Decreases in carbon isotopic gradients between surface and deep waters at the onset of the PETM are interpreted as a result of increased stratification, reduced nutrient supply and a less efficient biological pump (Zachos *et al.*, 2003). Interestingly, the benthic foraminiferal fauna suggests that there was no reduction in export production reaching the deep ocean, suggesting a better organic carbon preservation due to lower oxygen conditions (Thomas, 2007). There is no evidence for decreased biological carbonate production during the PETM (Gibbs *et al.*, 2010).

Phytoplankton can have significant feedbacks on atmospheric CO_2 and other atmospheric gases. For example, increased nitrogen fixation rates during glacial periods have been suggested as a result of increased airborne dust 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, diatoms have likely been less abundant during the glacial in polar waters while in the subantarctic 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 ppmv (Watson *et al.*, 2000) which may have been aided by an increased alkalinity pump due to 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, the nutrient addition from volcanic ash in an eruption in Alaska stimulated a large diatom bloom and hence enhanced productivity, but with little increase in the sequestration of atmospheric CO_2 (Hamme *et al.*, 2010).

Contemporary oceanic observations and opportunistic sampling of natural perturbations also provide robust evidence of long time-series records that detail how climate variability or natural perturbations affect marine biota. For example, increases in phytoplankton biomass have been detected in long time series from 1986 until present, likely as 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 effects. Other multi-decadal ocean time-series – such as HOT (Hawaii Ocean Time-series) and BATS (Bermuda Time-Series Study) have revealed feedbacks linked to climate variability such as NAO and ENSO, resulting in increase in rates of nitrogen fixation 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 nitrogen 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 nitrogen 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 and hence changes in nutrient distribution are likely to influence nitrogen 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*, and an increase in nanophytoplankton and low chlorophyll concentrations while the 1998 La Niña led to an increase in diatom dominance and increases in NPP due to enhanced upwelling (Masotti *et al.*, 2011).

Given, the potential for concurrent change in the role of marine biota in regulating climate, and the likelihood that an altered climate in the coming decades will result in multiple feedbacks where the sign and magnitude of the feedback are difficult to predict (Boyd and Doney, 2002), modelling simulations provide our most powerful tool to explore these issues. Modelling experiments provide some preliminary indications of the potential magnitude of climate feedbacks. Climate change 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 being more than offset by predicted decreases at low latitudes (Bopp *et al.*, 2002). 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), and hence represent a positive feedback on climate change. Only a few global models have so far been applied in quantifying the importance of changing pelagic carbonate production on the oceans ability to sequester CO_2. Predictions for the additional quantity of anthropogenic CO_2 taken up by the ocean by the year 2100, i.e. a negative feedback on climate change, fall in the range 5.9 and 18 PgC (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). Each of these modelling 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 oceans biological pump cannot be reliably modelled, as many of the factors controlling the functioning of this pump are poorly understood (Figure 6-13). 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 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 6-13 HERE
Figure 6-13: A schematic representation of the ocean's biological pump, an important conduit for carbon sequestration. 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 (Bopp *et al.*, 2002); B, floristic and faunistic shifts in the pelagical (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 (Engel *et al.*, 2004); E, warming and faster bacterial enzymatic rates of particle solubilisation (Christian and Karl, 1995); and faunistic shifts at depth (Jackson and Burd, 2001). Figure modified from Buesseler *et al.* (2008) by J. Cook (WHOI).]

Evidence from many studies, both in the geological past and present day, point to the significant effects that marine feedbacks can have on global climate. However, the ability to predict both the sign and magnitude of specific feedbacks to climate change with even a medium degree of certainty 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 ocean acidification may slow coral growth by nearly 50% by 2050 (Hoegh-Guldberg *et al.*, 2007; WGII, chapter 5). Therefore, the threats to reefs resulting from anthropogenic impacts, climate change, and ocean acidification are likely to make some islands and coastal areas more vulnerable with respect to tsunamis, as well as storm surges.

6.4.1.3. Cultural Services

Cultural services represent the non-material benefits people obtain from ecosystems through the development of spiritual, cognitive, aesthetic, and recreational activities. They are difficult to quantitatively value. A significant component of leisure and recreation depends upon marine biodiversity (e.g. bird watching, sea angling, rock pooling and diving), which in turn supports employment and small businesses. The rapid growth of sea angling is recognized as a significant opportunity for coastal economies. In addition, the occurrence of harmful or unpleasant algal bloom can reduce the aesthetics of beach recreation and has impacts on shelf fish landings (Jin *et al.*, 2008). The enormous biodiversity supported by coral reefs underpins substantial tourist industries for many tropical countries. Countries with coral reefs attract millions of SCUBA divers every year, yielding significant economic benefits to the host country. Globally, tourism is estimated to provide US$ 9.6 billion in annual net benefits (Cesar *et al.*, 2003) and a multiple of this amount in tourism spending. Coral reef biodiversity also has a high research and conservation value, as well as a non-use value, estimated together at US$ 5.5 billion annually (Cesar *et al*., 2003). Loss of coral reefs and their diversity would impact global tourism to these areas and their enjoyment by tourists, including those from the UK.

The harvesting of marine and terrestrial mammals is widely practiced amongst the Artic communities, with traditional foods contributing a significant portion of the community's nutritional intake (Van Oostdam *et al*., 2005). Inuit hunting is largely subsistence-based in the Canadian Arctic (Gombay, 2006). Sea ice is important for transportation as often the frozen ocean surface provides a link to 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).

6.4.1.4. Supporting Services

Supporting services are necessary for and support the existence of all other ecosystem services, essentially forming their foundation. They are not represented on the market, yet their "value" amounts to more than all of the above services combined. Further, because they are so diverse in nature and scales, their identification and description is virtually impossible. We can recognize, however, some processes that are particularly relevant for supporting ocean ecosystem services. One example involves certain organisms, such as calcifying algae and corals that provide living quarters for other marine species simply through their normal growth (6.3.5.2.). Changes in the conditions in which these ecosystem engineers produce the 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).

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6.4.2. Human Activities: Socioeconomics, Adaptation, Management Risks

The many effects, both known and as yet unknown, of a changing climate on the ocean will have widespread socio-economic and geopolitical ramifications, both positive and negative, for the future management of ocean resources ranging from adaptive changes to long-established industries such as the harvest of commercially valuable species, to the potential deployment of geoengineering methods to harness the potential of the ocean to help mitigate rising temperatures and carbon dioxide concentrations. Our understanding of the potential effects of climate change and cumulative effects in marine systems is not as advanced as for terrestrial systems (Brander, 2007; Richardson and Poloczanska, 2008).

6.4.2.1. Food Harvesting and Cultivation: Aquaculture, Fisheries, and Landings

Aquaculture provides nearly 20% of the total marine food production (102 million tons in 2006; FAO, 2007; 2008), mostly concentrated in coastal areas and based in molluscs and crustaceans. During the early 2000s this industry reported growth rates around 12% a year, but has recently decreased to nearly 7%, mostly because of the limited availability of suitable culture sites (FAO, 2007), which has motivated the exploration of open ocean culture technologies (FAO, 2007). The vulnerability of various human communities to these changes in seafood availability depends on their exposure to these changes. 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. 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 among these vulnerable nations, due to the importance of fishing, high exposure to predicted climate change, and relatively low adaptive capacity (Allison *et al.*, 2009). The study noted that the majority of countries that are most vulnerable to climate change impacts on their fisheries 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 the regional marine production system are uncertain, these changes overall are likely to have a negative 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).

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. 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; World Bank 2010).

How people respond to these changes in fish catch potential, in particular how the economic drivers of fisheries are managed, can have a greater impact on seafood security than the effects of climate change alone. 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 resulted in 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).

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). 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). A number of studies do however point to it being more likely than not that warming will be beneficial for fisheries productivity in for instance the North Atlantic (Arnason, 2007; Stenevik and Sundby, 2007). However, increasing stock fluctuations with resulting management and socioeconomic challenges are also apparent, though modelling exercises illustrate management issues in general to have greater impact on biological and economic conditions than climate change is expected to have (Eide and Heen, 2002; Eide, 2007; 2008).

