Ocean Acidification

A review of the current status of research

and institutional developments

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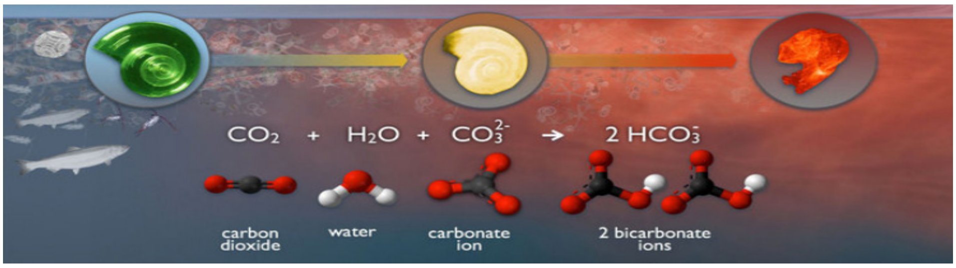

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Summary

Ocean acidification is defined as the change in ocean chemistry driven by the oceanic uptake of chemical inputs to the atmosphere, including carbon, nitrogen and sulphur compounds. Ocean acidification is also referred to as 'the other CO_2 problem' of anthropogenic carbon dioxide (CO_2) emissions alongside climate change.

Ocean acidification has become a hot topic on the international research agenda, whereby most publications are less than a decade old. Ocean acidification has also become an emerging topic on the international policy agenda. UNESCO supported the first global meeting on ocean acidification in 2004 and in 2007 the Intergovernmental Panel on Climate Change (IPCC) first recognized ocean acidification in its 4th assessment report as an associated disturbance of climate change caused by increasing CO_2 emission.

IMARES was commissioned by the Ministry of Economic Affairs, Agriculture and Innovation to provide an overview of the state of affairs on ocean acidification, in terms of global institutional developments and state-of-the-art research. Besides providing such an overview, objectives were to recommend relevant ocean acidification topics for the Netherlands and to identify key discussion partners for a dialogue on how to include ocean acidification on the Dutch policy agenda.

Scientific research into the effects of ocean acidification can broadly be divided in three topics, which are the effects on ocean chemistry, effects on organism level and effects on ecosystem level. A general overview of the current knowledge on these three topics is provided in this report.
The most important effect of oceanic uptake of atmospheric CO_2 is the increase of hydrogen ions (H^+) as a result of the reaction between water (H_20) and CO_2. Ocean acidification is caused by a decrease in the pH of the seawater as a result of an increased concentration of H^+ ions. The surface seawater is slightly alkaline with an average pH of about 8.2, although this varies across the oceans by approximately 0.3 units because of local, regional and seasonal variations. Another important change in ocean chemistry is a decreased concentration of carbonate (CO_3^{2-}). This has important consequences for the formation and dissolution of calcium carbonate ($CaCO_3$) commonly used by marine biota to form shells or skeletons.
The above effects on ocean chemistry are well-understood and largely predictable, unlike the uncertainty on biological responses of organisms which vary between and within taxa and the even larger uncertainty on ecological responses of populations, communities and ecosystems. The most important biological effects are on calcification rates of calcifying organisms such as corals, calcareous macroalgae, bivalves and crustaceans and planktonic organisms such as coccolithophores, foraminifera and pteropods. There is significant variability in the sensitivity of the calcification response between calcifying organisms.

Although there are still scientific knowledge gaps, especially on the long-term effects at organism level and large-scale ecosystem effects, and ocean acidification is still an invisible anthropogenic pressure on ecosystems, it is recommended to include ocean acidification as 'the other CO_2 problem' in climate change policy making. Recommendations to get ocean acidification on the Dutch policy agenda are to focus on important economic activities such as fisheries and aquaculture and on vulnerable habitats such as deltas and coral reefs.

Contents

1 Introduction

1.1 Research question

This research has been commissioned by the Dutch Ministry of Economic Affairs, Agriculture and Innovation (EL&I). The research question of EL&I was:

What is the state of affairs on ocean acidification, in terms of global institutional developments and state-of-the-art research?

The objective was to provide a general overview on the state-of-the-art of ocean acidification at a global level, by evaluating the literature and providing an overview of institutional organisations, research institutes and other stakeholders specifying their policy- and research programmes. Additional objectives, resulting from a progress meeting of the project team and EL&I policy officers, were to give recommendations of relevant ocean acidification topics for the Netherlands and to identify key discussion partners to involve in a dialogue on how to include ocean acidification at the Dutch policy agenda.

1.2 Scope

This report does only cover the natural processes and effects of increased CO_2 due to anthropogenic causes (i.e. fossil fuel burning). It does not cover artificial Carbon Capture and Storage (CCS) at sea and potential effects of elevated CO_2 levels in case of leaking.

2 Materials and Methods

For an overview of the state of the art of ocean acidification the literature between 2010 and August 2012 was evaluated, using a Web of Science search with ocean acidification in the title. This resulted in 184 hits. Papers that conducted a meta-analysis, review or analysis of a phylum were selected rather than species-specific or region-specific analyses. Other very comprehensive review articles were selected (Orr, Fabry et al. 2005; Raven, Caldeira et al. 2005; Doney 2006; Doney, Mahowald et al. 2007; Fabry, Seibel et al. 2008; Guinotte and Fabry 2008; Doney, Balch et al. 2009; Feely, Doney et al. 2009; Reid, Fischer et al. 2009; Schiermeier 2011) based on their citation in the above state of the art literature. In addition, topics of special interest for this report were selected, such as governance and policy responses to ocean acidification.

For an overview of the state of the art of warm-water and cold-water coral in relation to ocean acidification forthcoming literature, keynotes, proceedings and abstracts from the 12th International Coral Reef Symposium in July 2012 in Australia and the 5th Internationals Symposium on Deep-Sea Corals in April 2012 in The Netherlands were evaluated. Coordinated research initiatives were identified after expert consultation with Furu Mienis (cold-water coral expert of Royal NIOZ and MARUM, Center for Marine Environmental Sciences, part of University of Bremen) and Ronald Osinga (tropical coral expert of Wageningen University).

Publications concerning ocean acidification by European and intergovernmental organisations were identified.

3 Results

3.1 Ocean chemistry background

Ocean acidification is defined as the change in ocean chemistry driven by the oceanic uptake of chemical inputs to the atmosphere, including carbon, nitrogen and sulphur compounds. The main cause of today's ocean acidification is the increasing amount of anthropogenic carbon dioxide (CO_2) emitted into the atmosphere from human activities such as fossil fuel burning, deforestation, industrialization, cement production and other land-use changes (Guinotte and Fabry 2008). Ocean acidification is also referred to as 'the other CO_2 problem' (Turley 2005; Henderson 2006; Doney, Fabry et al. 2009) alongside climate change. A brief explanation of ocean chemistry, the carbon cycle and carbonate buffer is given in the first paragraph. The next paragraph addresses the chemical process of ocean acidification and its direct effects on carbonate saturation states and horizons. The last paragraph puts today's ocean acidification in the context of past events and future trends in a high CO_2 world.

3.1.1 Carbon cycle and carbonate buffer

Carbon exists in a variety of forms in several 'reservoirs' in the atmosphere, biosphere and oceans (figure 1). The exchange of carbon between these reservoirs is known as the carbon cycle (Raven, Caldeira et al. 2005). The ocean and the atmosphere exchange massive amounts of carbon dioxide (CO_2) and the ocean is not only an important carbon reservoir, but is also the most important long-term carbon sink of carbon sequestered in marine sediments.

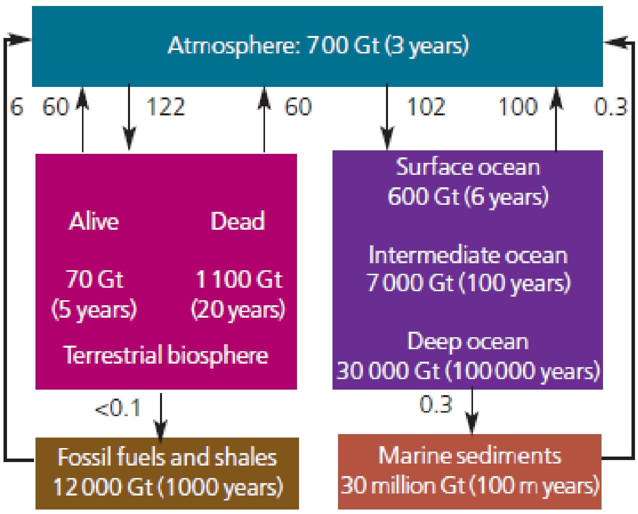

Figure 1. Global carbon cycle with carbon reservoirs in the atmosphere, biosphere and oceans (in giga tonnes) and exchanges between reservoirs (in giga tonnes per year). Also shown are residence times of carbon in each reservoir (Raven, Caldeira et al. 2005).

The carbon stored in the ocean occurs in different chemical forms. A small part is stored in organic compounds of marine biota (living beings), but the greatest part is contained in inorganic compounds which are referred to as DIC (dissolved inorganic carbon). Of these compounds, only 0.5% occurs as dissolved CO_2, 88% as bicarbonate (HCO_3^-) and 11% as carbonate (CO_3^{2-}) at a pH of 8.2 (Fabry, Seibel et al. 2008). Amounts vary slightly depending on temperature, salinity and pressure (Raven, Caldeira et al. 2005). The relationship between these three compounds is represented by the equilibrium equation:

$$CO_2 + H_20 + CO_3^{2-} \rightleftarrows 2\ HCO_3^-$$

The relative proportions of these three forms of DIC operate as the 'carbonate buffer' and maintain the pH value of the water within relatively narrow limits (figure 2).

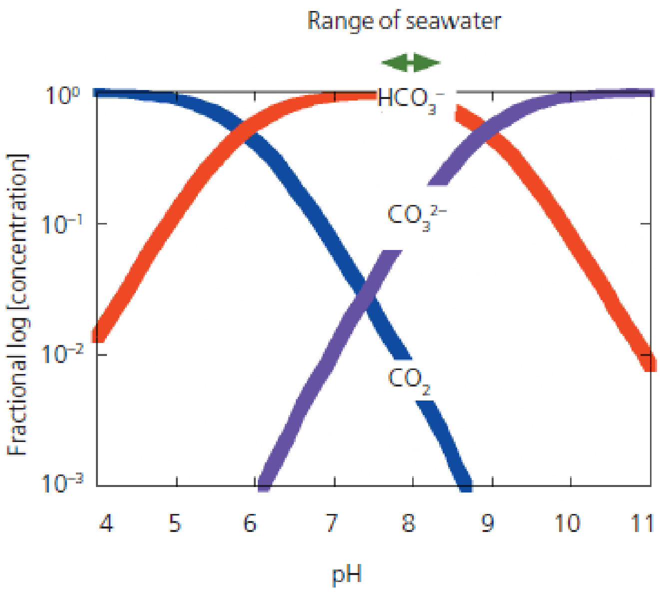

Figure 2. Relative proportions of the three inorganic forms of dissolved carbon. The green arrows at the top indicate the narrow range of pH (7.5-8.5) that is likely to be found in the oceans now and in the future. The vertical axis has a logarithmic scale (Raven, Caldeira et al. 2005).

One of the effects of CO_2 dissolving in seawater is the increase of hydrogen ions (H^+) as a result of an initial reaction between water (H_20) and CO_2 to form carbonic acid (H_2CO_3). This weak acid quickly dissociates and releases the H^+ ions to form other types of dissolved inorganic carbon.

$$CO_2\,^{(atmosphere)} \rightleftharpoons CO_2\,^{(aqua)} + H_20 \rightleftharpoons H_2CO_3 \rightleftharpoons HCO_3^- + H^+ \rightleftharpoons CO_3^{2-} + 2H^+$$

(from Zeebe and Wolf-Gladrow, 2001)

Acidity is determined by the concentration of H^+ ions and measured on pH scale, with an acid having a pH of less than 7 and alkali having a pH of more than 7. Because pH is measured on a logarithmic scale (pH = -log10 [H^+] a decrease of 1 unit corresponds to a 10-fold increase in the concentration of H^+ ions. Therefore the amount of CO_2 that dissolves in seawater has a strong influence on the pH of the oceans (Raven, Caldeira et al. 2005). The carbonate buffer is a natural buffer to the addition of H^+ ions, because when CO_2 dissolves in seawater the additional H^+ ions react with CO_3^{2-} and convert them to HCO_3^-. This reduces the concentration of H^+ ions such that the change in pH is much less than would otherwise be expected. The surface seawater is slightly alkaline with an average pH of about 8.2, although this varies across the oceans by approximately 0.3 units because of local, regional and seasonal variations (Raven, Caldeira et al. 2005).

3.1.2 Ocean acidification process and carbonate saturation

Through the uptake of atmospheric CO_2 the partial pressure of CO_2 (pCO_2) increases in the surface seawater, H_2CO_3 is formed and dissociates into a H^+ ion and HCO_3^-. H^+ ions can then react with CO_3^{2-} to form HCO_3^-. This results in increased concentrations of H_2CO_3, H^+ and HCO_3^-, and a decreased concentration of CO_3^{2-}. The decrease in CO_3^{2-} has important consequences for the formation and dissolution of calcium carbonate ($CaCO_3$) commonly used by marine biota to form shells or skeletons. This formation and dissolution of $CaCO_3$ is represented by the equilibrium equation:

$$CaCO_3 \underset{\text{Formation}}{\overset{\text{Dissolution}}{\rightleftharpoons}} Ca^{+} + CO_3^{2-}$$

Because of the decrease in CO_3^{2-} the formation of $CaCO_3$ is prevented and dissolution is promoted. There is a critical concentration of CO_3^{2-} below which $CaCO_3$ will start to dissolve, which increases with decreasing temperature and increasing pressure. The depth at which this occurs is called the 'saturation horizon', where the 'saturation state' (Ω) of seawater for a mineral is 1. Above the saturation horizon seawater is super-saturated ($\Omega > 1$), $CaCO_3$ will be preserved and formation of shells and skeletons is favoured. Below the saturation horizon seawater is under-saturated ($\Omega < 1$) and corrosive to $CaCO_3$, so in the absence of protective mechanisms dissolution will begin. Two common forms of $CaCO_3$ in seawater are the minerals calcite and aragonite, whereby the aragonite saturation horizon is shallower than that of the more stable, less soluble calcite (Raven, Caldeira et al. 2005).

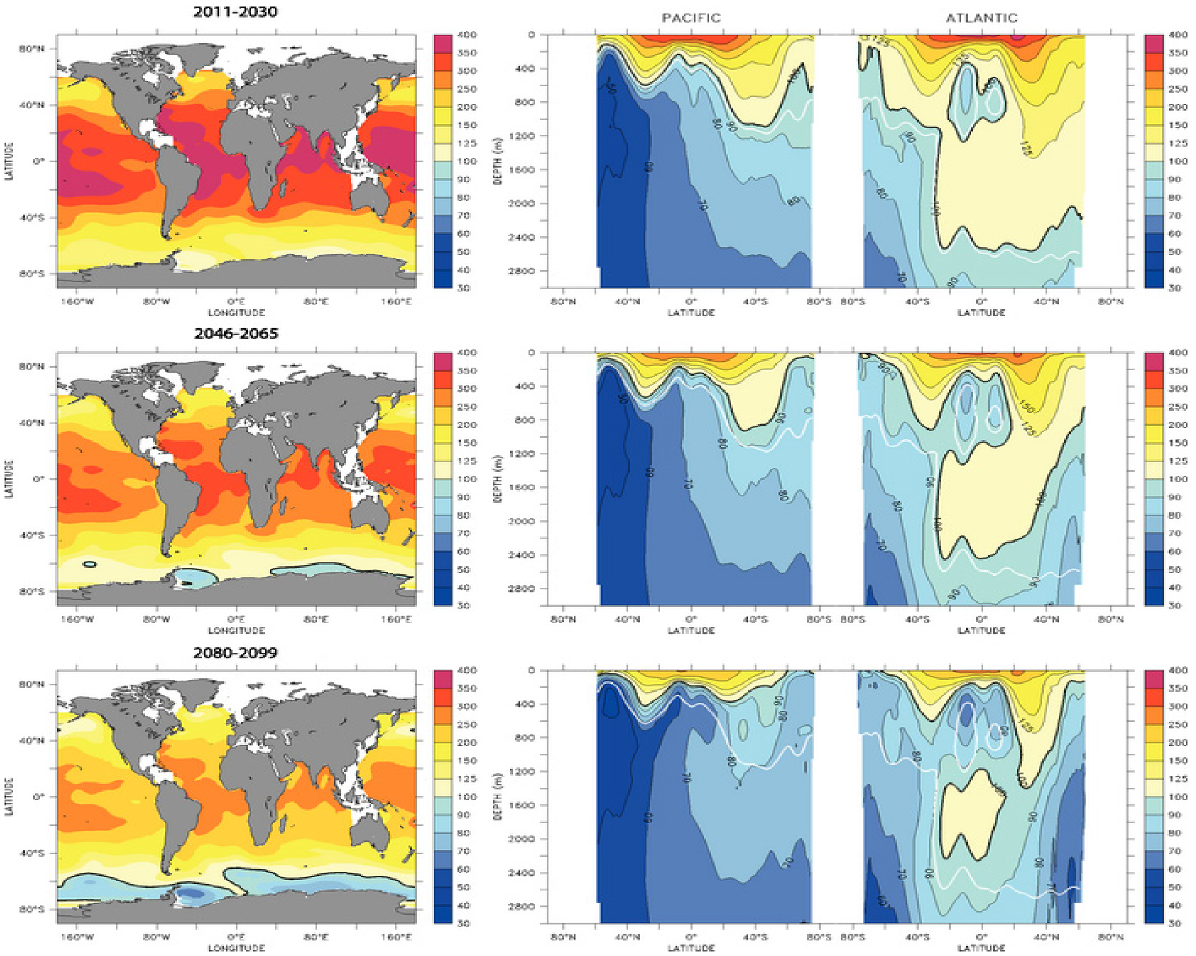

Figure 3. Multi-model projections of aragonite saturation states in the 21st century. Blue represents saturation states < 100% indicating under-saturation, yellow-orange-red represent saturation states > 100% indicating super-saturation and the black line indicates the saturation horizon. Maps on the left show saturation states in the surface oceans. Maps on the right show saturation states at each depth-latitude in the North and South Pacific and North and South Atlantic ocean. The white line in the right-hand maps indicates the 1994 observation-based saturation horizon. All projections are based on the Intergovernmental Panel on Climate Change (IPCC) IS92a business-as-usual (continual increasing) CO_2 emission scenario with average atmospheric CO_2 concentrations for the three time periods 2011 to 2030 (top), 2045 to 2065 (middle) and 2080 to 2099 (bottom) of 440, 570 and 730 ppm respectively (Meehl, Stocker et al. 2007) and an atmospheric CO_2 concentration of 788 ppm in 2100 (Orr, Fabry et al. 2005).

The projected direct effect of ocean acidification is the decrease of the seawater saturation state of aragonite (Ω_{arag}) and calcite (Ω_{cal}) and the consequent ascend of their saturation horizons. According to modelled projections for the 21st century (figure 3) the aragonite saturation state will decrease in surface oceans (left-hand maps) and the aragonite saturation horizon will shoal to shallower depths (right-hand maps). Aragonite will dissolve at all depths in the Southern Ocean, and low latitude regions and the deep ocean will be affected as well (Orr, Fabry et al. 2005; Meehl, Stocker et al. 2007). Therefore organisms that build aragonite skeletons are likely to be more sensitive to increased ocean water acidity (see paragraph 3.2).

3.1.3 Oceans in a high CO_2 world

The closest similarity in the geologic record to the present ocean acidification is the Paleocene-Eocene Thermal Maximum (PETM) 55.8 million years ago. The PETM was associated with large-sale release of carbon into the ocean-atmosphere system. The difference between this past event and the current acidification is that speed of change is arguably 10 times faster than in the PETM (Kerr 2010) and 100 times faster than any change in the past 650,000 years. Mean atmospheric CO_2 has ranged between 200 and 300 parts per million (ppm) in the past 650,000 years (Raven, Caldeira et al. 2005) and possibly in as much as 20 million years (Feely, Sabine et al. 2004). The rate of 100 ppm increase in 200 years is unparalleled for at least the last 300 million years (Honisch, Ridgwell et al. 2012). The longest record of direct measurement of atmospheric CO_2 (figure 4) started in 1958 and shows an increase from about 315 ppm to 397 ppm as measured in May 2012 [1].

