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The Oceans 2015 Initiative, Part I

An updated synthesis of the observed and projected impacts of climate change on physical and biological processes in the oceans

Ella L. Howes (Alfred Wegener Institut), Fortunat Joos (University of Bern), Mark Eakin (National Oceanic and Atmospheric Administration), Jean-Pierre Gattuso (Laboratoire d'océanographie de Villefranche-sur-Mer, CNRS-UPMC)

GREENHOUSE GASES: THE EFFECTS ON CHEMICAL AND PHYSICAL PROCESSES OF THE OCEANS

The oceans have absorbed approximately 93% of the excess heat caused by global warming. Warming increases stratification, limiting the circulation of nutrients from deep waters to the surface. There is evidence that enhanced stratification and increasing temperature are causing a decline in dissolved oxygen concentration and expanding existing oxygen minimum zones (OMZs). Approximately 26% of anthropogenic CO₂ is absorbed by the oceans, resulting in a reduction in pH and carbonate ion concentration, termed ocean acidification. Anthropogenic CO₂ has caused global ocean pH to decrease by 0.1 units since the start of the Industrial Revolution.

CHANGING OCEANS: THE EFFECTS ON BIOLOGICAL PROCESSES

The ocean ecosystems are responding to the changing environment, but at different rates and magnitudes and with interspecific and geographic variation in responses. Warming causes shifts in species' geographic distribution, abundance, migration patterns and phenology. Organisms that produce shells and skeletons from calcium carbonate are at most risk from ocean acidification as it lowers the saturation state of the mineral, favouring a dissolution reaction. To date, there are few observations of ocean acidification effects in natural communities; however, experimental evidence suggests that the risk to ecosystems will increase over the coming decades. Decreasing dissolved oxygen concentrations and expanding OMZs will favour anaerobic metabolisers such as bacteria and small microbes whilst reducing habitat for larger, oxygen dependant organisms.

WHAT DOES THE FUTURE HOLD FOR OCEAN ECOSYSTEMS?

The interaction of multiple drivers can amplify or alleviate each other's effects. It is likely that marine organisms will experience a combination of warming, acidification and declining oxygen concentrations as well as regionally specific local stressors. This makes it difficult to predict the responses of individual species to multiple drivers, and species interactions make ecosystem-based projections challenging. Using the available evidence, projections have been constructed of the potential impacts on ocean ecosystems by 2100, under two the Representative Concentration Pathways RCP4.5 and 8.5.

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1. INTRODUCTION

1.1. Major findings from the IPCC's WGI and WGII of AR5

Working Groups I and II (WGI and WGII) of the Intergovernmental Panel on Climate Change's (IPCC's) Fifth Assessment Report (AR5) synthesized research regarding observed and projected impacts of climate change on physical and biological processes in the oceans, at both global and regional levels. The impacts of these changes on human health and socio-economics were also discussed (see Cheung *et al.*, 2015).

Key findings on physical processes in the oceans highlighted, with an extremely high certainty, that the upper ocean had warmed over the last 40 years and predicted with *very high confidence* that this trend would continue over the coming century (Rhein *et al.*, 2013, Ciais *et al.*, 2013). It was considered *very likely* that this increase in temperature had contributed to significant global mean sea level rise (Rhein *et al.*, 2013). High agreement amongst data provided evidence that stratification caused by increasing sea temperatures has caused declining seawater oxygen concentrations (Rhein *et al.*, 2013). The report expressed high confidence that the oceans are absorbing anthropogenic carbon and that the resulting chemical reactions cause ocean acidification (Rhein *et al.*, 2013, Ciais *et al.*, 2013).

Key findings on biological processes highlighted the effect of increasing sea temperatures on the geographical distributions of organisms with observations lending evidence to poleward migrations of species (Pörtner *et al.* 2014, Poloczanska *et al.* 2014). Temperature was also shown to be affecting the timing of life history events such as reproductions and migration. Net primary productivity (NPP) was projected to decrease moderately by

2100 in the open ocean under both low- and high-emission scenarios, paralleled by an increase in NPP at high latitudes and a decrease in the tropics (Pörtner *et al.* 2014, Hoegh-Guldberg *et al.*, 2014). Despite a lack of field observations, ocean acidification was predicted to have a significant effect on many aspects of organisms' physiology, behavior and population dynamics (Pörtner *et al.* 2014). There was medium confidence that expansion of suboxic zones would benefit anaerobic microbes and limit oxygen dependent species (Pörtner *et al.* 2014). There was high confidence that the various environmental drivers would act simultaneously on organisms causing complex, interacting effects (Pörtner *et al.* 2014).

1.2. Key uncertainties remaining from AR5

AR5 identified key uncertainties regarding potential climate-related impacts on biological and physical systems. In particular, AR5 highlighted a need for an updated understanding regarding the following aspects:

- The extent of warming in deep water masses (below 700 m).
- While acknowledged as a critical process influencing ecosystem productivity, the likelihood of climate-induced changes to major upwelling systems (i.e., increased or decreased upwelling) was still uncertain (Lluch-Cota *et al.* 2014).
- Ways in which climate-induced changes in the physiology and biogeography of an individual species may alter ecosystem structures, species interactions, and food webs (Pörtner *et al.*, 2014).
- An improved understanding of climate sensitivity at the ecosystem level that considers multiple drivers (e.g., ocean warming, acidification, and hypoxia) and synergistic impacts (Pörtner *et al.*, 2014; Wong *et al.*, 2014).

- The degrees to which species can track changes in climate as well as the influence of multiple stressors on their capacities to respond remained uncertain (Poloczanska *et al.* 2014).
- The capacity for phenotypic and evolutionary adaptation over generations to respond to long-term climate change (Pörtner *et al.* 2014).

1.3. Study objectives

The objective of this report is to review existing knowledge published following AR5 and update our understanding of the observed and projected impacts of climate change on coastal physical and biological processes. The report endeavours to highlight key developments with respect to our scientific understanding of the relationships between different anthropogenic and climatic drivers on marine ecosystems. Lastly, the review calls attention to areas of agreement with, and points of departure from, AR5.

2. PHYSICAL SCIENCE

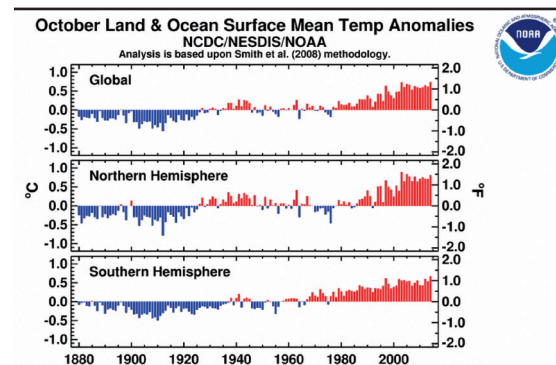
2.1. Earth climate and greenhouse gases

Earth’s climate and radiative forcing is strongly influenced by the atmospheric concentrations of greenhouse gases, mostly, carbon dioxide (CO₂), methane (CH₄) and nitrous oxide (N₂O). Since the start of the Industrial Era (1750 onwards), anthropogenic activities have resulted in increased concentrations of greenhouse gases and it is now *virtually certain* (for clarification on the language of certainty, see Annex 1) that atmospheric concentrations of greenhouse gases are at their highest in the last 800,000 years (Ciais *et al.*, 2013). Concentrations of CO₂, CH₄ and N₂O rose by 40, 150 and 20%, respectively, between 1970 and 2011. Accumulation of these gases in the atmosphere act to increase radiative forcing and, of the three, CO₂ has the greatest effect (Ciais *et al.*, 2013). This has resulted in a measureable increase in global air and sea temperatures (Fig. 1), with the beginning of the 21st century having the warmest years on record since 1880 (Ipcc, 2013; Table 1.1).

Prior to anthropogenic perturbation, concentrations of atmospheric CO₂ have been relatively stable over the last 800,000 years, oscillating between 180 ppm during glacial periods and 300 ppm during interglacial periods (Ciais *et al.*, 2013). Between 1750 and 2011, atmospheric CO₂ levels have risen from 278 ppm to 390.5 ppm, which corresponds to a mass of 236 Pg C (Ciais *et al.*, 2013). Total anthropogenic emissions between 1750 and

2011 amounted to 555 ± 85 Pg C (Ciais *et al.*, 2013). During this period, the burning of fossil fuels was the major contributor to total emissions, releasing 375 ± 30 Pg C, inclusive of emissions resulting from cement production of 8 Pg C (Ciais *et al.*, 2013). Changes to land use, mainly deforestation, have contributed to an increase in atmospheric CO₂ of 180 ± 80 Pg C (Ciais *et al.*, 2013). The IPCC AR5 states with *very high confidence* that the burning of fossil fuels and land use changes are the dominant cause of the increase in atmospheric CO₂ concentrations (Ciais *et al.*, 2013). Currently, anthropogenic emissions continue to rise; however, it depends on policy choices and socio-economic developments as to how carbon emissions and thus, atmospheric CO₂ will evolve in the 21st century. Several different emissions scenarios have been devised for use in model simulations to project environmental conditions over this century. These scenarios are referred to as representative concentration pathways (RCPs; see Annex 2) and are used by scientists as a standardised set of scenarios to allow a robust comparison of results from model simulations.

Figure 1. Global temperature anomaly means for October 2014



Source: <http://www.ncdc.noaa.gov/sotc/global/2014/11#temp>.

Note: Data are blended land and ocean values, calculated on a monthly and annual time scale. Blue bars indicate negative mean temperature anomalies, red bars represent positive temperature anomalies.

Table 1. List of the 10 warmest years between 1880-2013

Rank. 1 = warmest	Year	Anomaly (°C)
1	2010	0.66
2	2005	0.65
3	1998	0.63
4 (tie)	2013	0.62
4 (tie)	2003	0.62
6	2002	0.61
7	2006	0.60
8 (tie)	2009	0.59
8 (tie)	2007	0.59
10 (tie)	2004	0.57
10 (tie)	2012	0.57

Source: www.ncdc.noaa.gov/sotc/global/2013/13

2.2. Carbon in the oceans

A portion of the Earth's total carbon is stored in the ocean reservoir. Prior to the Industrial Revolution, this reservoir was in a relatively steady state, with a mass of approximately 38,000 Pg C in the form of dissolved inorganic carbon (DIC), 700 Pg C in the form of dissolved organic carbon (DOC), 3 Pg C as marine biota and 1,750 Pg C in ocean floor surface sediments. The ocean carbon inventory is more than 60 times larger than the inventory of the preindustrial atmosphere and oceanic processes set the natural CO₂ concentration of the atmosphere. Three major cycles or “pumps” control the surface-to-deep gradient of carbon and many other elements in the ocean (Volk & Hoffert, 1985) the solubility pump, the calcium carbonate pump and the organic matter pump (Ciais *et al.*, 2013). Generally, the ocean surface is depleted in carbon and nutrients relative to deep waters by the action of these three cycles. Consequently, the atmospheric CO₂ concentration is lower compared to a hypothetical ocean in which the concentration of carbon and other elements would be uniformly distributed and these pumps would not operate.

The solubility pump refers to the spatial distribution of temperature and CO₂ solubility; as CO₂ is more soluble in cold than warm water, the cold deep ocean is enriched in carbon relative to the warm surface waters. Similarly, marine organisms contribute, together with ocean circulation, to establish a deep ocean enrichment in carbon and other nutrients. Marine organisms assimilate carbon and other nutrients to form organic material and shells of calcium carbonate that are eventually transformed into non-living particles. This results in flux of organic carbon and calcium carbonate from the surface to the deep ocean where the majority of this particle-bound carbon is remineralized and turned back into dissolved inorganic carbon and nutrients. At steady state, the export of carbon and nutrients in biogenic material is balanced by upwelling of inorganic carbon and nutrients, resulting in closed cycles. The efficiencies of these pumps are governed by the decadal to century time scales, governing ocean overturning. On shorter time scales changes in wind speeds, upwelling events and natural climate variability such as El Niño, La Niña and the Pacific Decadal Oscillation also affect the flux of CO₂ between the atmosphere and the oceans (Ciais *et al.*, 2013).

In contrast to these approximately balanced cycles, the uptake of excess anthropogenic carbon by the ocean is predominantly a physico-chemical process. Excess CO₂ dissolves in surface waters and reacts to form bicarbonate and carbonate ions. This well-known carbonate chemistry, together with

the ocean volume, sets the capacity of the ocean to absorb excess CO₂ towards a new equilibrium with atmospheric CO₂. The dissolved inorganic carbon is transported by physical mechanisms such as large-scale advection, eddy mixing and convection to the ocean interior. This is the rate limiting step for the uptake of anthropogenic carbon as it takes decades to centuries to exchange deep waters with surface waters. The ventilation time scales of the ocean are quantitatively well understood thanks to the observed penetration of bomb-produced radiocarbon and industrially produced chlorofluorocarbons, as well as from the distribution of natural radiocarbon within the ocean. Perturbations in the three pumps discussed above, e.g. through changes in ocean circulation and biological processes, represent a feedback and can influence the uptake of excess CO₂ in addition to the first order physico-chemical process.

2.3. Observed and projected changes in the oceans

The accumulation of greenhouse gases in the atmosphere and the oceans produces widespread, global, and long-lasting physical changes in the ocean environment. These changes are summarised below, focusing on those that are anticipated to have the greatest effect on organism and ecosystem functioning.

2.3.1. Carbon uptake

The ocean acted as a net source of CO₂ to the atmosphere during the Holocene Era (the last 11,700 years). The situation has, however, reversed with modern oceans now acting as a net sink of CO₂. It is *virtually certain* that the oceans have sequestered 155 ± 30 Pg C (28% of total anthropogenic emissions) of anthropogenic CO₂ since the Industrial Revolution, *very likely* at a rate of between 0.1 and 3.2 Pg C yr⁻¹ (Ciais *et al.*, 2013). The increased CO₂ absorbed by the ocean is in response to the increasing concentrations of CO₂ in the atmosphere. Without ocean uptake, atmospheric CO₂ would be much higher, thus the oceans play an important role in mediating global climate change effects (Ciais *et al.*, 2013).

Model projections show that an increase in atmospheric CO₂ will always lead to an increase in ocean carbon storage, all other things being held constant (Ciais *et al.*, 2013). The proportion of carbon that remains in the atmosphere will increase with increasing input of carbon in the atmosphere-ocean system as the oceans' buffer capacity diminishes (Ciais *et al.*, 2013). The excess carbon will continue to invade the ocean for centuries, perturbing dissolved inorganic carbon (DIC), the

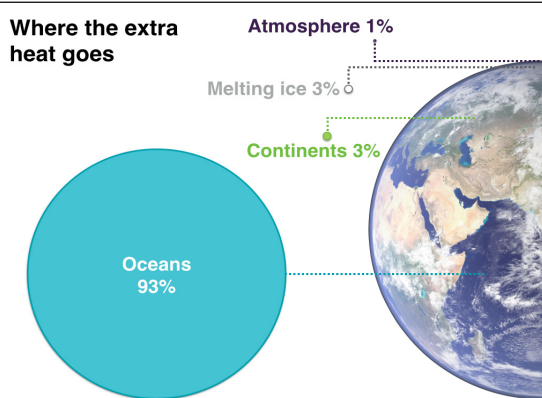
partial pressure of pCO₂ in seawater and pH, also in the deep oceans (Ciais *et al.*, 2013). Model projections show a widespread increase of CO₂ in the upper mixed layer from 0.1–0.2 mol m⁻³ in year 1990 to 0.2–0.4 mol m⁻³ in year 2100 under a high emissions scenario (Cocco *et al.*, 2013).

2.3.2. Warming

2.3.2.1. Upper Ocean (0-700 m)

There is *high confidence* that the ocean has absorbed the majority of the increasing amounts of energy trapped in the atmosphere by the increasing concentrations of atmospheric greenhouse gases (Rhein *et al.*, 2013). There is *high confidence* that 93% of the excess heat in Earth’s energy inventory from 1971 and 2010 ended up in the oceans. As a result of these processes, the upper (0 to 700 m) ocean has warmed, which accounts for about 64% of the total warming occurring in the ocean (Fig. 2; Rhein *et al.*, 2013).

Figure 2. The fate of the increasing heat that is trapped in the atmosphere by greenhouse gases.



Source: modified from <http://bit.ly/ipccceans>.

Note: Between 1971 and 2010, there is *high confidence* that the oceans have absorbed approximately 93% of the heat from global warming. The remaining 7% can be accounted for in warming of the continents (3%), melting ice caps (3%) and atmospheric warming (1%).

Conventionally, sea surface temperature is a variable that can be measured accurately with a minimum of technology. Due to the large number of measurements dating back significantly history, there is a high degree of certainty associated with surface ocean temperature observations. These measurements have been contributed to by high accuracy measurements from remote sensing by satellites. The upper ocean has warmed between 1971 and 2010; globally averaged increases from 0-200 m between 1971-2010 are 0.25°C (Rhein *et al.*, 2013). Warming has occurred at all depths but is most pronounced at the surface; during the same period, temperatures in the upper 75 m

are estimated to have increased by ~ 0.11°C decade⁻¹ (Rhein *et al.*, 2013). It is also *very likely* that warming was occurring earlier, between the 1870’s and 1971 (Rhein *et al.*, 2013). As for temperature, it is also *virtually certain* that the heat content of the upper oceans has also increased (Rhein *et al.*, 2013). Estimates for the heating rate between 1971-2010 vary between 74 and 137 Terawatts (TW; Rhein *et al.*, 2013).

The 2000’s were the warmest decade on record with the 1990’s being the second warmest (Goddard, 2014, Trenberth & Fasullo, 2013). However, several estimates used in the IPCC AR5 (3 out of 5) reported that the increase in upper ocean heat content seems to have slowed between 2003-2010, as, compared to the previous decades (Rhein *et al.*, 2013). These findings could be artefacts of a change in observation methods but it has also been suggested that there may be an impact of large scale, natural climate variability, a reduced radiative forcing, or a smaller warming response to atmospheric carbon dioxide concentrations (Lewis, 2013). The central and eastern Pacific are the areas which have exhibited the greatest slowing in the warming trend (Trenberth *et al.*, 2014) and it has been suggested that the negative phase of the Pacific decadal oscillation (PDO) may be responsible for this (Goddard, 2014, Trenberth & Fasullo, 2013, Trenberth *et al.*, 2014). Two recent studies suggest that the warming hiatus is caused by heat transported to deeper layers in ocean basins, although there is debate which basins, although are the main drivers (Chen & Tung, 2014, Trenberth *et al.*, 2014).

A recent study (Durack *et al.*, 2014) suggested that the IPCC AR5 estimates for increases in ocean heat content might be biased toward low values as a result of the relatively limited sampling of the Southern Hemisphere compared to the Northern Hemisphere. When satellite observations of sea surface height are used a model parameter to calculate changes in ocean heat content, the results show a more homogeneous warming, with larger magnitudes in the South Pacific and South Atlantic basins compared to IPCC estimates. The results yielded an increase in global upper ocean heat content of 2.2 to 7.1 × 10²² J above existing estimates for 1970 to 2004.

Based on the evidence presented in the IPCC AR5, it is considered *virtually certain* that the upper ocean has warmed during the last 40 years and *likely* that warming occurred from the beginning of the 20th Century (Rhein *et al.*, 2013). It is *very likely* that the warming trend has increased the stratification of upper 200 m of the oceans by about 4% during the period 1971-2010; in turn there is *medium confidence* that this has reduced

the dissolved oxygen concentration and decreased the availability of inorganic nutrients, limiting photosynthesis (Rhein *et al.*, 2013).

Regionally, the average sea surface temperature (SST) of the Indian, Atlantic and Pacific Oceans have increased by 0.65, 0.41 and 0.31 °C, respectively, between 1950 and 2009 (Hoegh-Guldberg *et al.*, 2014). There is *high confidence* that sea surface temperatures of in sub-tropical gyres of the Atlantic, Pacific, and Indian Oceans have increased (Hoegh-Guldberg *et al.*, 2014). In the Indian Ocean, there is *medium confidence* that the majority of the warming trend (90%) can be attributed to external forcing, of this 98.8% is thought to result from anthropogenic CO₂ (Dong *et al.*, 2014). Average sea temperatures have increased between 1950 and 2009 by 0.43 and 0.54 °C in the Pacific and Atlantic equatorial upwelling systems, respectively (Hoegh-Guldberg *et al.*, 2014). In the North Atlantic it is *likely* that surface waters have warmed by 0.07 °C decade⁻¹ between 1950 and 2009, causing an increase in sea temperature of 0.44 °C (Hoegh-Guldberg *et al.*, 2014), which has been suggested to be a contributing factor to the retreat of the Greenland ice sheet (Straneo & Heimbach, 2013).