Preliminary modelling studies (Cheung *et al.*, 2010; Fulton, 2011) are finding declines in the predicted potential catch in the tropics. Confidence in specifics remains low at this time, however, as predictions on regional ecosystem dynamics are still uncertain. Nevertheless, if such patterns are realised in the tropics, there is limited capacity for adaptation. These areas are dependent on fisheries economically and for food security (27% of the dietary protein is from fish compared to 13% in less vulnerable countries) and as their citizens are amongst the worlds poorest there is 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, it is highly certain that the impacts of climate change will be significant for marine ecosystems, the production of food from these systems 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 be 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). Ironically, it appears to be the more northerly (and developed) nations, which are likely to benefit from climate change, at least initially. Long-term consequences of climate change to capture fisheries production are highly uncertain and depend on what happens to marine primary production, the projections for which at present are highly variable.

6.4.2.2. Other Marine Economies

It is very likely that opportunities for new marine industries will arise as systems change into the future. It is likely that new fisheries opportunities will arise while others are lost (Cheung *et al.*, 2010; Fulton, 2011) if predicted large-scale ecosystem changes do occur (though the locations of these shifts is uncertain given the preliminary nature of the simulations to date) and industry members have sufficient socioeconomic capacity to respond. In other fledgling industries, such as marine pharmaceuticals, although a diverse range of phyla have been investigated (Hunt and Vincent, 2006), there is no current appraisal of the status of the industry and of any key species or phyla that could be used as a platform to explore how climate change might alter the industry in the future.

Currently, the most important energy industry operating in the ocean is the extraction of oil and gas supplying fossil fuels. Because of depletion of oil deposits, the industry is progressively moving towards deeper waters, which potentially exposes moored developments to greater storm hazards (see WG II, ch. 30). Extraction of kinetic energy from ocean currents and waves (see IPCC SRREN) has only been tested in pilot forms on tidal streams (Douglas *et al.*, 2008). Energy available is proportional to velocity cubed, and rotors are located close to the surface layers where velocity is highest. Very strong forces acting on the structure require heavy engineering. Future development of platforms should consider that potential changes in ocean dynamics due to climate change could influence their efficiency and security.

Opportunities will exist for other sectors too. New industries are already growing around alternative energy sources (Fraenkel, 2002; Henderson *et al.*, 2003), other industries may arise around geoengineering, new shipping routes will likely be possible with the reduction of sea ice levels in places like the Arctic (Wilson *et al.*, 2004; Granier *et al.*, 2006), and new tourism opportunities will arise as people travel to see disappearing ecosystem types (e.g. Antarctic tourism, Liggett *et al.*, 2011) or previously inhospitable areas open, peak seasons shift (e.g. Amelung *et al.*, 2007; Moore, 2010) or the location of key attractors shift (e.g. cetaceans, Lambert *et al.*, 2010). It is highly likely that climate change will pose some negative impacts for industries too (e.g. extreme events can disrupt oil and gas operations (Considine *et al.*, 2004), affect tourism and transport (Becken, 2005)**.** Together these shifts in industries using the marine system may further modify pressures on them.

6.4.2.3. Ecosystem Management, Marine Protected Areas

All of the potential ecological, social and economic shifts will pose new management questions and combinations, to the already highly demanding enterprise of managing ocean resources (Eide and Heen, 2002; Eide, 2007). Integrated, "whole-of-system" or adaptive ecosystem-based management (EBM) is already being increasingly adopted around the world 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 (Planque *et al.*, 2010; Eero *et al.*, 2011). Such an extension and a focus on integration (Miller *et al.*, 2010) is based on widespread and robust evidence that the effects of different human activities will undermine resilience to other impacts or attempts at mitigation and adaptation. For example, along coastal margins it is likely that existing infrastructure (e.g. roads and settlements) will prevent the landward migration of fringing ecosystems, such as saltmarshes (Hughes, 2004). In other cases, consequences are more subtle. Recruitment variability, or reduced larval survival, as a result of shifting climate or ocean acidification 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. Modelling 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 ocean acidification (assumed loss of shelled benthos as food), habitat degradation and altered water column properties. However, such projection is fraught with high levels of uncertainty.

Analyses of the North Sea regime shift in the 1980s indicate that there is a potential for early detection of ecosystem shifts. Quantification of the multivariate multiscale variance revealed that changes in ecosystem state were paralleled by an increase in variance. Rising variance can thus provide an early warning to ecosystem managers of an impending regime shift (Carpenter and Brock, 2006). Periods of low variance in the ecosystem state alternate with periods of more pronounced variability (shift). 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, at least in some circumstances, the physical effects of climate change likely lead to significant additional conservation pressures 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 ecosystem-based management (EBM) will be implemented and be successful in any location. For example, based on model predictions there may be the potential for significant change in biodiversity in some locations (Danovaro *et al*., 2004; Cheung *et al*., 2009; Fulton, 2011) 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). It 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).

6.4.2.4. Impacts 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, and that direct injection could avoid much of the atmospheric heat trapping. This method and now many others for active ocean manipulation or disposal (see Table 6-4) are currently being initially evaluated and given preliminary rankings on criteria such as efficacy, safety and cost (Boyd, 2008). Many of these schemes predate ocean acidification 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. 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). There has been a recent comparative assessment of how ecosystems will be altered by different geoengineering methods (Russell *et al*., 2011). Energy structure emplacement in the ocean such as offshore wind farms and tidal energy conversion are now proceeding apace with far fewer policy hurdles.

[INSERT TABLE 6-4 HERE
Table 6-4: 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 ocean acidification 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 6-4). 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 metabolisation and, thereby, remineralisation 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 net primary production 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 catabolisation of organic material in a fertilized ocean region causes enhanced oxygen demand and deep water oxygen depletion as confirmed by modelling 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.

6.4.2.5. Health Issues: Harmful Algal Blooms, Pathogen Proliferation

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). It seems likely that an important environmental stimulus for bloom formation is an increase in the presence of haline stratification in regions susceptible to fresh-water inputs. 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). Prediction of the impact of global climate change on HABs is fraught with a medium to low level of certainty.

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 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. cholerae* 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 seawater 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 seawater inundation due to sea level rise are all predicted to exacerbate the global threat of cholera.

Interaction with non-climate stressors

A further illustration is the recent discovery of increased windiness over the Southern Ocean due to the altered atmospheric pressure differential between high and mid-latitudes. This increased windiness has been associated with anthropogenic alteration of the ozone hole, and to date has resulted in both decreased oceanic carbon dioxide storage (Le Quéré *et al.*, 2007) and deepening of the surface mixed layer depth (Sallee *et al.*, 2010). Again, the interplay between and outcome for the biota of increased windiness and the on-going effects of climate change is highly uncertain.

6.5. Conclusions and Key Uncertainties

[to be developed after ZOD]

Frequently Asked Questions

[to be developed after ZOD]

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Supplementary Online Material

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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 ocean ecosystems[1].

	Size		**Stratification**			**Nutrient**[2]	
System	**Area ($km^2 x10^6$)**	**%**	**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: Preliminary assessment of effects of ocean acidification on marine taxa, giving the number of laboratory and field studies, parameters and total number of species studied in the range from $p\mathrm{CO}_2$ <650 to >10000 μatm. Parameters investigated in various life stages include growth, survival, calcification, metabolic rate, immune response, development, abundance, behaviour and others. Not all life stages, parameters and ranges of $p\mathrm{CO}_2$ were studied in all species. +: denotes that possibly more species or strains were studied, as only genus or family were specified; RCP 6.0: representative concentration pathway with projected atmospheric $p\mathrm{CO}_2 \approx 850$ μatm in 2100; RCP 8.5: representative concentration pathway with projected atmospheric $p\mathrm{CO}_2 > 1370$ μatm in 2100 (Moss *et al.,* 2010). Note that confidence is limited by the short to medium-term nature of various studies and the common lack of sensitivity estimates across generations, i.e. on evolutionary timescales. Certainty was estimated by considering the number of studies, the number of species studied and the level of agreement amongst studies (Literature base to be widened and included as suppl. material online).
TO BE COMPLEMENTED BY BACTERIAL PROCESSES AFTER ZOD