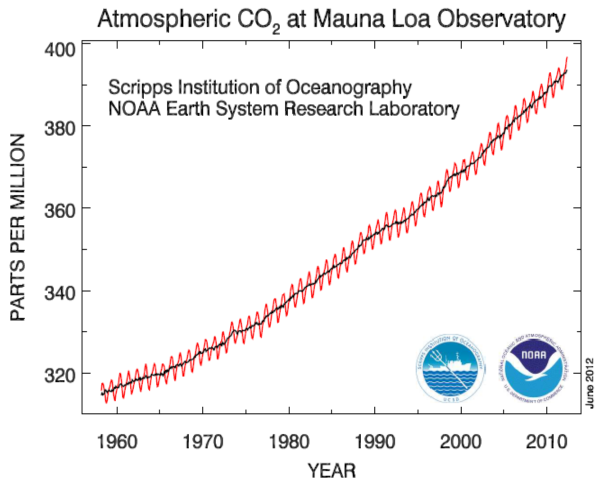

Figure 4. The longest record of direct measurement of atmospheric CO_2 in Mauna Loa Observatory (red curve) corrected for seasonal variation (black curve) [1].

Predictions under six different future scenarios of the Intergovernmental Panel on Climate Change (IPCC) calculate that CO_2 concentrations in 2100 will be 600, 700, 800, 850, 1250 and 1550 ppm for scenario B1, A1T, B2, A1B, A2 and A1FI respectively (figure 5a) (Solomon, Qin et al. 2007). Scenarios A1, A2, B1 and B2 [1] as described in the IPCC Special Report on Emissions Scenarios (SRES) are based on different assumptions regarding global demographic, economic and technological development, without additional climate policies above those existing in 2000 (IPCC 2007).

The uptake of increased anthropogenic CO_2 in the past two centuries has led to a reduction of the pH of surface seawater of 0.1 units, which is recorded on a logarithmic scale and the same as a 30% increase of the concentration of H^+ ions. The average pH of surface oceans of about 8.2 can fall with another 0.5 units if global emissions of CO_2 from human activities continue to rise (Raven, Caldeira et al. 2005). Modelled projections based on SRES scenarios give reductions in pH of between 0.14 and 0.35 units in the year 2100 (figure 5b) (Meehl, Stocker et al. 2007). Aragonite undersaturation in the Southern Ocean is projected for a number of scenarios (figure 5c), unlike calcite undersaturation (figure 6b).

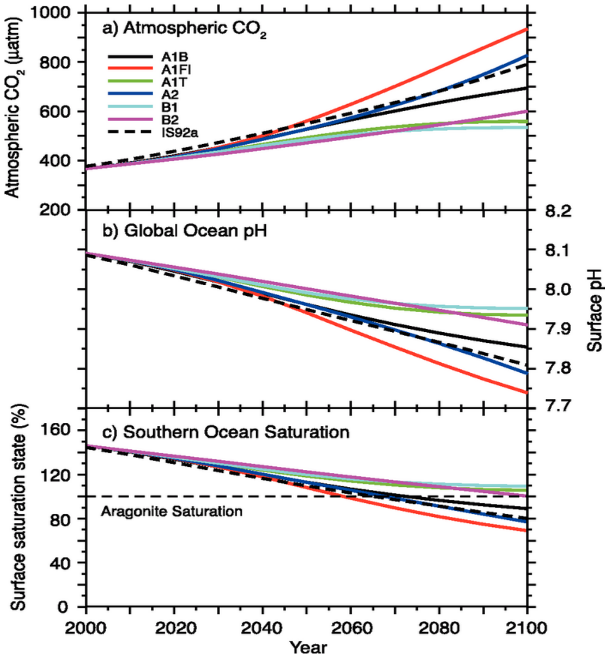

Figure 5. Changes in global average surface pH (b) and aragonite saturation state in the Southern Ocean (c) under the SRES scenarios of atmospheric CO_2 (a) (Meehl, Stocker et al. 2007)

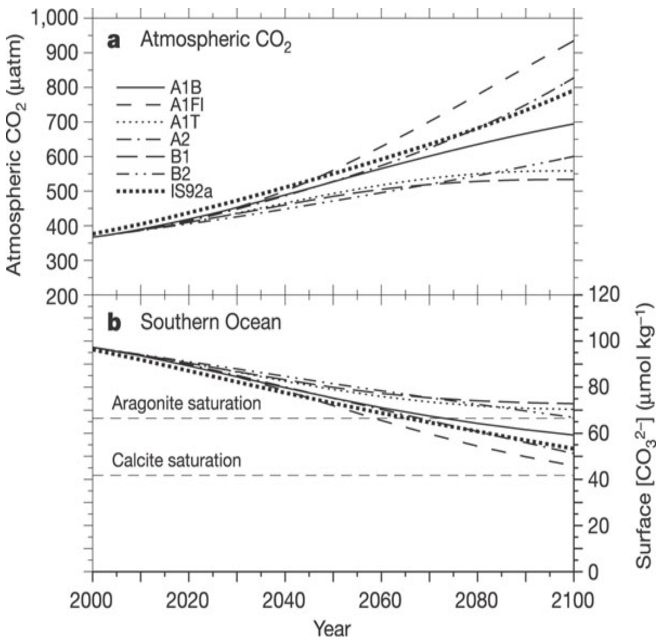

Figure 6. Changes in aragonite and calcite saturation state in the Southern Ocean (b) under the SRES scenario of atmospheric CO_2 (a) (Orr, Fabry et al. 2005)

[1] A1 assumes a world of very rapid economic growth, a global population that peaks in mid-century and rapid introduction of new and more efficient technologies. A1 is divided into three groups that describe alternative directions of technological change: fossil intensive (A1FI), non-fossil energy resources (A1T) and a balance across all sources (A1B).
B1 describes a convergent world, with the same global population as A1, but with more rapid changes in economic structures toward a service and information economy. B2 describes a world with intermediate population and economic growth, emphasising local solutions to economic, social, and environmental sustainability. A2 describes a very heterogeneous world with high population growth, slow economic development and slow technological change. No likelihood has been attached to any of the SRES scenarios. (IPCC, 2007)

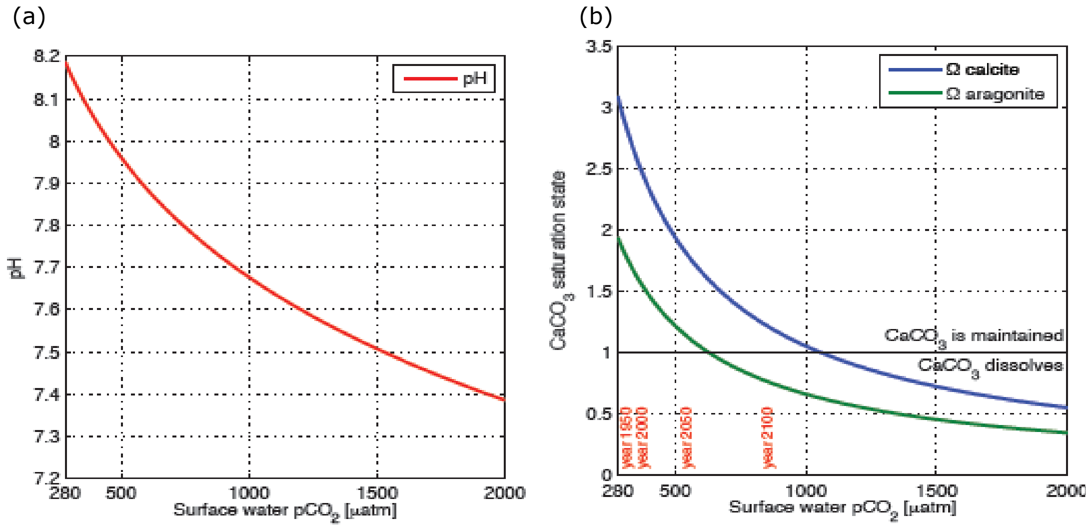

Figure 7. Surface water pH (a) and aragonite and calcite saturation state (b) in the year 2300 and beyond in the polar oceans (De Baar and Van Heuven 2012)

Beyond the year 2100, if fossil fuel burning continues at the current rate, pH is projected to decrease with 0.7 units by 2300 (Caldeira and Wickett 2003). Building on the modelled projections of Caldeira and Wickett (2003; 2005) for the year 2300 and beyond, De Baar and Van Heuven (2012) calculated the Polar Oceans remain basic at a pH of 7.39 (figure 7a).

In most SRES scenarios the aragonite saturation horizon will reach the surface waters of the Southern Ocean meaning aragonite will dissolve at some point in the second half of the 21st century (figure 5c). These projections are based on a study of Orr et al. (2005), who also included the calcite saturation state in his predictions (figure 6b) showing calcite is less likely to dissolve in the Southern Ocean under the SRES scenarios. The study of De Baar and Van Heuven (2012) calculated polar surface waters will also become under-saturated for calcite beyond the year 2100 (figure 7b).

According to the above predictions the oceans will never become acidic in any realistic scenario of fossil fuel CO_2 emission, as the pH remains well above 7. De Baar and Van Heuven (2012) argue it is therefore best to speak of the Ocean in a High-CO_2 World instead of ocean acidification, to avoid scepticism about the changes in ocean chemistry and to ensure the problem is not ignored by the public and decision makers.

The speed of ocean acidification makes a big difference, because it takes the ocean about 1000 years to flush carbon dioxide added to surface waters into the deep sea (Kerr 2010) and it will take up to a million years to restore ocean pH to its pre-industrial state by neutralizing the added acids. This neutralization process takes place through the dissolution of carbonate sediments on the sea floor and the weathering of rocks on land coupled with mixing of surface and deeper waters (Archer, 2005; Ridgwell and Zeebe, 2005 in Turley, Eby et al. 2010). The environmental changes associated with the PETM ocean acidification have been slow enough to avoid biological effects in the surface ocean, only causing extinction among tiny shell-forming organisms living on the deep sea floor (Kerr 2010).

Table 1. An overview of regional differences between oceans in projected carbonate chemistry changes under the IPCC IS92a business-as-usual (continual increasing) CO2 emission scenario with an atmospheric CO2 concentration of 788 ppm in 2100 (Orr, Fabry et al. 2005). The first and second column refer to the concentration of atmospheric CO2 [CO2] at which the surface oceans are projected to become under-saturated for aragonite (Ωarag<1) and calcite (Ωcal<1) resp. The last column refers to the shoaling of the aragonite saturation horizon in the oceans from current depths to projected depths in the year 2100.

	[CO_2] at which Ω_{arag} <1	**[CO_2] at which Ω_{cal}<1**	**Depth at which Ω_{arag}=1 (in 2005 versus 2100)**
North Pacific	740ppm	1040ppm	140m → 0m *
North Atlantic			2600m → 115m
Southern Ocean	560ppm	900ppm	730m → 0m
Arctic Ocean	Under research **	Under research **	Under research **
Tropics	Not applicable ***	Not applicable ***	Not applicable ***
Subtropics	Not applicable ***	Not applicable ***	Not applicable ***

** In parts of the North Pacific*
*** continuing research is evaluating how the Arctic Ocean differs from the Southern Ocean (Fabry, Seibel et al. 2008) where saturation states are further reduced by freshwater input, melting of sea ice and river runoff (IPCC 2011)*
**** warm surface waters of the tropics and subtropics will not become under-saturated with respect to aragonite and calcite under the projected conditions except in some regions with upwelling (Feely, Sabine et al. 2004)*

Apart from the level of atmospheric CO_2, acidification also depends on physical and biological factors, such as temperature, water mixing, ocean currents and biological productivity (Orr et al. 2005). Colder waters naturally absorb and hold more CO_2 and are therefore more acidic than warmer waters which favour release of CO_2 (Guinotte and Fabry 2008; Portner 2008). Surface waters are usually higher in pH because of CO_2 consumption for photosynthesis by primary producers, while deeper waters have lower pH because of respiratory demand and CO_2 production from organic material. The lower pH in deeper waters progressively decreases from the North Atlantic to the North Pacific in the direction of the large-scale deep-ocean currents, the so-called conveyor belt (Portner 2008). Therefore pH and saturation states vary depending on region and latitude (table 1). Short-term CO_2 variation occurs between day and night, when photosynthesis during the day increases pH and respiration during the night decreases pH (Truchot and Duhamel-Jouve 1980 in Portner 2008). Coastal waters show more variability due to high levels of biological productivity and respiration, coastal upwelling, fresh water runoff with associated high nutrient input and hypoxia and changes in stratification (Wanninkhof keynote 1-4 in IPCC 2011).

3.2 Effects of ocean acidification

Changes in ocean chemistry, especially rapid changes such as ocean acidification, could have substantial direct and indirect effects on marine organisms and on the habitats in which they live. Direct effects of ocean acidification include the impacts of increased $p\mathrm{CO_2}$ and decreased pH and $CaCo_3$ saturation states on all stages of the life cycle. Indirect effects include the impact on organisms arising from changes in availability or composition of nutrients and prey which changes the composition and dynamic interactions in food webs. Effects include negative as well as positive effects and can, besides effects on organism level, affect populations of species, trophic interactions between species, biodiversity and other ecosystem processes (Raven, Caldeira et al. 2005). Direct and indirect effects of ocean acidification on biological and ecological processes are discussed in the first paragraph. Marine organisms can adapt to their environment (Raven, Caldeira et al. 2005) and the extent to which adaptation to ocean acidification occurs is also addressed. In the next paragraph effects on the biogeochemical processes are addressed, which concerns chemical cycles consisting of biotic and abiotic compartments. The last paragraph addresses other effects of ocean acidification such as socio-economic effects.

3.2.1 Effects on biological and ecological processes

The most important effects of ocean acidification are the effect of reduced $CaCO_3$ saturation states on the process of calcification and formation of biogenic calcium carbonate; the effect of shallower depths of $CaCo_3$ saturation horizons on the process of dissolution of biogenic calcium carbonate; and the effect of elevated pCO_2 partial pressure (known as hypercapnia) on physiological processes of water-breathing animals and the acid-base regulation (Fabry, Seibel et al. 2008; Guinotte and Fabry 2008).

3.2.1.1 Effects on organism level

Calcifying organisms such as coccolithophores, foraminifera, pteropods, calcareous macroalgae, corals, echinoderms, gastropods, molluscs and crustaceans require calcite or aragonite to form biogenic calcium carbonate for their skeletons, shells and plates (table 2).
Calcifying organisms are expected to experience negative effects at lower carbonate saturation levels (Orr, Fabry et al. 2005; Raven, Caldeira et al. 2005; Doney 2006; Fabry, Seibel et al. 2008; Schiermeier 2011), because it is more difficult and/or requires more energy to form biogenic calcium carbonate. However, research shows that there are large differences between responses in organisms due to different mechanisms to control the internal micro environment, different resistance and adaptation of organisms and differences between life stages (Fabry, Seibel et al. 2008). Life stages of benthic invertebrates include planktonic (gametes, fertilization, embryos and larvae) and benthic (juvenile, adult) life stages with different sensitivities to ocean acidification. Early life history stages are of particular concern as this determines recruitment success and persistence of populations (Byrne 2011).

Table 2. Taxa of calcified marine organisms with indicators of their ability to photosynthesise, the form of $CaCO_3$ deposited and their habitat. Aragonite dissolves more rapidly at low carbonate concentrations than calcite. Photosynthesis in foraminifera and warm-water corals depends on symbiosis with algae (Raven, Caldeira et al. 2005).

Organisms	**Photosynthetic or non-photosynthetic**	**Form of calcium carbonate**	**Habitat**
Coccolithophores	Photosynthetic	Calcite	Planktonic
Macroalgae *	Photosynthetic	Aragonite or calcite	Benthic
Foraminifera	Some photosynthetic Non-photosynthetic	Calcite Calcite	Benthic Planktonic
Molluscs: Pteropods Non-pteropods *	Non-photosynthetic Non-photosynthetic	Aragonite Aragonite + calcite	Planktonic Benthic or planktonic
Corals: Warm-water Cold-water	Photosynthetic Non-photosynthetic	Aragonite Aragonite	Benthic Benthic
Echinoderms	Non-photosynthetic	Calcite	Benthic
Crustaceans *	Non-photosynthetic	Calcite	Benthic or planktonic

** Not all species of these taxa are calcified.*

The different responses of dominant groups are given in the following paragraphs. Until recently, the primary focus has been to test the effects of high CO_2 conditions on individual species under lab conditions. Presently, research has shifted towards adaptive strategies and more natural conditions including competition and interaction with other species or direct and indirect changes in environmental conditions. For example, indirect effects of ocean acidification, such as changes in nutrient availability or bioavailability of trace metals, may have an impact on growth (Shi et al., 2010) and calcification.

3.2.1.1.1 Photosynthetic calcareous organisms

Coccolithophores & calcifying dinoflagellates

Coccolithophores are calcifying nannoplankton (<20 um in size) that are characterised by small calcite scales (coccoliths) that cover their outer surface. Despite their small size, this group of marine phytoplankton is responsible for a significant amount of the carbonate produced by calcifying organisms. In addition, their coccoliths may function as ballasting, i.e. promote CO_2 drawdown through facilitating the downward export of organic matter, making them important players in the marine carbon cycle.
An experiment by Riebesell et al. (2000) suggested a negative effect on both calcification and organic matter production in two extant coccolithophore taxa. However, more recent studies have shown that the effects of high CO_2 conditions on coccolithophores are ambiguous, with some taxa showing negative impacts calcification and malformation of their coccoliths (Langer et al. 2006), whilst other taxa are not negatively affected by CO_2 (Langer et al., 2009). Such a resilience to high CO_2 conditions was shown during studies of the PETM (Stoll et al., 2007) and following high CO_2 events (Dedert et al., 2012). To further complicate matters, the discovery of crypto-species, i.e. different species with similar morphologies (deVargas et al., 2004) as well as genetic variety with a single species that each show different responses (Langer et al., 2009). Unlike many other calcifiers, coccolithophores calcify intracellularly, and thus can control and adapt their calcification process, resulting in a resilience to acidified conditions (Lohbeck et al., 2012). In addition, an organic coating that protects the coccoliths (Hassenkam et al., 2011) further adds to their resilience to acidified conditions. The calcifying dinoflagellate *Thoracosphaera heimii* appears to suffer negative consequences under lower pH (Hinga 2002), however, more studies are presently done that may clarify its sensitivity to high CO_2 further.

Calcifying macroalgae: coralline algae & Halimeda

Coralline algae play an important role in the ecology of coral reefs, as they promote settlement and recruitment of numerous invertebrates. Ocean acidification has a significant negative effect on photosynthesis and growth on calcareous algae (Kroeker, Kordas et al. 2010). For example, Kuffner et al. (2008) showed that acidification can significantly inhibit the recruitment rate and growth of coralline algae by ~90%. A cumulative negative effect was found by Martin & Gatusso (2009), who demonstrated a significant effect on calcification during high CO_2 conditions concomitant with elevated temperature.
Halimeda are calcareous forms of green macro-algae that deposit calcium carbonate in its tissues, and is an important group of sediment producing algae in tropical reef regions. They play an important role in the framework development on reefs because of their rapid calcium carbonate production and high turnover rates (Price et al., 2011). *Halimeda* appears to be negatively affected by high CO_2 concentrations under natural conditions near a volcanic vent (Hall-Spencer et al., 2008), although experiments with cultured *Halimeda* show a difference in effects between various species of *Halimeda* (Price et al., 2011). Ries et al. (2009) performed culture experiments under various CO_2 concentrations, which showed that *Halimeda* species grown under elevated CO_2 concentrations varying between 605-903 ppm demonstrated an increase in calcification. A decrease in calcification was observed under high CO_2 concentrations of ~2856 ppm. These results imply that *Halimeda* is able to sustain calcification at relatively high CO_2 concentrations.

3.2.1.1.2 Photosynthetic non-calcareous organisms

Seagrass & macroalgae

Seagrass is found in coastal regions all over the world, where it provides a key habitat for lifecycles of numerous marine animal species. Several seagrass species are threatened by human activities during the last decades, however, the impact of high CO_2 concentrations appears to promote growth in seagrasses. Hall-Spencer et al. (2008) found that the growth of a seagrass species near a volcanic vent was optimal at a pH of 7.6. Jiang et al. (2010) conducted a study with the seagrass *Thalassia Heimprichii*, and found that this species of seagrass responded positively to acidification of the coastal waters by stimulating photosynthesis. Additionally, Kroeker et al. (2010) showed that acidified conditions have a significant positive effect on growth on fleshy algae. As the present-day availability of CO_2 limits photosynthesis, an increase in CO_2 will promote the growth of photosynthesizing organisms (Guinotte & Fabry 2008), such as for seagrass. However, a recent study (Arnold et al., 2012) found that under high CO_2 conditions, marine plants as seagrass, show a reduced production of plant phenolics. These phenolic substances protect the plants from grazing. Arnold et al. (2012) found intensified rates of grazing near a volcanic CO_2 vent, indicating that grazing stimulated by decreased phenolic protective substances could pose a threat to seagrass. An increasing number of field studies applying new methods are carried out (Fig. 8) that allow for in situ experiments under high CO_2 conditions. These studies will help to increase our understanding of ocean acidification in natural circumstances.