Warming can be observed in all the sub-regions of coastal boundary systems (CBS), overall, CBS warmed by 0.14–0.80 °C from 1950–2009 (Hoegh-Guldberg *et al.*, 2014). Key sub-regions within the CBS such as the Coral Triangle and Western Indian Ocean warmed by 0.79 and 0.60 °C, respectively, from 1950–2009 (Hoegh-Guldberg *et al.*, 2014). It is *very likely* that the Gulf of Mexico and Caribbean Sea have warmed by 0.31 °C and 0.50 °C, respectively from 1982–2006 (Hoegh-Guldberg *et al.*, 2014). Variance in SST in many of the semi-enclosed seas is dominated by oscillations of large-scale climate modes, however all semi enclosed seas exhibit significant warming from the mid 1980's to 2009 (Hoegh-Guldberg *et al.*, 2014).

The Arctic Ocean has exhibited one of the strongest (but variable) warming trends. In areas where the warming trend is high, a novel study using isotope proxy analysis found up to 3.7 °C increase between 1920 and 2011. This is approximately 6 times higher than the observed global warming trend and double the previously suggested rate of warming for the area (Brand *et al.*, 2014). Conversely, observed SST measurements have decreased in the Southern Ocean, particularly around sea ice margins. One hypothesis is that runoff from melting shelf ice is cooling and freshening surface waters in the surrounding areas (Bintanja *et al.*, 2013).

2.3.2.2. Deep Ocean (below 700 m)

The uncertainties when assessing warming in the deep ocean are much higher than for the surface

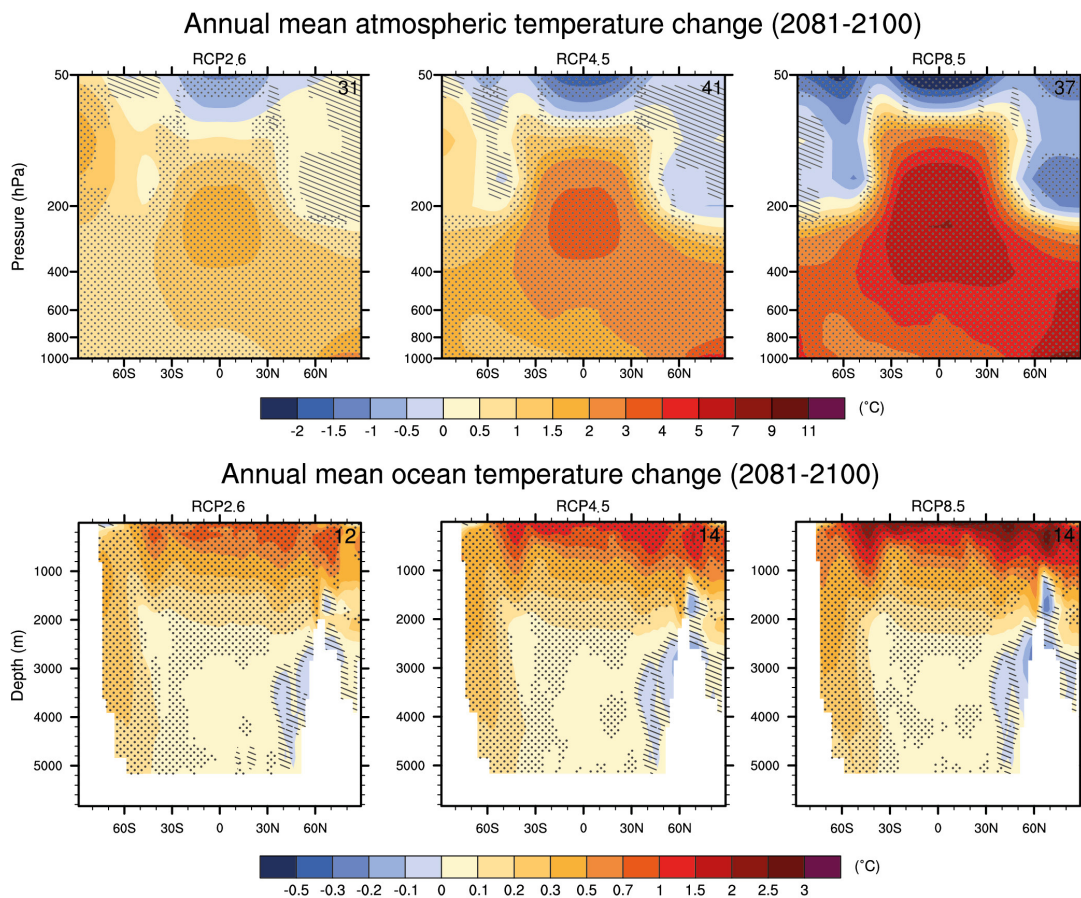
ocean due to under sampling. Before 2005, the data are too sparse to produce reliable estimates for annual global changes in temperature and ocean heat content. Studies confirm warming between 0 and 1500 m since 2005 and it is *likely* that waters between 700 and 2000 m have warmed, on average between 1957 and 2009 (Rhein *et al.*, 2013). A recent estimate suggested that, in the last decade, about 30% ocean warming has occurred below 700 m, contributing significantly to an acceleration of the warming trend (Balmaseda *et al.*, 2013). Conversely, it is *likely* that there has been no significant global warming trend between 2000 and 3000 m (1992–2005), although steep vertical gradients and water mass movements confound sparse sampling at mid-depths (Rhein *et al.*, 2013). Globally, waters from 3000 m to the bottom are thought likely to have experienced a warming trend greater than zero (Rhein *et al.*, 2013).

Some regions are better sampled than others allowing a more detailed assessment of temperature changes. It is *very likely* that N. Atlantic deep waters below 2000 m have warmed between 1955 and 1975, then cooled between 1975 and 2005 with a net cooling trend of -4 TW between 1955–2005 (Rhein *et al.*, 2013). It is considered *likely* that waters of Antarctic origin have warmed below 3000 m by 0.01 °C decade⁻¹ between 1992–2005 and that waters south of the Sub-Antarctic polar front have warmed by 0.03 °C decade⁻¹ for the same period (Rhein *et al.*, 2013). Improving observations of ocean heat content for the deep ocean are important for a better understanding of the fate of surface warming and may help to better understand the role of natural variability, e.g., as expressed in the recent hiatus in global mean surface air temperature (Goddard, 2014).

Based on the information presented in IPCC AR5, it is clear that there are variations in temperature and ocean heat content trends below 700 m, depending on the depth, region and water mass movements (Rhein *et al.*, 2013). Estimates are severely hampered by a lack of data, however a global estimate suggests an increase of 35 TW below 2000 m between 1992 and 2005. Warming of deep waters is thought to be particularly strong in the Southern Ocean (Rhein *et al.*, 2013) with a rate of up to 0.05 °C decade⁻¹ (Patara & Böning, 2014). The warming of deep Antarctic waters, may, in turn, strengthen the large-scale meridional overturning of the Atlantic Ocean (Patara & Böning, 2014).

There is considerable debate as to whether or not climate change will drive an intensification of upwelling in all upwelling regions in agreement with Bakun's 1990 hypothesis (see Annex 3; Hoegh-Guldberg *et al.*, 2014). There is *robust evidence* and *medium agreement* that the California Current

Figure 3. CMIP5 multi-model changes in annual mean zonal mean temperature in the atmosphere and ocean relative to 1986–2005 for 2081–2100 under the RCP2.6 (left), RCP4.5 (centre) and RCP8.5 (right) forcing scenarios.



Source: Collins *et al.*, 2013.

Note: Hatching indicates regions where the multi model mean is less than one standard deviation of internal variability. Stippling indicates regions where the multi model mean is greater than two standard deviations of internal variability and where 90% of the models agree on the sign of change.

has experienced a decrease in the number of upwelling events (23 to 40%), but *high confidence* that there has been an increase in the intensity of upwelling events between 1967 and 2010 (Hoegh-Guldberg *et al.*, 2014). In the Canary Current, there is *low agreement* on whether the strength of the upwelling has intensified over the last 60 years (Hoegh-Guldberg *et al.*, 2014). Meta analysis of upwelling favourable wind intensification over the last 60 years found an intensification over the California, Benguela, and Humboldt upwelling systems but produced inconclusive results for the Canary Current System (Sydeman *et al.*, 2014).

2.3.2.3. Warming; future projections

Despite the recent hiatus in the global mean surface air temperature trend, the consensus is that this can be attributed to natural variability and ocean heat content continues to increase again (Goddard, 2014, Huber & Knutti, 2014, Schmidt

et al., 2014b, Trenberth & Fasullo, 2013, Trenberth *et al.*, 2014). Projections of warming in the oceans show very little difference between RCP scenarios over the next couple of decades with differences starting to appear towards the end of the century (Fig. 3; Ciais *et al.*, 2013). Model projections of surface ocean warming are projected to be $+2.73 \pm 0.72$, $+1.58 \pm 0.48$, $+1.28 \pm 0.56$ and $+0.71 \pm 0.45$ °C for RCP8.5, RCP6.0, RCP4.5 and RCP2.6, respectively, by the end of the 21st century (Bopp *et al.*, 2013).

High variability is projected for future SSTs: the strongest warming trends are predicted in the Arctic Ocean, the tropics and the North Pacific with increases larger than 4 °C in all 3 regions, under scenario RCP8.5 (Bopp *et al.*, 2013). There is *high confidence* that strongest warming for the surface ocean will occur in the tropical and Northern Hemisphere in subtropical regions (Ciais *et al.*, 2013).

For deep waters warming of between 0.3 °C

(RCP 2.6) to 0.6°C (RCP 8.5) are projected (Ciais *et al.*, 2013). Depending on the emission scenario, global ocean warming between 0.5°C (RCP2.6) and 1.5°C (RCP8.5) will reach a depth of about 1 km by the end of the century (Ciais *et al.*, 2013). For deep waters, there is *high confidence* that the largest warming will occur in the Southern Ocean (Ciais *et al.*, 2013).

Warming also increases stratification and it is considered *very likely* that continued warming will continue to increase thermal stratification (Ciais *et al.*, 2013). This has the potential to impact the availability of inorganic nutrients to surface waters. It is thought *likely* that the response will vary from region to region as complex systems govern these water mass movements (Ciais *et al.*, 2013). Intensification of upwelling is predicted in the Southern Ocean, however there is *low confidence* in the current understanding of how eastern upwelling systems will be altered under future climate change (Ciais *et al.*, 2013). In the Benguela Current there is *medium agreement* and *limited evidence*, that upwelling will change as a result of climate change (Hoegh-Guldberg *et al.*, 2014). It is considered *likely* that warming in the Atlantic equatorial upwelling systems will weaken upwelling (Hoegh-Guldberg *et al.*, 2014).

2.3.3. Sea level rise

Sea level varies relative to changes in temperature (thermoelectric sea level rise) and fluxes of water between the oceans and the continents and ice sheets (mass sea level rise). Global mean sea level (GMSL) has risen by 0.19 ± 0.02 m over the period 1901–2010 (Fig. 4; Rhein *et al.*, 2013). It is very likely that the mean rate was 1.7 ± 0.2 mm yr⁻¹ between 1901 and 2010 and increased to 3.2 ± 0.4 mm yr⁻¹ between 1993 and 2010¹. Ocean thermal expansion and melting of glaciers have been the largest contributors, accounting for over 80% of the global mean sea level rise over the latter part of the time series (Church *et al.*, 2013). Although records for the deep sea are sparser, it is possible to estimate that warming below 2000 m contributed 0.1 [0.0 to 0.2] mm yr⁻¹ to global mean sea level rise between about 1992 and 2005 (Rhein *et al.*, 2013). The component of sea level rise that is attributed to changes in fluxes of water between the oceans and the continents and ice sheets has been increasing at a rate between 1 and 2 mm yr⁻¹ since 2002 (Rhein *et al.*, 2013).

There is *very high confidence* that there is high regional variability in sea level rise with relative sea level rise sometimes exceeding global mean sea level rise by an order of magnitude, reaching more than 10 cm yr⁻¹ (Church *et al.*, 2013). This variation is partly due to fluctuations in ocean circulation, tectonic activity and interactions with

climate mode variability such as the ENSO in the Pacific (Church *et al.*, 2013a). Anthropogenic activities such as oil and gas extraction and changes to the coastal sediment delivery *via* damming or consolidation from building work have also contributed to localized changes in relative sea level (Church *et al.*, 2013a). Sea level rise in coastal boundary systems is variable but, in some regions, has risen by up to 10 mm yr⁻¹ between 1950 and 2009 (Hoegh-Guldberg *et al.*, 2014). In the Pacific, changes in sea level have been highly variable, in the warm pool of the western Pacific, rates of sea level rise are up to three times higher than the global average (Rhein *et al.*, 2013), while the eastern equatorial Pacific has been declining by -10 mm yr⁻¹ (Hoegh-Guldberg *et al.*, 2014).

► Sea level rise: future projections

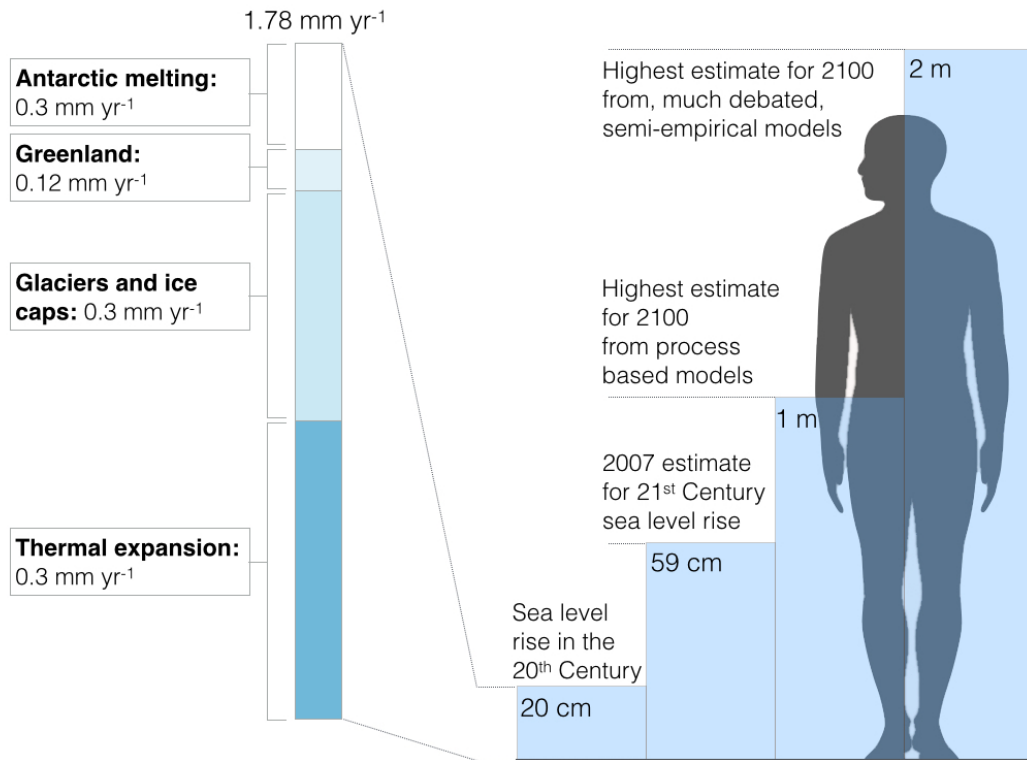
It is *virtually certain* that sea level rise will continue beyond the 21st Century (Fig 4; Church *et al.*, 2013). Future rates of GMSL rise over the 21st century are projected to exceed the observed rate for the period between 1971 and 2010 of 2.0 ± 0.3 mm yr⁻¹ (Church *et al.*, 2013) for all RCP scenarios. However there is *low agreement* on the projected magnitude of sea level rise due to the use of different models, some of which take into ice sheet dynamics (Church *et al.*, 2013). The IPCC AR5 predicts with *medium confidence* that the mean sea level rise will be 0.44m under RCP2.6, 0.53 m under RCP4.5, 0.55 m under RCP6.0, and 0.74 m under RCP8.5 (Church *et al.*, 2013). Higher amounts of sea level rise and a more recent study suggested it *very likely* that GMSL would reach 0.5–1.2m under RCP8.5 and 0.4–0.9 m under RCP4.5 (Kopp *et al.*, 2014).

2.3.4. Oxygen

Due to the solubility effect, warmer waters contain less dissolved oxygen. Increased stratification, as a result of warming, decreases ventilation of water masses, also causing decreased oxygen concentration. When O₂ concentrations are below 60 μmol kg⁻¹ conditions become hypoxic, when O₂ concentrations are lower than 4.5 μmol kg⁻¹, waters are termed suboxic and waters without dissolved oxygen are termed anoxic (Fig 5; Pörtner *et al.*, 2014).

The availability of oxygen is key for biological functions. There is *medium confidence* that dissolved O₂ concentrations have generally decreased since 1960 but with strong regional variations (Rhein *et al.*, 2013). The mean annual global oxygen loss during 1970–1990 between 100–1000 m is calculated as $0.55 \pm 0.13 \times 10^{14}$ mol yr⁻¹ (Rhein *et al.*, 2013). Stratification-induced, reduced ventilation is thought to be the major cause of this decline with solubility effect accounting for only 15% of the decrease (Rhein *et al.*, 2013). Naturally

Figure 4. The origins of the “extra” water causing sea level rise and the extent of current and projected sea level rise by the end of the century.



Source: Modified from Jones (2013).

occurring, periodic hypoxic events may be exacerbated by climate change (Rhein *et al.*, 2013).

Decreases in O₂ concentrations have been observed over the last 50 years in tropical basins (-2 to -3 μmol kg⁻¹ decade⁻¹), the subpolar North Pacific and below the thermocline in the southern Indian Ocean east of 75°E (Hoegh-Guldberg *et al.*, 2014). Over the same period, O₂ concentrations decreased in North Atlantic surface waters but increased in intermediate waters (Hoegh-Guldberg *et al.*, 2014). Conversely, it increased in the thermocline in the Indian Ocean and South Pacific Oceans between the 1990's and 2000's (Hoegh-Guldberg *et al.*, 2014). Results for the Southern Ocean are contradictory depending on region and time period and require further clarification (Rhein *et al.*, 2013). Along the continental shelf, large regions of the Eastern Pacific are low in dissolved oxygen and oxygen minimum zones (OMZ) are found at around 300 m depth (Hoegh-Guldberg *et al.*, 2014). The depths of OMZ are often associated with low pH waters.

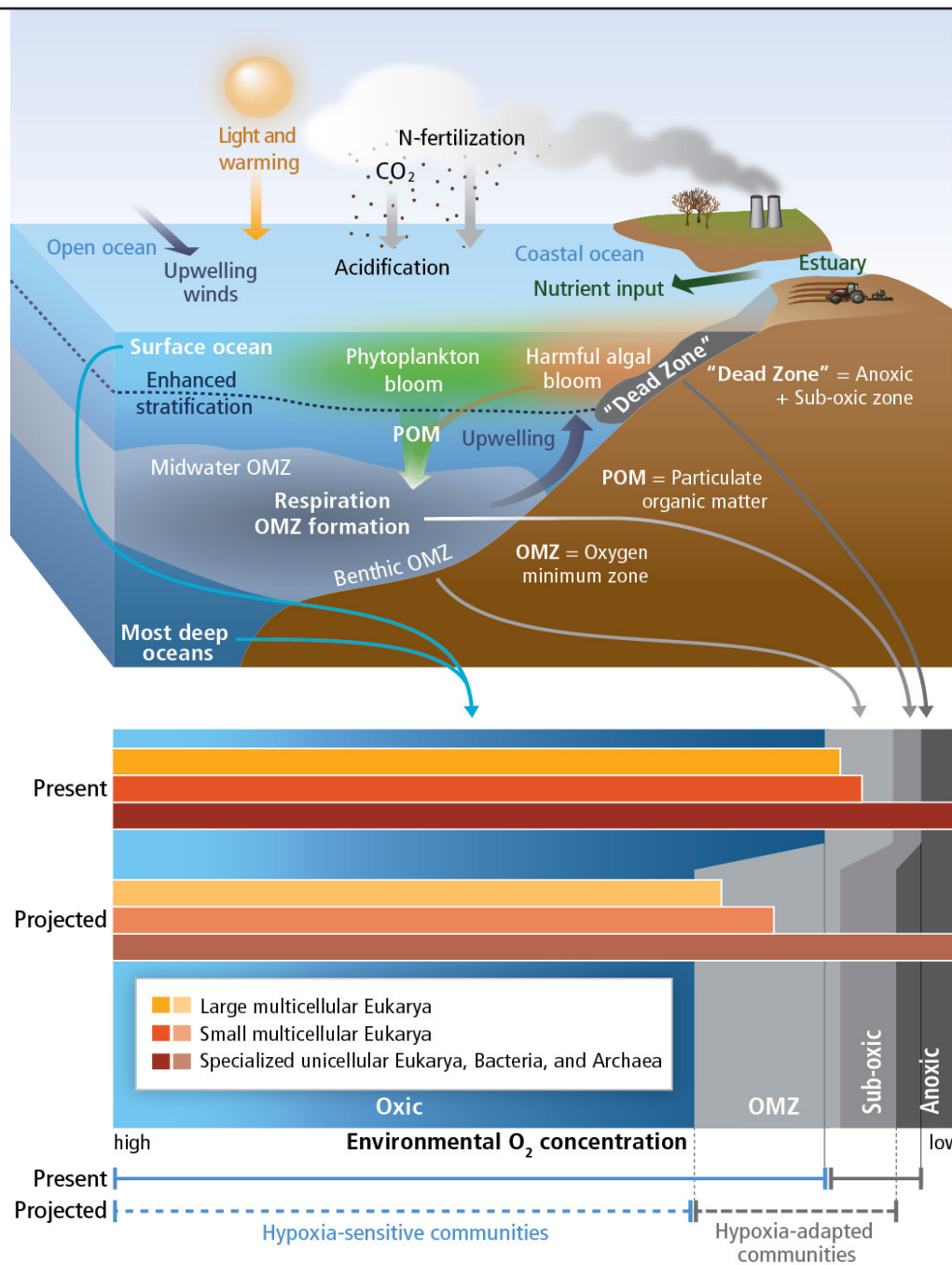
The shoaling lysocline as a result of ocean acidification means that it is *likely* that upwelling waters will be both depleted in oxygen and acidified (see 2.3.4; Rhein *et al.*, 2013).