Taxon	No. of studies	No. of parameters studied	Total no. of species studied	$p\mathrm{CO}_2$ where the most vulnerable species is negatively affected or investigated $p\mathrm{CO}_2$ range* (μatm)	Assessment of tolerance to RCP 6.0 (certainty)	Assessment of tolerance to RCP 8.5 (certainty)
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	Vulnerable (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	Vulnerable (low)	Vulnerable (low)
Annelids	4	6	4+	2800	Tolerant (medium)	Tolerant (medium)
Molluscs (bivalves, gastropods)	29	19	25+	600	Vulnerable (medium)	Vulnerable (medium)
Molluscs (pteropods)	6	7	3	750	Vulnerable (high)	Vulnerable (high)
Molluscs (cephalopods)	6	7	3	4000	Tolerant (low)	Tolerant (low)
Bryozoans	2	3	5+	2900	Tolerant (medium)	Tolerant (medium)
Corals (tropical, subtropical)	24	13	25+	640	Vulnerable (high)	Vulnerable (medium)
Corals (temperate, deep-sea)	5	4	6	570	Vulnerable (medium)	Vulnerable (medium)
Crustaceans (strongly calcifying)	10	11	9	700	Tolerant (low)	Vulnerable (low)
Crustaceans (weakly calcifying)	15	16	24+	1000	Tolerant (low)	Tolerant (medium)
Echinoderms	23	13	24+	600	Tolerant (medium)	Vulnerable (medium)
Fish	19	14	16	700	Vulnerable (low)	Vulnerable (low)

Table 6-4: 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	Complex system as yet untested in pilot processes. Involves mining and crushing large quantities of silicate	House *et al*., 2007; Köhler *et al*., 2010

	silicate minerals such as olivine for disposal. The net result is to add alkalinity to the ocean akin to natural silicate weathering processes.	minerals. Very long time scale consequences uncertain.	

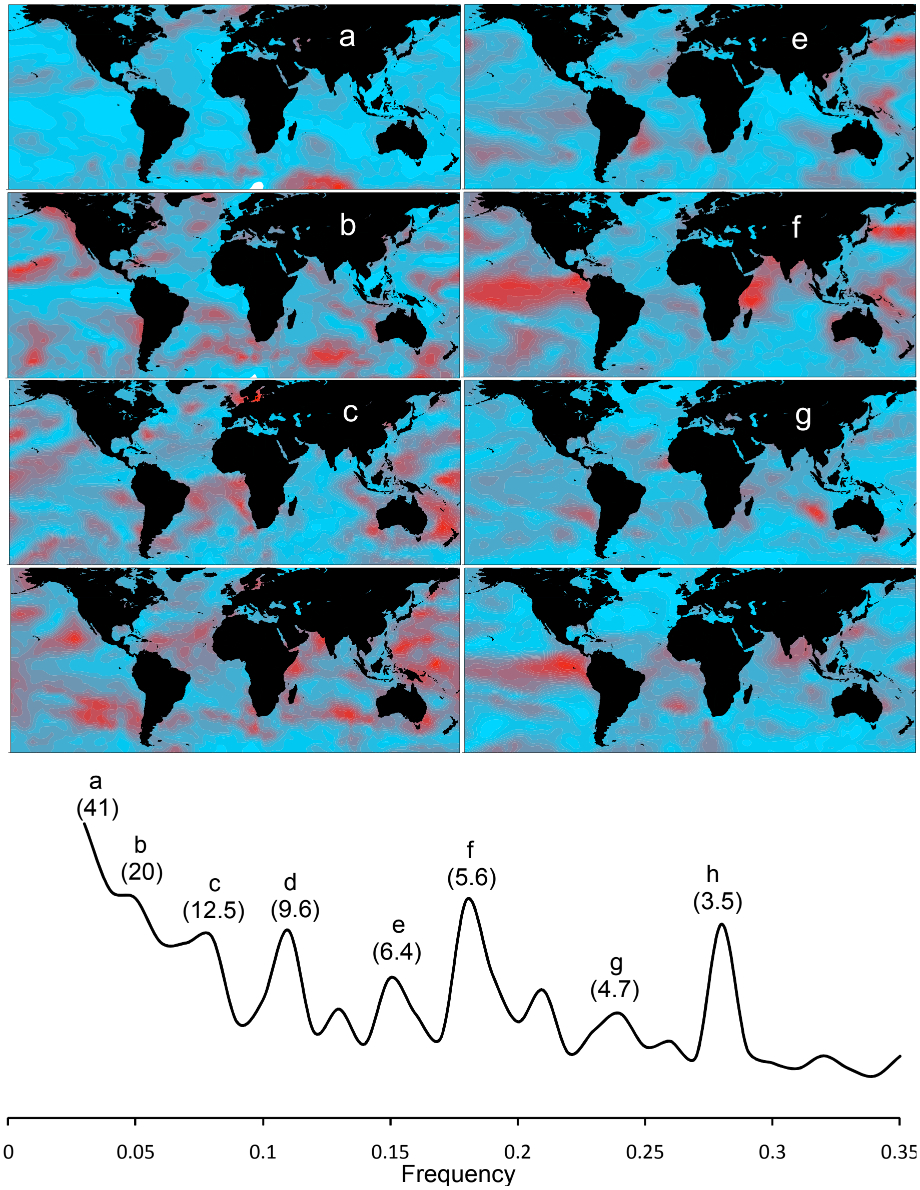

Figure 6-1: Spatial distribution of interannual temperature variability during the 1911 to 2010 period. Extended sea surface temperature data (ERSST) are available as 2°x 2° boxed time series from the National Climatic Data Center (http://www.ncdc.noaa.gov/ersst/). Each series was annualized, detrended and standardized before the computation of spectral density (as a proxy for temperature variability). The lower panel shows the accumulated spectral density values for each of the 8036 valid boxes of the World Ocean (no land, no ice, latitudes between 60°S and 70°N). Each map corresponds to one of the peaks in the series, identified by a letter. The number below each letter corresponds to the centered period value (years). Color scales are arbitrary, indicating maximum (red) and minimum (light blue) spectral density values for each frequency window. A general pattern reveals lower frequency variability (a) occurs mostly in polar regions, the interdecadal (10 to 20 years; b,c,d) at mid latitudes, and the strong peaks at higher frequencies (f,h) in the tropics. However, there are also important differences between maps suggesting the participation of different mechanisms. For example, the two peaks typically associated to the ENSO variability (f and h) exhibit strong differences, with the low frequency component (5.6 years) present in the north and south Pacific and the Indian ocean, while the high frequency (3.5 years) is concentrated in the eastern tropical Pacific.