Figure 8. In situ experiment with seagrass under high CO_2, from: Campbell & Fourqurean (2011)

Phytoplankton

Several experiments have shown that increased availability of CO_2 increases the primary productivity in marine ecosystems (Riebesell et al., 2007; Tortell et al., 2008). Among the various groups of phytoplankton, differences in response occur that may be directly linked to available CO_2, or to indirect effects resulting for climatic changes associated with increasing atmospheric CO_2 concentrations.

The dominant phytoplankton group, the diatoms, have a substantial variation in cell size, ranging from ~3μm up to over 100μm. While the smaller species are expected to be able to rely on their CO_2 uptake through diffusion, the bigger species may be to a larger extent dependent on a Carbon Concentrating Mechanism (CCM), that transports CO_2 into the cell at a high energetic cost. Boelen et al. (2011) demonstrated in an experiment that for small diatoms variations in CO_2 concentrations have no effect of the photophysiological functioning of the cell. However, larger diatom species may benefit from higher CO_2 availability, as an on-deck experiment with diatoms from the Southern Ocean showed a shift to larger chain-forming diatoms. An increased abundance of larger diatoms may function as a negative feedback to high CO_2, as larger cells more strongly promote the downward transport of organic matter and thus CO_2.

The genus of *Phaeocystis* is considered a harmful algae bloom genus, as the organic foam on beaches caused by degradation of the cells in spring can have a negative impact on tourism, and degradation can potentially result in anoxia, which poses a threat to aquaculture in coastal regions (Hoogstraten et al., 2012). The species *Phaeocystis globosa* has a highly efficient CCM (Rost et al. 2003; Reinfelder 2011), allowing it to regulate its CO_2 uptake. Wang et al. (2010) found changes at higher CO_2 concentrations both in growth rate and elemental composition of the cells, which may contribute to forecasting the occurrence of harmful blooms by this species.

Some species of dinoflagellates and cyanobacteria have the potential of forming toxins that at high concentrations may be a threat to human health. Environmental conditions associated with high atmospheric CO_2 such as higher temperatures and increased stratification promote the occurrence of these taxa, often in combination with higher nutrient availability. Lomas et al. (2012) found no negative effects of higher CO_2 on cyanobacteria, in fact, they demonstrate an increased N-fixation rate which may promote primary production by other taxa especially in more open ocean waters (Barcelos e Ramos et al., 2007).

Calcifying macroalgae
Based on research on the effect of increasing CO_2 levels on macroalgal communities at high-CO_2 volcanic vents it appears that many macroalgal species are tolerant to long-term elevations in CO_2 levels but that macroalgal habitats are altered significantly and differ at taxonomic and morphological group levels along a pH gradient. The vast majority of the 101 macroalgal species studied were able to grow with only a 5% decrease in species richness as the mean pH fell from 8.1 to 7.8. This small fall in species richness was associated with shifts in community structure as the cover of turf algae decreased disproportionately. Calcifying species were significantly reduced in cover and species richness and a few non-calcifying species became dominant. At a mean pH of 6.7, where carbonate saturation levels were <1, calcareous species were absent and there was a 72% fall in species richness. Under these extremely high-CO_2 conditions a few species dominated the simplified macroalgal assemblage. Very few species showed enhanced reproduction, while in other species reproduction was inhibited at these high-CO_2 conditions (Porzio, Buia et al. 2011).

3.2.1.1.3 Other planktonic calcareous organisms

Foraminifera
Foraminifera are widely distributed protists that live in the water column as well as on the ocean floor. They are significant contributors to the main carbonate production, although contrary to the other dominant carbonate producer, the coccolithophores, this group of organisms precipitate their calcite scales (tests) extracellularly in special vacuoles. This mechanism is potentially more sensitive to changes in marine carbonate chemistry, and several studies point to a negative effect on planktonic taxa. For example, field studies suggest a decrease in shell weight caused by reduced calcification of ~25% in the Arabian Sea (De Moel et al., 2009) and ~30 to 35% in the Southern Ocean (Moy et al., 2009).

Environmental conditions for benthic foraminifera differ substantially. They either live in or on top of the sediments. These sediments provide a buffer for changes in pH, if a substantial fraction is made up of carbonates. From fossil records it is know that high CO_2 events are accompanied by extinction of various benthic foraminifera (Thomas, 2007). However, whether this is the direct result of high CO_2 or other environmental changes such as rapid warming, decrease in oxygenation of the deep waters or changes in primary productivity is yet unknown. Experiments with cultured benthic foraminifera indicate negative effects (Kuroyanagi et al., 2009) for growth and calcification, however, species-specific responses (Fujita et al., 2009) may cause shifts in benthic assemblage composition (Haynert et al., 2012).

Pteropods
Pteropods are tiny free-swimming sea snails that form carbonate shells made up of aragonite. This type of carbonate is more solution-prone that calcite, which results in a high solution-susceptibility. Studies on the effect of ocean acidification on pteropods strongly focus on polar regions, as they are important to the local foodwebs and carbon biogeochemical cycles (Manno et al., 2010). Negative effects of high CO_2 include decrease in calcification by ~28% or shell degradation (Lischka et al., 2011). However, adaptation to environmental conditions through migration to deeper water layers or decreased oxygen consumption and ammonium excretion in non-migration species provide adaptive strategies that increase the resilience of these species to ocean acidification (Maas et al., 2012).

3.2.1.1.4 Higher trophic level calcareous organisms

Scleractinian (stony) tropical corals (Zooxanthellate)

Guinotte and Fabry (2008) reported that evidence from species tested to date indicate that calcification rates will be reduced by 20-60% at double preindustrial CO_2 concentrations of 560 ppm (Guinotte and Fabry 2008). This will have serious consequences for skeletal formation and probably result in weaker coral skeletons, reduced extension rates and increased susceptibility for erosion (Kleypas, Buddemeier et al. 1999). Coral reef growth is the net $CaCO_3$ accumulation when calcification takes place at faster rates than biological, physical and chemical erosion (Kleypas, Buddemeier et al. 1999). According to Hoegh-Guldberg et al. (2007) net reef accretion approaches zero or becomes negative at aragonite saturation states of 3.3 which occurs at atmospheric CO_2 concentrations of 480 ppm. The area with extremely low (<3) and marginal (3-3.5) aragonite saturation states is expected to expand considerable (Figure 9).

A mesocosm experiment revealed dissolution of reef-building corals will be faster than net reef accretion at atmospheric CO_2 concentrations of 560-840 ppm (Guinotte and Fabry 2008). Another experiment found two species of scleractinian corals were able to survive and recover from complete dissolution by recalcification of their skeletons (Fine and Tchernov, 2007 in Guinotte and Fabry 2008), but it was questioned whether these species were representative for zooxanthellate reef-building corals (Guinotte and Fabry 2008). Another study by Pelejero et al. (2005 in FAO 2009) suggested that adaptation to long-term pH change may be possible in coral reef ecosystems, based on their observations in 300-year old massive Porites corals from the southwestern Pacific which had adapted to 50-year cycles of large pH variations. A large number of experimental studies found a range of effects on calcification of corals, varying from strongly negative to weakly positive (Chan and Connolly 2012 in [10]). The first meta-analysis on the sensitivity of coral calcification to ocean acidification by Chan and Connolly (2012 in [10]) estimated an average decline of 15%, which is towards the low end of the range of likely responses to acidification that has been proposed in earlier work (13-40%). Variation was large, confirming that some coral response will be below this range and others will be towards the middle or upper end of the range (N. Chan, pers.comm.).

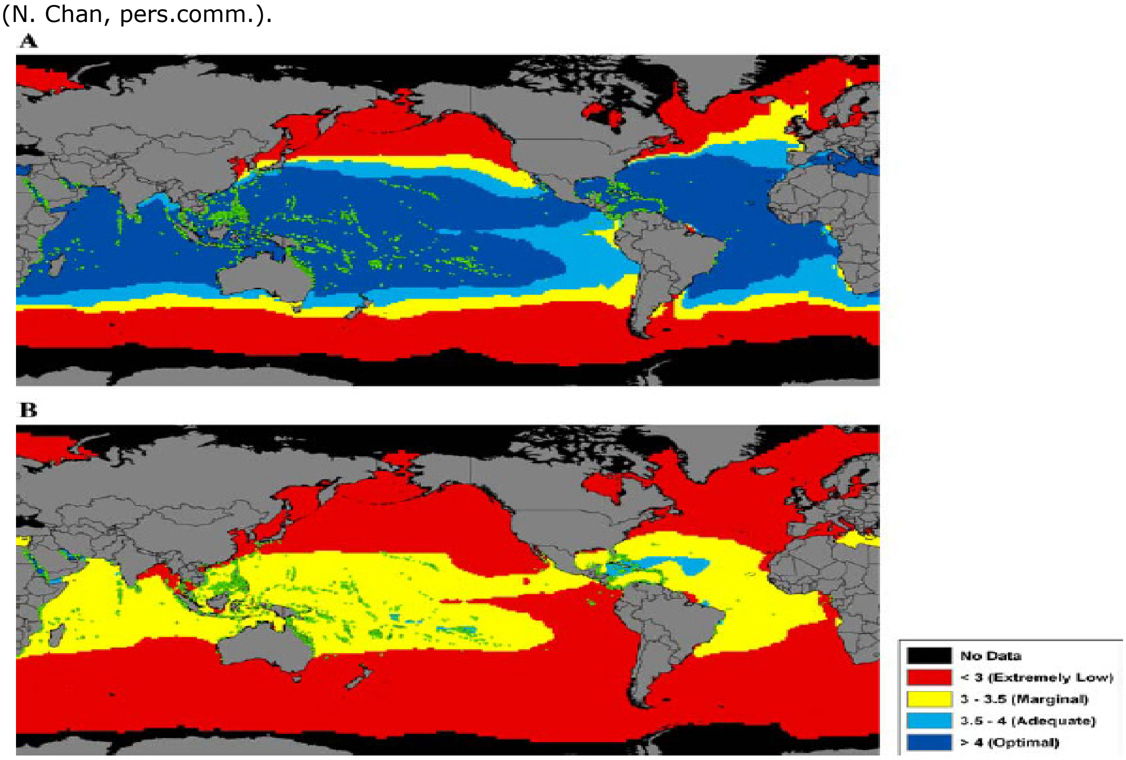

Figure 9. Zooxanthellate coral distribution (green dots) and projected surface aragonite saturation states in (A) preindustrial atmospheric CO_2 concentration of 280 ppm and (B) projected CO_2 concentration of 517 ppm (Guinotte and Fabry 2008).

Slower calcification and growth rates are hypothesised to reduce the ability to compete for space and light, which is a concern if global sea levels rise and light for photosynthesis becomes a limiting factor for corals deeper in the photic zone. The effects of reduced calcification rates on recruitment, settlement and juvenile life stages of the majority of coral are not well known (Guinotte and Fabry 2008). This is in line with the findings of a meta-analysis of 139 studies that quantified biological responses to ocean acidification by Kroeker et al. (Kroeker, Kordas et al. 2010). They found a significant negative effect of ocean acidification on coral calcification and growth, but could not identify significant effects of ocean acidification on coral reproduction, development and survival (Kroeker, Kordas et al. 2010).

Scleractinian (stony) cold-water corals (Azooxanthellate)

Cold-water corals are azooxanthellae, meaning they do not contain photosynthetic algae and are not limited to the photic zone. Cold-water corals occur on a global scale and are found at all latitudes and in all oceans (figure 10) and have a total surface area which at least equals the size of tropical coral reefs (Mienis 2008). Cold-water coral reefs and mounds create complex habitat and form local hotspots of biodiversity, because they attract various species for food and shelter (Jensen and Frederiksen, 1992, Mortensen et al. 1995 in Mienis 2008). Although there is only correlative evidence that they are essential fish habitat supporting commercial fisheries, there is evidence that cold-water corals function as habitat for fish larvae (Baillon, Hamel et al. 2012) and for oviparous (egg-laying) sharks (Henry and Roberts 2012). Most occurrences of cold-water corals have been reported from the Northeast Atlantic Ocean along the European continental margin (Mienis 2008). The majority of cold-water corals are found in depths of 200-1000 meter or above. Cold, deep waters have naturally high levels of CO_2 with a global average aragonite saturation state of 2, which probably is the reason for the slow calcification rate of cold-water corals (Guinotte and Fabry 2008). Projections of rising aragonite saturation horizons (figure 10) indicate that 70% of cold-water corals could be in undersaturated water by 2100 (Orr, Fabry et al. 2005) and could experience dissolution. Cold-water corals not only consist of stony corals, but also of octocorals (soft corals, stoloniferans, sea fans, gorgonians and sea pens) and stylasterids, the majority of which produce calcite spicules and holdfasts. The North Pacific is dominated by octocorals and stylasterids, and it is hypothesized that stony cold-water corals are absent there, because of the shallow depth of the aragonite saturation horizon and high dissolution rates. If this is true, then decreasing aragonite saturation state will probably impact stony cold-water corals earlier than warm-water corals (Guinotte and Fabry 2008).

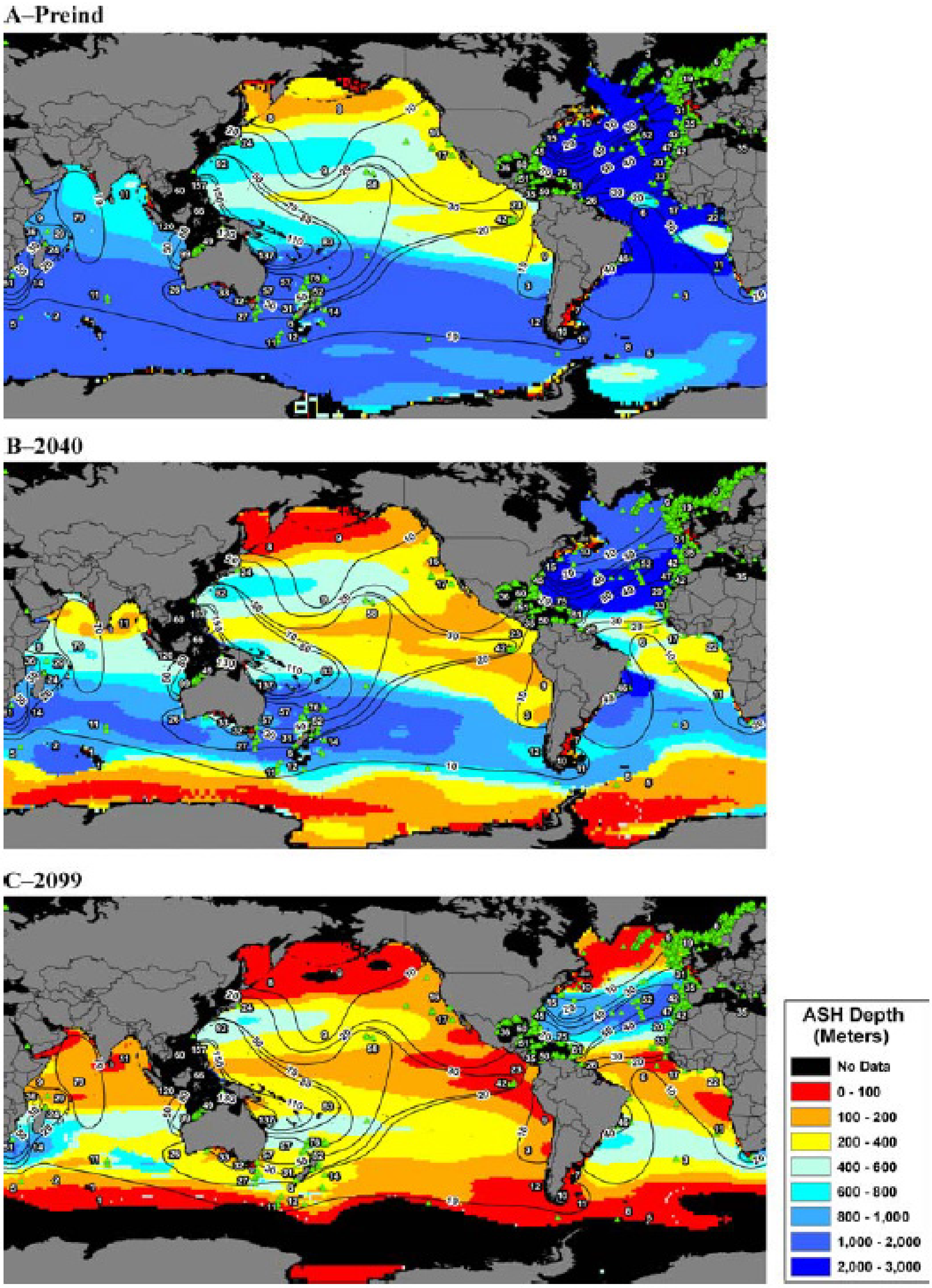

Figure 10. Azooxanthellate coral distribution (green dots) and projected aragonite saturation horizon (ASH) in (A) preindustrial atmospheric CO_2 concentration of 278 ppm (B) projected CO_2 concentration of 513 ppm and (C) projected CO_2 concentration of 788 ppm (Guinotte and Fabry 2008)

Laboratory perturbation experiments (Carreiro-Silva, Godinho et al. 2012; Form and Riebesell 2012; Lunden, Georgian et al. 2012) and *in situ* experiments (Jantzen, Laudien et al. 2012) to test sensitivity for decreasing aragonite saturation state have been conducted for the main species of stony cold-water coral (*Desmophyllum dianthus*, *Lophelia pertusa* and *Madrepora oculata*), but not for octocorals and stylasterids (Guinotte and Fabry 2008). Form and Riebesell (2012) found successful acclimatization of a coral species to ocean acidification. The stony cold-water coral *Lophelia pertus*, the dominant reef-builder in the North Atlantic (Maier, Watremez et al. 2012), showed reduced calcification in a 1-week experiment, but slightly enhanced calcification in a 6-month experiment. Jantzen et al. (2012) and Carreiro-Silva et al. (2012) found the same results for *Desmophyllum dianthus* and Jantzen et al. (2012) concluded cold-water corals in general or *Desmophyllum dianthus* in particular has a great ability to acclimatize or even adapt to a broad range of environmental conditions including pH. It is known that cold-water corals can show non-linear calcification responses and are able to maintain their calcification rate relatively constant with a certain range of CO_2 concentrations such as at pCO_2 levels projected for 2100.

Above and below a certain pCO_2 threshold significant negative and positive responses occur, such as decreasing calcification at much higher pCO_2 levels than those projected for 2100 (Ries et al. 2010 in Maier 2012; Maier, Watremez et al. 2012). Short-term and long-term (acclimatization) experiment are currently being researched to get insights in the combined effects of higher sea surface temperatures and high-CO_2 conditions (Buscher, Form et al. 2012; Hennige, Wicks et al. 2012). Indirect effects of ocean acidification, such as the shift in bacterial community and how this affects the resilience of cold-water corals remains to be explored (Maier 2012).

Echinoderms

Echinoderms (sea urchins, sea stars, brittle stars and sea cucumbers) are vital components of the marine environment, where they are often keystone ecosystem engineers, for example in bioerosion and sedimentation. A literature review analysed 19 studies including 16 species, which revealed that echinoderms are surprisingly robust to ocean acidification, but that important differences in sensitivity are observed between populations and species (Dupont, Ortega-Martinez et al. 2010). This is in line with the findings of a meta-analysis of Kroeker et al. (2010) who found a non-significant positive effect of ocean acidification on calcification on echinoderms. However, these results depend on exposure time, whereby short-term experiment may hide longer-term negative impacts. In addition, some physiological processes and life stages are more sensitive, based on negative effects in the larval and juvenile stage compared to positive effects in the adult stage, which is important for the response of the species as a whole. Fertilization of 10 echinoderm species proved to be robust to pH of 7.4 to 7.6. Echinoderm larvae produce their skeletons of the less soluble high-magnesium calcite in internal tissue that may be more protected from seawater chemistry, nevertheless 8 echinoderm species showed reduced growth and calcification in near-future CO_2 conditions (Byrne 2011). Responses are extremely species-specific and differ among species from different habitats, such as an intertidal and subtidal sea urchin (Byrne 2011). The literature review of Dupont et al. (2010) concludes that ocean acidification will have negative impact on echinoderm taxa with likely significant consequences at the ecosystem level (Dupont, Ortega-Martinez et al. 2010).