Coastal regions, particularly along the west coast of North America, have exhibited decreases

in O₂ concentrations due to increased stratification and it has been suggested that O₂ concentrations in coastal areas may be declining approximately 10 times faster than the open ocean, although more data are needed to confirm this hypothesis (Hoegh-Guldberg *et al.*, 2014). Due to the greater solubility of O₂ in cold waters and the low microbial activity, deep sea waters are relatively well oxygenated (Hoegh-Guldberg *et al.*, 2014). However, oxygen concentration is decreasing in the deep sea, with the largest decline at intermediate water depths (< 1000 m), some deeper waters are also decreasing in oxygen concentration. There is *high confidence* that increasing temperatures will cause widespread declines in dissolved O₂ (Hoegh-Guldberg *et al.*, 2014).

The Arabian Sea and Bay of Bengal host up to 50% of the area of global OMZ and there is *high confidence* that oxygen concentration in these areas is decreasing (Hoegh-Guldberg *et al.*, 2014). In the Baltic Sea, dissolved O₂ is low in the deep basins and increased thermal stratification has produced prolonged hypoxic conditions (Hoegh-Guldberg *et al.*, 2014). In the Black Sea, reduced nutrient upwelling and expanded anoxic areas have also been observed (Hoegh-Guldberg *et al.*, 2014).

Figure 5: (a) Principal mechanisms underlying the formation of hypoxic conditions and their biological background. The buoyant, fresh input from rivers produces sharp density stratification at the base of the freshened layer (also valid for ice melt and high precipitation) near the surface and, hence, vertical mixing is greatly reduced. In consequence, the nutrient inputs from the river and the atmosphere accumulate in a narrow upper layer, leading to blooms of phytoplankton. The increased oxygen consumption due to aerobic decomposition of sinking particulate organic matter (POM) results in hypoxic conditions of benthic and mid-water oxygen minimum zones (OMZs). Enrichment of nutrients (eutrophication) results in coastal dead zones. In the open oceans, heating of the upper layer increases stratification, while the wind-driven upwelling of hypoxic, nutrient-rich water from deeper layers adds to the formation of the OMZs. (b) Distribution of free-living marine organisms (microbes such as archaea, bacteria), in various water layers. Hypoxia tolerance is enhanced in small compared to large organisms, allowing unicellular species and small animals to thrive in extremely hypoxic habitats. Species richness and body size of animals decrease with falling oxygen levels.



Source: Pörtner *et al.* (2014).

› Oxygen: future projections

Recent model projections suggest a decrease in oxygen concentration under every RCP scenario. The modeled mean reduction in global ocean oxygen concentration is -3.4 , -2.5 , -2.3 and -1.8% by the end of the century relative to the 1990s, for RCP8.5, RCP6.0, RCP4.5 and RCP2.6, respectively (Bopp *et al.*, 2013). Ocean warming will *very likely* lead to further declines in dissolved O_2 , estimates of global decline range between 6 to 12 $\mu\text{mol kg}^{-1}$ by 2100, depending on the RCP scenario (Ciais *et al.*, 2013). The regions most affected by decreasing O_2 concentrations are the intermediate to deep waters of the North Atlantic, North Pacific and Southern Ocean with declines between 20 to 200 $\mu\text{mol kg}^{-1}$ by 2100 (Hoegh-Guldberg *et al.*, 2014).

In previous years, models have been limited in their simulation of present day O_2 concentrations (Cocco *et al.*, 2013) and as a result there is uncertainty surrounding the expansion of hypoxic and suboxic zones, the IPCC AR5 report considers it *as likely as it is unlikely* that they will expand (Ciais *et al.*, 2013). More recent model simulations have shown greater accuracy in simulating present day conditions and predict a decline in global oxygen content of seawater (Bopp *et al.*, 2013). Models also do not take into account feedbacks from changes in biogeochemical cycling or processes in coastal oceans, which may increase deoxygenation, it is therefore possible that current projections of future O_2 concentrations in coastal areas are too high (Ciais *et al.*, 2013).

2.3.5. Ocean acidification

CO_2 that is absorbed by the ocean reacts with the seawater and causes a decrease in pH and changes the relative abundances of the dissolved inorganic carbonate species: concentration of bicarbonate ions (HCO_3^-) increases while the concentration of carbonate ions (CO_3^{2-}) decreases, lowering the saturation state (Ω) of calcium carbonate ($CaCO_3$). Saturation state is also affected by temperature, salinity and pressure and, thus, varies regionally and with depth. The chemical response of the oceans to increasing CO_2 is well understood with *very high confidence* (see Annex 4; Rhein *et al.*, 2013).

There is *high confidence* that surface ocean pH has declined by 0.1 pH units since the beginning of the Industrial Era, corresponding to a 26% increase in the concentrations of H^+ ions (Rhein *et al.*, 2013). Direct measurements show that the rate of pH decrease is between -0.0014 and -0.0024 units yr^{-1} in surface waters (Rhein *et al.*, 2013). There is a *high level of agreement* between observed datasets from time series and repeat transects, lending *high confidence* to the IPCC AR 5 findings on ocean acidification (Rhein *et al.*, 2013).

Regional estimates vary, with some areas better sampled than others. There is less certainty in the Southern Ocean surface waters due to a paucity of time series measurements, the available data suggest rates similar to those seen globally (Rhein *et al.*, 2013). Repeat transects in the Southern Ocean found large inter-annual variability in salinity, SST, pH, total dissolved carbon (C_T), and total alkalinity (A_T) due to differences in sea-ice concentration, physical processes and primary production (Mattsdotter Björk *et al.*, 2014).

Baseline monitoring of the Western Arctic Ocean estimates that 20% of Canadian Basin surface waters are undersaturated with respect to aragonite (Robbins *et al.*, 2013) and that the saturation horizon is shoaling; over 67% and 22% of the bottom water of Hudson Bay was undersaturated with respect to aragonite and calcite respectively (Azetsu-Scott *et al.*, 2014). In the Arctic, acidification is modulated by the seasonal dynamics of the sea ice, resulting in a five times larger seasonal amplitude of the carbonate system, in the upper 20 m than observed in sea ice free systems (Fransson *et al.*, 2013). Saturation state decreases during ice formation, and increases during ice melt (Fransson *et al.*, 2013).

Calculated pH trends for the North Atlantic Gyre suggests a decrease of -0.0022 ± 0.0004 units yr^{-1} over the period 1981 to 2007 (Lauvset & Gruber, 2014). This rate is very close to that expected based on the assumption of thermodynamic equilibrium of CO_2 between the atmosphere and the surface ocean. In the North Pacific, a pH decrease of -0.0011 ± 0.0004 units yr^{-1} from 1997 to 2011 has been calculated (Table 1.2; Wakita *et al.*, 2013).

Anthropogenic CO_2 has reached at least 1000 m in all three ocean basins and deeper in the Atlantic (Hoegh-Guldberg *et al.*, 2014). As the waters at the bottom of some oceans basins are very old, it will take many centuries for full equilibration of deep ocean waters to recent global warming and CO_2 perturbation (Cao *et al.*, 2014, Hoegh-Guldberg *et al.*, 2014). It is predicted that when atmospheric CO_2 reaches four times its pre-industrial level, global mean aragonite saturation horizon will shoal from the pre-industrial levels of 1288 m to 143 m (Cao *et al.*, 2014). In upwelling areas, the upwelled water is high in dissolved CO_2 , which is exacerbating ocean acidification driven by anthropogenic activities (Hoegh-Guldberg *et al.*, 2014).

A recent study has shown that anthropogenic trends in ocean acidification emerge quickly from the background noise of natural variability on the local-to-regional scale. Anthropogenic trends in surface ocean pH (and pCO_2) emerge within roughly 12 years, for the majority of the global ocean area, compared to between 10 and 30 years

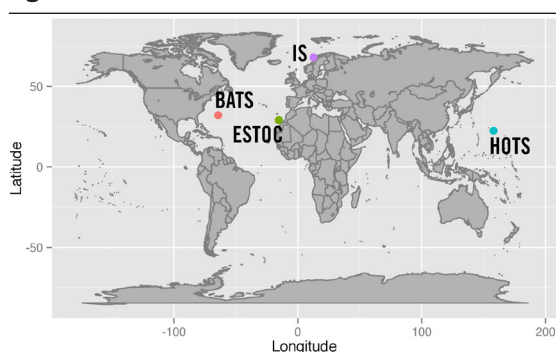
Table 2. Long-term trends of atmospheric pCO₂ and seawater carbonate chemistry at four ocean time series in the North Atlantic and North Pacific oceans

Site	Period	pCO ₂ ^{atm} (µatm yr ⁻¹)	pCO ₂ ^{sea} (µatm yr ⁻¹)	pH _T (yr ⁻¹)	[CO ₃ ²⁻] (µmol kg ⁻¹ yr ⁻¹)	Ω _a (yr ⁻¹)
BATS	1983-2009	1.66 ± 0.01	1.92 ± 0.08	-0.0019 ± 0.0001	-0.59 ± 0.04	-0.0091 ± 0.0006
	1985-2009	1.67 ± 0.01	2.02 ± 0.08	-0.0020 ± 0.0001	-0.68 ± 0.04	-0.0105 ± 0.0006
	1988-2009	1.73 ± 0.01	2.22 ± 0.11	-0.0022 ± 0.0001	-0.87 ± 0.05	-0.0135 ± 0.0008
	1995-2009	1.90 ± 0.01	2.16 ± 0.18	-0.0021 ± 0.0001	-0.80 ± 0.08	-0.0125 ± 0.0013
ALOHA	1988-2009	1.73 ± 0.01	1.82 ± 0.07	-0.0018 ± 0.0001	-0.52 ± 0.04	-0.0083 ± 0.0007
	1995-2009	1.92 ± 0.01	1.58 ± 0.13	-0.0015 ± 0.0001	-0.40 ± 0.07	-0.0061 ± 0.0028
ESTOC	1995-2009	1.88 ± 0.02	1.83 ± 0.15	-0.0017 ± 0.0001	-0.72 ± 0.05	-0.0123 ± 0.0015
IS	1985-2009	1.75 ± 0.01	2.07 ± 0.15	-0.0024 ± 0.0002	-0.47 ± 0.04	-0.0071 ± 0.0006
	1988-2009	1.70 ± 0.01	1.96 ± 0.22	-0.0023 ± 0.0003	-0.48 ± 0.05	-0.0073 ± 0.0008
	1995-2009	1.90 ± 0.01	2.01 ± 0.37	-0.0022 ± 0.0004	-0.40 ± 0.08	-0.0062 ± 0.0012

Source: Modified from Rhein *et al.* (2013).

Note: Long-term trends of atmospheric (pCO₂^{atm}) and seawater carbonate chemistry (i.e., surface-water pCO₂, and corresponding calculated pH, CO₃²⁻ and aragonite saturation state (Ω_a) at four ocean time series in the North Atlantic and North Pacific oceans: (1) Bermuda Atlantic Time-series Study (BATS, 31°40'N, 64°10'W) and Hydrostation S (32°10'N, 64°30'W) from 1983 to present; (2) Hawaii Ocean Time series (HOT) at Station ALOHA (A Long-term Oligotrophic Habitat Assessment; 22°45'N, 158°00'W) from 1988 to the present; (3) European Station for Time series in the Ocean (ESTOC, 29°10'N, 15°30'W) from 1994 to the present; and (4) Iceland Sea (IS, 68.0°N, 12.67°W) from 1985 to 2006.

for surface ocean DIC and 45–90 years for SST (Keller *et al.*, 2014). This implies that anthropogenic carbon emissions already forced surface pH values beyond the range of 20th century natural variability.

Figure 6. Locations of the times series stations used in table 2.

2.3.5.1. Ocean acidification; future projections

It is *virtually certain* that the continued uptake of CO₂ by the oceans will increase ocean acidification (Ciais *et al.*, 2013). Between 1986–2005 and 2081–2100, global decreases in seawater pH by 2100 are projected to be 0.065 for RCP 2.6, 0.145 for RCP 4.5, 0.203 for RCP 6.0 and 0.31 for RCP 8.5 (Ciais *et al.*, 2013).

As aragonite is the more soluble form of CaCO₃, waters will become undersaturated with respect to aragonite before calcite. It is *unlikely* that more than 10% of global surface waters will maintain Ω_a higher than 3 if atmospheric CO₂ exceeds 550 ppm by 2100 (Steinacher *et al.*, 2013). With subsurface waters becoming undersaturated, models predict that the lysocline will shoal from 200 to 40 m in the subarctic Pacific, from 1000 m to the surface in the Southern Ocean and from 2850 to 150 m in the North Atlantic (Hoegh-Guldberg *et al.*, 2014). Even

if atmospheric CO₂ does not exceed 450 ppm, most of the deep ocean is anticipated to be undersaturated within several centuries (Hoegh-Guldberg *et al.*, 2014). Under RCP8.5, pH reductions exceeding 0.2, units are projected in 23% of North Atlantic deep-sea canyons and 8% of seamounts (Gehlen *et al.*, 2014).

The extent of ocean acidification will vary regionally and seasonally, with undersaturated conditions first reached in wintertime (Ciais *et al.*, 2013). The largest decreases in the concentration of carbonate ions (CO₃²⁻) will be in warmer, low and mid latitudes as these areas are naturally high in CO₃²⁻ concentration (Ciais *et al.*, 2013). The areas that are projected to be come undersaturated first are the high latitudes and coastal upwelling areas. Recent work has found intermediate waters to be twice as sensitive to increased carbon concentrations as surface waters and project higher rates (–0.0008 to –0.0023 ± 0.0001 units yr⁻¹ depending on the scenario) of acidification in intermediate waters than surface waters over centennial timescales (Resplandy *et al.*, 2013).

The Arctic Ocean is of particular concern as increased freshwater input, due to sea ice melt, will exacerbate acidification (Steinacher *et al.*, 2009). It is estimated that increased ice melt in the Arctic would lead to enhanced oceanic uptake of inorganic carbon to the surface layer (Fransson *et al.*, 2013, Reisdorph & Mathis, 2014). As a result, the Central Arctic, Canadian Arctic Archipelago and Baffin Bay are projected to be the first to be undersaturated with respect to aragonite. Areas that are influenced by Atlantic seawater input such as the Greenland Sea and outer shelves of the Barents, Kara and Laptev seas are projected to become undersaturated much later, up to the year 2080 (Popova *et al.*, 2014). Within a decade, 10% of

Arctic waters will be undersaturated with respect to aragonite and by 2025, under all RCP scenarios, 10% of its waters are projected to be undersaturated with respect to calcite.

For the Southern Ocean, it is projected that wintertime undersaturation with respect to aragonite will occur within 10 to 30 years (Ciais *et al.*, 2013). It is considered *likely* that large regions of Antarctic and Sub-Antarctic surface waters will become undersaturated with respect to aragonite by 2030 (Ciais *et al.*, 2013, Mattsdotter Björk *et al.*, 2014). It is *likely* that aragonite undersaturation will be limited to 25% of the Southern Ocean surface by 2100 if atmospheric CO₂ stays below 625 ppm (Steinacher *et al.*, 2013). The California Current System is projected to follow similar trends to the Southern Ocean, due to the natural upwelling of waters rich in CO₂ (Hoegh-Guldberg *et al.*, 2014). Local drivers in other coastal systems such as river input, eutrophication and increased organic matter degradation will also cause more intense acidification effects.

2.3.5.2. Rates of change and irreversibility on human time scales

The rates of change in marine physical and biogeochemical variables and in ocean acidification influence the impacts on natural and socio-economic systems and their capabilities to adapt. Earlier analyses of ice core and atmospheric records show that the 20th-century increase in CO₂ and its radiative forcing occurred more than an order of magnitude faster than any sustained change during, at least, the past 22,000 years (Joos & Spahni, 2008). This implies that both global climate change and ocean acidification, which are anthropogenic in origin, are progressing at high speed.

The magnitude of 21st century CO₂ emissions by human activities pre-determines the range of atmospheric CO₂ concentrations, ocean temperature, sea level, and ocean acidification for the coming centuries, at least in the absence of the large-scale deployment of a technology to remove excess CO₂ from the atmosphere (Frölicher & Joos, 2010). In other words, the CO₂ emitted in the next decades will perturb the marine physical system, biogeochemical cycles, and ecosystems for centuries.

3. BIOLOGICAL IMPACTS OF CLIMATE CHANGE

The biological response to climate change drivers can be observed at different levels ranging from molecular to cellular, individual, population, community and ecosystem. In the following sections, the main findings for changes in temperature,

decreasing dissolved oxygen and ocean acidification are summarised for microbes, plants, animals and ecosystems. Corals and coral reefs have been treated separately as they represent a unique and important habitat that is particularly sensitive to the effects of climate change and ocean acidification.

3.1. Warming

All organisms have an optimum range of temperature (see Annex 5) at which physiological processes are most efficient. The impact of changing temperature depends on the organism's specific window of window of thermal tolerance, which varies greatly between species. Exceeding these limits can have effects on a wide range of physiological processes such as growth, body size, behaviour, immune defence, feeding, reproductive success, biogeography, phenology (timing of events) and, therefore, ecosystem structure and function (Mackenzie *et al.*, 2014b, Mackenzie *et al.*, 2014c, Poloczanska *et al.*, 2014, Pörtner *et al.*, 2014).

These organism-specific temperature ranges dictate the distribution of organisms. A common adaptation to changing temperature is the displacement of a species to areas of more favourable temperature (Poloczanska *et al.*, 2014, Pörtner *et al.*, 2014). Hence, under a warming scenario, poleward migrations are expected, but possibilities for migration are limited for polar organisms. Maximum temperature tolerances in multicellular organisms are within the range and, for some of them, close to maximum ocean temperature. Organisms also respond to temperature-driven changes in the physical environment such as stratification, reduced sea-ice cover and freshening (Pörtner *et al.*, 2014).

3.1.1. Microbes

Warming will enhance microbial growth. As thermal tolerances are species-specific, continued warming causes changes in species compositions with warmer conditions favouring smaller sized species (Pörtner *et al.*, 2014) and shifts in microplankton species compositions (Calbet *et al.*, 2014). This has implications for the global carbon pump as small size cells are less likely to be buried in the deep ocean.

The warming has been shown to enhance phytoplankton growth rates (De Senerpont Domis *et al.*, 2014, Marañón *et al.*, 2014); however, this is strongly modulated by nutrient availability, suggesting that under more stratified conditions warming many have a net negative effect on phytoplankton growth (Chust *et al.*, 2014, Lewandowska *et al.*, 2014, Marañón *et al.*, 2014). Models

predict that projected warming of 2.3 °C leads to a 6% reduction in phytoplankton biomass (Chust *et al.*, 2014). However, the coccolithophore *Emiliana huxleyi* has displayed evolutionary adaptation to ocean warming similar to that predicted under RCP8.5. (Benner *et al.*, 2013, Schluter *et al.*, 2014).

Phytoplankton are the taxon that has displayed the largest latitudinal range shifts concurrent with climate change, with average distribution shifts into cooler waters of over 400 km decade⁻¹ (Poloczanska *et al.*, 2014). Warming is thought to be one of the factors responsible for the increased frequency of harmful algal blooms (HAB) in the East China Sea (Hoegh-Guldberg *et al.*, 2014), and range expansions of HABs are predicted under the A1B emissions scenario (Glibert *et al.*, 2014). Warming may also be expanding the geographical range of coccolithophores with blooms forming for the first time in the Bering Sea and extending further south in the Southern Ocean (Hoegh-Guldberg *et al.*, 2014). Increasing temperatures have been attributed with *high confidence* to large, northward range shifts in North Atlantic phytoplankton (Poloczanska *et al.*, 2014, Pörtner *et al.*, 2014).

3.1.2. Macroalgae and seagrasses

There is *high confidence* that macrophytes (macroalgae and seagrasses) are limited in thermal tolerance and, thus, sensitive to warming, especially at their lowest latitudes of distribution (Pörtner *et al.*, 2014). However, inconsistencies are present in the literature as Brodie *et al.* (2014) predict, “seagrass will proliferate” in the North Atlantic under future warming. Thermal stress has been shown to affect photosynthesis, growth, reproduction and survival, with subsequent consequences for macrophytes’ abundance, distribution, and productivity. Sea ice retreat in polar areas has allowed an expansion of macroalgal distribution, via increased habitat availability (Pörtner *et al.*, 2014).