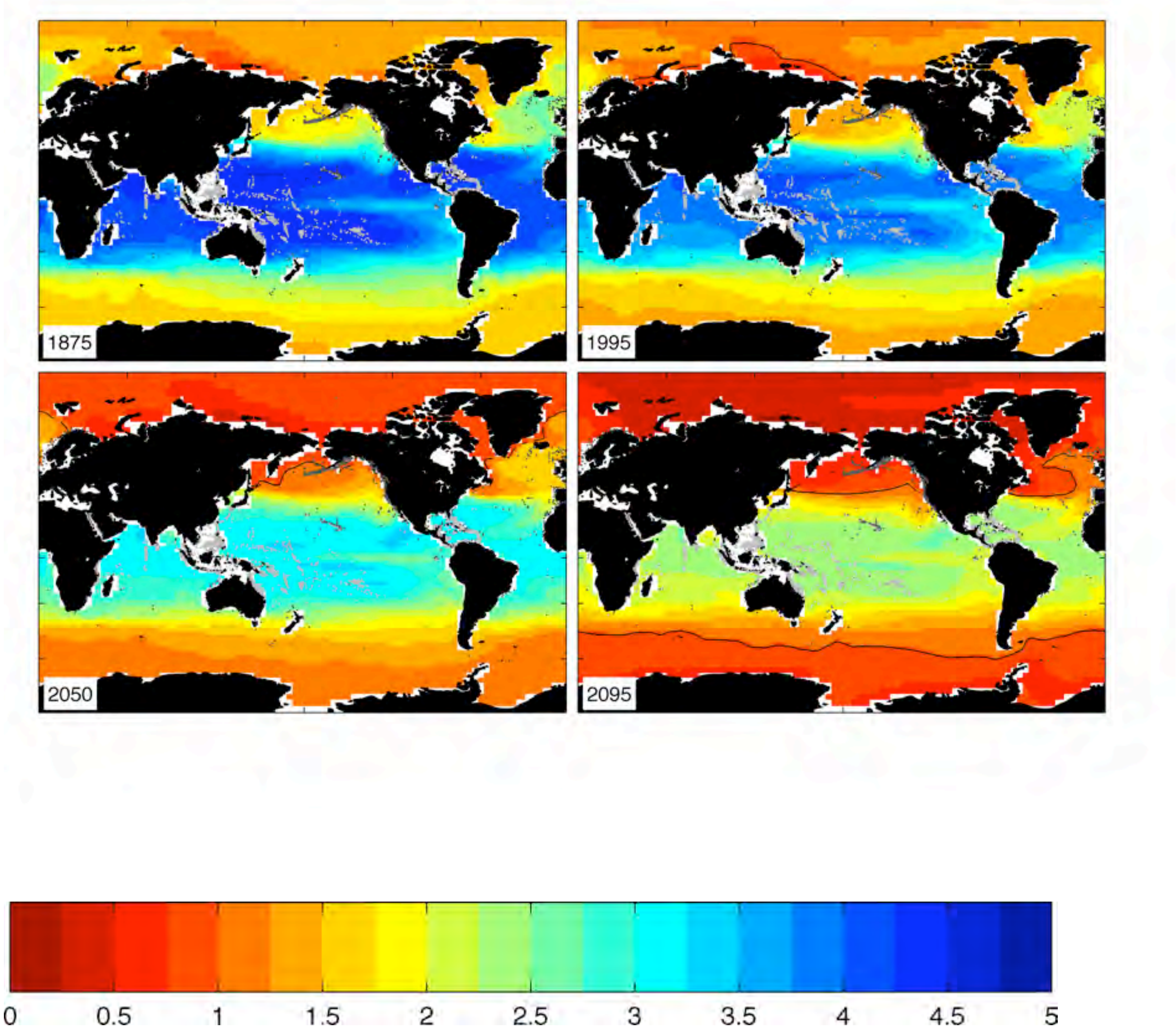

Figure 6-2: CCSM3-modeled decadal mean aragonite saturation (Ω) at the sea surface, around the years 1875, 1995, 2050, and 2095 following the SRES A2 emission scenario. The CO_2 concentration in 2100 approximates around 850 ppm similar to RCP8.5 (Moss *et al.*, 2010). Deep coral reefs are indicated by darker gray dots; shallow-water coral reefs are indicated with lighter gray dots. White areas indicate regions with no data (Feely *et al.*, 2009).

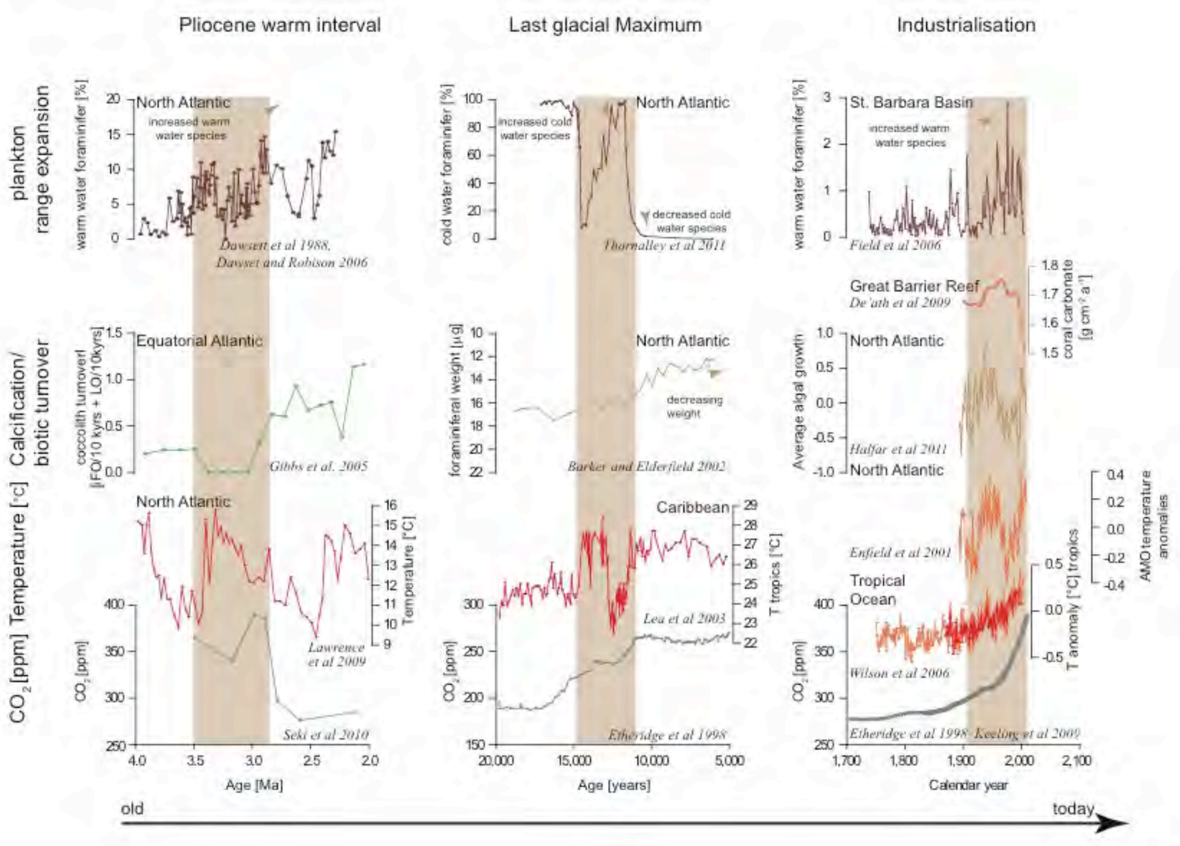

Figure 6-3: Atmospheric CO$_2$ (bottom) and temperature (middle) changes with associated biotic changes (top) for (from left to right) the industrial era, the last glacial to Holocene transition and the Pliocene warm period. Intervals of largest environmental change are indicated with brown bars. CO$_2$ data is based on measurements at Mauna Loa (Keeling *et al*., 2009), ice core records from Antarctica (Etheridge *et al*., 1998; Monnin *et al*., 2004) and proxy reconstructions (Seki *et al*., 2010). Temperature data is based on proxy data and models (Wilson *et al*., 2006, [tropical ocean]; Lea *et al*., 2003, [Caribbean]; Lawrence *et al*., 2009, [North Atlantic]) 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 coralline algae growth increment changes (Halfar *et al*., 2011), coral calcification as a product of density and linear extension (De'ath *et al*., 2009) and foraminiferal weight (Barker and Elderfield, 2002). Evolutionary turnover of coccolithophores is defined as the sum of first and last appearances per 10 kyrs (Gibbs *et al*., 2005). Abundance data of planktic foraminifers (Field *et al*., 2006, [St. Barbara Basin]; Thornalley *et al*., 2011, [North Atlantic]; Dowsett *et al*., 1988; Dowsett and Robinson, 2006, [North Atlantic]) indicates the temperature change and consequent range expansion or retraction in all three time intervals.