Molluscs

Molluscs (bivalves including mussels and oysters, gastropods including abalones and snails, and cephalopods including octopus, squid and cuttlefish) are a diverse group of filter feeders, grazers and predators with either an external (bivalves and gastropods) or internal (cephalopods) carbonate shell or no shell for some species of gastropods and cephalopods.

Adult bivalve molluscs are sensitive to elevated pCO_2 levels. Bivalves exposed to pH levels as expected later this century have been observed to have shells that were malformed and eroded. Calcification rates in the blue mussel *Mytilus edulis* and the Pacific oyster *Crassostrea gigas* decline linearly with increasing pCO_2 and may decrease by 25% and 10% respectively in 2100 (Gazeau, Quiblier et al. 2007). The energetic metabolism of *C. gigas* is also likely to be affected (Lannig et al. 2010 in ICES-WGMASC 2012) and increased pCO_2 has negative effects on physiology, rates of shell deposition and mechanical properties of the shells of the Atlantic oyster *C. virginica* (Beniash 2010 in ICES 2012). A number of studies on the blue mussel *M. edulis* came with contradictory results on growth and calcification rates,

which may be explained by a protective mechanism of the shells of *M. edulis* (Thomsen et al. 2010 in ICES-WGMASC 2012) or by adaptation of the mussel during longer experiments and less sensitive measuring methods.
Larval and juvenile bivalve molluscs that appear to be particularly sensitive to ocean acidification and high mortality rates have been linked to calcium carbonate dissolution (Fabry et al. 2008). Decrease in pH resulted in smaller larvae, impaired calcification, thinner shells and delayed metamorphosis in some species (*M. edulis, C. gigas,* Altantic oyster *C. virginica*, Sydney rock oyster *Saccostrea glomerata*, Atlantic bay scallop *Argopecten irradians,* hard clam *Mercinaria mercinaria*) but not in others (Asian oyster *C. ariakensis*, Mediterranean mussel *Mytilus falloprovincialis)* (Byrne 2011; ICES-WGMASC 2012).
The synergistic effects of ocean acidification and temperature has been investigated on the fertilization and embryonic development of *S. glomerata* and resulted in decreased fertilization, more abnormalities and smaller sizes. It was suggested that predicted changes in ocean acidification and temperature may have severe implications for this and other bivalve species (Parker et al. 2009 in ICES-WGMASC 2012). Changes in salinity may mitigate the decrease in biocalcification (Waldbusser et al. 2011 in ICES-WGMASC 2012).
Abalone larvae and early developmental stages are particularly sensitive to acidification, which causes significant reduction in thermal tolerance for some abalone developmental stages (pretorsion and late veliger larvae), but not for others (posttorsion and premetamorphic veligers). These results indicated that larval stages were differentially sensitive to low pH conditions and this variability may play into the resilience of individual species to withstand environmental change in the longer term.

Crustaceans
Crustaceans (cirripeds (barnacles), euphausiids (krill), decapods including lobster, crab, shrimp and prawn, copepods, isopods, amphipods and stomatopods) are a diverse group living in a range of habitats. Some are zooplankton and an important food source in the food web, such as krill. Others are important for the shellfish industry, such as decapods.
Marine crustaceans are currently considered to be tolerant to ocean acidification (Whiteley 2011), which could be the reason why research into the effects of ocean acidification on marine crustaceans has been limited (Byrne 2011). Most crustaceans have an exoskeleton and details of calcification of their exoskeletons still need to be determined (Luquet and Marin 2004 in Byrne 2011), but the high organic (chitin and protein) exoskeleton in the more stable form of calcite makes them more resilient to ocean acidification. In addition, direct exposure to changes in pH are avoided by their intra- and extra-cellular calcification processes. However, the vulnerability varies greatly between species and between life stages with lightly (copepods, amphipods, larvae) and heavily (lobsters, crabs) calcified exoskeletons (Byrne 2011). The first review of crustacean responses to ocean acidification by Whiteley (2011) concludes that crustaceans with strong iono- and osmoregulation are likely to be less vulnerable to ocean acidification, because they are able to maintain their acid-base balance. For example species in shallow coastal habitats and deep sea vents where natural variations in seawater salinity, temperature, pO_2 and pCO_2 occur. However, acid-base adjustments are likely to have high energetic and metabolic costs. In addition to poor iono- and osmoregulation, species living in low-energy environments such as deep-sea and polar habitats with low metabolic rates and low activity levels are also more vulnerable to ocean acidification.
Ocean acidification can affect calcification rates in two ways. First, the precipitation of calcium in the exoskeleton and second, the post-moult calcification of the new exoskeleton. One study of the blue crab (*Callinectes sapidus*) showed post-moult calcification took twice as long, which may indirectly increase mortality rates as the organism is vulnerable to predation, since it is unable to move and defend itself with a soft exoskeleton. Studies showed the calcification rate can be compensated by the blue crab, king prawn (*Penaeus plebejus*) and lobster (*Homarus americanus*), but at the expense of reduced growth rates and strength of the exoskeleton. If growth and reproductive capacity are influenced this may affect crustaceans at population level. There is growing interest in early life stages of crustaceans (Whiteley 2011). A review of Byrne (2011) into the impacts of ocean warming and acidification on marine

invertebrate life history stages included crustaceans. Impacts on crustacean early life stages are mixed for barnacle, copepod and amphipod. For lobster there was no effect in development, survival and growth up until the final larval stage, but in the final larval stage the mineral content of the exoskeleton which indicates negative effects for the adult lobster stage (Arnold et al. in Byrne 2011). This is not in line with the findings of a meta-analysis of Kroeker et al. (2010) who found a significant positive effect of ocean acidification on calcification on crustaceans. A review of Flores et al. (2012) on impacts of climate change on arctic krill found only one published study that embryonic development of krill could be negatively affected (Kawaguchi et al. 2011 in Flores et al. 2012), but preliminary results of long-term experiments by Kawaguchi suggest that growth, survival and recruitment of krill could also be directly or indirectly affected. Combined effects of ocean acidification and hypercapnia, increased sea surface temperatures and reductions in salinity have been poorly studied, but can have important synergistic effects (Whiteley 2011).

3.2.1.1.5 Higher trophic level non-calcareous organisms

Hypercapnia, the increased partial pressure of CO_2 (pCO_2) in seawater, has effects on physiological processes of fish and other water-breathing animals. Difference in pCO_2 of their body fluids and the ambient environment is very small and dissolved CO_2 in seawater diffuses across animal surfaces (Ishimatsu, Hayashi et al. 2005). As in seawater, CO_2 reacts with internal body fluids causing acidosis, an increased acidity in the blood and body tissue due to increased H^+ ions. Organisms with mechanisms for acid-base regulation of metabolically produced CO_2 and H^+ ions, use the same mechanisms to deal with acidosis. They include buffering capacity, ion exchange and CO_2 transport. Buffering capacity can be either passive or active. Active animals, such as epipelagic fish (e.g. tuna) and cephalopods (e.g. octopus and squid) have a high passive buffering capacity due to burst locomotion fuelled by anaerobic processes. Active buffering capacity occurs through accumulation of HCO_3^- as buffer to the increase of H^+ ions, when additional H^+ ions react with CO_3^{2-} and are converted to HCO_3^-. Ion exchange is the ability to transport acid-base equivalent ions such as HCO_3^- across cell membranes in exchange for Cl^-. When compensation of pH fails, mortality of all marine animals increases with the level of CO_2 and the duration of exposure (Fabry, Seibel et al. 2008).

Fish

According to a recent review of 116 papers published from 1969 to 2008 (Ishimatsu, Hayashi et al. 2008) studies on the effects of ocean acidification on fish are only based on laboratory experiments, with short exposure periods and much higher pCO_2 levels than under realistic future scenarios for the oceans, and studies focus on acid-base regulation and freshwater species. Fish appear to be most tolerant to hypercapnia among marine animals due to their acid-base regulation (Fabry, Seibel et al. 2008), with larval and juvenile stages being the most sensitive stages (Fabry, Seibel et al. 2008; Ishimatsu, Hayashi et al. 2008). If acid-base regulation is not achieved this may result in metabolic suppression. This adaptive strategy for the survival of short-term hypercapnia is not advantageous under chronic elevated pCO_2 levels as it will reduce growth and reproductive potential and will diminish the survival of species on longer time-scales (Fabry, Seibel et al. 2008).

Hypercapnia caused by anthropogenic CO_2 is not expected to cause fish mortality (Hayashi, Kita et al. 2004), although there is additional energy expenditure on acid-base regulation and ventilation. Oxygen consumption remains constant, but may shift from aerobic to anaerobic metabolism (Ishimatsu, Hayashi et al. 2008) and may affect aerobic performance (Munday, Crawley et al. 2009). All of the above effects may result in reduced fish growth. This was evident from studies under unrealistically high pCO_2 levels, but at the time of the review (Ishimatsu, Hayashi et al. 2008) no studies were available on the effects on fish growth and survival at realistic pCO_2 levels and at early life history stages. Since then, several studies at realistic pCO_2 levels were conducted with various results depending on the species. A study on a tropical reef fish, the orange clownfish (*Amphiprion percula*) did, apart from increased growth rate of some larvae, not detect effects on embryonic duration, egg survival and size at hatching and concludes thathypercapnia does not have significant disadvantages to growth and performance of larvae from benthic spawning marine fishes (Munday, Donelson et al. 2009). A study on early life history development of another tropical reef fish, the spiny damselfish (*Acanthochromis polyacanthus*) shows *that there is no effect on juvenile growth or survival of this species and perhaps also not on other tropical* reef fishes (Munday, Gagliano et al. 2011). Another study on the Baltic cod (*Gadus morhua*) did not find problems with sperm behaviour and fertilization success at high pCO_2 levels (Frommel, Stiebens et al. 2010). On the other hand, a study on an estuarine fish, the inland silverside (*Menidia beryllina*) concluded that the egg stage was much more vulnerable than the post-hatch larval stage to high pCO_2 levels (Baumann, Talmage et al. 2012).

Hypercapnia may also have effects on other physiological processes, such as skeleton and otolith (ear bones) formation, and on the sensory and feeding behaviour of fish.
Fish bones are composed of calcium phosphate. The only study on the effects at high CO_2 levels on fish bones at the time of the review (Gil-Martens et al., 2006 in Ishimatsu, Hayashi et al. 2008) found higher Ca and P (phosphorus) contents and higher bone remodelling (formation and desorption) activities, but no morphological difference. A later study on a tropical reef fish also did not find an effect on skeletal development (Munday, Gagliano et al. 2011).
Otoliths, used for postural balance and for sound detection, are composed of aragonite. High pCO_2 levels may reduce aragonite saturation in the endolymph where the otolith is formed. Otoliths are formed before hatching when acid-base regulation may not be fully developed. Otolith asymmetry (between left and right side of the body) may lead to higher mortality by impairing navigation (Ishimatsu, Hayashi et al. 2008). A few years later, studies found that otolith size, shape and symmetry are not affected by low pH in the spiny damselfish (*A. polyacanthus*) (Munday, Gagliano et al. 2011) and otolith development of the larval orange clownfish (*A. percula*) is even positively affected by low pH, because acid-base regulation in the endolymp can lead to larger otolith due to increased precipitation of $CaCO_3$ (Munday, Hernaman et al. 2011). They state, however, that otolith sensitivity varies considerable among species.
Fish behaviour affected by hypercapnia has been researched for changes in food consumption and foraging activity and for sensory behaviour. Sensory behaviour tested were the senses of smell (of predators), sound (of reef noise) and vision (the sight of a large fish). At highest realistic pCO_2 levels natural responses were absent in several experiments: with the orange clownfish (*A. percula*) to auditory cues that indicate risky locations (Simpson, Munday et al. 2011); with settlement-stage larvae of the orange clownfish (*A. percula*) to olfactory cues to smell predators and discriminate between predators and non-predators (Dixson, Munday et al. 2010; Munday, Dixson et al. 2010) and to olfactory cues to locate reef habitat and suitable settlement sites (Munday, Dixson et al. 2009); and with juvenile damselfish (*Pomacentrus amboinensis*) to visual cues of a potential threatening spiny damselfish (*A. polyacanthus*) (Ferrari, McCormick et al. 2012). All of this sensory behaviour provides strong evidence that the multi-sensory effects of high pCO_2 levels arise from systematic effects at the neural level (Ferrari, McCormick et al. 2012).
Foraging behaviour studies of a juvenile tropical reef fish, the anemonefish (*Amphiprion melanopus*) showed that high pCO_2 levels did only affect behaviour in combination with high seawater temperatures when the thermal optimum for food assimilation has been reached (Nowicki, Miller et al. 2012). Hypercapnia and hypoxia, a decreased dissolved oxygen content, in the ambient environment can narrow down the thermal window. This means the capacity of organisms to acclimatize to lower or higher ambient temperatures decreases, which is a potential concern with rising sea surface temperatures (SST) due to climate change (Portner and Peck 2010).

3.2.1.1.6 Meta-analyses on organism level

As described in the previous paragraphs marine organisms vary broadly in their sensitivity to ocean acidification. Three meta-analyses were identified on species sensitivity, one to construct a species sensitivity distribution per species for all effects of ocean acidification (De Vries, Tamis et al. in press) and two to analyse species sensitivity variation between taxa and between biological responses (Hendriks, Duarte et al. 2010; Kroeker, Kordas et al. 2010). Biological responses vary partly due to the variety of biological processes affected, such as calcification and dissolution, reproduction, survival, growth and metabolism. Calcification responses vary between organisms using different forms of $CaCO_3$, whereby organisms using high-magnesium calcite are more resilient than organisms using more soluble forms such as aragonite and low-magnesium calcite (Kroeker, Kordas et al. 2010). Andersson and Mackenzie (2011) challenged this outcome and it appeared that the form of calcium carbonate alone does not predict sensitivity to ocean acidification (Kroeker, Kordas et al. 2011). Calcification responses also vary, because some organisms are more resilient by increasing their calcification rate, controlling their internal pH or having symbiotic interaction with photosynthesis by autotrophs that may stimulate calcification. Calcification responses may result in altered energy allocation due to increased physiological costs of maintenance (e.g. acid-base balance), lower growth rates, reduced reproduction and decreased survival which also varies amongst calcifying organisms. Variation in sensitivity amongst organisms has important implications for ecosystem responses (Kroeker, Kordas et al. 2010). The meta-analysis by Hendriks et al. (2010) suggested that based on experimental differences in organism responses, many marine organisms are more resistant to ocean acidification than previously thought and long-term adaptive capacity is poorly understood. Dupont et al. (2010) showed that such a global meta-analysis can mask the complexity of biological systems such as differences in vulnerability in adult, juvenile and larval stages and that ocean acidification will have negative effects on some marine organisms with likely consequences at ecosystem level.

3.2.1.2 Effects on community and ecosystem level

It is apparent that ocean acidification will potentially have serious consequences for many marine calcifiers, but the direct effects on noncalcifiers and the indirect effects on higher trophic level organisms that rely on the calcifiers for shelter, nutrition and other core functions are less well known. These ecosystem responses are complex and difficult to quantify (Guinotte and Fabry 2008). Biological and ecological effects in the surface oceans will also affect the deeper waters, because organisms and habitats living there rely mainly on the products created by organisms in the surface waters. Organisms in deeper water may also become vulnerable to acidification on a longer timescale, as surface waters mix with deeper waters (Raven, Caldeira et al. 2005).

There are to date according to our knowledge two studies (Guinotte and Fabry 2008; Portner 2008) on the effects of ocean acidification at the ecosystem level. The first study reviewed effects at organism level and briefly addressed community level impacts in seagrass and coral reef ecosystems. The latter focussed on effects in the physiology of organisms as a first step to better understand and overcome uncertainty of ecosystem effects. There have been a few more systematic reviews (i.e. Hoegh-Guldberg and Bruno 2010; Doney, Ruckelshaus et al. 2012) on the impacts of climate change, including ocean acidification, on marine ecosystems. Ocean acidification cannot be considered in isolation from other high-CO_2 related effects and non-CO_2 related effects. The primary high-CO_2 related problem is climate change due to increasing atmospheric and ocean temperatures, which in turn create changes such as rising sea levels, retreating sea-ice, increased vertical ocean stratification, altered wind and ocean circulation patterns, and altered precipitation, runoff and freshwater input. In addition, warming and altered ocean circulation reduce subsurface oxygen concentrations. Non-CO_2 related pressures on marine ecosystems include intensive fertilizer use, coastal and benthic habitat degradation, fish stock overexploitation, growing aquaculture production and invasive species. Studies on ecosystem effects are complicated by the fact that these multiple stressors on marine ecosystems have integrated and synergistic effects (Doney, Ruckelshaus et al. 2012). Research on these interactive or cumulative effects on organisms and the consequent ecosystem responses are in its infancy (Guinotte and Fabry 2008). The most recent review of Doney et al (2012) does identify some of these complex responses and describes systematically how physiological responses at organism level manifest as population and community responses and ultimately determine ecosystem structure and function. These consequences of physiological responses to ocean acidification, as well as a case study of the effects on coral reef ecosystems are summarized here, because of its relevance for Caribbean Netherlands. For the other two case studies, on polar ecosystems and upwelling ecosystems, and for other CO_2 and non-CO_2 related effects is referred to this review of Doney et al (2012).

New environmental conditions like lower pH may be physiologically tolerable, allowing acclimatization (adjusted physiology within individuals) or adaptation (genetic change over generations) or intolerable, promoting migration (by individuals or populations), change in phenology (timing of biological recurring events) or local extinction (Parmesan 2006 in Doney, Ruckelshaus et al. 2012). These physiological responses of organisms lead to shifts in size structure, spatial organization (distribution and dispersion), productivity, variability and seasonal abundance of populations. These shifts in turn lead to alterations in species interactions, trophic structure, food web dynamics and biogeochemical cycles. Disruptions of existing species interactions can occur through asynchronous shifts in the seasonal phenologies of interacting predator and prey populations. Alterations of trophic structure can occur if changes in primary production cascade up to higher trophic levels and changes in ecologically dominant consumers cascade down to lower trophic levels. Food web dynamics can change if keystone species in the food web are affected by ocean acidification, such as calcifying pteropods. Ocean acidification and climate change will undoubtedly affect microbial food webs as well, although there are many uncertainties (Doney, Ruckelshaus et al. 2012).
Compared to terrestrial ecosystems, marine ecosystems respond much more sensitively and rapidly to climatic changes, for example through spatial shifts of populations (Schubert, Schellnhuber et al. 2006). Distribution shifts contribute to altered community composition and biodiversity and loss of functionally important species (Doney, Ruckelshaus et al. 2012). For example the mussel-dominated communities typical for the temperate rocky shores in the northeast Pacific gradually shifted to communities more dominated by fleshy algae and barnacles during eight years of declining pH (Wootton et al. 2008 in Doney, Ruckelshaus et al. 2012). In shallow benthic communities near natural high-CO_2 vents, calcareous corals and algae are replaced by non-calcareous algae, juvenile molluscs are sharply reduced or absent and biodiversity has decreased. This may benefit highly invasive non-native algal species (Hall-Spencer, Rodolfo-Metalpa et al. 2008). Another example is a naturally low-pH eastern tropical Pacific coral reef that is less cemented and more vulnerable to bioerosion (Manzello et al. 2008 Logan 2010). This can ultimately cause changes in ecosystem function, although the effects on ecosystem level depend on factors such as functional redundancy, the rate and sequence of community change and other features of population and community organization (Doney, Ruckelshaus et al. 2012). Ocean acidification effects on keystone and foundation species may be especially important. The calcification response of keystone species and critical habitat-forming marine benthic species, such as oysters or corals, could have a major impact on biogenic habitats such as coral reefs and oyster beds.

Since ocean acidification does not affect all species equally, it is critical that ecosystems are able to maintain functional capacity if species composition changes. A study by Hughes et al. (2012) into spatial variation in coral species composition and abundance at the Great Barrier Reef in Australia found flexibility in community composition. Spatial variation in coral reef assemblages among habitats (reef crest and reef slope) and along the length of the GBR is mainly caused by spatial patterns of larval recruitment, mortality and growth and physiological tolerance of individual species. Tolerance to reduced carbonate saturation state, increased water temperatures and other climate-related phenomena such as increased number and intensity of storms, varies substantially within and between taxa. The flexibility in community composition indicates climate change is likely to result in substantial changes in coral reef assemblages that could continue to function as highly altered ecosystems rather than complete loss of coral reef ecosystems, if CO_2 emissions are reduced sufficiently to avoid a complete collapse of coral reefs (Hughes, Baird et al. 2012).