Different distribution shifts and responses to warming can be observed in warm and cold water species (Brodie *et al.*, 2014, Komatsu *et al.*, 2014, Pörtner *et al.*, 2014). Species that are adapted to live in extreme temperatures have been observed to be more sensitive than temperate species that have wide thermal tolerance ranges (Pörtner *et al.*, 2014). As a result, increased instances of thermally tolerant invasive species have been observed (Brodie *et al.*, 2014, Pörtner *et al.*, 2014). There is *high confidence* that Antarctic and tropical species are most at risk from increasing sea temperature (Chambers *et al.*, 2013). There is evidence that, in temperate regions, kelp mortality, spore mortality and germination will be negatively affected by projected temperature increases under RCP8.5

(Brodie *et al.*, 2014, Gaitán-Espitia *et al.*, 2014). Seagrasses are thought to have higher tolerances than seaweeds (Brodie *et al.*, 2014) but shoot mortality of seagrasses has been linked to temperature increases of > 1 °C (Pörtner *et al.*, 2014). Additionally, eelgrass wasting disease has been shown to increase in both higher temperature seasons and locations (Bockelmann *et al.*, 2013, Bull *et al.*, 2012), suggesting that warming will increase the incidence and severity of this cause of mass die-off of eelgrass.

3.1.3. Animals

Surpassing species-specific heat tolerance limits during warming causes reduced abundance, mortality, shifts in the seasonal timing, and changes in individual growth, development, calcification and immunity, e.g. seen among corals or zooplankton biomass (Goberville *et al.*, 2014, Kanya *et al.*, 2014, Mackenzie *et al.*, 2014b, Mackenzie *et al.*, 2014c, Poloczanska *et al.*, 2014, Pörtner *et al.*, 2014, Queirós *et al.*, 2014, Rice *et al.*, 2014, Vehmaa *et al.*, 2013).

During early life, owing to incomplete development, or as adult spawners, owing to large body size, animals can become more sensitive to warming (Pimentel *et al.*, 2014a, Pörtner *et al.*, 2014). This may cause high vulnerability in seasonally spawning fish species (Crozier & Hutchings, 2014, Elettra *et al.*, 2014, Pörtner *et al.*, 2014). There is *medium confidence* that warming also affects the body size of marine fishes with a trend towards smaller body sizes that is predicted, with *medium to high confidence*, to continue as warming progresses (Pörtner *et al.*, 2014, Rice *et al.*, 2014).

There is *high confidence* that polar and tropical species are most vulnerable, and temperate species least vulnerable, to changes in temperature (Jones & Cheung, 2014, Pörtner *et al.*, 2014). As ocean temperatures are less variable in the Southern Hemisphere than the Northern Hemisphere, species from the Polar regions of the Southern Hemisphere are predicted to be the most vulnerable to increasing temperature (Chambers *et al.*, 2013, Constable *et al.*, 2014, Larsen *et al.*, 2014, McBride *et al.*, 2014, Pörtner *et al.*, 2014).

Although laboratory studies commonly use temperature means, observations of periods of localised, extreme temperature events suggest that these may exert a higher control on species response (Pörtner *et al.*, 2014). Mortality and/or latitudinal/depth range distribution shifts follow extreme temperature events and can lead to localised extinctions (*high confidence*) (Pörtner *et al.*, 2014). For example, there is *very high confidence* that, in the Mediterranean Sea, periods of extremely high temperatures in the late 1990’s and

2000's caused mass mortality of at least 25 species of invertebrates (Hoegh-Guldberg *et al.*, 2014).

As local temperatures approach the limits of a species' thermal tolerance, they are forced to acclimatise and, eventually, adapt to high temperatures or to migrate to areas with more favourable conditions to avoid death (Poloczanska *et al.*, 2014, Pörtner *et al.*, 2014). Zooplankton have exhibited some of the most extreme range shifts in response to increasing temperature of over 100 km decade⁻¹ (Poloczanska *et al.*, 2014). Significant distribution shifts of copepod species in the North Sea and North Atlantic have been observed in conjunction with warming between 1958 and 2009 (Beaugrand *et al.*, 2014). Latitudinal range shifts have also been observed in benthic cnidarians, benthic molluscs, benthic crustacea, larval bony fish, non-bony fish (sharks, rays, hagfish) and bony fish (Engelhard *et al.*, 2014, Poloczanska *et al.*, 2014, Potts *et al.*, 2014). Temperature also governs the distribution and abundance of large pelagic fish in the Indian, Pacific and Atlantic Oceans and there is *high confidence* temperature anomalies caused a major shift in tuna distribution in these areas (Hoegh-Guldberg *et al.*, 2014, Mackenzie *et al.*, 2014a).

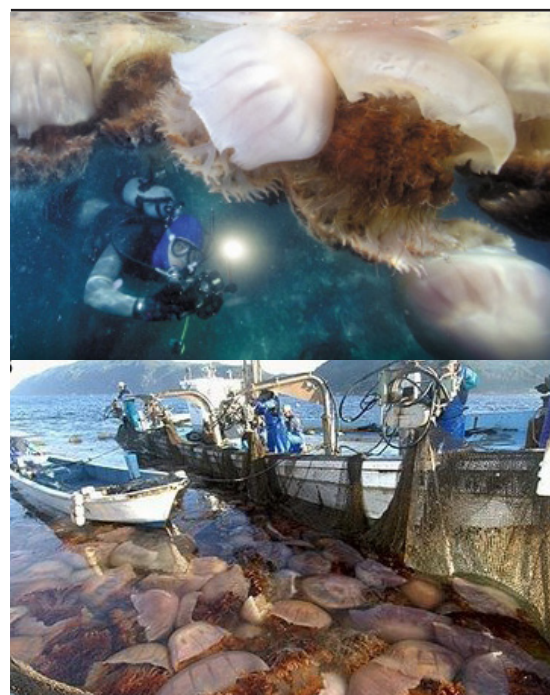
There is *low confidence* that increasing water temperatures have increased the frequency and size of jellyfish blooms, although contradictory evidence means that this is still under debate (Pörtner *et al.*, 2014). However, blooms of the giant jellyfish *Nemopilema nomurai* in the East China Sea have been observed to increase with warming (Fig. 7; Hoegh-Guldberg *et al.*, 2014).

Rising temperature has been shown to influence host-pathogen interactions, increasing infectious disease outbreaks (Burge *et al.*, 2014). Warming oceans have increased the incidence and/or severity of marine diseases affecting corals (Harvell *et al.*, 2009), shellfish (Travers *et al.*, 2009) and finfish (reviewed in; Bowden, 2008). Many marine pathogens have shifted their distributions poleward as ocean temperatures warm (e.g. Baker-Austin *et al.*, 2013, Nye *et al.*, 2009, Parmesan & Yohe, 2003), including bacterial infections of humans (Baker-Austin *et al.*, 2013, Martinez-Urtaza *et al.*, 2010) and disease of the eastern oyster, *Crassostrea virginica* (Bureson & Ragone Calvo, 1996, Ford & Tripp, 1996). Even the recent dramatic mortalities of sea stars along the Pacific coast of North America may be temperature related, as some echinoid diseases have been shown to increase with rising temperatures (Bates *et al.*, 2009, Staehli *et al.*, 2009).

Localised adaptations are possible, as organisms are already able to cope with seasonal variations. There is *medium confidence* that animals already acclimatized to a wide range of temperatures will

cope better with future conditions (Pörtner *et al.*, 2014, Zhang *et al.*, 2014). Although, secondary drivers such as ocean acidification, hypoxia and food availability affect the capacity of an organism to adapt to changing temperatures (Ko *et al.*, 2014, Mackenzie *et al.*, 2014b, Mackenzie *et al.*, 2014c, Madeira *et al.*, 2014, Pope *et al.*, 2014, Pörtner *et al.*, 2014, Vehmaa *et al.*, 2013). Some animals, such as those that undertake daily vertical migrations or live in tide pools, experience drastic physiochemical changes, close to the upper limits of their thermal tolerances. This may affect their ability to cope with climate change-induced alterations to their environment (Almén *et al.*, 2014, Rastrick *et al.*, 2014). Overall, there is *low confidence* in the understanding of the potential for long-term evolutionary adaptation (Pörtner *et al.*, 2014).

Figure 7. Blooms of the giant jellyfish *Nemopilema nomurai*.



Source: Schorpe (2012) and <http://eatingjellyfish.com/?tag=jellyfish-blooms>.

3.1.4. Warm and cold water coral communities

Tropical corals live in shallow water and differ from most other animals by hosting symbiotic dinoflagellates (*Symbiodinium* sp.) in their tissues, which provide the host with organic carbon from photosynthesis, nitrogen and enable the corals to build and sustain carbonate reefs. High light, rapid salinity changes and small increases in temperature can cause 'coral bleaching', the loss of symbionts and tissue colour (Fig. 8). Mass bleaching events are correlated temperature anomalies of only

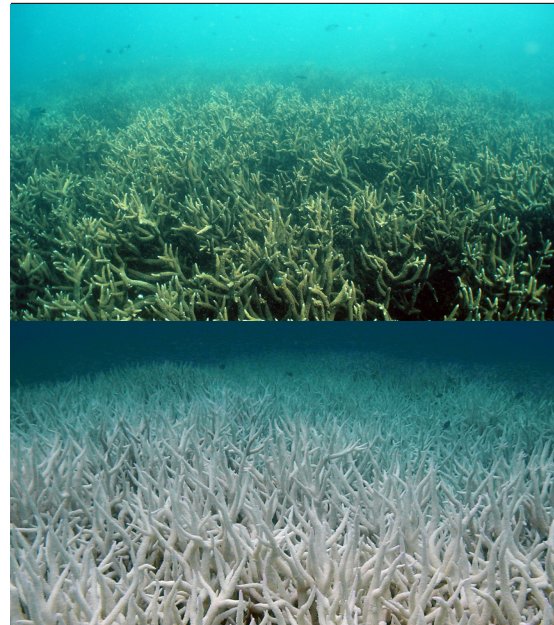
1 to 2 °C above the long-term summer maximum (Wong *et al.*, 2014). There is *very high confidence* that bleaching has the potential to lead to mass mortality of up to 50% mortality in bleached corals (Wong *et al.*, 2014). The effects of climate change can be seen as coral bleaching events become more widespread; 7% of the reef locations exhibited at least one bleaching event between 1985 and 1994 compared to 38% in the 1995-2004 period (Wong *et al.*, 2014). There is *high confidence* that increased temperatures cause mass mortality of warm water corals and a decline in coral abundance (Wong *et al.*, 2014). As with other phyla, thermal tolerance and recovery capacity of the both the coral host and the symbiotic dinoflagellates are geographically, and species specific (Alemu & Clement, 2014, Cantin & Lough, 2014, Falter *et al.*, 2014, McClanahan & Muthiga, 2014, Wong *et al.*, 2014).

There is *high confidence* that mass coral bleaching events have occurred in all three sub-tropical gyre (STG) regions, in conjunction with increasing temperature (Hoegh-Guldberg *et al.*, 2014). In the Pacific, there has been a steady decline in coral cover on coastal coral reef ecosystems ranging between 0.5 and 2.0% yr⁻¹ (Hoegh-Guldberg *et al.*, 2014). High temperature in the Atlantic STG caused mortality in the eastern Caribbean (Eakin *et al.*, 2010), and in the Indian Ocean there is *high confidence* that coral cover declined by an average of 38% following the 1998 temperature extremes (Hoegh-Guldberg *et al.*, 2014) and declined again in 2010 (Hoegh-Guldberg *et al.*, 2014). Reef recovery from mortality events is variable and it is likely that bleaching events will alter coral cover (Wong *et al.*, 2014). In the Red Sea, different species of coral have exhibited differential responses to increasing temperature with some species increasing growth with an increase in temperature of 0.74 °C between 1982 and 2006 (Hoegh-Guldberg *et al.*, 2014). However, there is *high confidence* that the average size of coral colonies has decreased over the last 20 years (Hoegh-Guldberg *et al.*, 2014). Coral bleaching has occurred in the Arabian Gulf and Red Sea and there is *high confidence* that bleaching and mortality is a result of warming corresponding to 0.09 and 0.07 °C decade⁻¹, respectively (Hoegh-Guldberg *et al.*, 2014). There is *medium confidence* that this coral decline has caused a decline in fish that feed on coral-associated invertebrates, concurrent with an increase in the abundances of herbivorous and planktivorous fish species (Hoegh-Guldberg *et al.*, 2014).

Several coral diseases have been found to be temperature sensitive and have increased with ocean warming (reviewed in; Burge *et al.*, 2014). Some coral diseases have been shown to be predictable using satellite-based temperatures

(Heron *et al.*, 2010, Maynard *et al.*, 2011) and this may lead to projections of potential coral disease increase as the climate warms. Temperature increases of 6 °C have also been observed to reduce the production of mucous, which may increase susceptibility to coral diseases (Pratte & Richardson, 2014). Dispersal of coral larva is reduced under high temperatures, this will weaken connectivity between populations, and so potentially slow down recovery if local populations are severely affected (Figueiredo *et al.*, 2014).

Figure 8. The same coral community before and after a bleaching event in February 2002 at 5 m depth, Halfway Island, Great Barrier Reef. Approximately 95% of the coral community was severely bleached in 2002.



Source: R. Berkelmans.

There is *high confidence* that bleaching susceptibility is geographically and species specific (Gattuso *et al.*, 2014) – this regional susceptibility has allowed for highly accurate satellite SST-based predictive tools and for projections of future climate impacts (Donner *et al.*, 2005, Eakin *et al.*, 2009, Van Hooidonk *et al.*, 2013). Some thermally tolerant species are able to divert cellular energy into mechanisms for survival and recovery of short-term heat stress but at the expense of growth and biomineralization (Maor-Landaw *et al.*, 2014). Studies have shown that even more thermally tolerant species are prone to bleaching and tissue breakdown (Rodolfo-Metalpa *et al.*, 2014) and that repeat bleaching may impact thermal tolerance with some species able to rapidly acclimatise while others becoming more susceptible (Grottoli *et al.*, 2014). There is *limited evidence* that some species are able to rapidly acclimatise to higher temperatures,

reflected in alterations in gene expression (Palumbi *et al.*, 2014). Model simulations also support the theory that corals have some capacity to acclimatise to high temperatures as the extent of present day bleaching would be expected to be higher if corals were not able to adapt or acclimate to warming that has already occurred (Logan *et al.*, 2014). Even if corals are able to adapt to thermal stress, model simulations predict that under RCP4.5, two thirds of the world's corals will be subject to long-term degradation (Gattuso *et al.*, 2014). Unfortunately, many of these impacts on coral reef ecosystems are likely to be long-lived even if emission reductions are achieved (Ortiz *et al.*, 2014).

Studies of the thermal sensitivity of deeper-living cold-water corals (without endosymbionts) are scarce. One species, *Lophelia pertusa* responds to about 3°C warming with a three-fold increase in metabolic rate, indicating a narrow thermal window in the cold (Pörtner *et al.*, 2014). Recent work has also suggested that increased temperatures and CO₂ concentrations may cause cold water corals to accumulate dimethylsulphoniopropionate (DSMP) from the water column. It has been suggested that they use DSMP in a similar way to algae, for example, in response to environmental challenges, implying an acclimation response to CO₂ stress (Burdett *et al.*, 2014).

3.1.5. Ecosystems

Ecosystems that are built around heat sensitive organisms such as coral reef or kelp forests may be at increased risk from warming-induced changes to and loss of habitat. Within ecosystems, different tolerances of individual species can cause changes in inter-specific competition, trophic dynamics (Arula *et al.*, 2014, Brodie *et al.*, 2014, Lewandowska *et al.*, 2014) and species compositions (Albouy *et al.*, 2014). Due to a lack of knowledge there is *low confidence* in predicting how ecosystems will react to immigration of animals as a result of climate change (Pörtner *et al.*, 2014).

There is *high confidence* that observed changes in distribution, phenology and reproduction of plants and animals in marine ecosystems are, at least partially, temperature induced (Beaugrand *et al.*, 2014, Chambers *et al.*, 2013, Goberville *et al.*, 2014, Hiddink *et al.*, 2014, Jones & Cheung, 2014, Kim *et al.*, 2014, Lambert *et al.*, 2014, Poloczanska *et al.*, 2014, Pörtner *et al.*, 2014, Rice *et al.*, 2014). As different species and groups have differential responses to warming, effects are seen at every trophic level and can also be amplified up the food chain (Chust *et al.*, 2014, Pinsky *et al.*, 2013, Pörtner *et al.*, 2014). Changes in phenology are not synchronous between phyla and so can cause predator-prey mismatches (Arula *et al.*,

2014, Behrenfeld, 2014, Pörtner *et al.*, 2014). Recent work has suggested that this maybe most pronounced in systems governed by seasonal blooms (Behrenfeld, 2014).

Changes in the frequency, intensity, and geographic distribution of marine diseases have had significant impacts on many ecosystems (Burge *et al.*, 2014). Disease-induced mortality has resulted in over 50% loss of live coral cover after severe thermal stress and coral bleaching (Eakin *et al.*, 2010, Miller *et al.*, 2009). Sea stars, the original keystone predators in Pacific rocky intertidal and subtidal ecosystems (Paine, 1969), have been catastrophically reduced in numbers in the last two years due to outbreak of a newly identified virus (Hewson *et al.*, 2014) that is more virulent at higher temperatures (Bates *et al.*, 2009). Removal of keystone predators can dramatically change intertidal ecosystems (Behrenfeld, 2014, Paine, 1969).

In the North Pacific, changes to the modes of climate oscillations are marked by abrupt reorganisation of the trophic regime and it is *very likely* that observed phenological shifts in zooplankton communities were in response to changes in climate oscillations (Hoegh-Guldberg *et al.*, 2014, Poloczanska *et al.*, 2014). Similarly, keystone predators like the sea star *Pisaster ochraceus* has been shown to be dramatically affected by small temperature changes associated with changes in upwelling patterns (Sanford, 1999).

There is *medium confidence* that in most semi-enclosed seas, temperature induced faunal latitudinal range shifts have also occurred and in the both the Mediterranean and the Black Sea, increased temperatures have prompted colonisation by invasive warm water species (Hoegh-Guldberg *et al.*, 2014). Sub-tropical species have also been observed to have invaded the Baltic Sea (Montero-Serra *et al.*, 2014). In the Mediterranean, synchronous changes in the diversity and abundance of zooplankton, decreases in anchovy abundance and increased mucilage events have occurred alongside increasing temperatures (Hoegh-Guldberg *et al.*, 2014). In the Baltic Sea there has been a substantial decline in phytoplankton biomass, there is *medium confidence* that this has been caused by changes to nutrient loads and it is *very likely* exacerbated by increasing temperature (Hoegh-Guldberg *et al.*, 2014).

There is *medium confidence* that loss of summer sea ice and increased ocean temperature will enhance secondary pelagic production in some regions of the Arctic (Larsen *et al.*, 2014, McBride *et al.*, 2014). There is *high confidence* that these changes will alter the species composition and carrying capacity with subsequent effects on fish and shellfish populations (*medium confidence*; Larson *et al.*, 2014).

3.1.6. Warming; future projections

Via alteration of energy demands, thermal tolerance affects almost every physiological process. It is also responsible for defining biogeography, community compositions and the timing of biological events. It is, therefore, possible to state with *very high confidence* that organisms are limited in thermal range and sensitive to temperature extremes.

RCP8.5

Average global primary production is projected to decrease under RCP8.5 due to a lack of nutrients as the result of stratification (Pörtner *et al.*, 2014). However, in high latitude spring blooms systems, photosynthesis is projected to increase. There is *high confidence* that warming is also driving changes in phenology of plankton groups and will continue to do so under RCP 8.5 (Behrenfeld, 2014, Hoegh-Guldberg *et al.*, 2014, Poloczanska *et al.*, 2014).

As fleshy macroalgae are cool water adapted and stressed by elevated temperatures, it is predicted that under temperatures predicted for the end of the century under RCP8.5, they will undergo significant changes in their distribution (Brodie *et al.*, 2014).

Reduced ocean productivity will reduce the energy available to higher trophic levels such as those of pelagic fish that are important for fisheries (Hoegh-Guldberg *et al.*, 2014). Fishery catches are projected to decrease in temperate and equatorial biomes by 38 and 15%, respectively under RCP8.5 (Pörtner *et al.*, 2014).

It is *virtually certain* that climate change will cause major changes to ecosystems in high latitude spring bloom systems; warming is a primary driver of ecosystem changes in the North Atlantic (*high confidence*) (Goberville *et al.*, 2014, Hoegh-Guldberg *et al.*, 2014). There is *high confidence* that expansion and contraction of faunal ranges have been observed, with an associated increase in diversity as warmer water species colonize new areas, particularly in the North Atlantic (Hoegh-Guldberg *et al.*, 2014, Poloczanska *et al.*, 2014).

