We manage land and the coasts for carbon – so why not the ocean as well?

IUCN GLOBAL MARINE AND POLAR PROGRAMME
The Significance and Management of Natural Carbon Stores in the Open Ocean

We manage land and the coasts for carbon – so why not the ocean as well?
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(clockwise from top): Antarctic (John Weller); globally distributed coccolithophore *Emiliania huxleyi* (Gustaaf Hallegraeff UTAS); floating Sargassum sp. in the Gulf of Mexico (Sylvia Earle); shell of the foraminifera *Globigerina bulloides* (Andrew Moy AAD); and adult Antarctic krill (Rob King).

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In 2009 IUCN published a now landmark report\(^1\) that synthesized a significant quantity of new scientific information on coastal ecosystems containing rich, stored carbon resources. At that time we stressed the need for prudent management to ensure that the carbon trapped in these ecosystems remains there – thus serving the triple objectives of mitigating carbon emissions, protecting nature, and supporting livelihoods that depend on such intact ecosystems. This led to global recognition and renewed efforts around the world to safeguard these ecosystems on land.

The question then remains – what about the other half of planet Earth - the open ocean - which is frequently referred to as the largest carbon sink on Earth? In this report we highlight the carbon-critical role of the open ocean by explaining how the system works, and then illustrating the criticality of managing carbon in the sea - as on land - using a number of case studies. Our aim is to bring scientific knowledge together in a way that shows the open ocean in a new light, in a new important context but one with wide resonance, in order to stimulate a global debate on improving the management and protection of the ocean and at the same time ensure the stability of the vast stored carbon resources.

The 2009 report showed that when damaged or destroyed, coastal habitats reduce or stop fixing carbon and can release significant amounts of carbon dioxide (CO\(_2\)), derived from the carbon in the living vegetation or below in the sediment, back into the air. Coastal habitats differ from the more readily-recognized terrestrial carbon sinks, such as forests, because they store a higher volume of carbon per unit area, and in some circumstances they are much less affected by emissions of other powerful greenhouse gases, such as methane. There is now consensus that recognition of this so-called coastal “blue carbon” is a major driving force for changes to improve the management, conservation and restoration of coastal ecosystems.

In this current report we set out to answer a series of equally critical questions for the open ocean. What and where are these open ocean carbon sinks or pools? Are we already impacting them through the consequences of our activities, and is it possible to better manage them to help mitigate against climate change? Does any of this affect how we might seek to mitigate climate change? Is management action even possible, and if so what modifications to human uses of the ocean are needed? Through these questions and others, we would like to stimulate a discussion on the role of oceanic blue carbon in mitigating climate change, just as the 2009 publication did for coastal ecosystems.

It is hoped that this report will add an ocean voice and scientific substance to the urgent need to drastically cut anthropogenic carbon emissions coupled with a twin track approach of rebuilding and sustaining resilience in ocean ecosystems. This could be through, for example, strictly enforced marine protected areas (MPAs) and making our uses of the ocean more truly sustainable, whilst factoring the carbon role of ecosystems and species into day-to-day management, impact assessments and decision making.

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The Significance and Management of Natural Carbon Stores in the Open Ocean

This report focuses on the open ocean, which is often referred to in the literature as the largest carbon sink on Earth. The report has been produced to promote better understanding of how atmospheric carbon is captured, stored and mobilized in the ocean, and how this has a significant bearing on sustainability, the welfare of people, and the future scale and intensity of climate change and ocean acidification. Whilst there has been a significant effort on managing carbon in natural environments on land in places such as forest and peatlands, we have been largely ignoring the ocean that is now responding to the full impact of the consequences of our activities.

The report sets out the importance of carbon in the open ocean and, through examples, illustrates the significance and values of some of its major carbon pools and sinks. This analysis ranges from microscopic organisms in the plankton that drive the biological pump, which take CO$_2$ out of the air and ultimately trap a proportion of solid carbon permanently in the sediments of the deep ocean, through to groups of animals, which perhaps hitherto have not been considered as very relevant in carbon management, such as krill and fish – and in so doing introduces the notion of 'mobile carbon units'. The report ranges in its attention from the surface waters, where carbon capture is powered by photosynthetic activities, through to the deep ocean. It describes the role and importance of deep sea microbes, and the recently discovered, increasingly important chemosynthetic pathways through which carbon is converted in the deep dark ocean to organic matter.