Theoretical concerns and preliminary research have identified coastal margins, deep-sea ecosystems, high-latitude regions (Raven, Caldeira et al. 2005; Kleypas, Feely et al. 2006; Fabry, Seibel et al. 2008; Guinotte and Fabry 2008), and especially tropical coral reefs ecosystems (Kleypas, Feely et al. 2006; Hoegh-Guldberg, Mumby et al. 2007) as areas of concern. Additional ecosystem effects arise when habitat forming animals such as corals are unable to form and cement reef structures as refuge, feeding and nursery habitat for a variety of invertebrates and fish (Kleypas, Feely et al. 2006). Coral reefs make up only 1% of the oceans, but may support up to 25% of marine biodiversity and cold-water corals have extremely high biodiversity, including commercially fished species (Husebø et al. 2002, Freiwald et al. 2004 in Logan 2010).

Coastal ecosystems are in addition to ocean acidification vulnerable to multiple anthropogenic disturbances (such as runoff of pollutants and nutrients, habitat alteration, aquaculture and fishing). These ecosystems are economically important economically as they make up only 7% of the oceans but support approximately 10% to 30% of marine primary productivity worldwide (Fabry, Seibel et al. 2008). Coastal acidification may be enhanced somewhat by acidic freshwater inputs and runoff, and acidic atmospheric inputs near major industrial centers (Doney, Fabry et al. 2009). Strong seasonal upwelling along parts of the west coasts of North and South America, Africa, and Australia brings up naturally acidic waters that are under-saturated with respect to aragonite. Although this is a natural phenomenon it was found that shoaling aragonite saturation horizons combined with seasonal upwelling, allowed undersaturated water to reach the surface along the west coast of North America (Feely, Doney et al. 2009; Feely et al. 2008 in Logan 2010).

Polar regions already have some of the lowest saturation states because of their cold temperatures, and will likely experience undersaturation with respect to aragonite first (Orr et al. 2005). Pteropods may be the first affected of the major calcifying organisms at high latitudes. Pteropods occur in the surface waters of the Southern, Arctic, and subarctic Pacific oceans and play a key role in the food web as they are prey to commercially fished species (Orr et al. 2005). In addition they export both carbonate and organic carbon from the surface to the seafloor (Logan 2010).

3.2.2 Effects on biogeochemical processes

Changes in biogeochemical processes in the ocean are considered to be an indirect effect of the increased atmospheric CO_2 concentrations (Gehlen et al., 2011). Ocean acidification through the oceanic uptake of CO_2, can have major consequences for processes such as $CaCO_3$ preservation, and the production and export of organic matter by the biological pump. Ocean acidification increases the Revelle buffer factor, which is a measure for the ability of the oceans to take up CO_2. An increased Revelle factor indicates a decrease in uptake by ocean water of CO_2, resulting in less uptake of CO_2 by the oceans and a transient increase of CO_2 in the atmosphere. Apart from this chemical process, the majority of feedbacks on biogeochemical cycles affect the functioning of the biological pump. Furthermore, changes in carbonate chemistry can also result in altered chemistry and bioavailability of weak acids of trace metals (Doney et al., 2009; Shi et al, 2010).

As described in paragraph 3.2.1, an increased availability of CO_2 in the oceans could stimulate production in certain photosynthesizing groups, which results in an increased production of organic matter and thus uptake of CO_2 by the marine ecosystem when preserved or exported to the deep ocean. Particularly the increased growth in larger phytoplankton taxa, such as found for diatoms (Tortell et al., 2008) will potentially enhance the CO_2 drawdown through ballasting (Balch et al., 2010). For calcifying organisms, a more acidic environment may have a negative effect on their calcification process (Fabry et al., 2008), thereby hampering their growth and productivity. As the carbonate mineral provides better ballasting material than the silicate frustules of diatoms (Balch et al., 2010), a decrease in carbonate production by the main carbonate producers (coccolithophores, foraminifera and pteropods) could decrease the strength of the biological pump. On the other hand, the calcification process releases CO_2 to the

atmosphere (Zondervan et al., 2001) and therefore a decreased calcification could function as a negative feedback to high atmospheric CO_2. Similarly, dissolution of carbonates, either from organisms present in the water column, or carbonate deposits on the ocean floor, will increase oceanic CO_2 uptake, albeit on long timescales (>1000y) (Archer et al., 2005). In addition, local conditions, e.g. through the input of nutrients that promote primary productivity (Borges and Gyphens, 2010) can result in a stronger change in the marine carbonate system than ocean acidification. Another stimulus for productivity associated with ocean acidification is the increased N_2-fixation (the conversion of atmospheric nitrogen N_2 into ammonia NH_3) by cyanobacteria. As briefly discussed in paragraph 3.2.1, elevated CO_2 concentrations enhance the rate of N_2 fixation. Fixation in the best studied species *Trichodesmium*, shows an increase of ~40 +/- 20% averaged over six experiments (Hutchins et al., 2009). Particularly in nitrogen limited oceanic regions, such an addition could enhance productivity substantially, and in turn strengthen the biological pump. Cyanobacteria prefer warm, more stable conditions, therefore it can be expected that cyanobacteria will become more abundant as climate change continues to warm the surface oceans. An increased temperature of the ocean waters will however also increase microbial activity, which will result in intensified decomposition of organic matter and subsequently reduce the carbon export and increase the respiratory CO_2 production (Piontek et al., 2010). As a direct consequence, the ocean's ability to take up CO_2 will be reduced. Furthermore, both increased water temperature and intensified organic matter degradation are processes that result in lower oxygen levels, and may lead to an expansion of the Oxygen Minimum Zone (OMZ). Oxygen depletion may be a threat to organisms living at these depths.
Finally, an increased weathering rates on land due to higher atmospheric CO_2 will lead to a larger influx of nutrients to the coastal waters. In addition to nutrient concentrations that will increase primary productivity, alkalinity will also increase, which counterbalances ocean acidification and positively affects calcifying organisms.

3.2.3 Other effects

Physical effects on sound and light absorption

A recently highlighted physical impact of ocean acidification is that lowered pH will also affect underwater sound propagation. Chemical pH-dependent decline in dissolved borate ions within the oceanic boric acid system will result in decreases in ocean sound absorption. A 'noisier' ocean at lower pH levels could have implications for communication of marine organisms (Hester, Peltzer et al. 2008). Decreased ocean sound absorption will affect low frequencies (below 10mHz) which will reach 70% farther by 2050 (Brewer and Hester, 2009 in Reeder and Chiu 2010), but the potential effect on whales and other marine mammals is largely unknown (Doney, Fabry et al. 2009). Reeder and Chiu (2010) further analysed ocean noise and concluded that several important physical concepts minimize the impact of ocean acidification on ocean noise levels. An effect could only be expected in very quiet regions, very distant from shipping lanes, and at depths experiencing the least change in pH. In deep water a negligible change in ocean noise levels was found, but no observable change was found in shallow water and surface duct environments, two environments where most of the marine mammal populations are found.
Light propagation might also be affected due to reduced light scattering and deeper euphotic zones in a decalcified ocean with reduced calcium carbonate particles such as microscopic coccolithophores. This scenario could have consequences for such biogeochemical aspects as export production (Balch and Utgoff 2009 in Doney, Fabry et al. 2009). This concern has according to our knowledge not been further investigated.
Physical chemistry of seawater might change such that rates of redox reactions associated with metal oxidation and electrolysis can change. This more applied chemistry would be of strategic importance to both shipping and naval interests, particularly as it affects the integrity of ship hulls (Doney, Fabry et al. 2009). Because this does not have biological or ecological consequences this potential impact has not been reviewed any further.

Ecosystem services

Ecosystem services are the benefits humans derive from ecosystems. The Millennium Ecosystem Assessment divided ecosystem services into four categories: provisioning, regulating, cultural and supporting services (MEA 2005). Coastal ecosystems like estuaries, marshes, mangroves and coral reefs provide relatively more of each service category. Seagrass beds, kelp forest and lagoons provide ecosystem services at lower levels (table 18.2 in MEA 2005). Ocean acidification is likely to affect each of the service categories by affecting organisms, communities and ecosystems thereby altering marine ecosystem functioning (Cooley, Kite-Powell et al. 2009). The response of mangroves to ocean acidification is unknown, seagrass beds and kelp forests are less likely to be damaged by ocean acidification, and the other above-mentioned coastal ecosystems are more likely to be damaged. Ecosystem services that experience multiple stressors could be most harmed.

A recent study by Cooley (2012) identified for all ecosystem services whether they are likely to be affected by ocean acidification and two other stressors, pollution and deoxygenation (table 3).

Services that may be affected by ocean acidification according to Cooley (2012) include capture fisheries and aquaculture harvests of particularly shellfish (provisioning services), coastal protection by carbonate reef structures (regulating service), habitat provisioning by structural complex reefs, biodiversity, biological regulation by food web dynamics and the carbon cycle (supporting service), tourism and cultural identity (cultural services).

Table 3. Anthropogenic changes in ocean biogeochemistry and their negative (--) positive (++) or mixed (+-) effects on marine ecosystem services (adapted from Cooley 2012)

Ecosystem services		**Ocean acidification**	**Pollution**	**Deoxygenation**
Provisioning	Food			
	- Fish	+-	--	--
	- Invertebrates/shellfish	--	--	--
	- Plants/seaweed	++	--	
	Clean water		--	
	Building materials			
	- Wood		--	--
	- Limestone	--		
	Fuel			
	- Timber		--	--
	- Fossil fuel			
	Medicines & genetic resources	?	--	--
	Ornamental resources	--	--	--
Rgulating	Regulation			
	- Air quality		--	
	- Climate	++		
	- Hydrological cycle			
	Human disease control			
	Wastewater processing		--	--
	Flood & storm protection	--		--
	Erosion control		--	

Ecosystem services		Ocean acidification	Pollution	Deoxygenation
Supporting	Habitats & nurseries	--		--
	Biodiversity	--	--	--
	Biological regulation			
	- Predator-prey relationships	--	--	--
	- Keystone species	--	--	--
	Freshwater storage & retention			
	Primary productivity		--	
	Nutrient cycling & fertility	--	--	--
Cultural	Cultural & spiritual	--	--	--
	Tourism & recreation	--	--	--
	Aesthetic	--	--	--
	Education & research	-+	--	--

The effect of ocean acidification on ecosystem services and their economic value is difficult to quantify, and to date only four economic valuation studies have attempted to quantify impacts on shellfish harvests (Cooley and Doney 2009, Cooley et al. 2009 and Narita et al. 2012 in Cooley 2012) and on coral reef ecosystem services (Brander et al. 2009). Cooley et al. (2009) examined global marine harvest patterns and dividing this into biological groups with different vulnerability to ocean acidification. The global annual economic value of fisheries has been estimated at USD 91.2 billion and for aquaculture at USD 78.8 billion (FAO, 2009 in Cooley, Kite-Powell et al. 2009). The heavy reliance of Atlantic and Pacific fisheries on vulnerable groups suggests that if ocean acidification decreases harvest of calcifying species, economic values could decline by billions of dollars. Most affected will be developing countries in the Pacific depending heavily on calcifying species (molluscs, sponges and corals) with small island nations having limited agricultural alternatives for their provisioning services (Cooley, Kite-Powell et al. 2009). Brander et al. (2009) estimated the annual economic damage of ocean-acidification-induced coral reef area loss for four SRES scenarios (A1, A2, B1 and B2, see footnote in paragraph 3.1.3). The estimation is based on the value of coral reefs from a meta-analysis of 160 coral reef valuation studies and on the projected loss of coral reef area. The Netherlands Antilles was included with a reef area of 250 km^2. The average value was estimated at USD 177.000 per km^2 in the year 2000, including ecosystem services tourism, fishing, coastal protection, biodiversity and preservation. The value was projected to rise by a factor 67 for scenario A2 up to a factor 681 for scenario A1 in the year 2100. The total area loss was projected to be between 16% or 30.000 km^2 for scenario B1 and 27% or 65.000 km^2 for scenario B2 in the year 2100. The estimated economic loss was up to USD 870 billion in the A1 scenario in 2100. Scenario B1 had the lowest damage, because it had the lowest area loss. However, the proportional economic loss as a percentage of the global GDP was higher in scenarion B1 with 0.18% compared to 0.14% in scenarios A1 and A2. The study concluded ocean acidification adds 10% to the total impact of climate change.

All the above mentioned studies are unable to provide accurate insight in the effects of ocean acidification on ecosystem services, either because they are very general or extremely specific and because they focus on monetizable services only. Two recent reviews on the impacts of climate change on marine fisheries (Cheung, Pinnegar et al. 2012) and aquaculture (Callaway, Shinn et al. 2012) in the UK and Ireland do not monetize impacts on these ecosystem services. They do however provide a very comprehensive overview of effects on fisheries and aquaculture resources and management measures, knowledge gaps and policy recommendations. Because of similarities in geographic range, marine resources, fisheries management and policies between The Netherlands and the UK, ocean acidification effects on fisheries and aquaculture identified in both reviews are summarized here. The reviews acknowledge the major difficulty is to directly attribute changes in fisheries and aquaculture to climate and ocean change rather than other non-CO_2 related pressures such as overfishing (Cheung, Pinnegar et al. 2012). Also ocean acidification effects cannot be considered in isolation from climate change effects, nevertheless only identified effects of ocean acidification are addressed here.

Marine fisheries

From a fisheries ecology perspective ocean acidification can affect fisheries directly and indirectly through recruitment, growth, mortality (Fabry et al. 2008) and migration. Recruitment is the most variable parameter in the productivity of fish stock (Cheung, Pinnegar et al. 2012). Direct effects of ocean acidification are anticipated through recruitment, because early life stages of fish (eggs and larvae) are likely to be most vulnerable to pH changes and survival of early life stages may be reduced by ocean-acidification-induced changes in the plankton community which affect food quality, food quantity, phenology and predation. Direct physiological effects of ocean acidification on growth and mortality are unknown, but indirect ecological effects of change in food quality, quantity and phenology may be reduced growth which may result in reduced fertility and survival.

A review of FAO (2009) on current scientific knowledge of climate change impacts on marine fisheries concluded the effects of ocean acidification on organisms with calcium carbonate shells and skeletons such as bivalve molluscs, some crustaceans, corals, echinoderms and some phytoplankton species, will potentially results in reduced production and declines in yields for calcifying marine resources and ecologically related species. However, research shows large variations between and within taxa (Cheung, Pinnegar et al. 2012) and a meta-analysis by Hendriks et al. (2010) suggests that many marine organisms are more resistant to ocean acidification that previously thought and long-term adaptive capacity is poorly understood. The real question is therefore who will be the winners and losers and what will be the population and community effects of ocean acidification (Dulvy, Reynolds et al. 2011).

The recent review of Cheung et al. (2012) on marine fisheries in the UK elaborates on the effects of climate and ocean change by dividing them into effects on: (1) resource availability (2) fishing operations (3) fisheries management and conservation measures and (4) profits from fisheries.

(1) Climate change could have major effects on resource availability. Resource availability is already affected by observed distribution shifts, changes in productivity and variability in resources. International fisheries landings data for the whole north-east Atlantic region show both northerly (such as for Atlantic cod *Gadus morhua* and plaice *Pleuronectes platessa*) and southerly (such as for sole *Solea solea*) shifts over recent decades. Warm-water species expand their northern boundary (such as sea bass, *Dicentrarchus labrax* and red mullet *Mullus barbatus*) and cephalopods (squid, octopus and cuttlefish) generally become more abundant in the North Sea. Distributions of exploited and new target species will continue to shift in the next five decades globally and in the north-east Atlantic specifically (Cheung et al. 2009, 2010, 2011 in Cheung, Pinnegar et al. 2012). Pelagic fisheries targeting mainly herring (*Clupea harengus*) and Atlantic mackerel (*Scomber scombrus*) are known to respond dramatically to environmental fluctuations (Barange et al. 2009 in Cheung, Pinnegar et al. 2012). Aerobic scope (oxygen availability for metabolism), temperature, food availability and ocean chemistry are the major factors determining distribution and growth. Changes in ocean chemistry, particularly ocean acidification and reduced oxygen levels, can reduce the aerobic scope of organisms (Portner 2010 and Cheung et al. 2011 in Cheung, Pinnegar et al. 2012). Tolerable organisms may acclimatize or adapt to lower pH while intolerable organisms may alter their distribution (Dulvy, Reynolds et al. 2011). Ocean acidification may have direct impacts on recruitment, growth and survival of commercial shellfish. European lobster (*Homarus gammarus*) showed to be potentially vulnerable, without significant change in carapace length, but with lower carapace mass during the final developmental stage of the larvae (Arnold et al. 2009 in Cheung, Pinnegar et al. 2012). Larvae of oysters (*Crassostrea virginica and C. Ariakensis*) also showed lower shell area (Miller et al. 2009 in Cheung, Pinnegar et al. 2012). Current evidence on direct impacts of ocean acidification on commercial finfish is limited. They may be less impacted in terms of direct physiological effects, but they may be impacted indirectly by changes in the marine foodweb. Larvae and juveniles of most fish are reliant on planktonic crustaceans which may or may not be impacted by future

acidification. Adult commercial fish species such as haddock *Melanogrammus aeglefinus* and plaice *Pleuronectes platessa* are reliant on bivalve molluscs or echinoderms which are predicted to decline (Dulvy, Reynolds et al. 2011). The Dynamic Bioclimate Envelope Models (DBEMs) projecting future distributions and resource availability, assume negative effects of ocean acidification, reduced oxygen and changes in size structure of phytoplankton, and project a reduction in the maximum potential catch up to 30% in the North Sea. If effects of ocean acidification are ignored a small gain of less than 5% is projected in the North Sea (Cheung et al. 2011 in Cheung, Pinnegar et al. 2012). Because of assumptions and uncertainties model projections should focus on the general trend rather than numerical outputs. The review concludes the valuable UK lobster fisheries is potentially the most vulnerable to ocean acidification, although the sensitivity is still unclear and long-term sustainability of this sector remains highly uncertain.

(2) Fishing operations are affected directly by climate change through extreme weather events and indirectly through catchability of fishing gear. Some fish and invertebrate species show increased consumption rate with increased temperature, resulting in increased vulnerability to baited fishing gear (such as lobster traps). Bottom trawl gear does not show significant changes in catchability, but changes in vertical ocean stratification may affect catchability of pelagic gears. Ocean acidification is not mentioned as indirect effect.

(3) Fisheries management and conservation measures are also not specifically affected by ocean acidification, but changes in resource availability caused by climate and ocean change will effect fisheries management. Shifts in species abundance and increased variability make it more difficult to set quota, because many stock assessments are based on the assumption that environmental conditions are stationary. Shifts in species distribution affect the allocation of quota across international boundaries with potential territorial disagreement. Shifts in both species abundance and distributions compromise the effectiveness of spatial fisheries management measures such as temporary closed area (i.e. the Plaice box in the Wadden Sea) and marine protected area (i.e. spawning populations moving outside the boundaries of the protected area).

(4) Fishing profits will shift as a result of changes in productivity and prices of high-value finfish, crustaceans and molluscs are expected to increase in the future. Fishing costs will increase with shifting distribution of demersal fisheries resources and increased fuel usage. A study has been done on costs of adaptation to climate change of the fisheries sector, which was estimated to be between USD 15 and 30 million in Europe for measures such as buy-backs, transferable quotas and investments in alternative sources of employment and income (Sumaila and Cheung 2010 in Cheung, Pinnegar et al. 2012). The impact of climate change on marine fisheries was assumed to primarily occur through changes in primary productivity, shifts in species distribution and ocean acidification (Cheung et al. 2011 in Cheung, Pinnegar et al. 2012).

Vulnerability of 132 national economies to climate change impacts on fisheries has been assessed by Allison et al. (2009) based on three key elements: exposure to physical effects of climate change, the degree of intrinsic sensitivity of the fisheries resources or the dependence of the national economy on the fisheries sector and the adaptive capacity to offset potential impacts. The Netherlands was ranked 127 with very low vulnerability to climate change, good adaptive capacity and a relatively small anticipated impact.