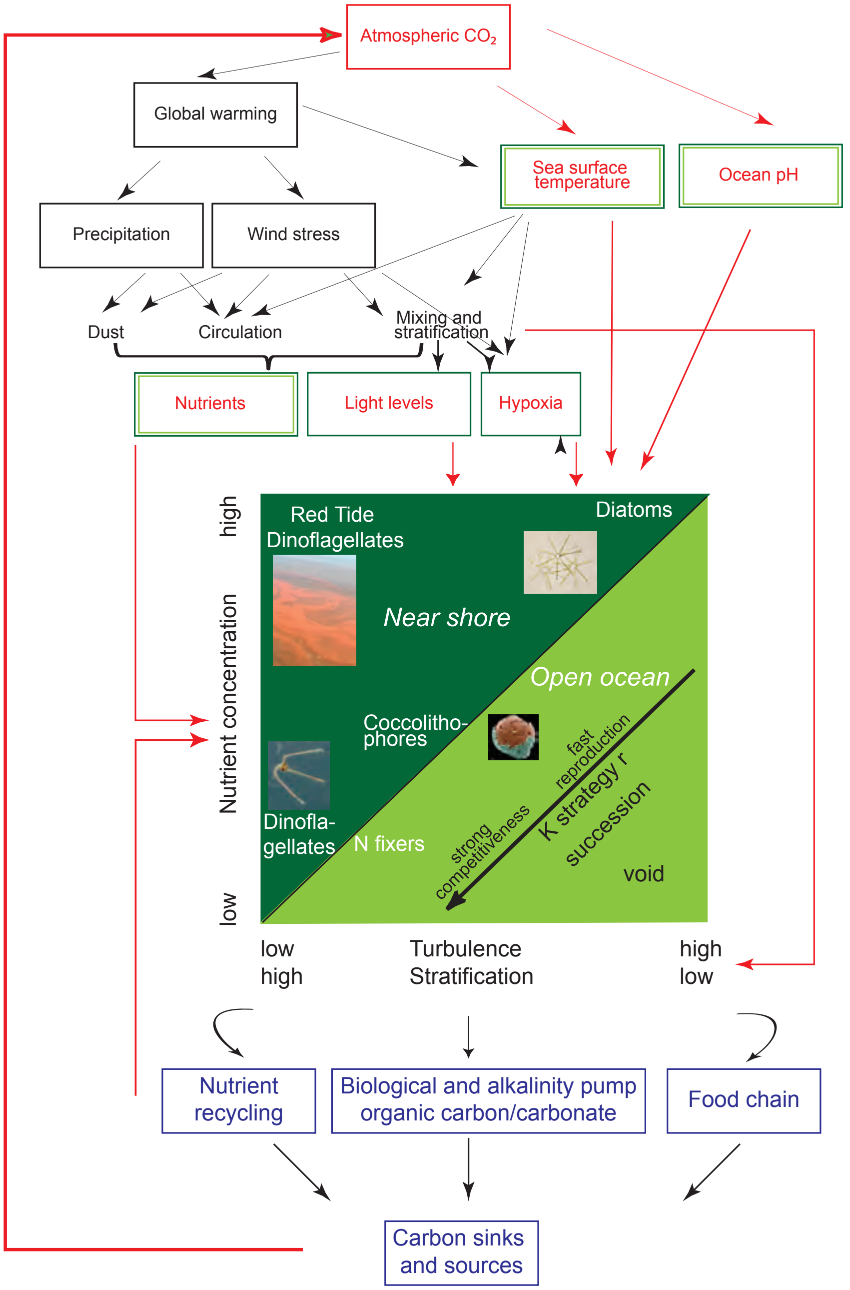

Figure 6-4: Climate impacts on phytoplankton succession. Margalef's Mandala (Margalef, 1978; Margalef *et al.*, 1979) with additions on harmful algal blooms (Cullen *et al.*, 2007) described in a simplified framework of how the phytoplankton community structure changes in relationship to turbulence and nutrients, factors which have a strong influence on phytoplankton reproduction and competitiveness. This model provides no quantitative predictions, but it is generally consistent with observation, experimentation, and theory (Kiørboe, 1993). As these factors are expected to vary with 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.

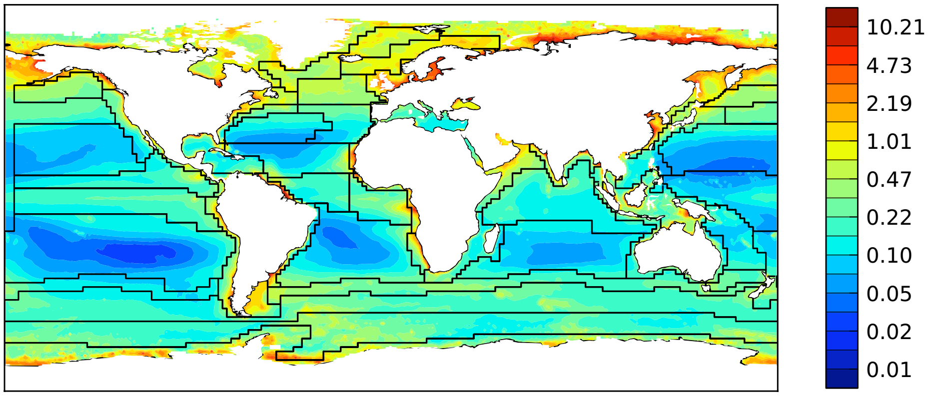

Figure 6-5: Productivity in 51 distinct global ocean biogeographical provinces as represented by a grid of thin black lines (after Longhurst, 1998), overlaid with an annual composite plot of ocean colour, i.e. a proxy for phytoplankton stocks in the upper ocean) from the NASA/Orbimage SeaWiFs satellite. These provinces or biomes span several orders of magnitude in phytoplankton stocks from < 0.1 mg m^{-3} in the low latitude oligotrophic regions (denoted by purple and blue) to 1-10 mg m^{-3} in coastal upwelling regions in Eastern boundary currents (denoted by red).