It is known with *medium confidence* that export of organic matter to the deep sea is controlled by temperature. There is *medium confidence* that warming and changes to primary productivity in the upper ocean will reduce the export of organic matter to the deep sea. This has the potential to affect the distribution, abundance and composition of faunal communities in the deep sea (Hoegh-Guldberg *et al.*, 2014).

There is *very high confidence* that, as warming progresses, coral bleaching and mortality will increase in frequency and magnitude over the next decade. Under the A1B CO₂ emission scenario

(~ RCP6.0), 99% of the reef locations will experience at least one severe bleaching event between 2090 and 2099 (Wong *et al.*, 2014). Long-term degradation is predicted by 2020 under scenario RCP8.5 (Pörtner *et al.*, 2014). Even if coral acclimation is taken into account, more than 50% will experience high frequency bleaching under RCP8.5 (Logan *et al.*, 2014). There is *limited evidence* and *low agreement* that corals will be able to acclimate or adapt to increasing temperatures enough to limit bleaching events (Wong *et al.*, 2014). There is *high confidence* that bleaching events will negatively impact coral community structure and diversity with *medium confidence* of bleaching affecting the abundance and species composition of fish communities (Pörtner *et al.*, 2014).

RCP4.5

From a global perspective, net primary productivity under RCP4.5 will show similar patterns to those projected under RCP8.5, decreasing moderately overall by 2100 but with increases in high latitude systems (Pörtner *et al.*, 2014)

The effects of warming will be less severe under the conditions predicted by the end of the century under emissions RCP4.5 than for RCP8.5. Nonetheless, many plants and animals will still be severely affected, as thermal tolerance is species specific (Pörtner *et al.*, 2014). However, species distributions and phenological shifts are likely to be less extreme with fewer negative implications on trophic interactions.

In models that account for coral acclimation ability, fewer than 50% of corals, globally, will experience high frequency bleaching under RCP4.5 throughout the 21st century, however there is significant doubt as to whether this is a realistic scenario (Logan *et al.*, 2014).

3.2. Sea level rise

Sea level rise will have an indirect effect on many biological processes via habitat loss for several key coastal ecosystems.

› Ecosystems

Vegetated habitats such as mangroves, seagrass meadows, intertidal rocky reefs and wetlands are the natural systems most affected by changes in sea level (Cazenave & Cozannet, 2014, Di Nitto *et al.*, 2014, Murray *et al.*, 2014b, Saintilan *et al.*, 2014, Thorner *et al.*, 2014, Wong *et al.*, 2014). There is *high confidence* that these habitats are in decline with the loss estimated to release 0.04-0.28 PgC yr⁻¹ (Wong *et al.*, 2014). Increasing sea levels as a result of warming have also caused reductions and range shifts in seagrass and mangrove systems in the Pacific region

(Hoegh-Guldberg *et al.*, 2014). There is *medium confidence* that some coral reefs will be able to keep up with the projected rate of sea level rise (Hamilton *et al.*, 2014, Wong *et al.*, 2014, Woodroffe & Webster, 2014). However, increasing evidence suggests increased erosion and export of land-based sediments and pollutants will exacerbate existing stress to nearshore corals, perhaps preventing them from keeping up (Storlazzi *et al.*, 2011).

3.3. Decreasing dissolved oxygen concentration

When O₂ concentrations are below 60 μmol kg⁻¹ conditions become hypoxic and can have detrimental effects on animals, which rely on aerobic respiration. Under hypoxic conditions, species with higher O₂ demands are lost and, if hypoxic conditions are sustained, characteristic communities that thrive in low O₂ environments replace them (Pörtner *et al.*, 2014).

Even above hypoxic concentrations, oxygen can be limiting. Oxygen demand depends on species, body size, life stage, metabolic activity and temperature. In extreme temperatures, critical O₂ concentration is almost the same as fully O₂ saturated water, indicating increased sensitivity to hypoxia in increased temperatures. Critical O₂ concentrations for a species are defined by the efficiency of their ventilation and circulation systems. Below critical O₂ concentrations, organisms switch to fulfil the energy deficit by anaerobic respiration. Most animals can only sustain anaerobic metabolism temporarily, even if they are energy-efficient and survive long periods of anoxia (Pörtner *et al.*, 2014).

3.3.1. Microbes

Oxygen minimum zones (OMZs) form habitat for both anaerobic and aerobic microbes that can utilize very low (< 1 μmol kg⁻¹) O₂ concentrations. In OMZs, microbial respiration drives O₂ concentrations down and maintains low concentration of oxygen. Therefore, there is *high confidence* that microbial life will benefit from expanding OMZs (see Fig. 4; Pörtner *et al.*, 2014), with communities shifting to smaller, multicellular Eukarya, Bacteria and Archaea (Storch *et al.*, 2014).

3.3.2. Animals and plants

In mid-water oxygen minimum zones, zooplankton also contribute to the development of hypoxia. During daytime, zooplankton congregate at the upper margin of OMZs, where the degradation of organic material causes intensified respiration and lowers oxygen concentration (Pörtner *et al.*, 2014). Special adaptations to hypoxia and lower energy demand are present in animals that live

permanently in the OMZ as they still rely on aerobic respiration. This is only possible for animals of small size (< 1 mm) in cold temperatures. Larger, more active animals tend to have high O₂ demands and so mostly avoid OMZs. Few animals have developed strategies to temporarily cope with hypoxic conditions and there is *high confidence* that hypoxia-adapted life forms, such as the jumbo squid will benefit from expanding OMZs (Pörtner *et al.*, 2014, Seibel *et al.*, 2014, Stewart *et al.*, 2014). Some non-hypoxic specialists are resilient to a short term decreases in oxygen concentration, including mussels, urchins and tubeworms (Frieder *et al.*, 2014, Mukherjee *et al.*, 2013, Taylor *et al.*, 2014b)

There is little information on the sensitivity of macrophytes to hypoxia. However negative responses have been observed in eelgrasses so there is *medium confidence* that expanding benthic OMZs will constrain the distribution of macrophytes (Pörtner *et al.*, 2014).

3.3.3. Ecosystems

There is *medium confidence* that expansions of OMZs, will result in habitat and abundance losses for taxa with high O₂ demands (Pörtner *et al.*, 2014, Sadorus *et al.*, 2014). As many pelagic species migrate vertically on a daily and seasonal basis, the shoaling of OMZs will affect these migrations and change microbial and faunal compositions to organisms which can tolerate brief exposure to hypoxia (*medium confidence*; Pörtner *et al.*, 2014). Expansions of OMZs are predicted to compress habitat depth for hypoxia-intolerant fish such as tuna and halibut (Hoegh-Guldberg *et al.*, 2014, Sadorus *et al.*, 2014).

Incursion of hypoxic waters onto continental shelves has been observed to cause mortality large benthic invertebrates, in the California Current System, it is *likely* that changes in oxygen concentration have decreased the habitat available for benthic species (Cheung *et al.*, 2014, Hoegh-Guldberg *et al.*, 2014). Larval stages are particularly sensitive, suggesting that the impacts could threaten population survival and affect higher trophic levels (Pörtner *et al.*, 2014). There is *high confidence* that, as a result of increased energy demand, calcifiers are particularly sensitive to hypoxia (Gobler *et al.*, 2014, Pörtner *et al.*, 2014). Oxidation reactions in OMZs release nitrogen into the atmosphere meaning that less fixed nitrogen is available to primary producers, as a result there is *medium confidence* expansion of OMZs will limit primary productivity (Pörtner *et al.*, 2014). Decreases in coral photosynthesis under hypoxic conditions suggests that decreasing oxygen concentrations could have potential negative implications for reef ecosystems (Wijgerde *et al.*, 2014).

3.3.4. Future projections

The global average oxygen saturation of seawater is projected to decrease by 2.3% under RCP4.5 and 3.4% under RCP8.5 (Bopp *et al.*, 2013). However, it is considered *as likely as it is unlikely* that OMZs will expand as a result of climate change (Ciais *et al.*, 2013).

The expansion of OMZs will *likely* affect trophic interactions, species distribution, migration and composition. Small-bodied (< 1 mm) hypoxia-tolerant animals and microbes will benefit at the cost of large bodied, active animals with high metabolic oxygen demands. There will be a loss of biodiversity as communities shift to specialists that are adapted to tolerate hypoxic conditions (Pörtner *et al.*, 2014).

Under suboxia, only highly specialized species can survive, thus there is *high confidence* that expansion of suboxic and anoxic centres of pelagic OMZs and benthic dead zones will lead to loss of habitat (Pörtner *et al.*, 2014). Due to the specialized nature of animals living in hypoxic conditions, there is *high confidence* that expansion of OMZs will decrease biodiversity (Pörtner *et al.*, 2014). As average global oxygen concentrations are predicted to decrease more under RCP8.5 than RCP4.5, the effects described above will be more pronounced under RCP8.5, with potentially larger areas becoming hypoxic and suboxic.

3.4. Ocean acidification

Many biological processes require organisms to exert a tight control on internal pH; thus, ocean acidification inevitably alters individual fitness. A wide range of organismal functions are affected by ocean acidification including: membrane transport, calcification, photosynthesis, neuronal processes, growth, reproductive success and survival. Some processes can be enhanced by ocean acidification; photosynthesis requires CO₂ as a substrate so, theoretically, ocean acidification can benefit primary producers and nitrogen fixers. Conversely, calcification is generally negatively impacted by acidification (Pörtner *et al.*, 2014).

The magnitude of organism response to pH change depends on their ability for acid-base regulation, although there is *low to medium confidence* in our understanding of these mechanisms in many phyla (Pörtner *et al.*, 2014). In acidified conditions, some species increase their metabolic rate, possibly indicating that they are directing energy into pH mediation measures. Some organisms are able to acclimate to pH by up and down regulating genes related to affected processes and there is *medium to low confidence* that pH tolerance is higher in animals living in environments that are

naturally lower in pH (Pörtner *et al.*, 2014). Very little is known about the capacity for evolutionary adaptation as most experiments investigating the effects of ocean acidification are run over relatively short time periods.

3.4.1. Microbes

Due to insufficient field observations there is *limited evidence* and *low agreement* on how future conditions will affect microorganisms (Pörtner *et al.*, 2014). New research has suggested that ocean acidification might benefit bacterial communities by elevating growth (Endres *et al.*, 2014) and increased benthic bacterial diversity has been observed along natural CO₂ gradients (Taylor *et al.*, 2014a). Other studies have found no detectable effects of ocean acidification on natural microbial communities, possibly because their quick generation time allows fast adaptation to acidified conditions (Ahrendt *et al.*, 2014, Gazeau *et al.*, 2014).

Due to contradictory findings of *in situ* and laboratory experiments, there is *low to medium confidence* on the effects of ocean acidification on nitrogen (N₂) fixing cyanobacteria. A wide range of N₂ fixation responses to conditions predicted under RCP8.5 have been observed in laboratory experiments (Böttjer *et al.*, 2014, Eichner *et al.*, 2014, Gradoville *et al.*, 2014), possibly due to species specific differences in the mechanisms of N₂ fixation (Eichner *et al.*, 2014).

Certain species of both diatoms and dinoflagellates are thought to produce more toxic by-products under higher pCO₂ (Pörtner *et al.*, 2014). However, work with dinoflagellates has shown that toxin production per cell is not affected but toxin production increases due to increased growth rates (Errera *et al.*, 2014). There is evidence that ocean acidification may induce longer diatom chain lengths (E Ramos *et al.*, 2014) and make them less susceptible to photo inhibition (Wu *et al.*, 2014). However, the magnitude of their response can be strongly modulated by the length of acclimation period (Hennon *et al.*, 2014).

Coccolithophore growth and calcification responses exhibit highly varied responses depending on species, strain (Pörtner *et al.*, 2014) and secondary environmental controls such as irradiance, bloom species composition and nutrient availability (Benner *et al.*, 2013, Horigome *et al.*, 2014, Muller & Nisbet, 2014, Poulton *et al.*, 2014, Sett *et al.*, 2014, Young *et al.*, 2014b). Thus, a wide range of responses have been observed under conditions projected under RCP8.5 and there is *medium evidence* and *low agreement* on how they will be affected by future conditions (Pörtner *et al.*, 2014, Young *et al.*, 2014a). There is evidence that the coccolithophore, *Emiliania huxleyi*, has the capacity

to evolve genetic adaptations to both warming and ocean acidification expected under RCP8.5 (Benner *et al.*, 2013, Lohbeck *et al.*, 2014, Schluter *et al.*, 2014).

Ocean acidification can drastically alter the species composition of microbial assemblages, and this has been linked to increased occurrences of harmful algal blooms (HAB) of diatoms and dinoflagellates (Pörtner *et al.*, 2014). Community composition of diatom blooms is also altered by ocean acidification under iron replete conditions (Hoppe *et al.*, 2013).

There is *medium* to *high confidence* that foraminiferal calcification is negatively affected by acidification. Decreasing calcification, shell weight and ornamentation with increased dissolution and deformation, concurrent with increasing $p\text{CO}_2$, has been observed in laboratory cultures (Khanna *et al.*, 2013, Pörtner *et al.*, 2014). This is reflected in observed changes in fossilised foraminifera during periods of lower pH (Pörtner *et al.*, 2014). The severity effects on benthic foraminifera are species and symbiont specific (Doo *et al.*, 2014). Planktonic foraminifera are predicted to experience the greatest decrease in diversity and abundance in sub-polar and tropical areas, under RCP8.5 conditions (Roy *et al.*, 2014).

3.4.2. Macroalgae and seagrasses

Non-calcifying species generally exhibit positive growth responses to increasing CO_2 concentration although these responses are season and species specific (Longphuir *et al.*, 2013, Pörtner *et al.*, 2014). There is *high confidence* that conditions of 720 to 1800 $\mu\text{atm CO}_2$ (approximate values for 2100 under RCP8.5 = 950 $\mu\text{atm CO}_2$) stimulate increases in primary production, shoot density, reproductive output and below ground biomass (Mcminn *et al.*, 2014, Pörtner *et al.*, 2014), although these effects can be modulated by nutrient availability (Martínez-Crego *et al.*, 2014). It has been suggested with *low confidence* that some species maybe exposed to higher grazing pressure due to impacts on the production of grazer-deterrent substances (Betancor *et al.*, 2014, Pörtner *et al.*, 2014).

Calcifying species of macrophytes display complex and varied responses to ocean acidification (James *et al.*, 2014, Johnson *et al.*, 2014b, Mcminn *et al.*, 2014). There is *medium confidence* that impacts on calcification and respiration are observed when species-specific $p\text{CO}_2$ thresholds are surpassed (Mccoy & Ragazzola, 2014, Pörtner *et al.*, 2014). One study has shown evidence that thickly calcified species of crustose coralline algae will remain heavily calcified, whilst thin walled species will get thinner under future ocean acidification conditions (Mccoy & Ragazzola, 2014). Changes in

species composition along natural CO_2 gradients have been observed (Ordoñez *et al.*, 2014) but negative effects on calcification can be mediated by inter-specific interactions (Reyes-Nivia *et al.*, 2014, Short *et al.*, 2014) and acclimatization (Johnson *et al.*, 2014a). There is *medium confidence* that significant dissolution of living and dead maerl beds will occur, both of which provide important habitat for associated fauna (Brodie *et al.*, 2014).

3.4.3. Animals

Species-specific responses to ocean acidification are mixed (Duarte *et al.*, 2014, Pörtner *et al.*, 2014). Amongst benthic invertebrates, calcifying organisms are more sensitive than non-calcifying and amongst those that calcify, studies have shown reduced calcification, reduced rates of repair calcification and weakened calcified structures under acidified conditions in corals, echinoderms, molluscs, and larval crustaceans (Bressan *et al.*, 2014, Coleman *et al.*, 2014, Fitzer *et al.*, 2014, Pörtner *et al.*, 2014, Wei *et al.*, 2015).

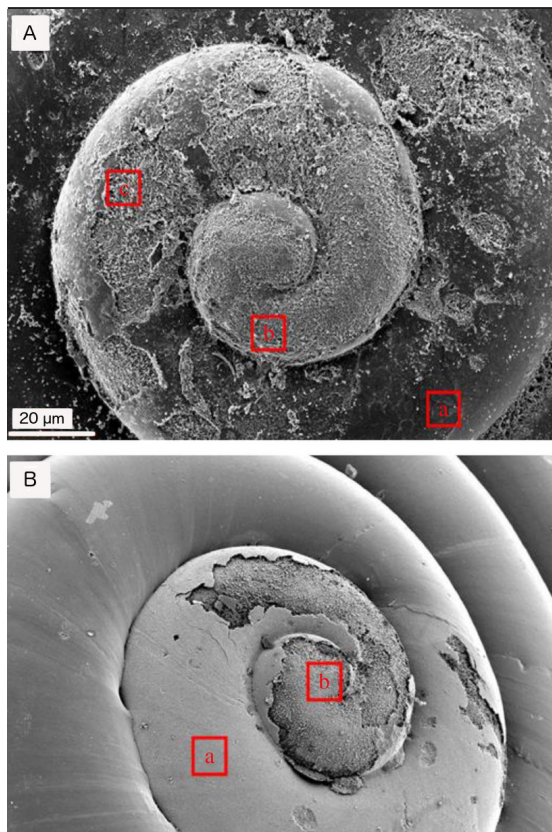
Some species have been observed to increase calcification rates at $p\text{CO}_2$ ranging from 600 to 900 μatm (approximately the CO_2 atm predicted for 2100 under RCP4.5 - RCP8.5), before decreases were exhibited at higher $p\text{CO}_2$ (Collard *et al.*, 2014, Dery *et al.*, 2014, Langer *et al.*, 2014, Pörtner *et al.*, 2014). There is *medium confidence* that increased calcification under lowered pH increases energetic costs at the expense of other physiological processes (Pörtner *et al.*, 2014, Rastrick *et al.*, 2014) and deformities have been observed in juvenile lobsters raised at high $p\text{CO}_2$ (Agnalt *et al.*, 2013).

Decreasing pH can also have species-specific, negative impacts on fertilization success, in sea urchins and scallops (Bögner *et al.*, 2014, Frieder, 2014, Scanes *et al.*, 2014, Sewell *et al.*, 2013, Sung *et al.*, 2014). Early life stages are thought to be more sensitive to ocean acidification drivers and there is *high confidence* in attributing fatalities at oyster farms to upwelling CO_2 , rich waters (Pörtner *et al.*, 2014). Projected future ocean acidification under RCP8.5 has also been shown to have negative effects on clam larval dispersal (Clements & Hunt, 2014).

Studies on calcifying zooplankton focused on pteropods. In the California Current System (Fig. 9) and Southern Ocean, pteropod shell dissolution due to undersaturated waters can already be observed (Bednaršek *et al.*, 2014, Pörtner *et al.*, 2014). There are fewer studies on non-calcifying zooplankton but there is some evidence of negative effects. Results of experiments using projected future levels of pH and temperature under RCP8.5, indicate a variety of sub-lethal effects, including decreased egg production, lower hatch success and decreased survival of nauplii

in copepods (Pedersen *et al.*, 2014, Vehmaa *et al.*, 2013, Zervoudaki *et al.*, 2013). There is *high confidence* that embryos of Antarctic krill are vulnerable to increased seawater concentrations of CO₂ (Larsen *et al.*, 2014) but Atlantic species have been found to be resilient to decreased pH (Sperfeld *et al.*, 2014).

Figure 9. Scanning electron microscope (SEM) images of shells of the pteropod *Limacina f. pacifica* from the California Current System showing signs of *in situ* dissolution



Source: Bednaršek *et al.* (2014).

Note: Scanning electron microscope (SEM) images of shells of the pteropod *Limacina f. pacifica* sampled during a 2011 cruise in the California Current System showing signs of *in situ* dissolution from (A) an onshore station, with the entire shell affected by dissolution, and (B) from the offshore region, with only the protoconch (first whorl) affected. Indicated in the figure are: (a) intact surface, (b) Type I dissolution, (c) severe dissolution.

Fish, including some commercially important species such as cod and herring, have been shown to be reasonably resistant to the effects of ocean acidification (Chambers *et al.*, 2014, Jutfelt & Hedgärde, 2013, Maneja *et al.*, 2014). However, deformities in calcified structures (Pimentel *et al.*, 2014b) and damage to internal organs have been observed under conditions predicted for the end of the century under RCP8.5 (Frommel *et al.*, 2014). The strongest effects observed in fish are behavioural, lower pH has been observed to affect

predator avoidance, prey detection, odour detection, lateralization, boldness and swimming behaviours in fish (Caprio *et al.*, 2014, Dixon *et al.*, 2014, Domenici *et al.*, 2014, Munday *et al.*, 2014, Murray *et al.*, 2014a, Welch *et al.*, 2014). It has also been observed to reduce retinal function in reef fish (Chung *et al.*, 2014). Effects on predator avoidance and prey detection have also been observed in reef fish (Munday *et al.*, 2014).

At the community level, there is *medium confidence* that naturally high CO₂ environments are associated with species compositions that favour non-calcifying species, suggesting that calcifiers are outcompeted once pH reaches 7.8-7.7 (Pörtner *et al.*, 2014). There is *high confidence* that elevated CO₂ causes losses in diversity, biomass and trophic complexity of benthic marine communities (Pörtner *et al.*, 2014).