Marine aquaculture
A review of FAO (2009) on current scientific knowledge of climate change impacts on marine aquaculture concluded ocean acidification may negatively affect shellfish aquaculture as it could impair the growth and shell formation of oysters and mussels (Gazeau, Quiblier et al. 2007) and positively affect seaweed

or macroalgae aquaculture. Positive effects of increased atmospheric CO_2 on seaweed aquaculture depends on the species. Many species have CO_2 concentrating mechanisms that ensure macroalgae are not carbon limited for growth, and growth rates of 13 species did not increase at higher CO_2 levels (Israel and Hophy 2002 in ICES 2012). However, gross chemical composition of macroalgae may change (Zou and Gao 2010 in ICES 2012) which may be important for the eventual utilization of the seaweed.

The combined effect of ocean acidification with ocean warming could have positive and negative effects on marine aquaculture. The positive effect for filterfeeding shellfish may be enhanced coastal plankton productivity provided that nutrients are available. The negative effect may be eutrophication-induced occurrence of toxic algal blooms and the spread of diseases, which is one of the most feared threats to aquaculture (FAO 2009). Shellfish aquaculture is entirely dependent on the availability of natural food sources, including phytoplankton. It is expected that the largest changes in marine ecosystems will occur at the lower trophic levels, and there is evidence to suggest that phytoplankton seasonal cycles have shifted (Edwards and Richardson 2004 in ICES-WGMASC 2012) including occurrence of harmful algae blooms causing shellfish poisoning (Hallegraeff 2010 in ICES-WGMASC 2012). Ocean acidification is recognized as contributing factor to algal blooms. Algal blooms themselves result in a CO_2 reduction and a pH rise. This pH rise is detrimental to algal growth and stops further algal growth or succession. With ocean acidification the starting pH for this process is lower and the succession events may be altered (Callaway, Shinn et al. 2012). Higher temperature may affect succession further and increase primary production. However, rising surface water temperature will also lead to increased stratification and greater nutrient limitation. The net result is expected to be a reduction in global primary production, but the present ability to predict future changes is limited (ICES-WGMASC 2012).

A recent review by ICES WGMASC (2012) on the state of scientific knowledge of climate change impacts on shellfish aquaculture found that studies on ocean acidification effects on commercial marine calcifiers is limited to a small number of species: Blue mussel *Mytilus edulis*, Pacific or Japanese oyster *Crassostrea gigas,* Altantic or Eastern, American, Virginia oyster *C. virginica*, Asian or suminoe oyster *C. ariakensis*, Sydney rock oyster *Saccostrea glomerata*, pearl oyster *Pinctada fucata* , hard clam *Mercinaria mercinaria*, (Atlantic) bay scallop *Argopecten irradians*, Japanese or Chinese scallop *Chlamys farreri*, and red abelone *Haliotis rufescens*. The studies to date generally suggests that the rise in pCO_2 can impact physiology, growth and calcification rate. The available data also give reason to speculate that recent declines in bivalve populations may be connected to ocean acidification. Two of the largest oyster hatcheries in the Pacific Northwest reported an 80% decline in production rates. It is suspected that wind-driven coastal upwelling events have exposed the bivalves to deep acidic waters (Miller et al. 2009 in ICES-WGMASC 2012). Coastal upwelling areas are some of the most productive regions for shellfish aquaculture. Organism can be tolerant to ocean acidification by acclimatization or adaptation, or migrate or go extinct if they are intolerant. Estuarine species may be better adapted to ocean acidification than open-ocean species, because they are used to being exposed to very fluctuating conditions. On the other hand estuarine species may experience acidification sooner and more severely, because estuaries are more ssusceptible to acidification because they are subject to multiple acid sources and are less buffered than marine waters (Callaway, Shinn et al. 2012; ICES-WGMASC 2012). The ICES review (2012) concludes that current and future increases in temperature and CO_2 are likely to have significant negative consequences for the spatial distribution and productivity of shellfish aquaculture as their ecological roles and economic potential may be altered. However, research on the direct and indirect effects of climate change and ocean acidification on many species is largely in its infancy. The review states that ocean acidification responses of cultured and wild bivalve populations are not sufficiently known in terms of calcification response, organism response, ecosystem response and socio-economic response.

Another recent review of Callaway et al. (2012) on marine aquaculture in the UK found that the biological effects of ocean acidification by 2100 are well researched. Although organism responses are species specific and differ between closely related species and between and within populations, the principal biological effect is on calcifying species with reduced calcification rates, especially during the early life stages, resulting in reduced survival rates. As a result ocean acidification could significantly reduce recruitment and is expected to affect the shellfish aquaculture most. This could mean increased reliance on hatchery produced seed or culture of bivalve species more tolerant to ocean acidification. The latter can be achieved through selective breeding of broodstock with higher tolerance or research into species with naturally high tolerance such as those living near hydrothermal high CO_2 vents (Callaway, Shinn et al. 2012). In comparison to bivalves, culture of fish, lobster and crab is less likely to be affected by ocean acidification. However, as part of climate change it has the potential to change entire food chains and community structure, which may influence the success of aquaculture because of the close relationship with environmental conditions such as temperature, salinity and oxygen solubility (Callaway, Shinn et al. 2012).

Bivalve and seaweed aquaculture can also have an effect on atmospheric CO_2. Seaweed or macroalgae culture can sequester CO_2 and at the current levels of cultivation remove nearly 0.7 million tons of carbon, which has a very small impact on total carbon emissions (Turan and Neori 2010 in ICES 2012). An area of 1000 km^2 of seaweed could potentially sequester up to 1 million tons of CO_2 per year (Issar and Neori 2010 in ICES 2012). Bivalves are a biogenic CO_2 source and can influence inorganic carbon cycling by generating CO_2 to the surrounding water. This CO_2 source is increasing, because of global translocation of molluscs, their successful colonization of new habitats and the rapidly growing aquaculture production (Chauvaud et al. 2003 in ICES-WGMASC 2012). High-density bivalve aquaculture and invasive species could have a substantial influence on the carbon cycle, particularly in coastal regions (ICES-WGMASC 2012). A study by Lejart et al. (2012 in ICES-WGMASC 2012) suggests that *C. gigas* populations increase CO_2 release to the atmosphere in coastal ecosystems in France and consequently contribute to the global warming that facilitates the northerly spread of this invasive species.

3.3 Institutional and research developments

3.3.1 Policy developments and policy documents

This section provides an overview of institutional organizations and their policy programme in relation to ocean acidification with most important policy developments and policy documents on ocean acidification and the policy options currently available to take action on ocean acidification.

3.3.1.1 International policy

International policy has developed through various United Nations (UN) bodies. These include the United Nations Framework Convention for Climate Change (UNFCCC), the Intergovernmental Oceanographic Commission (IOC) as part of the United Nations Educational, Scientific and Cultural Organization (UNESCO), the United Nations Environmental Programme (UNEP), the United Nations Commission on Sustainable Development (CSD) and the Convention on Biological Diversity (CBD). Ocean acidification is relevant to all these intergovernmental bodies and they each offer opportunities to inform policy makers (Turley and Gattuso 2012) and to influence policy making. However, since the only policy action to mitigate ocean acidification on a global scale is to reduce anthropogenic CO_2 emissions, it is important that policy makers consider this 'other CO_2 problem', so not only impacts of CO_2 on climate change, but also on the ocean (Turley and Gattuso 2012). The UNFCCC offers the best chance for mitigation of ocean acidification, which is explained below.

Intergovernmental Panel on Climate Change (IPCC)

In 2007 the IPCC first recognized ocean acidification in its 4th assessment report as an associated disturbance of climate change caused by increasing CO_2 emission (IPCC 2007). IPCC is the leading international body for the assessment of climate change established by UNEP and the World Meteorological Organization [2], but does not recommend policy (Turley and Gattuso 2012). The IPCC Special Report on Emissions Scenarios published in 2000 gave predictions of CO_2 concentrations under six different future scenarios of global demographic, economic and technological development (IPCC 2007), which are used as realistic future scenarios in research on ocean acidification and its effects. Ocean acidification will be even more substantially addressed in its 5th assessment report due in 2013-2014 (Turley and Gattuso 2012). A number of expert meetings and workshops have been held to support the process of preparing the Fifth assessment report [2]. A 3-day IPCC workshop on ocean acidification was held in 2011 in Japan, which was attended by 82 expert scientists and policy makers to synthesise the scientific understanding of ocean acidification effects on organisms, ecosystems and ecosystem services (IPCC 2011).

UNFCCC Conference of the Parties (COP)

In 2011 at the UNFCCC COP17 in Durban ocean acidification was first addressed as a side event on the ocean. One side event brought the risks of ocean acidification to the attention in the policy document 'Hot, sour and Breathless: ocean under stress' (Turley et al. 2011 in Turley and Gattuso 2012). UNFCCC is an international treaty established in 1992 for countries to cooperatively consider what they could do to limit average global temperature increases and climate change and to cope with the impacts [3]. A recent paper by Turley and Gattuso (2012) recommends the climate change discussions in the UNFCCC COP as the best chance for the mitigation of ocean acidification, especially because ocean acidification and climate change together give a compelling rationale for CO_2 emissions reduction. IOC/UNESCO made a point in 2011 in their report 'A blueprint for ocean and coastal sustainability' that UNFCCC should include atmospheric CO_2 impacts on ocean chemistry and ecosystems (Turley and Gattuso 2012). COP18 will take place in Qatar from 26 November to 7 December 2012.

IOC/UNESCO

In 2011 the IOC/UNESCO and three other UN agencies, Food and Agriculture Organization (FAO), International Maritime Organization (IMO) and United Nations Development Programme (UNDP), launched 'A blueprint for ocean and coastal sustainability'. This inter-agency paper is a proposal to implement a number of urgent actions to mitigate and adapt to ocean acidification and to improve the management of oceans, prepared for consideration by the UN conference on sustainable development (Rio+20) in June 2012 (IOC-UNESCO, IMO et al. 2011). One action in the paper is to launch a global inter-disciplinary program on ocean acidification risk assessment, to assist countries in formulating mitigation responses and to identify regions most at risk of impact from ocean acidification (Turley and Gattuso 2012). In 2004 UNCESCO supported the first global meeting on ocean acidification, 'Oceans in a High CO_2 World', which is addressed in paragraph 3.3.2.

CBD

In 2011 the CBD became interested in ocean acidification impacts on biodiversity and published a 'Scientific synthesis of the impacts of ocean acidification on marine biodiversity'. In 2011 an expert meeting was held to develop expert review processes to monitor and assess the impacts of ocean acidification on marine and coastal biodiversity. Furthermore it was agreed that CO_2 emissions must be reduced and ecosystem resilience managed to preserve biodiversity (Laffoley and Baxter 2011). In 2012 the CBD will report on ocean acidification with respect to its impacts on marine biodiversity (Turley and Gattuso 2012).

Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES)
In April 2012 IPBES was established by UNEP, in collaboration with UNESCO, FAO and UNDP (http://www.ipbes.net/). This platforms aims to build capacity for and strengthen the use of science in policy making. IPBES will be an interface between the scientific community and policy makers. Like the IPCC it will not recommend policies, but it will conduct periodic biodiversity and ecosystem services assessments on global, regional and sub-regional level (Turley and Gattuso 2012), advocate new topics in biodiversity to policymakers such as ocean acidification and write authoritative reports on request of governments and conventions. The thematic content of the first IPBES work programme has been established in January 2012, which is a general work programme without addressing specific topics yet.

UN Commission on Sustainable Development
In June 2012 the CSD organised the Rio+20 UN Conference on Sustainable Development. Rio+20 was the 20-year follow-up to the historic Earth Summit, the 1992 UN Conference on Environment and Development also held in the same city. CSD was established after the Earth Summit to review progress at international, regional and national level in the implementations of commitments made at the Earth Summit [4]. Rio+20 was mentioned as an opportunity for policy action on ocean acidification by Turley and Gattuso (2012), because in the zero-draft declaration for Rio+20 it was proposed to implement an international observing network for ocean acidification and to work collectively to prevent further ocean acidification [5] and there were a number of side events on ocean acidification (Turley and Gattuso 2012). 'The future we want', the outcome document of the conference, calls for support to initiatives that address ocean acidification and to scientific research and monitoring of ocean acidification through enhanced international cooperation [6]. It does not specifically advise to implement an international observing network.

3.3.1.2 European policy

An EU report recently reviewed how European policy adapts to marine climate change (ICES-WGMASC 2012). The Water Framework Directive does not directly respond to the effects of climate change, but aims to obtain a 'good status' of water bodies. This iterative management system, with 6 year cycles of monitoring, assessments and planning, should be robust to responding to climate change effects. The OSPAR Commission Contracting Parties will establish ways in which to incorporate both climate change and ocean acidification considerations into future work. The Assessment and Monitoring Committee is currently taking this work forward using the latest pan European overview of climate change, produced by the European Science Foundation as one starting point to critically evaluate future science needs and to identify the 'added value' OSPAR might provide in this area. The Nature 2000 legislation, designed to protect the most seriously threatened habitats and species across Europe, also does not directly address climate change. However, directives listing the habitat types and organisms protected can adapt in response to scientific advice. An important concept of The Common Fisheries Policy is the precautionary approach. This approach may be used to adapt policy to the anticipated consequences of climate change (ICES-WGMASC 2012).

3.3.2 Research programmes and state-of-the-art research

This section provides an overview of the most important research programmes and key scientific reports and publications that together provide a comprehensive source of knowledge on ocean acidification. A turning point was at the 2004 symposium 'Oceans in a high CO_2 world'. Until that time the term ocean acidification was not widely used and scientists were primarily studying the beneficial effects of the ocean taking up CO_2 to mitigate the increased atmospheric CO_2 from human activities. At the symposium there was growing awareness of problems associated with changes in ocean chemistry due to this uptake of CO_2. In the 4 years between the first and second symposium in 2008 the number of publications on ocean acidification was more than in the preceding 55 years (Orr, Caldeira et al. 2009) and this number is increasing exponentially. State-of-the-art research on ocean acidification has been incorporated in the overview on effects of ocean acidification in section 3.2 as much as possible within the timeframe of this assignment.

3.3.2.1 Research programmes

European project on ocean acidification (EPOCA)

In 2008 the European Commission funded EPOCA (http://www.epoca-project.eu/), a 4-year project that has just come to an end, to investigate ocean acidification and its consequences in a multinational effort that includes 32 partners located in ten European countries. Four partners from the Netherlands are: NIOZ (Koninklijk Nederlands Instituut voor Zeeonderzoek), KNAW (Koninklijke Nederlandse Akademie van Wetenschappen), University of Utrecht and Vrije Universiteit Amsterdam. The research interests of EPOCA are divided into four themes :

1. "First, EPOCA aims to document the changes in ocean chemistry and geographical distribution of marine organisms across space and time. Paleo-reconstruction methods will be applied to several geological archives of foraminifera and deep-sea corals, to determine past variability in ocean chemistry (carbonate, nutrients and trace metals) and to tie these to present-day chemical and biological observations.
2. Second, EPOCA devotes much effort to quantifying the impact of ocean acidification on marine organisms and ecosystems. Key climate-relevant biogeochemical processes such as calcification, primary production and nitrogen fixation will be investigated using a large array of techniques, ranging from molecular tools to physiological and ecological approaches. Perturbation experiments are being carried out both in the laboratory and in the field. Key organisms are selected on the basis of their ecological, biogeochemical or socio-economic importance.
3. Third, the modelling component of EPOCA integrates the chemical, biological and biogeochemical impacts of ocean acidification into biogeochemical, sediment and coupled ocean-climate models. Special attention will be paid to feedbacks of physiological changes on the carbon, nitrogen, sulphur and iron cycles and in turn how these changes will affect and be affected by future climate change.
4. Finally, EPOCA assesses uncertainties, risks and thresholds ('tipping points') related to ocean acidification at molecular, cellular, organismal, local and global scales. It also assesses pathways of CO_2 emissions required to avoid the identified thresholds and describe the state change if these emissions are exceeded and the subsequent risk to the marine environment and Earth system."

Biological impacts of Ocean Acidification (BIOACID) Germany

In 2009 the 3-year project BIOACID (http://www.bioacid.de/) started, a national initiative of the German Ministry of Education and Research (BMBF), closely coordinated with EPOCA. The overarching questions of BIOACID are:

1. What are the effects of ocean acidification on marine organisms and their habitats?
2. What are underlying mechanisms of responses and adaptations on population and community level?
3. How are they modulated by other environmental stressors, and what are the consequences for marine ecosystems and ocean biogeochemical cycles?

In order to achieve the objectives of BIOACID, five thematic areas have been identified which cover the range of processes from the base of the marine food chain to the community and ecosystem level, and of mechanisms from the subcellular to the whole organism level. In view of their distinct sensitivities to ocean acidification, calcification and carbonate dissolution processes will be the focal point of a separate theme. According to these research priorities the scientific programme of BIOACID is structured under the following five themes:

Theme 1: Primary production, microbial processes & biogeochemical feedbacks.

Theme 2: Performance characters: Reproduction, growth & behaviours in animal species.

Theme 3: Calcification: Sensitivities across phyla and ecosystems.

Theme 4: Species interactions and community structure in a changing ocean.
Theme 5: Integrated assessment: Sensitivities and uncertainties.

BIOACID will pursue a multidisciplinary approach, involving over 100 scientists from 14 German universities with expertise in cell and molecular biology, microbiology, physiology, evolutionary biology, marine ecology, marine chemistry, biogeochemistry and numerical modelling. BIOACID will employ a wide range of scientific approaches and methodologies, extending from field monitoring of ocean acidification sensitive areas and ecosystems to joint mesocosm perturbation experiments, combined with closely coordinated ecosystem and biogeochemical modelling activities using parameterizations of observed biological responses and their biogeochemical implications.

Kiel Off-Shore Mesocosm for future Ocean Simulations (KOSMOS) Germany
The largest field experiment until now is KOSMOS (http://mesoaqua.eu/kiel_kosmos), an offshore study by EPOCA, involving algae and bacteria in mesocosms exposed to varying levels of CO_2. The research took place between May and July 2010, off the island of Spitsbergen in the Arctic Ocean. Daily measurements of variables affecting the 'mesocosm' were collected, such as nutrient cycling and trace-gas production by calcifying algae. The experiment was repeated in April and May 2011 off Bergen in Norway (Schiermeier 2011).

Mediterranean Sea Acidification in a changing climate (MedSeA)
In 2011 the European Commission funded the 3-year project MedSeA (http://medsea-project.eu/) which assesses uncertainties, risks and thresholds to Mediterranean Sea acidification and warming at organism, ecosystem and economic scales, as well as potential regional adaptation and mitigation strategies. MedSeA involves 16 institutes from 10 countries mainly from the Mediterranean Sea.

UK Ocean Acidification (UKOA) research programme
In 2011 the 5-year UKOA research programme (http://www.oceanacidification.org.uk/) was launched involving over 120 researchers in 26 laboratories. UKOA is funded by the British Natural Environment Research Council (NERC), the Department for Environment, Food and Rural Affairs (DEFRA) and the Department of Energy and Climate Change (DECC). The programme will collaborate with BIOACID, EPOCA, MedSeA and potentially with the emerging US ocean acidification research programme. The programme focuses on the North East Atlantic, Antarctic and Arctic Oceans and aims to deliver 7 main outputs:
1. Improve estimates of ocean CO_2 uptake and associated acidification.
2. Evaluate the impact of acidification on ocean biogeochemical processes.
3. Identify and improve understanding of the potential impacts and implications of acidification on key ecosystems, communities, habitats, and species, focussing on the continental shelf and slope.
4. Improve the understanding of the potential population, community and ecosystem impacts and implications for commercially important species.
5. Provide evidence from the paleo-record of past changes in ocean acidity and resultant changes in marine species composition and Earth System function.
6. Identify and understand the indirect impacts of decreasing pH on atmospheric chemistry and the climate system.
7. Improve the understanding of the cumulative or synergistic effects of ocean acidification on ecosystem structure and function with other global change pressures.

International Geosphere-Biosphere Programme (IGBP)
IGBP was established in 1987 as an international research programme to investigate global change. Main aim of the IGBP is to develop and coordinate international research on global-scale and regional-scale interactions between Earth's biological, chemical and physical processes and their interactions with

human systems. The programme constitutes eight projects that investigate different parts of the Earth system, which also focus on social and economic dimensions. One programme run by IGBP is Integrated Marine Biogeochemistry and Ecosystem Research (IMBER), an international project that aims to investigate the sensitivity of marine biogeochemical cycles and ecosystems to global change, on time scales ranging from years to decades, of which ocean acidification is an important component including the projects BIOACID and EPOCA. For the next ten years, IGBP will more strongly focus on socio-economic forcing and work with relevant partners to support solutions to societal transformation.