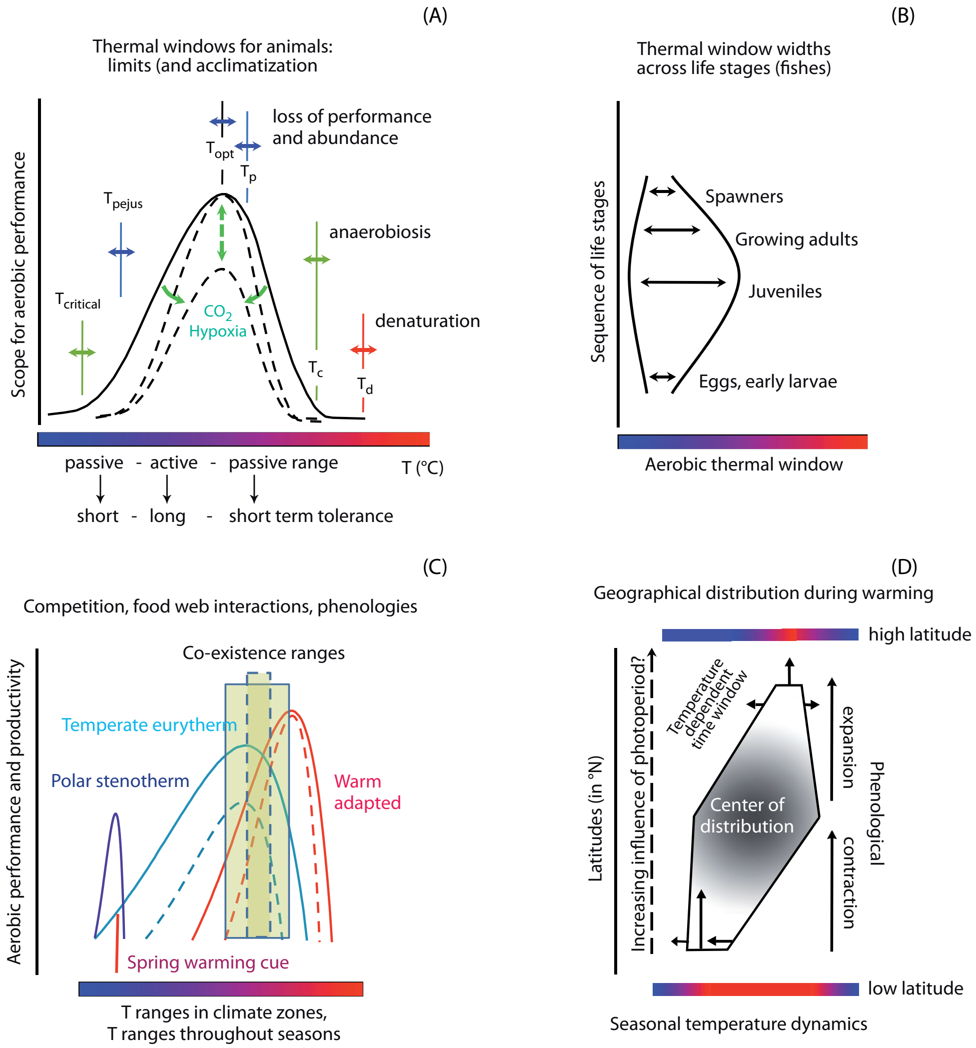

Figure 6-6: Mechanisms linking organism to ecosystem response (A) Concept of oxygen and capacity limited thermal tolerance (OCLTT) characterizing the specialization of animals on limited thermal windows set by (aerobic) performance capacity (shaping fitness; growth, specific dynamic action (SDA), exercise, behaviours, immune capacity, reproduction) and, as a consequence, the why, how, when and where of climate sensitivity. Pejus temperatures (T_p) indicate limits to long-term tolerance, critical temperatures (T_c) the borders of short-term passive tolerance and transition to anaerobic metabolism (after Pörtner and Farrell, 2008, and Pörtner, 2010). 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. 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) (A, C). Applicability of such reaction norms to other organisms (phytoplankton, macroalgae, bacteria) is likely. Temperature-dependent performance forms the basis of shifts in phenologies, namely the seasonal timing of biological processes, of changes in species co-existence ranges and interactions as well as in biogeography during climate warming (D). Here, the black line surrounding the polygon limits 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 (modified after Beaugrand, 2009).

Figure 6-7: (OPTIONAL, TO BE DEVELOPED AFTER ZOD) Ranges of oxygen concentrations (and temperatures) covered by various groups of organisms (archaea to animals), reflecting a narrowing of life options with rising levels of organisational complexity.

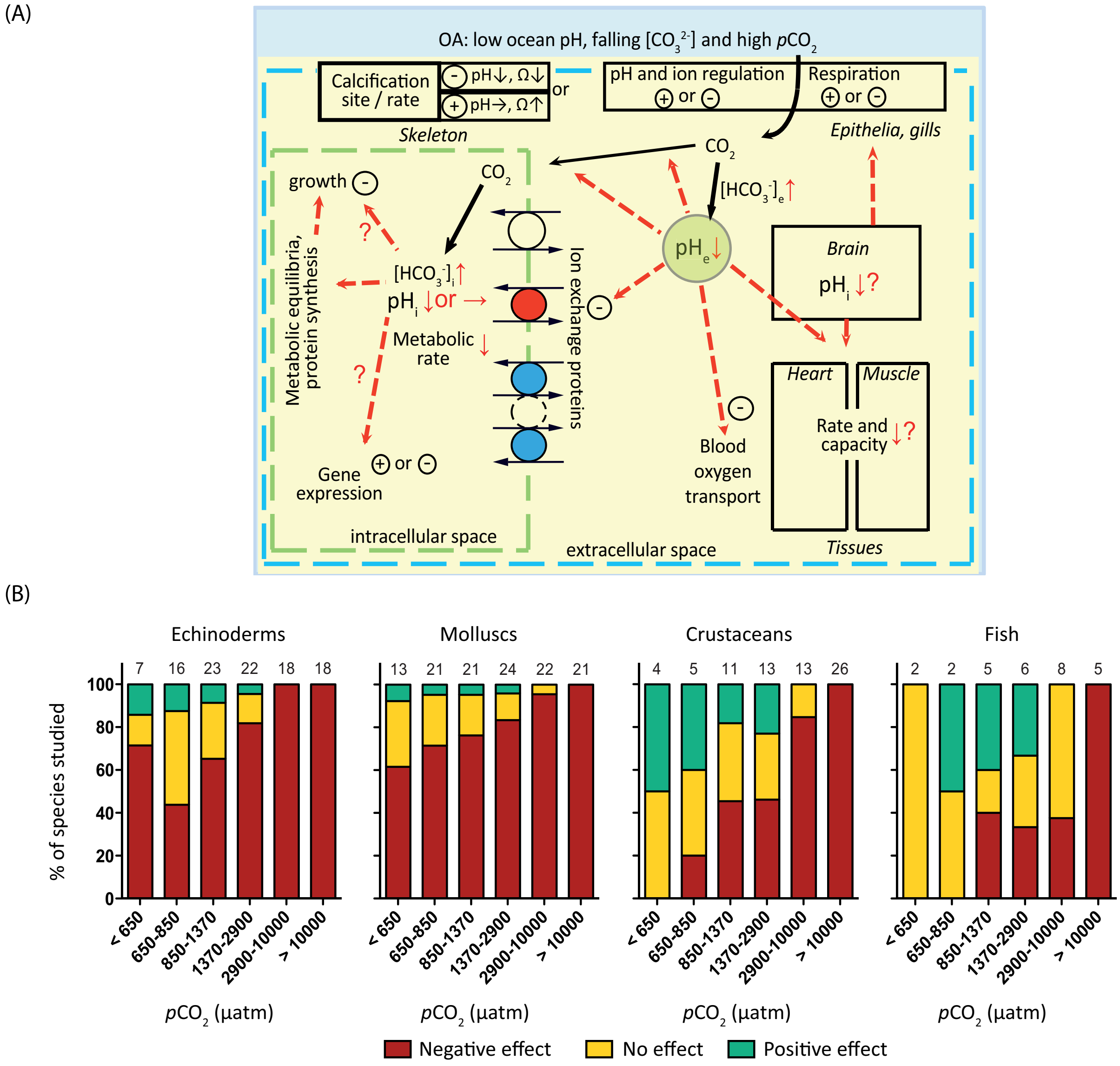

Figure 6-8: (A) Unifying physiological principles characterizing the responses of a schematized marine water breathing animal (dashed blue line) sensitive to ocean acidification (OA), mediated via entry of CO_2 (black arrows) resulting in a permanent drop in extracellular pH and its putative effects (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). In less sensitive species, pH compensation would occur extracellularly and/or 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). (B) % fraction of studied molluscan, echinoderm, crustacean and fish species affected negatively, positively or not at all by various levels of elevated ambient CO_2. Effects considered include those on various life stages and processes reflecting changes in physiological performance (oxygen consumption, aerobic scope, calcification, growth, immune response, maintenance of acid-base balance, fertilization rate, sperm motility, developmental time, production of viable offspring, morphology). Behavioural effects have not been widely studied and thus not considered in this comparative analysis. Also, 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 (Literature base in online supplementary material).