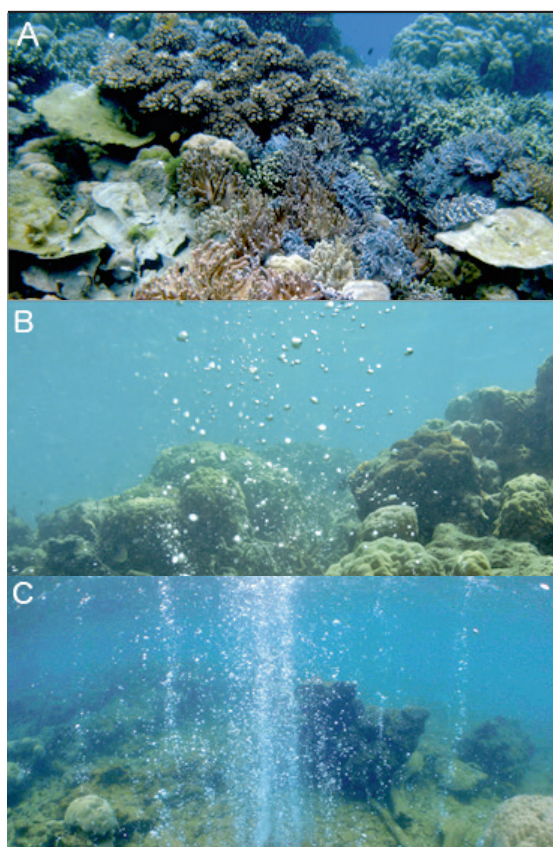
3.4.4. Warm and cold water corals

There is *high confidence* that warm water corals will be sensitive to future ocean acidification (Wong *et al.*, 2014). Reductions in calcification are species specific and affected by the internal pH of the calcifying fluid (Holcomb *et al.*, 2014), with fast calcifiers affected more than slow calcifiers (Comeau *et al.*, 2014d). The magnitude of calcification response to acidification is also highly geographically specific, suggesting that secondary factors such as irradiance, nutrient availability and interactions with other ecosystems, such as mangroves, can mediate the effects on calcification (Comeau *et al.*, 2014a, Comeau *et al.*, 2014c, Enochs *et al.*, 2014, Gibbin *et al.*, 2014, Tanaka *et al.*, 2014, Wendel, 2014, Yates *et al.*, 2014). Unfortunately, recent work has shown that local factors have caused the pH on corals reefs around the globe to increase at over three times the rate of the open ocean (Cyronak *et al.*, 2014). There is *high confidence* that warm water corals will be sensitive to future ocean acidification (Wong *et al.*, 2014). Reductions in calcification are species specific and affected by the internal pH of the calcifying fluid (Holcomb *et al.*, 2014), with fast calcifiers affected more than slow calcifiers (Comeau *et al.*, 2014d). The magnitude of calcification response to acidification is also highly geographically specific, suggesting that secondary factors such as irradiance, nutrient availability and interactions with other ecosystems, such as mangroves, can mediate the effects on calcification (Comeau *et al.*, 2014a, Comeau *et al.*, 2014c, Enochs *et al.*, 2014, Gibbin *et al.*, 2014, Tanaka *et al.*, 2014, Wendel, 2014, Yates *et al.*, 2014).

Ocean acidification has been shown to have significant effects on dissolution of warm water corals (Comeau *et al.*, 2014b, Silbiger & Donahue, 2014)

with up to 59% lower net community calcification observed under RCP8.5 conditions (Comeau *et al.*, 2014b) and is already resulting in enhanced erosion of reef framework carbonates (Silbiger & Donahue, 2014). There is also evidence that acidified conditions can reduce fertilization and settling success of larvae (Uthicke *et al.*, 2013). Decreasing pH is projected to decrease community calcification and increase dissolution effects (Silverman *et al.*). Although the response of coral calcification to ocean acidification is species specific (Fig. 10), reef ecosystems may be disproportionately affected by the affected by negative effects on keystone species (Alvarez-Filip *et al.*, 2013).

Figure 10. Three CO₂ seeps in Milne Bay Province, Papua New Guinea.



Source: Fabricius *et al.* (2011).

It should be noted however, that warm-water corals as well as cold-water corals may display resistance to lowered pH and can maintain positive net calcification under aragonite saturation states < 1 (Movilla *et al.*, 2014, Pörtner *et al.*, 2014). It is thought that they achieve this by increasing pH at the site of calcification (Venn *et al.*, 2011, Venn *et al.*, 2013). However, like warm-water corals, calcification response is species-specific (Movilla *et al.*, 2014, Pörtner *et al.*, 2014).

3.4.5. Ecosystems

As the effects of ocean acidification are complex and species specific, it is difficult to accurately assess the impacts at the ecosystem level. There is *high confidence* that ocean acidification will have a wide range of direct and indirect effects on ecosystems (Pörtner *et al.*, 2014), although the severity and the magnitude will vary with the type of ecosystem, geographical location, species composition and the influence of secondary environmental drivers (Garrard *et al.*, 2014, Hendriks *et al.*, Martínez-Crego *et al.*, 2014, Park *et al.*, 2014, Richier *et al.*, 2014). There is *high confidence* that ecosystems that are built around heavily calcified structures such as coral and vermetid reefs or maerl beds are at high risk from ocean acidification (Alvarez-Filip *et al.*, 2013, Brodie *et al.*, 2014, Comeau *et al.*, 2014b, Milazzo *et al.*, 2014).

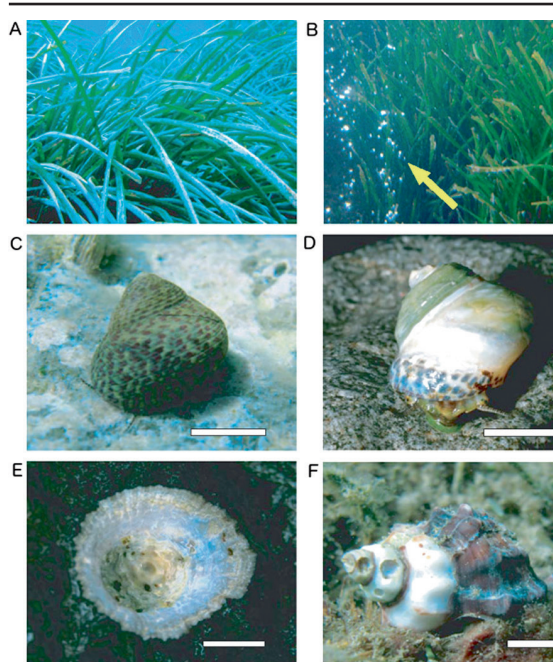
There is *high confidence* that areas prone to low saturation states such as eastern boundary upwelling systems and the polar seas will be strongly affected by ocean acidification. There is high confidence that Arctic ecosystems are also at high risk due to the exacerbating effects of freshwater from melting sea ice. The Arctic food web is relatively simple, with pteropods acting as an important trophic link (Amap, 2014). As pteropods are predicted to be highly affected by ocean acidification, there is *medium confidence* that there will wider consequences for the Arctic ecosystem, potentially affecting important fisheries, including salmonids (Amap, 2014). It is *likely* that there will be negative effects on shellfish hatcheries located along the continental shelf in the North Pacific where there are upwelling waters that are low in pH and dissolved O₂ (Gobler *et al.*, 2014, Gobler & Talmage, 2014, Hoegh-Guldberg *et al.*, 2014).

Biodiversity has been observed to decrease by 30% around natural CO₂ vents in the Mediterranean Sea and transplants of invertebrates in these areas suggest low vulnerability to projected conditions for 2100, although there is *low confidence* in this finding (Fig. 11; Hoegh-Guldberg *et al.*, 2014, Ziveri *et al.*, 2014). Coral diversity has also been observed to decrease around natural CO₂ vents in Papua New Guinea (Gattuso *et al.*, 2014). An 8-year trend of (variable) pH decline in upwelled waters along the Northeast Pacific coast was paralleled by shifts in community composition, where shelled species like mussels were replaced by fleshy algae and barnacles (Pörtner *et al.*, 2014).

Deep waters already have low saturation states for aragonite and calcite and ocean acidification is projected to cause decreases in calcification and increased dissolution of existing carbonate structures such as dead coral mounds, which are

important habitats. However, there is *limited evidence, medium agreement, and low confidence* on how organisms will be affected, with some studies suggesting that the impacts may not be as severe as first thought.

Figure 11. Organism samples from the surrounding area of volcanic CO₂ vents in the Mediterranean Sea



Source: Hall-Spencer *et al.* (2008).

Note: Organism samples from the surrounding area of volcanic CO₂ vents in the Mediterranean Sea, showing the impacts of lowered saturation states for calcium carbonate a, b, *Posidonia oceanica* with heavy overgrowth of Corallinaceae at pH 8.2 (a) and lacking Corallinaceae at mean pH 7.6 (b); arrow indicates bubbles from the CO₂ vent field. c, d, Typical examples of *O. turbinata* with the periostracum intact at pH 8.2 (c) and with old parts of the periostracum removed at mean pH 7.3 (d). e, f, Live *P. caerulea* (e) and *H. trunculus* (f) showing severely eroded, pitted shells in areas of minimum pH 7.4. Scale bars represent 1 cm.

3.4.6. Future projections

Individual level responses to ocean acidification are highly species-specific and can be affected by a range of other environmental factors and the degree of control that the organism exerts on the calcification process (Goffredo *et al.*, 2014, Pörtner *et al.*, 2014). There is *low confidence* that primary production will be enhanced under future conditions and *medium confidence* that ocean acidification will increase abundances of non-calcifying primary producers but be detrimental to calcifying primary producers and animals (Pörtner *et al.*, 2014). There is *high confidence* that ecosystems built around coral reefs are at high risk under future conditions (Pörtner *et al.*, 2014). There is also *low to medium confidence* that shifts in predator-prey relationships could occur as species distributions and fitness change in response to changing pH (Pörtner *et al.*, 2014).

RCP8.5

There is *medium to low confidence* that the levels of ocean acidification projected under RCP8.5 will be beneficial for most non-calcifying phytoplankton and cyanobacteria (Pörtner *et al.*, 2014). There is *medium confidence* that coccolithophores are vulnerable to projected end of century pH but evidence from natural populations found in high CO₂ waters and long-term laboratory experiments lends *medium confidence* that they will be able to adapt to future conditions (Benner *et al.*, 2013, Lohbeck *et al.*, 2014, Pörtner *et al.*, 2014).

There is *low confidence* that seagrasses and non calcifying macroalgae will also benefit under RCP8.5 conditions (Brodie *et al.*, 2014, Gutow *et al.*, 2014, Johnson *et al.*, 2014b, Longphuir *et al.*, 2013, Pörtner *et al.*, 2014), potentially leading to increased abundance, expanding habitat for associated species that are tolerant to ocean acidification.

There is *high to medium confidence* that calcifying invertebrates, including commercially important species such as oysters, mussels and clams, will be vulnerable to end of century ocean acidification, with implications for reproductive success (Clements & Hunt, 2014, Pörtner *et al.*, 2014, Scanes *et al.*, 2014). Fish are also projected to be vulnerable under RCP8.5 conditions and there is *low confidence* from model predictions that ocean acidification, will generally reduce fish biomass and catch (Pörtner *et al.*, 2014). There is *low confidence* that crustaceans will be able to tolerate the projected pH decrease (Harms *et al.*, 2014, Pörtner *et al.*, 2014). In mesocosm studies, losses of calcifiers occurred around 0.5 units below the pH values expected from ocean acidification under RCP8.5 by 2100 (Pörtner *et al.*, 2014). These projections have profound implications for future trophic interactions and ecosystem functioning; it is *likely* that many calcifiers will be out-competed by non-calcifying species. There is *high confidence* that elevated CO₂ will cause losses of diversity, biomass and trophic complexity in benthic marine communities (Pörtner *et al.*, 2014). The fossil record shows that ocean acidification events in geological history are marked by mass extinctions of calcifying taxa. Current rates of ocean acidification are progressing at least 10 times faster than comparable events in geological history (Pörtner *et al.*, 2014), therefore it is *likely* that species extinctions will occur.

There is *high confidence* that warm waters corals will be vulnerable to RCP8.5 levels of acidification. Under RCP8.5 there is *medium confidence* that dissolution of reefs will be widespread by the end of the century (Wong *et al.*, 2014) and *low confidence* that projected pH levels will also

impact larval dispersal and settlement. This is *very likely* to reduce habitat and refugia for associated fauna and further reduce the fitness of calcifying fauna, such as benthic foraminifera, which are already predicted to be vulnerable to future conditions. There is *high confidence* that calcifying algae are also vulnerable under RCP8.5 scenarios, many species are important for reef stability and function, therefore losses may further impact coral reef health. Degradation of reef ecosystem health will have negative impacts on fisheries, tourism and coastal protection (Pörtner *et al.*, 2014).

RCP4.5

Under the conditions predicted for the end of the century under RCP4.5, the effects of ocean acidification are less severe than those for RCP8.5. Non-calcifying photosynthesizers will still benefit but may have slightly less of a competitive advantage over calcifying species. There is *low confidence* that levels of CO₂ predicted under RCP4.5, remains within the tolerance levels of coccolithophores (Pörtner *et al.*, 2014).

There is *low confidence* that certain groups of calcifying invertebrates will be tolerant to RCP4.5 conditions including foraminifers and some pelagic molluscs and *medium confidence* that crustaceans will also be able to tolerate these conditions (Pörtner *et al.*, 2014). There is also *low confidence* that many fish species will be resistant under the conditions in 2100 (Pörtner *et al.*, 2014).

There is *medium to low confidence* that both warm and cold water corals are vulnerable to end of century and *medium confidence* that an atmospheric CO₂ concentration expected under RCP4.5 (560 ppm) is the threshold at which global dissolution of reefs will occur (Wong *et al.*, 2014). The habitat loss associated with reef dissolution under RCP4.5 will be less severe than for RCP8.5. There is *low confidence* as to whether future conditions will alter distribution of cold corals (Pörtner *et al.*, 2014).

3.5. Effects of multiple drivers

There is *high confidence* that the effects of climate change will act on organisms and ecosystems as a suite of simultaneous, multiple environmental drivers which will interact with each other to have synergistic or antagonistic effects on the fitness of the individual or the ecosystem.

3.5.1. Microbes

Both synergistic and antagonistic effects of multiple drivers on microbial biota in the surface ocean have been observed in manipulation or modeling experiments (Pörtner *et al.*, 2014). The effect of RCP8.5 levels of CO₂ on growth is species specific and can be

strongly modulated by nutrient availability (Hoppe *et al.*, 2013, Marañón *et al.*, 2014), light conditions and temperature (Errera *et al.*, 2014, Pörtner *et al.*, 2014, Sett *et al.*, 2014). These differences can alter bloom species compositions, with potential impacts on predator-prey interactions (Hoppe *et al.*, 2013, Pörtner *et al.*, 2014). Shifts to different phytoplankton species compositions can alter the sinking rates of particles. As these particles are decomposed by bacteria, it can alter the levels of dissolved oxygen, potentially expanding OMZs (Pörtner *et al.*, 2014).

The coccolithophore *Emiliania huxleyi* has demonstrated the ability to adapt to the concurrent drivers of ocean warming and acidification (Lohbeck *et al.*, 2014, Schluter *et al.*, 2014).

3.5.2. Plants and animals

There is *high confidence* that the interaction between temperature increase and pH decrease predicted under RCP8.5 for the 2100 have synergistic negative effects on the growth, survival, fitness, calcification and development of organisms (Gaitán-Espitia *et al.*, 2014, Gobler *et al.*, 2014, Hyun *et al.*, 2014, Mackenzie *et al.*, 2014b, Madeira *et al.*, 2014, Maudgendre *et al.*, 2014, Pörtner *et al.*, 2014, Rastrick *et al.*, 2014, Rosa *et al.*, 2014a, Rosa *et al.*, 2014b, Roy *et al.*, 2014, Schmidt *et al.*, 2014a, Schram *et al.*, 2014, Vehmaa *et al.*, 2013). In some cases, hypoxic conditions have been observed to mediate the negative effects of ocean acidification (Mukherjee *et al.*, 2013).

Conversely, hypoxia reduces heat tolerance and vice versa (see Annex 5). There is *high confidence* that warming will expand the area of ecosystems affected by hypoxia even if oxygen concentrations remain unchanged. This is likely to restrict geographic and depth ranges, particularly in upwelling areas (Pörtner *et al.*, 2014).

There is also growing evidence that the interactions of other environmental drivers such as irradiance, nutrient availability, geographic location and species community composition can strongly modulate the biological effects of warming, ocean acidification and hypoxia (Comeau *et al.*, 2014a, Comeau *et al.*, 2014c, Hoppe *et al.*, 2013, Ko *et al.*, 2014, Pörtner *et al.*, 2014, Poulton *et al.*, 2014, Richier *et al.*, 2014).

There is *high confidence* that warming acts synergistically with CO₂ to decrease calcification and increase sensitivity to bleaching in warm-water corals, although the effects can be modulated by irradiance levels (Comeau *et al.*, 2014a, Pörtner *et al.*, 2014). Combined warming and ocean acidification in mesocosms following approximately RCP4.5 and RCP8.5 scenarios caused losses of symbionts and corals, and a nocturnal decalcification of the reef community in summer (Pörtner *et al.*, 2014).

3.5.3. Ecosystems

There is *high confidence* that the effects of climate change are already causing changes to the physical and chemical characteristics of habitats and altering food webs (Pörtner *et al.*, 2014). There is *high confidence* that the indirect effects of climate change, such as shifts in stratification and productivity, expanding oxygen minimum zones, and the changing composition and biomass of food are exacerbating the effects on ecosystems (Pörtner *et al.*, 2014). This complicates predictions of future consequences for organisms and ecosystems.

There is *high confidence* that the combined effects of increased temperature, hypoxia, and ocean acidification will have significant impacts on organisms that act as ecosystem engineers, organisms that create, significantly modify, maintain or destroy a habitat, such as coral or kelp (Dove *et al.*, 2013, Pörtner *et al.*, 2014). Thus, climate change could drastically alter ecosystems by reducing habitat quality and extent, if ecosystem engineers are affected.

There is *high confidence* that species' range distributions and phenologies will be affected by climate change. The rate and extent of these changes will vary geographically and between different groups of organisms and alter the trophic interactions in a given area (Pörtner *et al.*, 2014). It is likely that some of these changes may be irreversible. The knock-on effect of changes at the base of the food web on the next trophic level can be amplified throughout the food web and drive the ecosystem to a new regime that may become permanent (Fig. 12; Pörtner *et al.*, 2014).

3.5.4. Future projections

Due to the relative lack of knowledge on the interacting effects of environmental drivers and the complexity of the marine trophic web, it is difficult to make ecosystem wide projections. It is *likely* that under both RCP scenarios there will be significant poleward migrations and phenological shifts in many groups of organisms (Pörtner *et al.*, 2014). It is *very likely* that these effects will be amplified under RCP8.5 compared to RCP4.5 (Fig. 13; Pörtner *et al.*, 2014). It has also been suggested that there will be losses in biodiversity, particularly in the tropics (Pörtner *et al.*, 2014). Following OCLTT theory (see Annex 5) there may be shifts to smaller body sizes due to thermal stress, exacerbated interactions with other drivers (Pörtner *et al.*, 2014).

Storch *et al.* (2014) provide evidence that small, less complex unicellular Eukarya, Bacteria and Archaea will benefit and proliferate under climate change as they evolve rapidly and can survive anaerobic conditions and higher temperatures than more complex, multicellular animals (Fig. 13).

Although non-calcifying phytoplankton are thought to be relatively resilient to the effects of ocean acidification (Pörtner *et al.*, 2014), recent work has shown that nutrients play an important role in controlling growth. As a result, it is likely that low nutrient availability due to enhanced thermal stratification will limit phytoplankton growth under both RCP scenarios but especially 8.5 (Fig. 13; Marañón, *et al.*, 2014).

While potentially benefiting from increased dissolved CO₂, macrophytes are limited in their thermal tolerance and, therefore, may be somewhat negatively affected by climate change (Pörtner *et al.*, 2014, Brodie *et al.*, 2014). Kelps have been shown to be sensitive to conditions projected under RCP8.5 (Fig. 13; Brodie *et al.*, 2014, Gaitán-Espitia *et al.*, 2014). Seagrasses are thought to be more tolerant of increasing temperatures and may proliferate under climate change conditions, particularly if they are able to take advantage of ecological niches provided by the decline of less tolerant groups of organisms (Fig. 13; Brodie *et al.*, 2014, Pörtner *et al.*, 2014).