Scientific Committee on Oceanic research (SCOR)
SCOR is an international non-governmental organisation focused on promoting and coordinating international research activities. The main activity of SCOR is to facilitate international oceanographic research through promoting cooperation, for example through providing travel grants to scientists from developing nations. SCOR has formed partnerships with numerous international non-governmental and intergovernmental organisation, such as the IGBP and the IOC.

Future of Reefs in a Changing Environment (FORCE)
FORCE is an EU-funded integrated research project running until 2014, which takes an ecosystem approach, linking social and ecological aspects towards managing Caribbean coral reefs in the face of climate change. It contains 10 research projects into ecological and social processes that affect coral reef health and aims to create tools for effective coral reef management. One project studies the impacts of climate change on corals including coral bleaching and ocean acidification [12] by conducting laboratory experiments with Caribbean coral species on the combined effects of ocean acidification, increased ocean temperatures, eutrophication and current or a lack thereof (R. Osinga, pers. comm.).

3.3.2.2 Key scientific publications

'Oceans in a high CO_2 world' symposia
In 2004 and 2008 two symposia on 'Oceans in a high CO_2 world' were held and the third symposium will be held from 24-27 September 2012 in Monterey, California. The symposium offers the opportunity for the scientific community to share results and develop new research collaborations [7].
The first symposium was a turning point, because of growing awareness that the uptake of CO_2 by the oceans also had detrimental and not just beneficial effects. Papers from the first symposium were published in high-profile scientific journals (Feely, Sabine et al. 2004; Sabine, Feely et al. 2004; Orr, Fabry et al. 2005) and scientific reviews were released by the UK Royal Society (Raven, Caldeira et al. 2005), the OSPAR commission (OSPAR 2006), US federal agencies NSF, NOAA and USGS (Kleypas, Feely et al. 2006) and the German Advisory Council (Schubert, Schellnhuber et al. 2006). The second symposium most important results were that [8]:

- It was agreed guidelines were needed to standardize research methods which resulted in the EPOCA 'Guide to best practice for ocean acidification research and data reporting' by Riebesell et al. in 2010;
- Atmospheric CO_2 should not exceed 450 ppm to limit severe conditions of aragonite undersaturation in the surface waters of polar oceans;
- Shell weights of Southern Ocean foraminifera and pteropods are decreasing, which may be due to ocean acidification and that the rate of calcification of an Arctic pteropod declines at lower pH;
- Cold-water coral calcification decreases under high-CO_2 conditions;
- Increased ocean CO_2 and temperature has negative effects on larval stages of oysters, but less severe effects in oysters bred selectively to resilience to disease;
- Ocean acidification has deleterious effects on invertebrate reproduction and larval stages;
- In ecosystems with naturally high CO_2 conditions near seafloor vents, ecosystem changes generally follow expected trends based on understanding gained from laboratory perturbation experiments;
- Ocean acidification is affecting sound propagation and noise in the ocean.

‘Avoiding dangerous climate change’ symposium
In 2005 this international conference ‘Avoiding dangerous climate change: a scientific symposium on stabilisation of greenhouse gases’ (http://stabilisation.metoffice.com/) was the first time many policy advisers became aware of ocean acidification. This symposium took place under the UK presidency of the G8 with 200 internationally well-known scientists from 30 countries participating. It examined the link between atmospheric greenhouse gas concentration and the 2°C ceiling on global warming that was considered necessary to avoid the most serious effects of global warming. Previously the ceiling was a CO_2 concentration of 550 ppm that was not linked to a temperature ceiling (Laffoley and Baxter 2011).

The Royal Society
In 2005 the UK Royal Society (http://royalsociety.org) published the policy document ‘Ocean acidification due to increasing atmospheric carbon dioxide’, which provided an overview of the state of scientific knowledge of ocean acidification and its likely impacts on marine organisms (Raven, Caldeira et al. 2005) and recognized ocean acidification as a threat to many calcifying organisms with the potential to alter food chains and other ecosystem processes and to reduce biodiversity (Laffoley and Baxter 2011). The Royal Society is a self-governing fellowship of many of the world’s most distinguished scientists drawn from all areas of science, engineering, and medicine. The Society’s fundamental purpose, as it has been since its foundation in 1660, is to recognize, promote, and support excellence in science and to encourage the development and use of science for the benefit of humanity [9]. The report listed policy recommendations, including limiting the accumulation of CO_2 emissions (Laffoley and Baxter 2011).

German Advisory Council
In 2006 the German Advisory Council released ‘The future oceans: warming up, rising high, turning sour’ (Schubert, Schellnhuber et al. 2006). This document presents the effects of ocean acidification in the context of other climate change processes in the ocean. Policy makers were urged to acknowledge the role of CO_2 as an ocean hazard during future negotiations under the UNFCCC (Laffoley and Baxter 2011).

National Science Foundation (NSF), National Oceanic and Atmospheric Administration (NOAA) and the US Geological Survey (USGS)
In 2006 the report ‘Impacts of ocean acidification on coral reefs and other marine calcifiers: a guide for future research’ was released by US federal agencies NSF, NOAA and USGS (Kleypas, Feely et al. 2006). It summarised the state of the science regarding the biological effects of acidification, mainly on calcifying organisms. The report recommended research priorities and underscored the need for research to place the long term biological changes induced by acidification into a historical perspective.

OSPAR Convention for the Protection of the Marine Environment of the North East Atlantic
In 2006 the OSPAR Convention organized a scoping workshop on ocean acidification research which resulted in the report ‘Effects on the Marine Environment of Ocean acidification resulting from elevated levels of CO_2 in the atmosphere’ (OSPAR 2006).

From 2008 onwards ocean acidification regularly featured in a large number of key reports. A summary of each report is provided in the briefing paper ‘Messages for Rio+20’ from the EPOCA International ocean acidification Reference User Group (Laffoley and Baxter 2011). Key reports include:

2008: Research recommendations ‘Present and future impacts of ocean acidification on marine ecosystems and biogeochemical cycles’ by the US Ocean Carbon and Biogeochemistry program (OCB), National Aeronautics and Space Administration (NASA), NSF and NOAA;

2008: Policy document ‘Position analysis: CO_2 emissions and climate change: ocean impacts and adaptation issues’ by the Australian government;

2008: Strategy meeting paper 'The Honolulu Declaration on ocean acidification and reef management' by the Nature Conservancy and the International Union for Conservation of Nature (McLeod, Salm et al. 2008) adopted by participants of a workshop convened by the Nature Conservancy in Hawaii;
2008: 'Position statement on ocean acidification' by the European Geosciences Union, Asia Oceania Geosciences Society and the Japan Geosciences Union;
2009: 'The Monaco Declaration' by 'The ocean in a high- CO_2 world' 2008 symposium;
2009: 'Summary for policy makers' by 'The ocean in a high- CO_2 world' 2008 symposium;
2009: Introductory guide ' Ocean acidification the facts' by the EPOCA;
2009: 'IAP statement on ocean acidification' by the Interacademy panel (IAP) of over 100 national academies;
2009: 'Science-policy briefing on impacts of ocean acidification' by the European Science Foundation;
2009: 'Overview of scientific knowledge of ocean acidification related to fisheries by the FAO;
2009: 'Exploring ecosystem linkages' by the UK Marine Climate Change Impacts Partnership (MCCIP);
2009: A special issue of 'Oceanography' a quarterly journal of the Oceanography Society;
2010: 'Ocean acidification frequently asked questions' by OCB, EPOCAL and UKOA;
2010: 'Ocean acidification question answered' by EPOCA;
2010: 'Environmental consequences of ocean acidification: a threat to food security' by UNEP emerging issues bulletin;
2010: 'Ocean acidification. A national strategy to meet the challenges of a changing ocean' by the National Research Council of the US national academies;
2011: 'Southern Ocean acidification report card' by the Antarctic Climate & Ecosystems Cooperative Research Centre;
2011: The first authoritative book 'Ocean acidification' edited by Gattuso and Hansson.

3.4 Recommendations for policymakers and research

3.4.1 Policy recommendations

Ocean acidification has moved from a purely scientific subject to one of wider public interest. This move has been slow and recent, primarily because, unlike climate change, ocean acidification is invisible and it involves the use of chemical terms. This point is well illustrated by coral reefs: mass bleaching due to increased sea surface temperatures is destructive and well known, while acidification impacts are almost entirely predictions without visible component. Nevertheless, public interest has been fuelled by the potential seriousness and irreversibility of ocean acidification (Veron 2011).
Although the perception may be that that the global problem of ocean acidification cannot be addressed at local level, Kelly et al. (2011) describe policy options for the US by which local and regional governments, as opposed to federal and international bodies, can reduce 'hot spots' of ocean acidification. Suggestions include several mitigation strategies and a focus on data collection and development of biological water quality standards for acidification to assess if a water body is impaired on the basis of biological indicators. This could lead to future regulatory revisions that would allow local governments to regulate the activities of local contributors to coastal acidification.
Recommendations for policy makers from key reports as listed in paragraph 3.3.2.2 all state that the risks of significant adverse effects of ocean acidification should be taken into account by policy makers and other relevant national and international bodies at all discussions and negotiations about climate change (Raven, Caldeira et al. 2005; Schubert, Schellnhuber et al. 2006; McLeod, Salm et al. 2008). Ocean acidification adds a powerful reason, in addition to climate change, for reducing global CO_2 emissions. There is no practical way to remove this additional CO_2 from the oceans after it has been absorbed, nor a realistic way to reverse its widespread chemical and probable biological effects (Royal Society report on 'Geo-engineering the climate: science, governance and uncertainty' 2009 in Dulvy, Reynolds et al. 2011). It will take many thousands of years for natural processes to remove the excess

CO_2 and return the oceans to a level close to their pre-industrial state. Therefore the only practical way to minimise large and irreversible damage to the oceans is to reduce CO_2 emissions to the atmosphere (Raven, Caldeira et al. 2005).

Although research into geo-engineering falls outside the scope of this research, some findings from key reviews are mentioned here. Geo-engineering is the deliberate intervention in the climate system to counteract anthropogenic global warming. There are two main methods: direct carbon dioxide removal (CDR) and solar radiation management (SRM) that aims to cool the planet by reflecting more sunlight back to space . The findings of the Royal Society review in 2009 on geo-engineering were summarized by Shepherd (2012), including the climate effects, costs, risks and research and governance needs for various approaches. Key findings include: (1) Geo-engineering is not a magic bullet and not an alternative to emissions reductions. (2) Greenhouse gas emissions must remain our highest priority, but because this has proven to be difficult geo-engineering may be useful to support it. (3) Geo-engineering is very likely to be technically possible, but there are major uncertainties and potential risks concerning effectiveness, costs and social and environmental impacts. (4) Much more research is needed, as well as public engagement and a system of regulation. (5) The acceptability of geo-engineering will be determined not only by scientific and technical factors, but also by social, legal and political issues. Some methods involve release of materials to the environment, either to the atmosphere or to the oceans, in areas beyond national jurisdiction. There are therefore international implications to deploy geo-engineering methods, which require early and collaborative consideration (Shepherd 2012). Earlier studies showed that changes in geo-engineering did have secondary effects on ocean acidification Cao et al. (2007 in Gosling, Warren et al. 2011) and SRM could slow ocean acidification Matthews et al. ((2009 in Gosling, Warren et al. 2011). However, a more recent study of Williamson and Turley (2012) into ocean acidification and bioengineering concluded that some ocean-based CDR methods would relocate acidification from the upper ocean to the seafloor or elsewhere in the ocean interior. SRM might reduce the increase of atmospheric CO_2 due to preventing the net release of biogenic CO_2 in addition to anthropogenic emissions. However, ocean acidification would continue to be driven by increases in atmospheric CO_2 and SRM could have two other indirect effects. First, SRM-induced changes in light could affect primary production of phytoplankton and ocean chemistry. Second, ocean acidification could be slightly exacerbated if sulphate aerosols were used for SRM due to their effect on precipitation pH (Williamson and Turley 2012).

Ocean acidification will be substantially addressed in the IPCC Fifth assessment report due in 2013-2014 (Turley and Gattuso 2012). A review of the developments since the IPCC Fourth assessment report (Gosling, Warren et al. 2011) concluded that methodological inconsistencies make it impossible to state the magnitude of ocean acidification impacts on marine organisms with a higher degree of confidence than the medium confidence given by the 4^{th} assessment report. The IPCC workshop report on ocean acidification (IPCC 2011) made a synthesis of current scientific understanding of ocean acidification effects on three levels: ocean chemistry, organism level and ecosystem level.

More specific policy recommendations of The Royal Society (Raven, Caldeira et al. 2005) included:

- Targets for CO_2 emission reductions should take into account the impacts on climate change as well as ocean acidification and should be considerably less than 900 Gt carbon by 2100;
- Ocean acidification and its effects need to be taken into account by the IPCC (and perhaps the UNFCCC) and need to be kept under review by international scientific bodies such as the Intergovernmental Oceanic Commission, the Scientific Committee on Oceanic research and the International Geosphere-Biosphere Programme. This cannot be done by any country alone and it is recommended that the UK takes a lead on international policy and research by developing and extending its research and international scientific networks;

- Additional investment is required for research in to ocean acidification. The scale of internationally coordinated research and monitoring should be similar to that on the effects of climate change. The necessary funding should be additional and not be diverted from research into climate change;
- Research should address the effects on sensitive organisms, functional groups and ecosystems, focus on getting a better understanding of various metabolic processes at different parts of the life cycle and how these effect ecosystems. Research needs to include global monitoring, laboratory, mesocosm and field studies, and models at different pH scales, linked to climate change models to predict synergistic impacts;
- The increased fragility and sensitivity of marine ecosystems as a result of environmental impacts (not only ocean acidification, but also climate change, deteriorating water quality, coastal deforestation, fisheries and pollution) need to be taken into consideration when developing policies related to their conservation, sustainable use and exploitation.

Recommendations for policy makers from the German Advisory Council report (Schubert, Schellnhuber et al. 2006) include specific policy- and management options:
- Create Marine Protected area (MPA) for coral reefs and fish nursery grounds, ecosystem approach;
- Stop fisheries subsidies, levy charges on shipping and earmark revenues, micro insurance, divert emergency relief to preventive action;
- Strictly regulate mining of methane hydrate, because naturally methane is stable under high pressure and low temperature, so global warming makes gradual release possible;
- Engineering approaches such as liming are not feasible in the ocean;
- Improve understanding of anthropogenic disturbance, biodiversity and resilience;
- Do research into the consequences for biogeochemical cycles and ecosystem services;
- Ensure pH does not drop with more than 0.2 below pre-industrial average.

The Honolulu declaration on ocean acidification and reef management, as prepared and adopted by 14 scientists of The Nature Conservancy and universities in the USA and Australia, gives policy- and management recommendations for coral reef ecosystems. Policy recommendations include (McLeod, Salm et al. 2008):
- Focus conservation efforts on the reduction of all anthropogenic stresses to enhance ocean ecosystem health and resilience, as chances of survival are better if the pressures of ocean acidification and not combined with other threats;
- Reduce land-based sources of pollution and inputs of nitrogen and sulphur oxides and ammonium compounds that contribute to lowering pH in coastal and ocean water;
- Mandate the inclusion of climate change into MPA management plans to address ocean acidification, sea temperature and sea level rise as these management plans are routinely developed or revised. Specific actions are specified in the management recommendations of the Honolulu declaration;
- Expand the content of ocean acidification in the IPCC 5th assessment report due in 2013-2014;
- Establish a coordinated international program on coral reef acidification to link government agencies, research institutions, NGOs and coral reef managers, building on existing structures.

The economic valuation study of Brander et al. (2009) estimated ocean-acidification-induced coral reef loss adds 10% to the total impact of climate change and recommended to include ocean acidification into climate change policy interventions from an economic perspective.
- First, because ocean acidification changes the trade-offs between the reduction of greenhouse gasses. Since ocean acidification is exclusively driven by CO2 as opposed to climate change which is also caused by other greenhouse gases, there are additional cost associated with CO2 emissions.
- Second, because ocean acidification changes the dynamics of optimal emission control and makes the discount rate less important. Reason is that absorption of CO2 by the oceans and ocean

acidification occur over short time scales while atmospheric temperature increase lags behind the increase of greenhouse gasses.

- Third, because ocean acidification changes the instrument choice for the potential solution to climate change such as the Pigouvian tax required to achieve efficient greenhouse gas emissions (Tol 2005 in Brander, Rehdanz et al. 2009). Climate change may be countered by geo-engineering such as sulphur particles to cool the planet (Schelling 1996 in Brander, Rehdanz et al. 2009), but ocean acidification will continue unabated or may even accelerate.

A specific recommendation of this report is to estimate the economic loss from ocean acidification for the coral reefs in the Netherlands Caribbean, which based on its coral reef area of 250 km^2 (Brander, Rehdanz et al. 2009) can presumably be derived from the study of Brander et al. (2009) and the valuation studies currently taking place and commissioned by EL&I in the Netherlands Caribbean (Wolfs 2011).

From a marine fisheries and aquaculture perspective policy- and management measures to minimize negative combined effects of ocean acidification and climate change should:

- Fully consider the implications of climate and ocean change which are threatening the effectiveness of fisheries management measures and international fisheries agreements (Cheung, Pinnegar et al. 2012). Ocean acidification cannot be changed by fisheries management, but negative effects can be reduced.
- Make fishery resources more robust to climate and ocean change by minimizing other non-CO2 related stressors from overfishing, habitat degradation, pollution and other anthropogenic factors. Rebuilding over-exploited fish populations, minimizing loss of genetic diversity and improving habitat quality will result in more productive fish stocks, higher biodiversity and higher resilience and adaptive capacity to climate and ocean change (Cheung, Pinnegar et al. 2012).
- Incorporate shifts in species abundance and distributions by for example larger networks of marine protected areas to ensure effective conservation of spatially shifting and/or more variable resources under climate change, including ocean acidification. This accommodates migrating populations, shifts of spawning populations outside the boundaries of protected area and uncertainty about the effects of climate and ocean change. Marine protected area and no-take zones also act as control sites for long-term monitoring programmes (Cheung, Pinnegar et al. 2012).
- Not delay climate change mitigation and adaptation policy actions because of scientific gaps, because it is already known that reduced greenhouse gas emissions limit impacts of climate and ocean change on fisheries and other sectors (Cheung, Pinnegar et al. 2012). The fisheries sector itself can only play a small part in reducing CO2 emissions to mitigate against future climate change (Dulvy, Reynolds et al. 2011; Cheung, Pinnegar et al. 2012). The global marine fishing fleets are estimated to burn 1.2% of global annual fossil fuel use, equivalent to that consumed annually by The Netherlands (Tyedmers et al. 2005 in Dulvy, Reynolds et al. 2011).
- Improve education and communication within the fishing industry about climate change to make climate change mitigation and adaptation policies more effective. The fishing sector should also contribute to reducing greenhouse gas emissions (Cheung, Pinnegar et al. 2012).
- Develop a decision-making processes for mitigation of shellfish aquaculture impacts and a proactive strategy for adaptation (ICES-WGMASC 2012).

3.4.2 Research priorities

The EPOCA 'Guide to best practice for ocean acidification research and data reporting' (Riebesell, Fabry et al. 2010) is a good bridge between science and policy, because the recommendations for future research take into account the needs for policy makers and ecosystem managers. The research needs for policy makers include:

- Effective communication of research results with policymakers, to increase the impact of ocean acidification science in the development of climate adaptation policy. Effective communication can be achieved through standardisation of atmospheric CO2 levels and use of this standard and realistic levels in perturbation studies. Standardisation aims to increase comparability among studies, to provide a clear link to atmospheric targets relevant to climate policy development and to develop coherent recommendations for policymakers. Effective communication also requires that all relevant information is available and accurately reported, for which guidelines on data reporting are provided;
- A key method for synthesising information into a useful format for policymakers are predictive models. The EPOCA guide acknowledges that models pose a problem and use of model results by policymakers requires some care, because prediction of the carbonate chemistry response is robust, but predicting ecosystem response is at a very early stage. Because of variable predictions models can also create uncertainty, which undermines the speed with which climate change became globally recognized;
- Identification of potential ecological tipping points for atmospheric CO2 levels, which can be crucial for climate policy development and for increased awareness to the potentially non-linear response of ecosystems to climate change.

The most important research priorities identified at the 2008 symposium 'Oceans in a high CO_2 world' included the following [7]. For a more detailed summary is referred to Orr et al. (2009).