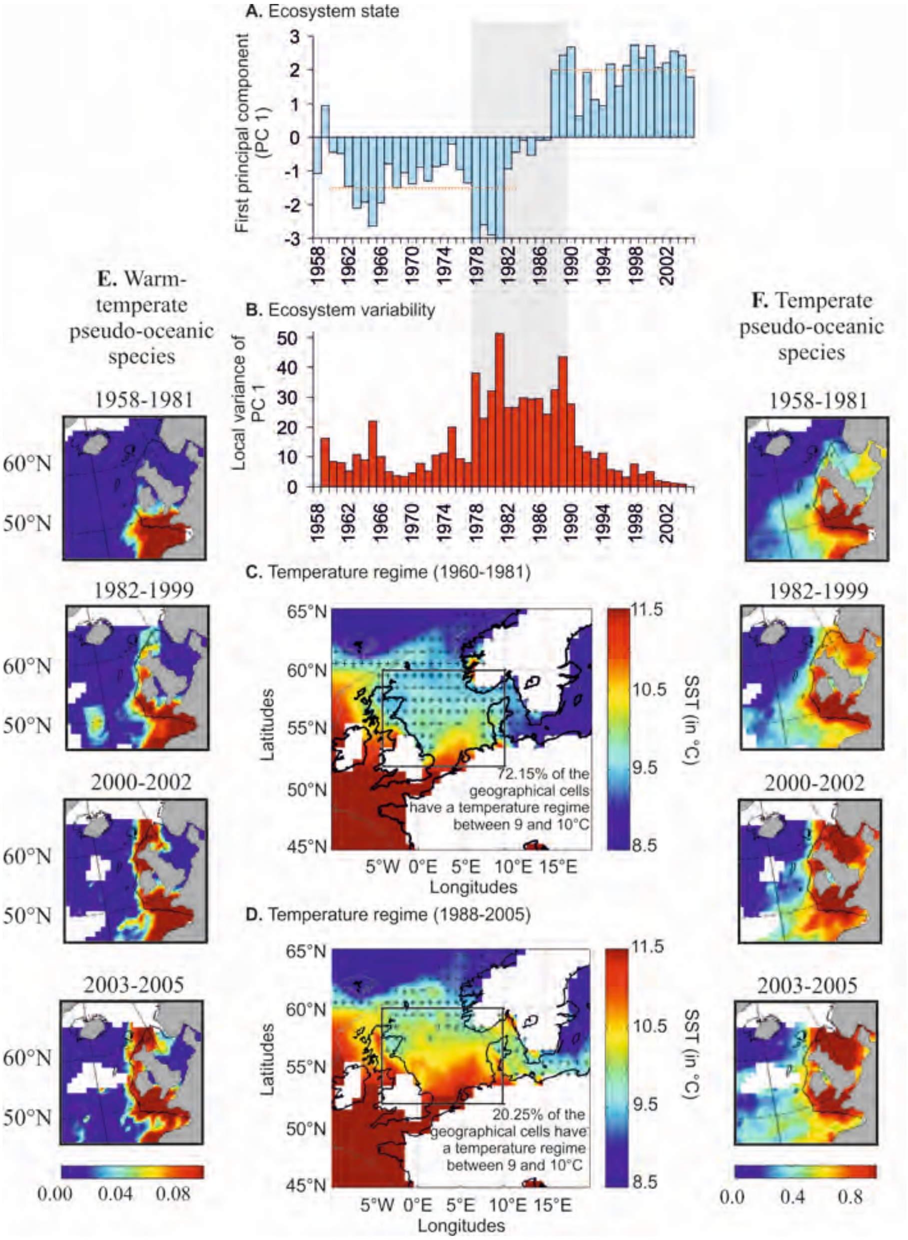

Figure 6-9: A. Long-term changes in the state of the ecosystem calculated by applying a principle component analysis (PCA) on 5 biological parameters (phytoplankton colour index: correlation r with first principal component: 0.91; mean size of calanoids: r=0.84; mean calanoid diversity (Gini index): 0.82; plankton change index: 0.76; cod recruitment: -0.69). B. Long-term changes in ecosystem variability (in red) from a multiscale multivariate non-parametric quantification of the variance. The light gray rectangle shows the unstable period (1980-1989). C. Observed mean annual sea surface temperature in the North Sea during 1960-1981. D. Observed mean annual sea surface temperature in the North Sea during 1988-2005. 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 maximum values are rarely superior to 1 because they are averages based on every 2-month and both daylight and dark periods. Many species are not found near the surface during the daylight period (e.g. *Pleuromamma robusta*) while some overwinter in deeper water (e.g. *Calanus finmarchicus*). After Beaugrand *et al*. (2008) and Beaugrand *et al*. (2009).

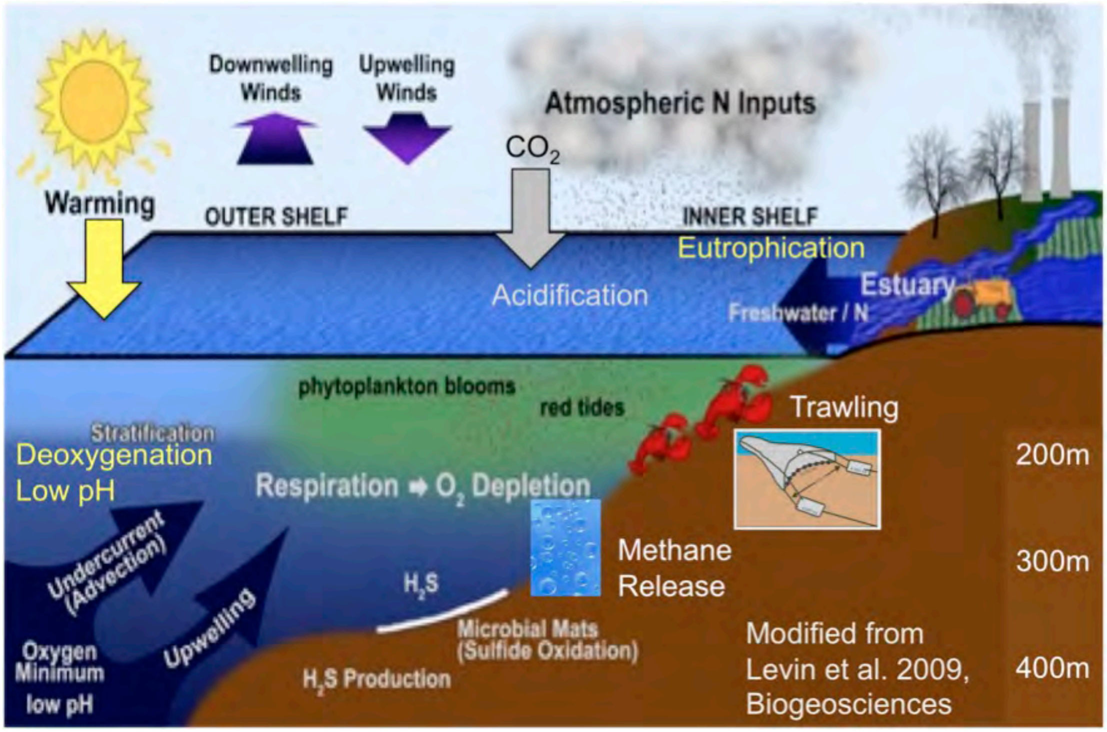

Figure 6-10: Diagram schematizing the principal mechanisms underlying the formation of hypoxic conditions along continental margins (modified from Levin *et al*., 2009; Levin and Sibuet, in prep., Ann. Rev. Mar. Sci.).
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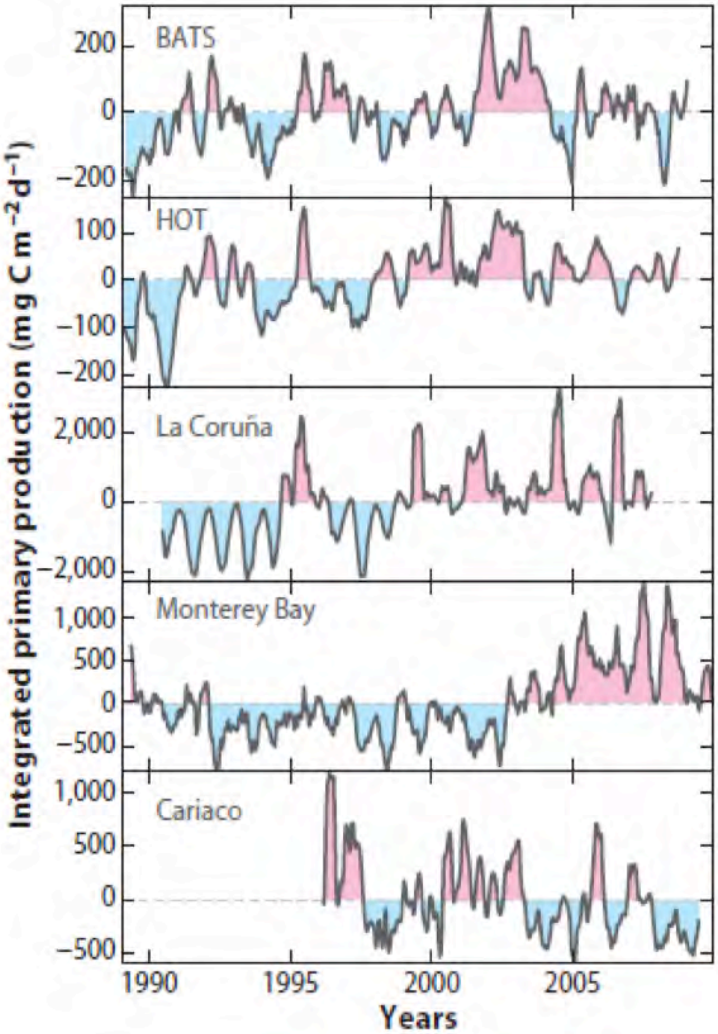

Figure 6-11: Time-series of water column integrated primary production (PP) anomalies for time-series sites: Northwestern Spain, La Coruña (43◦ 25.2 N, 8◦ 26.4 E); HOT (22◦ 45 N, 158◦W); BATS (31°50 N, 64°10 W); Monterey Bay, Central California Current (37°N, 122°W); Cariaco Basin, Venezuela (10°30 N, 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.