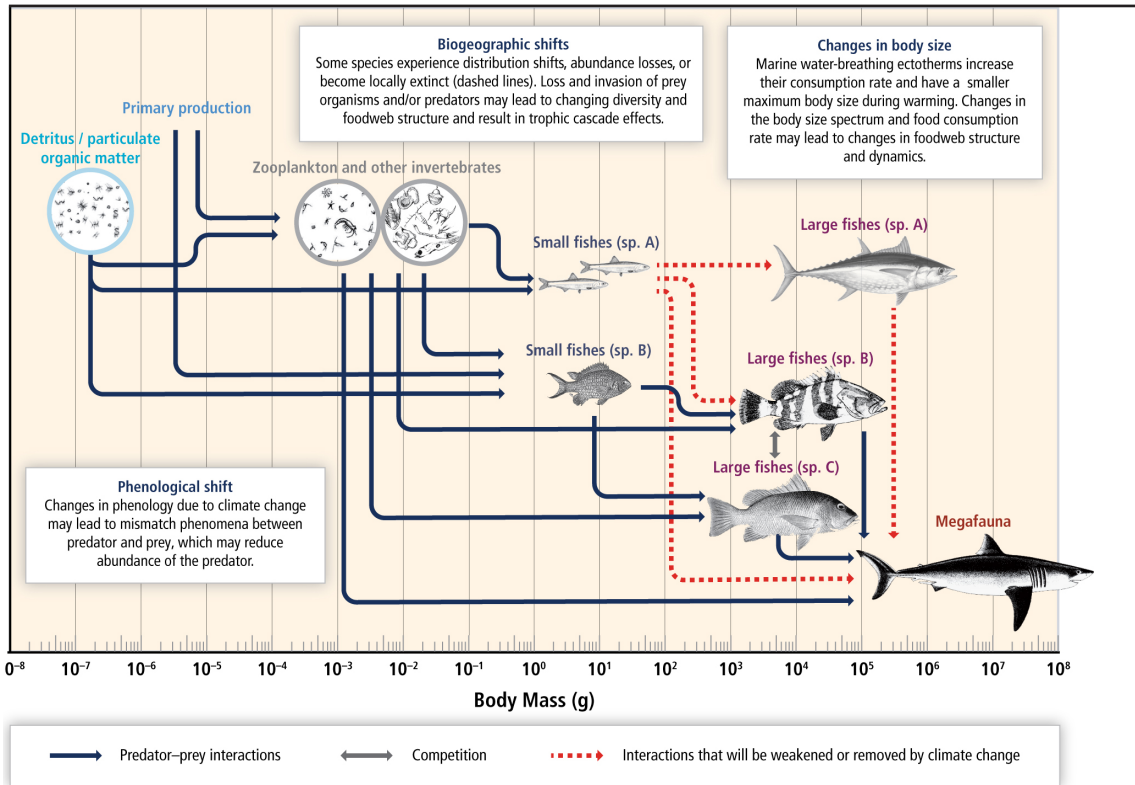
Non-calcifying zooplankton are thought to be reasonably resilient to the effects of ocean acidification, however, some calcifying groups, such as pteropods have been shown to be highly sensitive to declining saturation states (Bednaršek *et al.*, 2014, Pörtner *et al.*, 2014). It is *likely* that zooplankton will continue to display large geographic and phenological shifts under increasing temperatures (Fig. 13; Poloczanska *et al.*, 2014, Chambers *et al.*, 2014).

Studies of benthic calcifiers have shown them to be sensitive to the effects of climate change, particularly ocean acidification (Pörtner *et al.*, 2014). Observations of communities around natural CO₂ vents have shown decreases in biodiversity and species losses under increasing CO₂ concentrations (Hoegh-Guldberg *et al.*, 2014). It is likely that these effects will be more pronounced under RCP8.5 than 4.5. Experimental work has shown crustaceans to be more tolerant of lowered pH than other benthic species (Pörtner *et al.*, 2014) so it may be that they will be more tolerant to the effects of climate change than other benthic invertebrates, particularly under RCP4.5 (Fig. 13).

Pelagic fish could be affected by predator prey mismatches as effects are amplified up the trophic web to higher levels. Temperature increase will lead to poleward migrations with potentially negative impacts on low latitude fisheries and positive impacts for high latitude fisheries (see Cheung *et al.*, 2015).

Coral reefs are predicted to be sensitive to the effects of both warming and ocean acidification,

Figure 12. Schematic diagram of expected responses to climate change in a marine food web.



Note: A coupled pelagic and benthic food web is structured by the body size spectrum of species. Combined warming, hypoxia, and ocean acidification reduce body size, shift biogeographies, change species composition and abundance, and reconfigure trophic linkages and interaction dynamics. Fishing generally removes large-bodied species and truncates the body-size spectrum of the community. This confounds the detection and attribution of food web responses to climate change. Arrows represent species interactions (e.g., between predator and prey or competitors for food or space). Broken lines reflect the potential loss of populations and trophic linkages due to climate change. Source: Pörtner *et al.* (2014).

although warming will have the greatest detrimental effects, the drivers will act synchronously to increase bleaching events, reduce recovery from bleaching, impair reproduction and increase dissolution (Wong *et al.*, 2014, Gattuso *et al.*, 2014). Some species of coral have been shown to be more resilient to the effects of climate change than others, but it is likely that reef biodiversity will be severely affected under both RCP scenarios (Comeau *et al.*, 2014d, Wong *et al.*, 2014).

4. DISCUSSION

Research published following AR5 endeavored to address many of the key uncertainties highlighted by the IPCC. In particular, ecological advances included studies assessing climate-related impacts to different developmental stages of various taxa, as well as an improved understanding of impacts arising from ocean acidification. Studies have recently begun to investigate ecosystem-level responses to climatic stressors, and have identified additional

evidence of changes in community size structure and food web composition, with observed examples of community phase shifts across polar, temperate and tropical marine ecosystems. Predator-prey dynamics are also projected to change under ocean acidification and other drivers. Empirical and theoretical evidence continues to support the role of climate velocity in influencing species range shifts.

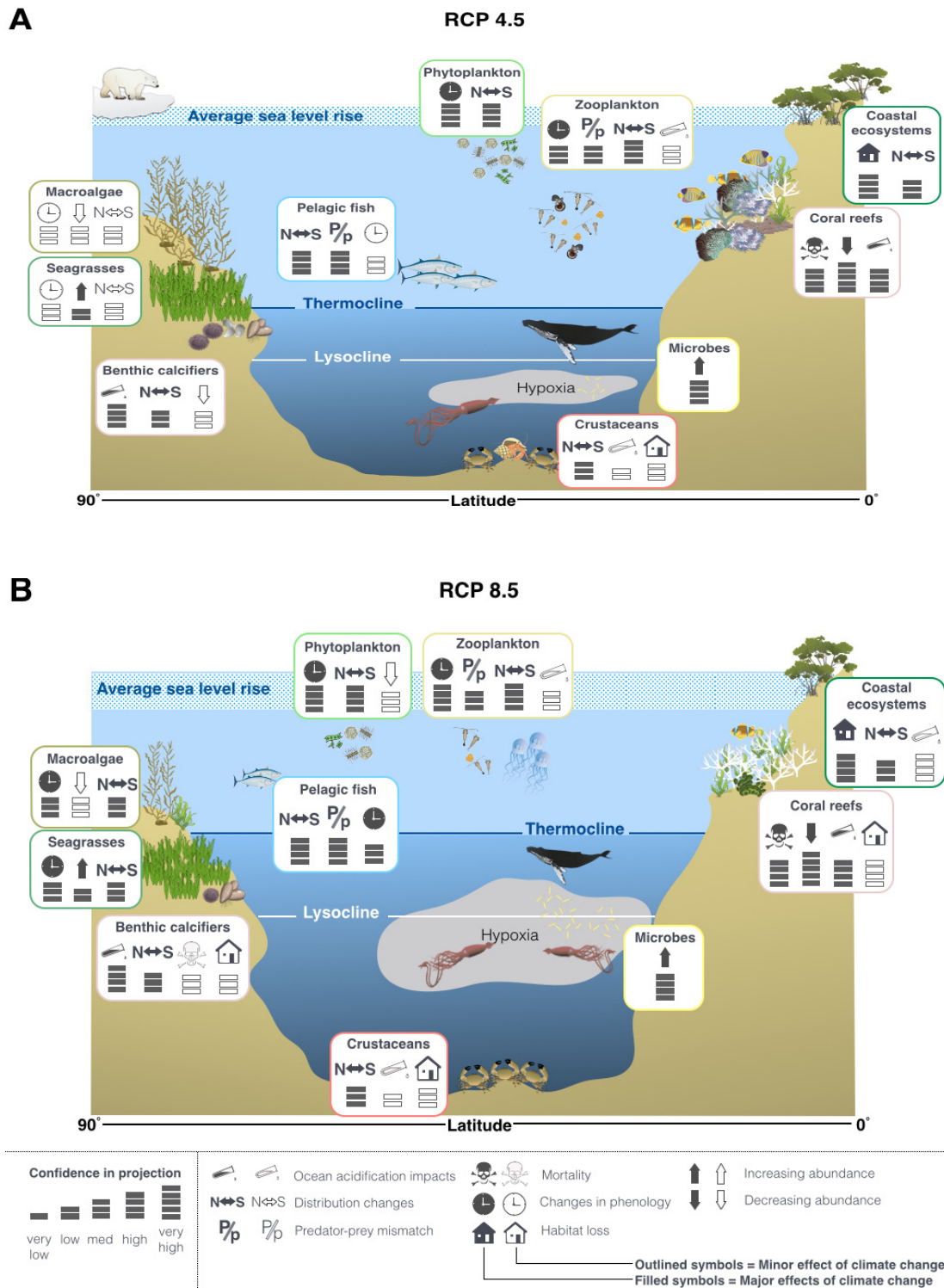
4.1. Agreement and points of departure from AR5:

In most cases the studies published since AR5 agree or add further weight to a growing body of evidence.

New studies suggest that the warming hiatus in sea surface temperatures may be caused by heat sequestration in deep ocean basins.

Trenberth *et al.*, (2014) and Chen & Tung, (2014) proposed that the heat has been transported to deeper waters in cooling cycles that might last

Figure 13. Projected changes to physical features in the oceans and some of the potential impacts on biology under RCP 4.5 (A) and 8.5 (B)



Note: Impressions of the projected changes to physical features in the oceans and some of the potential impacts on life in the oceans under RCP 4.5 (A) and 8.5 (B), based on the findings reported in the IPCC AR5 and literature published since the AR5. It is projected that thermocline and lysocline will shoal to a greater extent and OMZs will expand more under RCP8.5 compared to 4.5. These changes will favour bacteria and hypoxic specialists (Pörtner *et al.* 2014, Storch *et al.*, 2014) and limit the depth ranges of many species, causing habitat loss (Pörtner *et al.* 2014). In general, it is predicted that there will be a shift towards smaller body sizes and that many species will exhibit poleward migrations in response to increasing sea temperatures (Pörtner *et al.* 2014). Symbols provided by <http://ian.umces.edu/imagelibrary.html>.

between 20 to 35 years. However, there is uncertainty as to whether the Atlantic or the Pacific basin is the site of the excess heat storage.

Satellite observations of sea surface height have been used to propose higher heat content in the Southern Hemisphere.

Durack *et al.*, (2014) suggested that the IPCC AR5 estimates for increases in ocean heat content might be biased toward low values due to under sampling of the Southern Hemisphere compared to the Northern Hemisphere. Results of calculations using sea surface height show a more homogeneous warming between the two hemispheres, with larger magnitudes in the South Pacific and South Atlantic basins compared to IPCC estimates.

Improved understanding on the timescales involved in the emergence of anthropogenically induced changes demonstrates that anthropogenic forcing has already pushed changes in surface pH beyond the range of 20th century variability.

New research by Keller *et al.*, (2014) found that, for the majority of the global ocean area, anthropogenic trends in surface ocean pH (and pCO₂) emerge within roughly 12 years compared to between 10 and 30 years for surface ocean DIC and 45–90 years for sea surface temperature. The ability to quantify the time it takes for trends to emerge has enabled the separation of anthropogenically induced changes from natural cycles.

Evidence continues to strongly support the findings from AR5 that many species are undergoing geographical and phenological shifts as a result of warming.

(Beaugrand *et al.*, 2014, Chambers *et al.*, 2013, Goberville *et al.*, 2014, Hiddink *et al.*, 2014, Jones & Cheung, 2014, Kim *et al.*, 2014, Lambert *et al.*, 2014, Poloczanska *et al.*, 2014, Pörtner *et al.*, 2014, Rice *et al.*, 2014). Different species and groups have differential responses to warming, effects are seen at every trophic level. As changes are not synchronous, it remains difficult to predict the effects that this will have on food webs.

*Recent research has suggested some coral species may have some capacity to recover from bleaching events (Maor-Landaw *et al.*, 2014), and to acclimatize to higher temperatures (Palumbi *et al.* 2014, Logan *et al.*, 2014).*

Modeling historical coral populations indicates that corals have some capacity to adapt to increasing temperature, although it is doubtful that they will be able to adapt quickly enough to maintain populations under high emissions

scenarios (Logan *et al.*, 2013). Gene expression work has shown that some species display a rapid acclimatization to warming, however the capacity for coral reefs to respond to multiple stressors remains uncertain (Palumbi *et al.*, 2014).

Coccolithophores demonstrate evolutionary adaptation under ocean warming and acidification.

Benner *et al.* (2013) and Schlüter *et al.* (2014) both demonstrated that a coccolithophore species has the ability to adapt to significant ocean acidification and warming, demonstrating no significant changes in calcification or growth rates. It is uncertain whether other physiological processes will be strongly affected by these adaptations.

Shifts in nutrient availability as a key driver for phytoplankton growth.

Marañón, *et al.* (2014) demonstrated that resource supply overrides temperature as a controlling factor of marine phytoplankton growth. This suggests that nutrient availability as a result of stratification may limit primary productivity in some regions.

4.2. Conclusions

Anthropogenically produced greenhouse gases have caused measurable physical changes in the oceans. The oceans absorb 93% of the excess energy produced by global warming and approximately 28% anthropogenic CO₂, buffering the effects of climate change (Rhein *et al.*, 2013). This buffering is not without cost and there have been changes in ocean temperature, pH and oxygen content have been observed over the second half of the 20th century (Rhein *et al.*, 2013). Increasing atmospheric CO₂ will always lead to an increase in ocean carbon storage, all other things being held constant (Ciais *et al.*, 2013), thus, 21st century emissions will determine the condition of the world's oceans for centuries to come (Ciais *et al.*, 2013). Under both RCP4.5 and 8.5, physical changes are projected to continue but with greater severity under RCP8.5 (Bopp *et al.*, 2013, Ciais *et al.*, 2013).

Impacts of warming on biological processes can already be observed (Poloczanska *et al.*, 2014, Pörtner *et al.*, 2014) as organisms shift their distributions polewards (Poloczanska *et al.*, 2014), alter the seasonal timing of life events (Pörtner *et al.*, 2014) and instances of coral bleaching increase in frequency (Wong *et al.*, 2014). Experimental evidence has shown many organisms to be sensitive to projected future levels of ocean acidification, with calcifiers showing the strongest responses. However, observations of the effects

of ocean acidification on natural populations are scarce, except in areas which have naturally high concentrations of dissolved CO₂ (Pörtner *et al.*, 2014, Bednaršek *et al.*, 2014). Changes in dissolved oxygen concentrations are highly variable between regions, but it is predicted that expanding OMZs will favour bacteria and hypoxic specialists, whilst reducing habitat for organisms with higher oxygen demands (Pörtner *et al.*, 2014).

The overarching findings of both the AR5, and many of the studies published since, is that the effects of anthropogenically produced climate change on organisms is highly species specific. Impacts also varying regionally in response to local drivers and synchronously with other climate change drivers in unpredictable ways. As a result, there is limited ability to project the future for marine ecosystems. ■

APPENDIX

Annex 1. Language of certainty

The IPCC report employs a specialized language to quantify confidence and certainty in the findings they report, for consistency, the same language is also used throughout this report. In this box the standard terms used to define levels of confidence and certainty are explained.

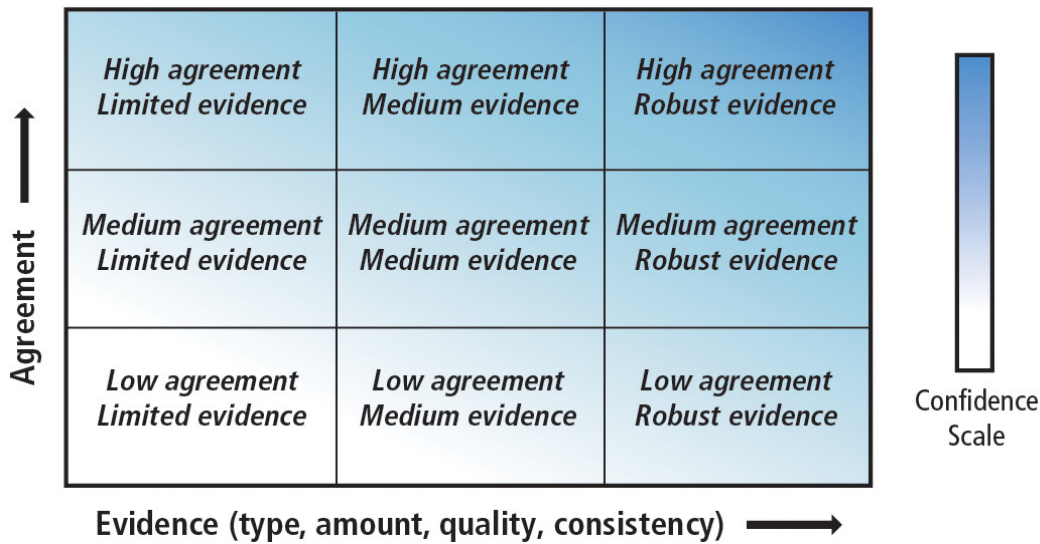
Confidence terminology

- Very high confidence*: at least 9 out of 10 chance
- High confidence*: about 8 out of 10 chance
- Medium confidence*: about 5 out of 10 chance
- Low confidence*: about 2 out of 10 chance
- Very low confidence*: less than 1 out of 10 chance

Likelihood terminology

- Virtually certain*: 99-100% probability of occurring
- Very likely*: 90-100% probability
- Likely*: 66-100% probability
- About as likely as not*: 33-66% probability
- Unlikely*: 0-33% probability
- Very unlikely*: 1-10% probability
- Exceptionally unlikely*: 0-1% probability

Figure 14. The basis for defining a confidence level for a statement based on levels of evidence (limited, medium, robust) and agreement (low, medium and high).



Source: Mastrandrea *et al.* (2010).

Annex 2. CO₂ and Emissions RCP scenarios

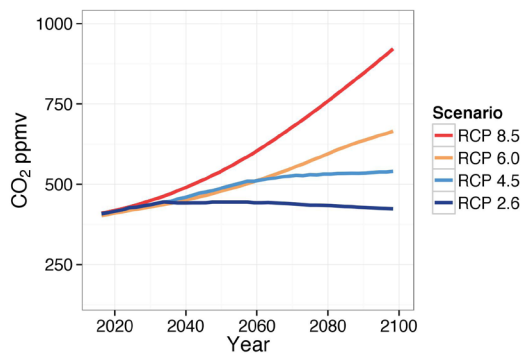
The IPCC projections of CO₂ emissions over the 21st century are broken down into 4 representative concentration pathways extending up to the year 2100 (RCP; Fig. 15). These are based on 4 different emissions scenarios published in existing literature and designed for use in studies that assess the risks of crossing certain physical and biological thresholds. All modelled scenarios show with *very high confidence* that ocean uptake of CO₂ will continue across all scenarios with higher uptake for the higher CO₂ concentration scenarios.

RCP2.6: One pathway where radiative forcing peaks at approximately 3 W m⁻² before 2100 and then declines after the turn of the century. Median temperature in 2100: 1.6°C, range to be considered

RCP4.5 and RCP6.0: Two intermediate *stabilization pathways* in which radiative forcing is stabilized at approximately 4.5 W m⁻² and 6.0 W m⁻² after 2100. Note that 4.5 is similar to the 2° C warming limit agreed as an upper limit in some international negotiations

RCP8.5: One high pathway for which radiative forcing reaches greater than 8.5 W m⁻² by 2100 and continues to rise for some amount of time after the turn of the century.

Figure 15. Atmospheric CO₂ concentrations for the 21st century based on the different RCP scenarios.