Often the science is incomplete and sometimes aspects are missing, with important topics yet to be fully investigated, but we already know enough at a broad level to recognize the significance of these ocean carbon processes, pools and sinks. The sheer geographical scale of the world ocean is such that the carbon pathways and pools are very significant and highly relevant to discussion on carbon management and climate change – and that is what now needs to happen. We know human pressures on the open ocean are growing – aside from familiar pressures like pollution and fishing, the International Seabed Authority has now entered into eleven 15-year contracts with nations leasing an area for deep sea mining more than twice the size of Germany\(^1\) – so the need for action and proper assessment and management is all the more urgent.

Evidence from ecosystem and species case studies in this report underlines the importance of retaining the nature and resilience of the ocean and of respecting the open ocean carbon processes by highlighting the unprecedented changes we believe we are now making to them. There are a number of recommendations that therefore naturally flow from this report:

- Urgent action is needed to address ocean carbon and protect the systems that regulate planetary processes – the essential role of mitigation of CO$_2$ is demonstrated through the case studies in this report, and the urgency illustrated by views across all case studies that our use and abuse of the ocean will alter the status quo in carbon management.
- Further analysis and research is needed to further develop the analysis presented in this report - just like IUCN’s original report in 2009 on coastal carbon sinks this report is only the beginning, and further work both technically and politically is needed.

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Limits on time and resources meant that issues such as the carbon role of large vertebrates or the benthos could not be covered. More research is also needed to understand how ocean acidification not only affects calcification, but how it (perhaps in turn) affects photosynthesis, and hence primary productivity in the ocean. The focus in this report is mainly on calcification processes in calcifiers, whilst research on these other impacts is needed to help clarify the current uncertainties around open ocean carbon pool quantification.

- Ocean carbon issues need to be addressed through international climate policy routes such as the UNFCCC to develop new processes and strengthen relevant existing measures.
- An Implementing Agreement is needed under the UN Convention Law of the Sea to secure a proper conservation and management framework for the High Seas – through which relevant supporting measures for ocean carbon could be taken.
- Sectoral ocean management bodies need to recognize and address ocean carbon budgets and undertake full environmental assessments of their activities – for example regional agreements such as CCAMLR and entire extractive industries such as capture fisheries and krill fisheries and the algal harvesting sector need to include carbon into their day-to-day decisions and activities to improve their ecosystem management.

The core message is that the significance of carbon processes, pools and sinks in the open ocean now need to be centrally factored into decision making at all scales – from global policy issues on climate change, through to resource management at sectoral (e.g. fisheries) and national levels, and even as a criterion in the selection of prospective MPAs. Unless there is a greater appreciation and action on the role and importance of ocean carbon systems it is more than probable that efforts to avoid dangerous climate change risk reducing carbon dioxide only by enough to stabilize Earth’s surface temperature, rather than the more aggressive cuts in emissions needed to tackle issues such as ocean acidification. Factoring in ocean carbon processes and issues such as tackling ocean acidification will require much more dramatic cuts to emissions to ensure we avoid dangerous changes. At the regional scale examples are included in the report where there are clear interactions between ocean carbon and human activities, e.g. fishing, krill extraction, etc. This report demonstrates from multiple angles that continuing with excessive CO$_2$ emissions from human activities, whilst ignoring carbon management through the various ways we use and interact with the ocean, is imperiling the ocean system that shields us from more rapid dangerous climate change impacts.

The footprint of our current carbon emissions will not only bear heavily on the shoulders of many generations to come but, such is the scale of the changes being set in train to the ocean, that they now have the very real potential to jeopardize the very functioning of the ocean in the future. The ocean absorbs almost a quarter of our annual emissions of CO$_2$, and much more besides in terms of absorbing excess heat resulting from the greenhouse effect, and it has thereby bought us time and shielded us from what otherwise would be much more accelerated climate-induced changes. We impact the functioning of the largest carbon sink on the planet, at our peril. Understanding how it functions, respecting those processes, and factoring them into how we manage the ocean must now be our priority.
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Abbreviations, acronyms and units used