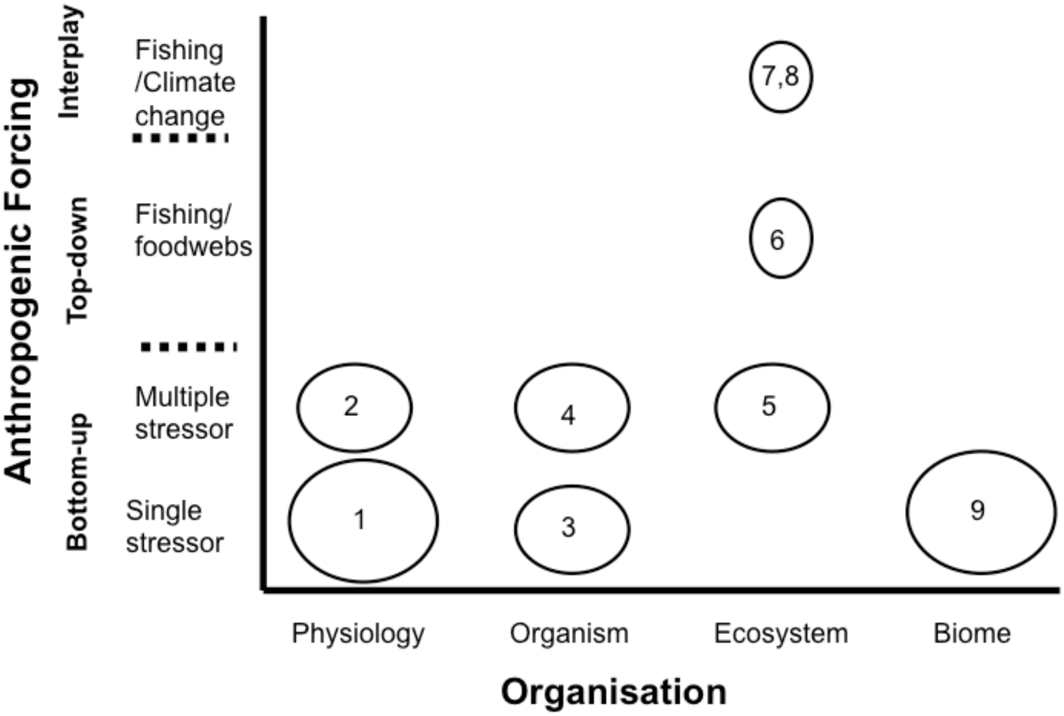

Figure 6-12: A schematic highlighting the potential interactions between modes of anthropogenic forcing on different levels of biological organisation. These interactions, from simple to complex, are illustrated with published examples and each is assigned a circle to indicate our degree of confidence in the findings of the study, ranging from low for modelling studies such as (8; Griffith *et al.*, 2011) to large for lab physiological studies placed into context of field data (1; Pörtner and Knust, 2007). The space populated by the circles points to the extent of our understanding of this relationship between forcing and its effect on organisational level. 1 denotes the effects of a single stressor - warming on alteration of organismal physiology and field abundance (Pörtner and Knust, 2007); 2 the synergistic effects of multiple stressors - warming and increased [CO_2] on coccolithophore calcification (Feng *et al.*, 2009); 3 a single stressor - altered pH and the different responses of coccolithophore species (Langer *et al.*, 2006); 4 differential responses of cyanobacterial groups to multiple stressors - warming and increased [CO_2] (Fu *et al.*, 2007); 5 differential effect of multiple stressors, light and temperature, on copepods versus diatoms (Lewandowska and Sommer, 2010); 6 the effect of fishing on ecosystem structure (Frank *et al.*, 2005); 7 the interplay of fishing pressure and climate change on ecosystems (Kirby *et al.*, 2009); 8 the interplay of ocean acidification and fishing pressure on benthic communities (Griffith *et al.*, 2011); 9 detailed time-series observations on warming and the alteration of zooplankton biomes (Beaugrand *et al.*, 2009).
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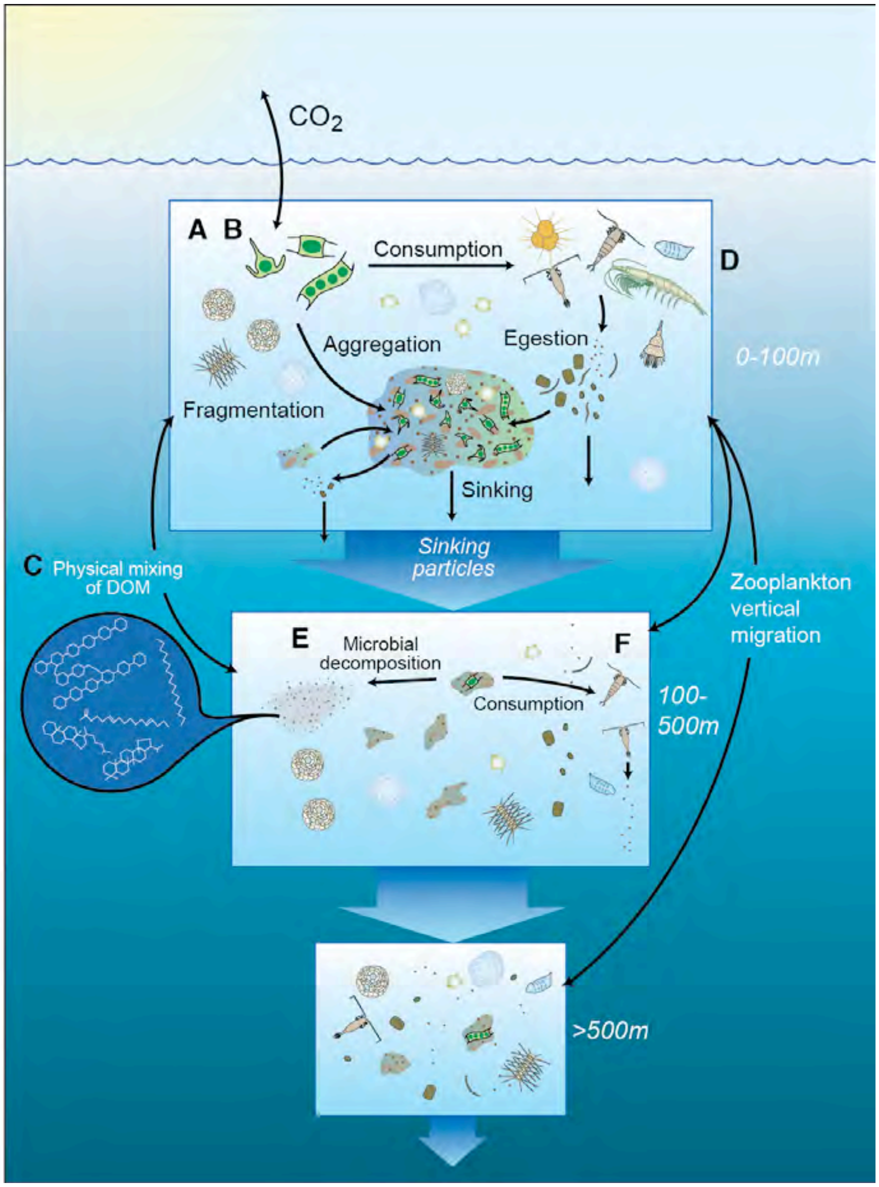

Figure 6-13: A schematic representation of the ocean's biological pump, an important conduit for carbon sequestration. In a changing climate it is difficult to predict how the pump might be altered and hence whether it would represent a positive or negative feedback to climate change. Factors reported to be altered by a changing climate include: A, changes to NPP (Bopp *et al*., 2002); B, floristic and faunistic shifts in the pelagical (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 (Engel *et al*., 2004); E, warming and faster bacterial enzymatic rates of particle solubilisation (Christian and Karl, 1995); and faunistic shifts at depth (Jackson and Burd, 2001). Figure modified from Buesseler *et al*. (2008) by J. Cook (WHOI).