Annex 3. Upwelling

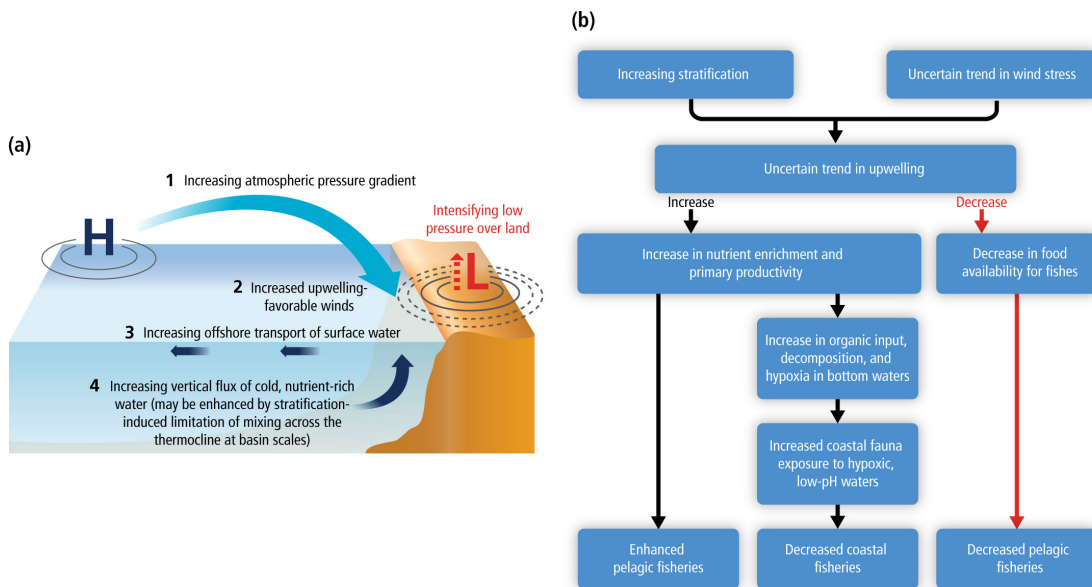
Upwelling is the vertical transport of cold, dense, nutrient-rich, relatively low-pH and often oxygen-poor waters to the euphotic zone where light is abundant. These conditions trigger high levels of primary production and a high biomass of benthic and pelagic organisms. The driving forces of upwelling include wind stress and the interaction of ocean currents with bottom topography. Upwelling intensity also depends on water column stratification. The major upwelling systems are the Equatorial Upwelling System (EUS) and the Eastern Boundary Upwelling Ecosystems (EBUS) represent only 10% of the ocean surface but contribute nearly 25% to global fish production (Lluch-Cota *et al.*, 2014).

It is hypothesized that the difference in rates of warming between the land and ocean increases the coastal air pressure gradient. This increases alongshore winds, leading to intensified offshore transport of surface water and the upwelling of nutrient-rich, cold waters (Fig. 16). As the nutrient input from upwelling waters supports a significant portion of global primary productivity, any changes in the strength of upwelling can be amplified up the food chain, affecting zooplankton, foraging fish, seabirds, and marine mammals (Lluch-Cota *et al.*, 2014).

There is *high confidence* that increased upwelling would enhance fisheries yields. However, the export of organic material from surface to deeper layers of the ocean may increase and stimulate its decomposition by microbial activity, enhancing oxygen depletion and CO₂ enrichment in deeper water layers. Once this water returns to the surface through upwelling, benthic and pelagic coastal communities will be exposed to acidified and deoxygenated water which may combine with anthropogenic impacts to negatively affect marine life and ecosystems in the upper ocean (Lluch-Cota *et al.*, 2014).

Reduced upwelling would also reduce the productivity of important pelagic fisheries, such as for sardines, anchovies and mackerel. However, under projected scenarios of reduced upward supply of nutrients due to stratification of the open ocean, upwelling of both nutrients and trace elements may become increasingly important to maintaining upper ocean nutrient and trace metal inventories (Lluch-Cota *et al.*, 2014).

Figure 16. (a) Hypothetic mechanism of increasing coastal wind driven upwelling at Equatorial and Eastern Boundary upwelling systems, where different warming rates between land and ocean results in increased land-ocean (1) pressure gradients that produce (2) stronger alongshore winds and (3) offshore movement of surface water, and (4) increased upwelling of deep, cold, nutrient rich waters to replace it. (b) Potential consequences of climate change in upwelling systems.



Source: Lluch-Cota *et al.* (2014).

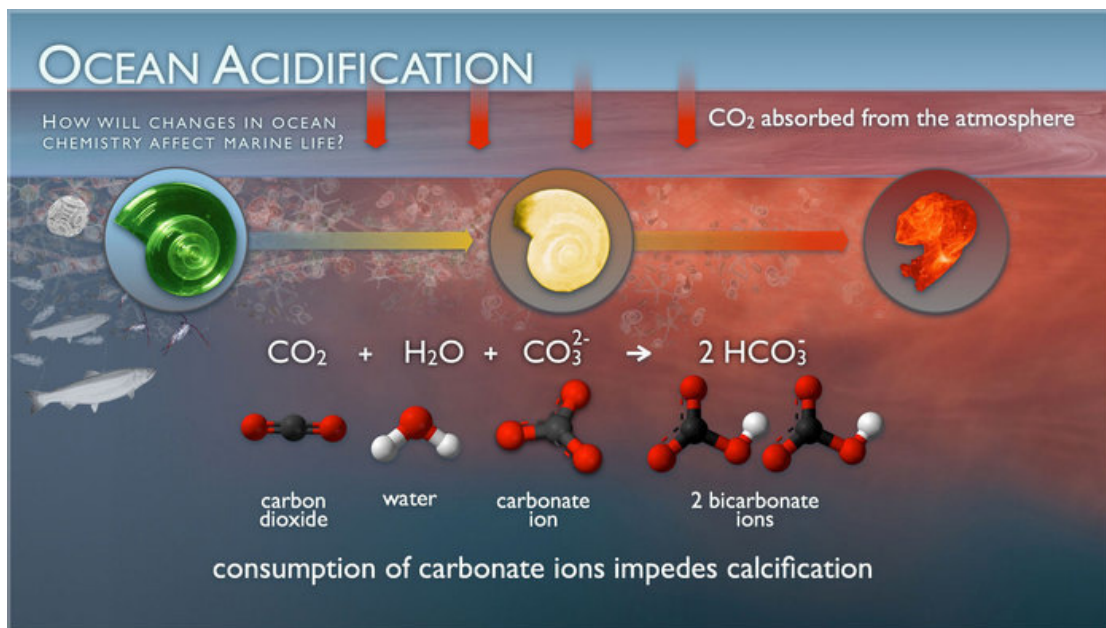
Annex 4. Ocean acidification

Ocean acidification refers to a decrease in seawater pH over an extended period, typically decades or longer, caused primarily by the uptake of carbon dioxide (CO₂) from the atmosphere. Ocean acidification can also be caused by other chemical additions or subtractions from the oceans that are natural (e.g., increased volcanic activity or long-term changes in net respiration) or human-induced (e.g., release of nitrogen and sulphur compounds into the atmosphere). Anthropogenic ocean acidification refers to the component of pH reduction that is caused by human activity (Rhein *et al.*, 2013).

When carbon dioxide (CO₂) is absorbed by seawater, chemical reactions occur that reduce seawater pH, carbonate ion (CO₃²⁻) concentration, and saturation states of calcium carbonate minerals. Together, these chemical reactions are termed “ocean acidification”. The reduction in CO₃²⁻ concentration caused by ocean acidification has potentially negative effects for calcifying organisms as it will cause the calcium carbonate saturation state (Ω) to decrease. If Ω is less than 1, the mineral phase is under saturated and dissolution will occur. Conversely, if Ω is greater than 1 it means that the mineral phase is supersaturated and precipitation is favoured. Different polymorphs of CaCO₃ are precipitated by marine calcifiers; calcite and aragonite, aragonite is approximately 50% more soluble than calcite.

Ocean acidification is causing many parts of the ocean to become undersaturated with respect to calcite and aragonite. Consequently, calcifying organisms have been observed to exhibit the strongest negative responses to ocean acidification, with analysis revealing reductions in calcification, growth, abundance and survival rate with increasing pCO₂ (Rhein *et al.*, 2013).

Figure 17. The chemistry of ocean acidification



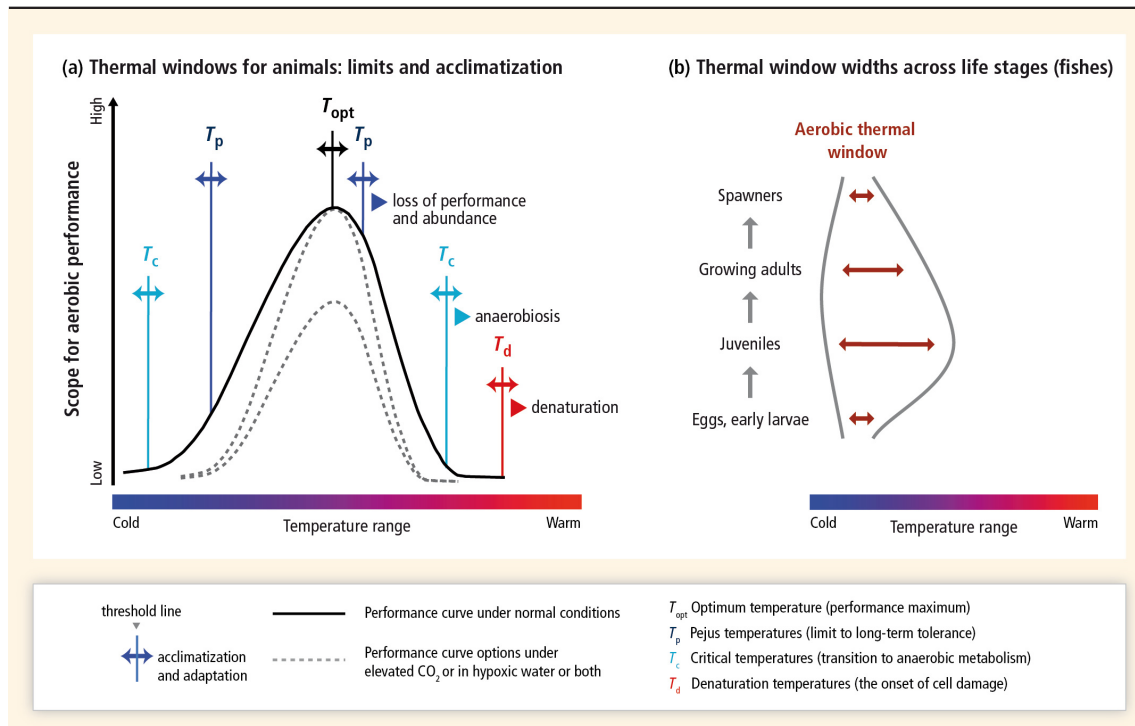
Source: www.pmel.noaa.gov

Note: Anthropogenic ocean acidification occurs as the oceans absorb CO₂ from the atmosphere. Carbon dioxide dissolved in seawater undergoes a series of chemical reactions, which result in a lowering of pH and carbonate ion concentration. This lowers the saturation state of calcium carbonate, making it more difficult for animals to produce calcium carbonate structures such as shells and skeletons.

Annex 5. OCLTT and thermal strategies

The mechanisms shaping an animal's thermal performance curve and, thereby, its thermal niche have been explained by the concept of “oxygen and capacity limited thermal tolerance”, which is applicable to marine invertebrates and fishes. The temperature range at which animals can function best, results from optimal oxygen supply at minimal oxygen usage. At temperature extremes, oxygen supply capacity becomes constrained in relation to demand, and metabolism becomes thermally limited. Beyond upper and lower temperature thresholds (T_p , Annex 6) growth, reproduction, and other key functions decrease. These thresholds change during the individual life cycle, and with body size. At large body size, limitations in oxygen supply are exacerbated and heat tolerance limits shift to lower temperatures. Motile animals with wide thermal tolerance windows that have adapted to a wide distributional range of temperatures are termed **eurytherms**. Conversely, **stenotherms** have narrow thermal windows and low energy demand lifestyles, making them sensitive to temperature change (Pörtner *et al.*, 2014). Adopting OCLTT principles has enabled modelling studies to project climate effects and paleo-studies to explain climate-induced mass extinction events and evolutionary patterns in Earth history (Pörtner *et al.*, 2014).

Figure 18. (a) The thermal tolerance range and performance levels of an organism are described by its performance curve. Each performance (e.g., exercise, growth, reproduction) is maximal at its optimum temperature (T_{opt}), and becomes progressively constrained during cooling or warming. Surpassing the first low- and high-temperature thresholds (T_p ; p, pejus: getting worse) means going into time-limited tolerance. Once further cooling or warming surpasses the next low or high thresholds (T_c ; c, critical), oxygen availability becomes insufficient and an anaerobic metabolism begins. Denaturation temperatures (T_d) are even more extreme and characterized by the onset of damage to cells and proteins. Horizontal arrows indicate that T_p , T_c , and T_d thresholds of an individual can shift, within limits, between summer and winter (seasonal acclimatization) or when the species adapts to a cooler or warmer climate over generations (evolutionary adaptation). Under elevated CO_2 levels (ocean acidification) and in hypoxic waters, performance levels can decrease and thermal windows narrow (dashed gray curves). (b) The width of the thermal range (horizontal arrows) also changes over time when an individual develops from egg to larva to adult and gains weight and size. Blue to red color gradients illustrate the range between cold and warm temperatures.



Source: Pörtner *et al.*, (2014).

Annex 6. Glossary

Acclimation

A change in functional or morphological traits occurring once or repeatedly (e.g., seasonally) during the lifetime of an individual organism in its natural environment. Through acclimatization the individual maintains performance across a range of environmental conditions. For a clear differentiation between findings in laboratory and field studies, the term acclimation is used in ecophysiology for the respective phenomena when observed in well-defined experimental settings. The term (adaptive) plasticity characterizes the generally limited scope of changes in phenotype that an individual can reach through the process of acclimatization.

Accretion

An increase by natural growth or by gradual external addition.

Adaptation

The process of adjustment to actual or expected climate and its effects. In human systems, adaptation seeks to moderate harm or exploit beneficial opportunities. In natural systems, human intervention may facilitate adjustment to expected climate and its effects.

Benthic

Region at the lowest level of a body of water such as an ocean or a lake, including the sediment surface.

Biodiversity

The variability among living organisms from terrestrial, marine, and other ecosystems. Biodiversity includes variability at the genetic, species, and ecosystem levels.

Biogeography

The distribution of species and ecosystems in geographic space.

Biomass

The total mass of living organisms in a given area or volume; dead plant material can be included as dead biomass. Biomass burning is the burning of living and dead vegetation.

Climate feedback

An interaction in which a perturbation in one climate quantity causes a change in a second, and the change in the second quantity ultimately leads to an additional change in the first. A negative *feedback* is one in which the initial perturbation is weakened by the changes it causes; a positive feedback is one in which the initial perturbation is enhanced.

Cnidarian

Phyla containing corals and jellyfish.

Coccolithophores

Calcifying group of phytoplankton.

Crustose coralline algae

Red calcifying algae.

Cyanobacteria

Phylum of bacteria that obtain their energy through photosynthesis. Cyanobacteria are also nitrogen fixers.

Denaturation

Denaturation is a process in which proteins or nucleic acids lose the quaternary structure, tertiary structure and secondary structure which is present in their native state, by application of some external stress or compound such as a strong acid or base, radiation or heat. If proteins in a living cell are denatured, this results in disruption of cell activity and possibly cell death.

Diatoms

Diatoms are a major group of algae, and are among the most common types of phytoplankton.

Dimethylsulphoniopropionate (DMSP):

Algal metabolic by-product produced in response to environmental stress.

Dinoflagellates

Single-celled aquatic organisms bearing two dissimilar flagellae and having characteristics of both plants and animals.

Dead zones

Extremely hypoxic (i.e., low-oxygen) areas in oceans and lakes, caused by excessive nutrient input from human activities coupled with other factors that deplete the oxygen required to support many marine organisms in bottom and near-bottom water.

Ecophysiological processes

Processes in which individual organisms respond continuously to environmental variability or change, such as climate change, generally at a microscopic or sub-organ scale. Ecophysiological mechanisms underpin individual organisms' tolerance to environmental stress, and comprise a broad range of responses defining the absolute tolerances by individuals of environmental conditions. Ecophysiological responses may scale up to control species' geographic ranges.

Ecosystem

An ecosystem is a functional unit consisting of living organisms, their non-living environment, and the interactions within and between them. The components included in a given ecosystem and its spatial boundaries depend on the purpose for which the ecosystem is defined: in some cases they are relatively sharp, while in others they are diffuse. Ecosystem boundaries can change over time. Ecosystems are nested within other ecosystems, and their scale can range from very small to the entire biosphere. In the current era, most ecosystems either contain people as key organisms, or are influenced by the effects of human activities in their environment.

El Niño-Southern Oscillation (ENSO)

The term El Niño was initially used to describe a warm-water current that periodically flows along the coast of Ecuador and Peru, disrupting the local fishery. It has since become identified with a basin-wide warming of the tropical Pacific Ocean east of the dateline. This oceanic event is associated with a fluctuation of a global-scale tropical and subtropical surface pressure pattern called the Southern Oscillation. This coupled atmosphere-ocean phenomenon, with preferred time scales of two to about seven years, is known as the El Niño-Southern Oscillation (ENSO). It is often measured by the surface pressure anomaly difference between Darwin and Tahiti or the sea surface temperatures in the central and eastern equatorial Pacific. During an ENSO event, the prevailing trade winds weaken, reducing upwelling and altering ocean currents such that the sea surface temperatures warm, further weakening the trade winds. This event has a great impact on the wind, sea surface temperature, and precipitation patterns in the tropical Pacific. It has climatic effects throughout the Pacific region and in many other parts of the world, through global teleconnections. The cold phase of ENSO is called La Niña.

Euphotic zone

The layer closer to the surface that receives enough light for photosynthesis to occur.

Eurytherms

Animals with wide thermal tolerance windows that have adapted to a wide distributional range of temperatures.

Foraminifera

A phylum or class of amoeboid protists, usually with a calcium carbonate shell.

H⁺ ions

The amount of hydrogen ions in a substance is used as a measure of acidity.

Lysocline

The lysocline is the depth in the ocean below which the rate of dissolution [of calcium carbonate minerals] increases dramatically.

Maerl

Collective name for Coralline red algae, which forms extensive beds.

Mesocosm Experiments

Experiments which isolate a small part of the natural environment to bring it under controlled conditions.

Mole fraction

Mole fraction, or *mixing ratio*, is the ratio of the number of moles of a constituent in a given volume to the total number of moles of all constituents in that volume. It is usually reported for dry air. Typical values for well-mixed greenhouse gases are in the order of $\mu\text{mol mol}^{-1}$ (parts per million: *ppm*), nmol mol^{-1} (parts per billion: *ppb*), and fmol mol^{-1} (parts per trillion: *ppt*). Mole fraction differs from *volume mixing ratio*, often expressed in ppmv etc., by the corrections for non-ideality of gases. This correction is significant relative to measurement precision for many greenhouse gases

Nauplii

The free-swimming first stage of the larva of certain crustaceans.

Nitrogen fixers

Bacteria that can convert nitrogen into ammonium; see cyanobacteria.

Otoliths

Calcified structures found in the inner ear of vertebrates.

Oxidative stress.

A disturbance in the balance between the production of reactive oxygen species (free radicals) and antioxidant defenses.

Oxygen minimum zone

The midwater layer (200 to 1000 m) in the open ocean in which oxygen saturation is the lowest in the ocean. The degree of oxygen depletion depends on the largely bacterial consumption of organic matter, and the distribution of the OMZs is influenced by large-scale ocean circulation. In coastal oceans, OMZs extend to the shelves and may also affect benthic ecosystems.

Pacific decadal oscillation (PDO)

The pattern and time series of the first empirical orthogonal function of sea surface temperature over the North Pacific north of 20°N. The PDO broadened to cover the whole Pacific Basin is known as the Inter-decadal Pacific Oscillation (IPO). The PDO and IPO exhibit similar temporal evolution.

Pelagic

Zone of ocean or lake waters that are neither close to the bottom nor near the shore.

Petagram

A unit of mass equal to 1,000,000,000,000 grams.

pH

pH is a dimensionless measure of the acidity of water (or any solution) given by its concentration of hydrogen ions (H⁺). pH is measured on a logarithmic scale where $\text{pH} = -\log_{10}(\text{H}^+)$. Thus, a pH decrease of 1 unit corresponds to a 10-fold increase in the concentration of H⁺, or acidity.

Phenology

The study of periodic plant and animal life cycle events and how these are influenced by seasonal and interannual variations in climate.

Pteropod

Free-swimming, pelagic sea snails and sea slugs, some of which produce aragonite shells.

Refugia:

A location of an isolated or relict population of a once more widespread species.

Saturation state (Ω)

The saturation state of seawater for CaCO₃ is a measure of its potential to corrode the CaCO₃ shells and skeletons of marine organisms. Without protective mechanisms, undersaturated seawater ($\Omega < 1$) is corrosive to calcifying organisms.

Stenotherms

Animals that have narrow thermal windows and low energy demand lifestyles, making them sensitive to temperature change.

Terawatt

The terawatt is equal to one trillion (10,000,000,000,000) watts.

Thermocline

The layer of maximum vertical temperature gradient in the ocean, lying between the surface ocean and the abyssal ocean. In subtropical regions, its source waters are typically surface waters at higher latitudes that have subducted and moved equatorward. At high latitudes, it is sometimes absent, replaced by a halocline, which is a layer of maximum vertical salinity gradient.

Trophic amplification

The increasing of effect size as it moves up the food web.

Trophic interactions

Interactions relating to feeding and nutrition.

Vermetid reefs

A reef composed of *vermetid* gastropods (a family of marine snails) built on some substrate such as coralline algae or bivalve shells.

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The Oceans 2015 Initiative, Part I

An updated synthesis of the observed and projected impacts of climate change on physical and biological processes in the oceans

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