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>ANAMMox</td>
<td>Anaerobic Ammonium Oxidation</td>
</tr>
<tr>
<td>CCAMLR</td>
<td>Commission for the Conservation of Antarctic Marine Living Resources</td>
</tr>
<tr>
<td>CCS</td>
<td>Carbon Capture and Storage</td>
</tr>
<tr>
<td>DIC</td>
<td>Dissolved Inorganic Carbon</td>
</tr>
<tr>
<td>DOC</td>
<td>Dissolved Organic Carbon</td>
</tr>
<tr>
<td>DOM</td>
<td>Dissolved Organic Matter</td>
</tr>
<tr>
<td>EFH</td>
<td>Essential Fish Habitat</td>
</tr>
<tr>
<td>HNLC</td>
<td>High Nutrient Low Chlorophyll</td>
</tr>
<tr>
<td>MPA</td>
<td>Marine Protected Area</td>
</tr>
<tr>
<td>MSY</td>
<td>Maximum Sustainable Yield</td>
</tr>
<tr>
<td>OML</td>
<td>Oxygen Minimum Layer</td>
</tr>
<tr>
<td>OMZ</td>
<td>Oxygen Minimum Zone</td>
</tr>
<tr>
<td>PCB</td>
<td>Polychlorinated Bi-phenol</td>
</tr>
<tr>
<td>PETM</td>
<td>Palaeocene – Eocene Thermal Maximum</td>
</tr>
<tr>
<td>pH</td>
<td>Logarithmic scale of measure of acidity. A pH below 7 indicates acidic, and above 7 alkaline</td>
</tr>
<tr>
<td>POC</td>
<td>Particulate Organic Carbon</td>
</tr>
<tr>
<td>ppm</td>
<td>parts per million</td>
</tr>
<tr>
<td>rDOC</td>
<td>Recalcitrant (i.e. non-reactive) Dissolved Organic Matter</td>
</tr>
<tr>
<td>µm</td>
<td>Micrometre ($10^{-6}$m)</td>
</tr>
</tbody>
</table>
Getting the most from this report – an essential guide to the main types of ocean carbon

In developing this report we have tried wherever possible to keep things simple, but by its very nature ocean carbon is a complex subject.

A fundamental starting point to get the most from this report is to understand a little about the main forms of carbon in the ocean.

Carbon (C) is the building block of life and occurs in two main forms:
- Organic Carbon molecules, which are produced by living organisms, contain carbon bound to hydrogen (C-H), and are often large and complex structures. The simplest organic carbon molecule is methane (CH₄), and a more complex example is glucose (C₆H₁₂O₆).
- Inorganic Carbon, which is generally of mineral origin and does not contain hydrogen. For example carbon dioxide (CO₂) and calcium carbonate (CaCO₃).

Organic carbon molecules occur in the ocean in dissolved and particulate forms:
- Dissolved Organic Carbon (DOC): non-living organic carbon molecules dissolved in water, which can pass through filter paper of ~0.45 μm pore size. In general, DOC compounds result from the decay of organic matter such as algae, and are important food to microorganisms.
- Particulate Organic Carbon (POC): particles containing organic matter that are too large to be filtered out of water (using a ~0.45 μm filter). POC can be either living (e.g. picoplankton, bacteria and viruses) or non-living (e.g. faecal pellets).

Atmospheric CO₂ dissolves in the surface ocean through the process of gas exchange, to form Dissolved Inorganic Carbon (DIC) compounds in the ocean as follows:

\[
\text{CO}_2 + \text{H}_2\text{O} \leftrightarrow \text{H}_2\text{CO}_3 \leftrightarrow \text{HCO}_3^- + \text{H}^+ \leftrightarrow \text{CO}_3^{2-} + 2\text{H}^+
\]

- The main DIC compounds in the ocean are therefore carbonic acid (H₂CO₃), bicarbonate ions (HCO₃⁻) and carbonate ions (CO₃²⁻).
- Elevated CO₂ concentrations lead to more H⁺ ions, which lower the pH of sea water and result in ocean acidification.
The Significance and Management of Natural Carbon Stores in the Open Ocean

Making the ocean carbon numbers visible

The aim of this report has been to start to quantify the role that particular habitats and species make to open ocean carbon processes. One of the problems with such work, and in fact any work on carbon around climate change, is that the subject – carbon dioxide – and the processes of carbon sequestration are invisible. Few if any of us have a sense of the scale of the figures quoted when it comes to carbon management through natural systems. The challenge is to explain the significance of the numbers that have been identified in a way people can more readily relate to, making the figures visible and tangible.