- improving international coordination to facilitate agreements on protocols, methods, and data reporting and to optimize sharing of materials, facilities, expertise, and data;
- developing strong links with end-users of ocean acidification research results, in order to guide information and product development and to better disseminate this information to appropriate audiences;
- scaling-up understanding of biological responses of individual organisms to meaningful predictions how ocean acidification will affect food webs, fisheries, and tourism;
- developing easy-to understand information that would be particularly useful to end-users, such as simple indicators of change and thresholds beyond which the ecosystem will not recover;
- integrating results from ocean acidification research, which is a different research community than for climate change and still in its infancy, into the IPCC process and UNFCCC negotiations that are aimed at reducing CO2 emissions.

To date some of these research priorities still seem valid, although the first priority was achieved in 2010 with the EPOCA 'Guide to best practice for ocean acidification research and data reporting' (Riebesell, Fabry et al. 2010). A recent review of ocean acidification perturbation studies by Hoppe et al. (2012) concluded that there are still inconsistencies in calculated parameters in the carbonate system such as pCO_2 and saturation states with implications on the interpretation and comparability of perturbation studies. De Vries et al. (in press) did a meta-analysis of *in vitro* laboratory experiments to get a species sensitivity distribution to ocean acidification. Based on this meta-analysis there is still a need to standardize test protocols, use uniform methods such as the unit and measure of exposure. However, research on coral responses to ocean acidification has adopted the EPOCA guide (R. Osinga, pers. comm.). Scaling up of *in vitro*, short-term, rapid perturbation experiments on isolated elements of the ecosystem to *in situ,* long-term effects on food webs and ecosystems has progressed through *in vitro* and *in situ* mesocosm studies (e.g. KOSMOS), but according to our knowledge not through ecosystem perturbation studies. For this, increasing focus is given to regions with natural high CO_2 conditions that serve as *in situ* laboratories which allow for analysing the long-term consequences of ocean acidification (e.g. for coral reefs see Fabricius et al. 2011). Russell et al. (2011) proposed to conduct a more integrated research approach that includes macroecology, experimentally derived data and modelling that incorporates energy budgets in life cycle models. These kind of studies will allow for a better interpretation of results obtained during experiments using several parameters to test the impact of ocean acidification and the few experiments done with species that are difficult to keep alive under laboratory conditions.

From a fisheries perspective knowledge gaps exist on:

- more informed ecological models to scale up from laboratory experiments to populations and to consequences for fisheries. This includes improving global climate models such as those used by the IPCC to regional and local scale relevant to important biomes and fisheries, a better understanding of the energy flow along food chains from primary productivity to fish and fisheries, an improved understanding of adaptation and species interactions in marine food webs, and a better understanding of adaptive capacity of the fisheries sector to change (Cheung, Pinnegar et al. 2012).
- the sensitivity of crustacean species to ocean acidification, and the consequent uncertainty in the long-term sustainability of the lobster fisheries (Cheung, Pinnegar et al. 2012), which is a potential issue of concern for the lobster fisheries at the Saba bank.
- the sensitivity of early life stages of fish and physiological effects of ocean acidification.

From an aquaculture perspective knowledge gaps exist on:

- Studies on the effects of climate change and ocean acidification on commercially cultured shellfish species, and particularly their sensitive early life stages. Research priorities include sensitivities to perturbations under ecologically relevant conditions (i.e. exposure to predicted food web interactions), cumulative effects of warming and acidification and the capacity of key species to acclimatize and/or genetically adapt to climate changes (ICES-WGMASC 2012).
- Assessments of regional susceptibilities for aquaculture impacts and the socio-economic consequences, given that climate change scenarios related to temperature, precipitation, storms and deep water upwelling of acidic water vary across countries (ICES-WGMASC 2012).

3.4.3 Coral reef agenda

The coral reef research agenda has moved along with the research recommendations as listed in the previous paragraphs (1) from organism level to ecosystem level (2) from perturbation studies to mesocosm and *in situ* studies (2) from single stressor to multiple stressor effects. This is evident from the agenda at the International Coral Reef Symposia (ICRS). Was the focus at the ICRS 2008 in Florida USA still on species, the ICRS 2012 in Cairns Australia focussed on combined effects of ocean acidification and warming sea surface temperatures. Also the EU call FP7-ENV-2013 , following EPOCA that has come to an end in July 2012, calls for research proposals on multiple stressor effects. Under section 6.1.1 'climate related ocean processes and combined impacts of multiple stressors on the marine environment' will be funded [14]. Not only global stressors but also local stressors should be taken into account, such as fisheries, nutrient enrichment and current patterns (R. Osinga, pers. comm.).
The ICRS is the largest coral reef conference, which is held every four years. ICRS 2012 was attended by 2500 scientists from 80 countries. All agreed that reefs around the world are in trouble. Together these scientists issued a consensus statement urging governments to take action for the preservation of coral reefs for the benefit of present and future generations. Increased acidity was mentioned as one of the major threats, impairing calcification of corals and reef growth. Action should be taken by reduction of carbon dioxide and other greenhouse gases emissions, as well as by improved local protection of coral reefs [13]. Actions on a local scale matter, from safeguarding reefs from pollution and destruction to sustainable fisheries and proper use of its coastal resources [12].

Over half of the publications about ocean acidification are about coral reefs (Veron 2011). Calcification of tropical reef-building corals has been well studied in laboratory and mesocosm experiments, but not in *in situ* field experiments under 'natural' conditions (Guinotte and Fabry 2008). Very few *in situ* field studies have emerged since then, although a number of studies were presented at the ICRS 2012. A distinction can be made between *in situ* observations, *in situ* controlled experiments and natural experiments such as at CO2 vents. The latter relates to often extreme pH variations associated with high-CO2 vents in the Mediterranean (Hall-Spencer et al., 2008) and Papua New Guinea (Fabricius et al. 2012 in [10]). The only *in situ* field experiment is the Coral-Proto Free Ocean Carbon Enrichment System (CP-FOCE) at the Great Barrier Reef in Australia. The CP-FOCE experiments since December 2009 with realistic pH scenarios in a natural setting with ecosystem interactions, whereby lowered pH varies according to the natural environmental conditions such as diel and seasonal changes instead of experimenting with a constant pH. The study concludes this first *in situ* study demonstrates the ability to alter the seawater carbonate chemistry and simulate ocean acidification conditions. It recommends the method can be used in a variety of habitats and can offer insights of the biological impacts from species to ecosystems (Kline, Teneva et al. 2012). The *in situ* field observations are more numerous, such as the Atlantic Ocean Acidification Test Bed (AOAT) in Puerto Rico (Moyer et al. 2012 in [10]), the Bermuda ocean acidification and coral reef investigation (BEACON) (Bates et al. 2012 in [10]), field monitoring efforts by NOAA in US affiliated pacific islands (Young et al. 2012 in [10]) and *in situ* observations across tropical oceans with natural gradients in ocean acidification (Cohen et al. 2012 in [10]. BEACON and AOAT provide a natural laboratory to autonomously measure seawater chemistry and calcification and monitor interactions and feedbacks between seawater chemistry and benthos in reef and seagrass habitats. AOAT decoupled seasonal patterns in aragonite saturation state from subtle changes in soft coral and calcareous algae abundance and investigation into the relationship between algal abundance and ocean chemistry is ongoing (Moyer et al 2012 in [11]). BEACON observed highly seasonal variation in seawater pCO_2 driven by seasonality in temperature (~8-10°C) and coral calcification rates that induces a strong flux of CO_2 from the ocean to the atmosphere (Bates et al. 2012 in [10]). Ocean Acidification Flow Thru Experimental Raceway Units (OAFTERU) which are land-based seawater systems similar to mesocosm studies (Crosby et al. 2012 in [10]).

A debate in ocean acidification research currently is whether ocean acidification matters, with conflicting opinions between scientists. One group considers ocean acidification a serious threat and another group argues increasing sea surface temperatures will have such a detrimental impact that ocean acidification does not matter and is only used as a means to justify continuous research and to get funds (R. Osinga, pers.comm.). For example Byrne (2011) who reviewed marine invertebrate tolerance to ocean warming and acidification and argued that if the bottleneck for species is embryonic thermal tolerance, then embryos may not reach the calcifying stage and the effect on calcification due to acidification may not be relevant. An example of a counter-argument is that ocean acidification is the assassin of deeper reefs at 10-20 meter depth. At these depths corals are less susceptible to coral bleaching due to ocean warming, but more susceptible to ocean acidification which does occur at these depths (R. Osinga, pers.comm.).

3.4.4 Discussion partners

Key discussion partners to involve in a dialogue on how to include ocean acidification at the Dutch policy agenda were identified. These initial discussion partners were selected based on the relevance of their research topics for the Netherlands and Caribbean Netherlands and/or based on their ability to give strategic advice on relevant research topics and how to include ocean acidification in EL&I programs and other funding sources of the Dutch government. The following discussion partners are proposed:

Ronald Osinga is researcher at Wageningen University on invertebrate biology and biotechnology of corals and sponges. He is an expert in controlled aquarium and mesocosm research, was chair of the organising committee of the European Conference of the International Society for Reef Studies (ISRS) in December 2010 in Wageningen and is involved in the FORCE project 'impacts of climate change on corals' researching multiple stressors on Caribbean corals including ocean acidification [12]. Ronald Osinga expressed his interest to participate in this initiative of EL&I.

Hein de Baar is a professor at Rijksuniversiteit Groningen in Oceanography and head of Biological Chemical Oceanography Group at the Royal Netherlands Institute for Sea Research (NIOZ). His main research interests comprise climate regulation, the ocean carbon cycle, in particular the Southern ocean, in combination with phytoplankton ecology and trace metal limitation. He has been involved in various national and international programmes, such as CARBOOCEAN, and has led several scientific expeditions.

Gerald Ganssen is head of the sub-department Marine Biogeology at the Vrije Universiteit Amsterdam. His main research activity involves the impact of climate change and ocean acidification on marine ecosystems. He is involved in various research programmes on ocean acidification, such as EPOCA. Gerald Ganssen is the former president of the European Geosciences Union and presently a member of several national and international scientific committees and programmes dealing with paleoceanography, modern and past climate and global change in research, training and outreach.

Jaap Kaandorp is associate professor at the Section Computational Science of the Faculty of Mathematics, Computer Science, Physics & Astronomy of the University of Amsterdam. He works on research projects modelling calcification and growth in corals.

Jelle Bijma is a Dutch biogeochemist working at the Alfred Wegener instituut in Bremerhaven Germany doing polar research. He is involved in the Helmholtz research programme PACES (Polar regions and coasts in a changing Earth System) and investigating organisms and their changing role in marine ecosystems due to ocean warming and acidification as part of the first research topic 'The changing Arctic and Antarctic' [15].

Jean-Pierre Gattuso is research professor at the Laboratoir d'Oceanographie de Villefranche. His main research activity relates to the cycling of carbon and carbonate in coastal ecosystems. More recently he focused on the response of marine organisms and ecosystems to ocean acidification. He published his first paper on this topic in 1998 and edited the first authoritative book on ocean acidification, published in 2011. He is the scientific coordinator of EPOCA and co-editor of the 'Guide to best practice in ocean acidification research and data reporting' [16].

Ulf Riebesell is research professor at the Helmholtz Centre for Ocean Research in Kiel Germany who published mostly on planktonic research. In 2012 he received the Leipzig Prize of the German Research Foundation for his research on the effects of global change on marine ecosystems. He is chair of the organising committee of the 'Oceans in a high-CO_2 world' symposium and member of several European and US research programmes and committees, such as EPOCA, BIOACID, UNESCO-IOC, the US National Research Council (NRC) and the Natural Environment Research Council (NERC) [17].

Carol Turley is senior scientist at Plymouth Marine Laboratory. Her research mainly focused on biogeochemical cycles, and over the last 7 years she has been intensely involved in ocean acidification. In recent years she also worked on the socio-economic and policy implications of ocean acidification (Turley, Eby et al. 2010; Turley and Gattuso 2012). She lead or contributed to various programmes and reports, such as the UK Government (DEFRA) review on impact of pH change on the marine environment, was a lead author on the 2007 IPCC 4th assessment report and is a member of The Royal Society working group on ocean acidification.

Katrin Rehdanz is assistant professor for environmental and resource economics at the Christian-Albrechts University of Kiel associated with the Kiel Institute for the World Economy. Her main areas of research are environmental and climate policies research, global environmental problems, sustainable development, computable general equilibrium modelling. She was second author in the publication of Brander et al. (2009). Furthermore she is the coordinator and principal investigator of several research programmes focusing on ecosystem services and social issues relating to change climate and implementation of environmental regulations.

4 Conclusions and recommendations

Ocean acidification is an emerging topic on the international research agenda and on the policy agenda, either exclusively or as part of climate change. The IPCC 5th assessment report due in 2013-2014 is expected to address ocean acidification substantially. In preparation of this report an IPCC workshop on ocean acidification was held in 2011 in Japan, where 82 participants, including many renowned ocean acidification scientists, synthesised scientific understanding of ocean acidification effects on organisms, ecosystems and ecosystem services. The IPCC does not recommend policy. The UNFCC is recommended as the best chance for policy and decision-making to mitigate and adapt to ocean acidification (Turley and Gattuso 2012), with their next COP18 coming up in November 2012 in Qatar. UNESCO-IOC is contributing to the policy agenda, for example with their inter-agency paper 'A blueprint for ocean and coastal sustainability' which recommended policy and management measures as preparation for the Rio+20 UN conference in 2012 in Brazil. UNESCO also supported the first global meeting on ocean acidification in 2004. This 1st 'Oceans in a high CO_2 world' symposium was a turning point, because of the global awareness that the uptake of CO2 by the oceans also had detrimental and not just beneficial effects. It was followed by a large number of acknowledged papers and scientific reviews from 2005 onwards. In the 2nd 'Oceans in a high CO_2 world' symposium in 2008 agreement was reached on the need for standardization, which resulted in the 'Guide to best practice for ocean acidification research and data reporting' by Riebesell et al. in 2010. In 2012 at least three global symposia will address or have addressed ocean acidification: the 3rd 4-yearly 'Oceans in a high CO_2 world' symposium, which will be held from 24-27 September in Monterey USA; the 12th 4-yearly International Coral Reef Symposium, which was held in July in Australia and the 5th 3-yearly International Symposium on Deep-Sea Corals, which was held in April in Amsterdam. Ocean acidification was one of the themes on the latter two symposia. There are numerous international research initiatives, of which the main large-scale European initiatives are listed in this report. EPOCA was the first large EU-funded research program running from 2008-2012 in which four Dutch research institutes took part. A new EU call is currently open for submission of proposals on multiple stressors in the marine environment. Ocean acidification research proposals have been submitted by well-established researchers, including Gattuso, Riebesell and Bijma (Osinga, pers.comm.). Worth mentioning is another EU-funded research program which focusses on managing Caribbean coral reefs in the face of climate change. Ocean acidification research is taking place by five researchers from universities in Mexico, Israel and Wageningen as part of the climate change project (Griffith-Mumby, pers.comm.).

Most publications about ocean acidification are less than a decade old (Veron 2011). Scientific research into the effects of ocean acidification can broadly be divided in three topics, which are the effects on ocean chemistry, effects on organism level and effects on ecosystem level. Ocean chemistry is well-understood and largely predictable, unlike the uncertainty on biological responses of organisms which vary between and within taxa and the even larger uncertainty on ecological responses of populations, communities and ecosystems.

Effects on ocean chemistry in the surface oceans due to the uptake of increased atmospheric CO_2 , which increases the partial pressure of CO_2 and decreases the surface ocean pH and calcium carbonate saturation states, are generally well-understood. Future changes in carbon chemistry based on realistic scenarios of atmospheric CO_2 are largely predictable, although there is a need that models include not only surface and open oceans, but also subsurface and coastal waters.

Effects on organism level can be divided in effects on microbes and microbial and biogeochemistry processes, phytoplankton and calcification and photosynthetic processes, calcification and dissolution of corals and coralline algae, calcification an dissolution of other calcifying invertebrates, and physiological effects on other invertebrates and fishes. It is apparent that there is significant variability in the sensitivity of the calcification response between calcifying organisms

Scientific research is currently shifting from short-term culture experiments to the development of longer term experiments that allow for evaluating mechanisms of adaptation. Furthermore, numbers of field studies are increasing, during which locations with naturally high CO_2 concentrations, such as upwelling regions and underwater volcanoes, are regarded to be representative of actual impacts of ocean acidification. These studies, in combination with increasingly detailed studies of geological record, may provide new insights into the effect of ocean acidification on marine ecosystems.

Although ocean acidification is an invisible anthropogenic pressure on ecosystems, for policymaking it is recommended to include ocean acidification as 'the other CO_2 problem' in all discussions and negotiations about climate change, because it adds a powerful reason for the reduction of global CO_2 emissions and because there are no solutions to remove CO_2 already absorbed by the oceans and to reverse the chemical and biological effects. Geo-engineering measures such as carbon dioxide removal and solar radiation management may support emission reductions, but are not an alternative to it. Besides, much more research is needed into major uncertainties and potential risks of geo-engineering. Meanwhile, scientific gaps should not be an excuse to delay climate change mitigation and adaptation policies. Although ocean acidification is a global problem, it is recommended to incorporate local pressures and local measures into policy action. Minimizing local and non-CO_2 related stressors from habitat degradation, pollution, overfishing and other anthropogenic factors helps to make ecosystems and its resources more robust and resilient to climate and ocean change (Cheung, Pinnegar et al. 2012). This can be achieved through local measures to monitor, regulate and reduce these stressors, as well as with conservation measures.

Aquaculture, particularly shellfish, is an important economic activity in The Netherlands. Research shows that certain shellfish species are vulnerable to ocean acidification. Research into selective adaptation or species-specific resilience to ocean acidification will help the aquaculture sector to identify species that are able to cope with high-CO_2 conditions or selectively culture more resilient species. A review of the potential threats, mitigation strategies and opportunities of ocean and climate change for the Dutch fisheries and aquaculture sectors is recommended, similarly to the impact studies carried out in the UK. These studies were commissioned by the Marine Climate Change Impact Partnership (MCCIP), a co-ordinating body in the UK which aims to transfer knowledge of impacts and guidance on adaptation to policy advisors and to communicate complex issues to a wide range of stakeholders-makers [18].

The Dutch coastal waters contain two fragile systems that might suffer negative impacts from increasingly acidified waters. As mentioned above, aquaculture in the Delta and Waddenzee may be at risk. In addition, the tropical coral reefs of the Caribbean are ecosystems particularly threatened by ocean acidification and the islands of the Caribbean Netherlands are largely dependent on the ecosystem goods and services provided by coral reefs. This includes fisheries, tourism, recreation and less tangible benefits such as coastal protection, habitat provision and cultural services. It is recommended to consider expanding the valuation study of Wolfs (2011) which is currently taking place in the Netherlands Caribbean, by estimating the economic loss from ocean acidification for the coral reefs in the Netherlands Caribbean, using the methodology of Brander et al. (2009). Furthermore a recent study by Unsworth et al. (2012) shows that seagrass may mitigate the effects of ocean acidification through modifying the marine carbonate system through uptake of CO_2. This is another ecosystem service of seagrass beds, in addition to habitat provisioning, sediment stabilisation and primary productivity, which gives an additional justification for the restoration and protection of seagrass habitats. Besides the mitigating capacity of seaweed, marine aquaculture of seaweed such as sea lettuce (*Ulva lactuca*) is another possibility to mitigate the effects of ocean acidification [19].

Key discussion partners to involve in a dialogue on ocean acidification research topics and policy action for the Netherlands and Caribbean Netherlands were identified. Recommended discussion partners are Ronald Osinga for coral reef research in the Caribbean, Jelle Bijma for polar research, Hein de Baar for biological and chemical oceanography, Jaap Kaandorp for modelling, Gerald Ganssen, Jean-Pierre Gattuso and/or Ulf Riebesell for their (key) role in EPOCA and other large-scale european research programmes, Carol Turley for socio-economic and policy implications and Katrin Rehanz for economics and ecosystem services.

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Quality Assurance

IMARES utilises an ISO 9001:2008 certified quality management system (certificate number: 57846-2009-AQ-NLD-RvA). This certificate is valid until 15 December 2012. The organisation has been certified since 27 February 2001. The certification was issued by DNV Certification B.V. Furthermore, the chemical laboratory of the Environmental Division has NEN-AND-ISO/IEC 17025:2005 accreditation for test laboratories with number L097. This accreditation is valid until 27 March 2013 and was first issued on 27 March 1997. Accreditation was granted by the Council for Accreditation.

Justification

Report C116/12
Project Number: 430.87010.11

The scientific quality of this report has been peer reviewed by a colleague scientist and the head of the department of IMARES.

Approved: Dr. T. van der Hammen
Researcher

Signature:

Date: 17-10-2012

Approved: F.C. Groenendijk, MSc.
Head of Department

Signature:

Date: 18-10-2012