At the core of this is the fact that a large family car weighs about 1.5 tonnes. So if we imagined the weight of carbon processed by the ocean each year, what would it look like by weight in terms of numbers of family cars per person per year based on the population of the UK?

<table>
<thead>
<tr>
<th>Scale of Units Used</th>
</tr>
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<tbody>
<tr>
<td>Value</td>
</tr>
<tr>
<td>$10^3$ g</td>
</tr>
<tr>
<td>$10^6$ g</td>
</tr>
<tr>
<td>$10^9$ g</td>
</tr>
<tr>
<td>$10^{12}$ g</td>
</tr>
</tbody>
</table>

One hectare = 10,000 m$^2$

Figures for land and ocean uptake based on Fact box 2.1. Other figures as given in case studies.
The last 10 years have seen an increased interest in nature-based solutions to climate change – both for mitigation and adaptation. There is now widespread recognition of the role some ecosystems play in mitigating climate change, notably forests and peatlands. In recent years significant progress has been made through the Reducing Emissions from Deforestation and Forest Degradation agenda (REDD+), as well as the recognition of similar opportunities in the coastal zone, although many challenges remain. This lends impetus to understand, assess and value more closely the carbon value of the open ocean, and potentially whether and how such ocean ecosystems might be managed directly, wholly or in part, as carbon sinks, or indirectly by better management of human activities that are driving changes to the marine environment. An understanding of the consequences of existing human impacts affecting carbon processes in the open ocean is similarly needed, especially given the feedback loops that are potentially exacerbating current levels of climate change, and the strong potential to continue to do so in the future.

Two landmark reports\(^1\) released in late 2009 provide a much-needed overview of the importance and role of coastal ecosystems as carbon sinks, focusing on mangroves, seagrass beds, saltmarshes, coral reefs and kelp forests. This has enabled a shift in and a broadening of the discussion around nature-based climate change mitigation options in coastal and inshore waters. However, the reports also illustrate that much scientific information is required in order to move the political agenda forward. Both reports focused on coastal ecosystems, but a significant gap remains in understanding oceanic carbon sinks, covering around half of the Earth’s surface.

The purpose of this new report on carbon in the open ocean is to provide what could be called ‘a policy adviser and decision-makers guide’ to this topic – an introductory document to explain why this is relevant and to whom, what there is of importance described in ways they can relate to, and what can or should be done to recognize and build such issues into decision-making.

This report has three broad target audiences:

- Scientists focusing on oceanic ecosystems and in particular carbon pools and sinks who are involved directly in research activities and are both the primary recipients and beneficiaries of new scientific findings. It is hoped that this report will trigger debate, and inspire the identification of key research priorities.

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1. Why this report?

- Government advisers and decision-makers, as well as climate change planners and policy makers who can benefit from enhanced awareness about the ecosystem services provided by the open ocean. This is particularly in relation to its role in the carbon cycle, how this can be better recognized through protection, management, restoration, positive and negative feedback loops to climate change, and actions needed to avoid further significant disruption of carbon processes and stores arising from the impact of human activities on specific aspects, in so far as this can/could be achieved.
- Those responsible for ocean stewardship whom can similarly gain knowledge that can improve management of habitats and species in the open ocean. In addition, awareness raising activities will also benefit conservation-minded NGOs and companies working on climate change mitigation or those that need to address their ‘carbon footprint’.

This report addresses the policy gap in broad scale understanding of the role of the ocean and carbon stores in four ways:

- By describing readily recognizable features of the ocean ecosystem that have important roles to play in the carbon cycle. This approach provides compelling ways to tell the story and ‘make it real and meaningful’ to people.
- By taking stock of and, to the extent possible, quantifying the amount of CO₂ that such key features of ocean ecosystems sequester (carbon sinks) and hold (carbon pools – net productivity). Revealing the role these key features play in natural global carbon management thus dispelling the widely held myth that focusing on forest and peatland management alone will save the day.
- By trying to provide an understanding of the consequences for carbon in the ocean through current feedback loops to climate change, and the influence human actions have on such processes. The latter being a consequence of degradation or changes resulting from human impacts coupled with poor management. This is as much about promoting reasoned, prudent ocean management as about specific tangible steps that can be taken.
- By promoting the understanding of whether, and if so how, features of ocean ecosystems can be enhanced through focused management and stewardship. Are there things we should do or should avoid doing to better ‘manage’ our interactions with specific components of ocean carbon, e.g. fisheries? The net result of this should be a greater policy and legislative respect for how the ocean supports and contributes to sustaining all life on Earth.

This report has been developed through working with key experts in the field of ocean carbon to review and synthesize the latest scientific information and present it in a format suitable for informing and influencing ocean planning, management and governance. In particular it is aimed at enhancing awareness in decision making on the impact of human exploitation on ocean carbon sinks and carbon pools, on the ocean’s ability to buffer climate change, and on possible actions to safeguard and enhance these functions. This full report is accompanied by a smaller separately available summary report directed more at policy advisers and decision makers.
2.1 The need for comprehensive carbon management

Much attention has been paid in recent decades to the role that the conservation and sustainable management of terrestrial and coastal ecosystems such as tropical forests and mangroves can play in mitigating climate changes. These ecosystems contain a significant amount of carbon, and to ensure that they continue to store carbon they must be maintained in a healthy natural condition, or be restored by (re-) planting efforts (e.g. such as through Reducing Emissions from Deforestation and Forest Degradation (REDD+)). To date there has been comparatively less analysis of similar opportunities available to maintain and restore carbon stores and pools in the open ocean.

In open ocean environments the uptake of atmospheric carbon is primarily controlled by biological activity and by seasonal and long-term changes in ocean heat content, as well as by the chemistry of surface and deep waters. It is important to understand these processes. The fixation of organic and mineral carbon by plankton productivity, and the resulting sedimentation of particulate carbon through oceanic waters have a major impact on the atmospheric concentration of \( \text{CO}_2 \). Although the carbon storage by plants in terrestrial (e.g. forests) and coastal marine ecosystems (e.g. mangroves) is relatively well understood, comparatively less information has been synthesized on the role that different open ocean ecosystems play in the uptake of atmospheric \( \text{CO}_2 \).

Although several aspects of open-ocean carbon cycles are relatively well understood, they have been poorly communicated to policy advisers and decision makers to date – hence the production and promotion of this report. The importance of communicating this scientific knowledge is especially pertinent for situations in which human activities are directly or indirectly having an impact on ocean carbon processes. Through this report we hope to raise awareness and understanding amongst key decision makers, and thereby help them (i) recognize and appreciate the global importance of ocean carbon processes, and (ii) identify ways in which selected open ocean ecosystems could be managed to protect or enhance their carbon roles, and thereby lower atmospheric \( \text{CO}_2 \) concentrations and mitigate climate change.

While reading this report, it is important to remember that the ocean plays an important but extremely complex role in global carbon cycles. This complexity can partly be attributed to the multiple interactions and feedback loops between different oceanic processes (e.g. hydrological, chemical, biological, geological, food-webs), and because human activities are already significantly modifying the natural processes that control the preservation of particulate carbon in the ocean sediments.
For example, the increasing level of atmospheric CO$_2$ is leading to elevated concentrations of dissolved CO$_2$ in oceanic surface waters, which is lowering the pH of the ocean and resulting in more acidic conditions, which is in turn reducing the preservation of mineral carbon in oceanic waters (see later in this chapter). Major issues remain unresolved about the future capacity of marine ecosystems to act as significant carbon sinks, and as a buffer to atmospheric CO$_2$ in the forthcoming decades.

2. Setting the scene: the importance of carbon in the ocean

The annual natural fluxes of CO$_2$ between the land and atmosphere and the ocean and atmosphere result in an uptake of CO$_2$ of approximately $5 \times 10^{15}$ grams of carbon per year (PgC.yr$^{-1}$) partially offsetting the human-caused CO$_2$ emissions ($\sim 9 \times 10^{15}$ gC.yr$^{-1}$ from fossil fuels burning, cement production and land-use change) (Ciais et al., 2013). The natural sinks of carbon are mainly controlled by photosynthetic activity that captures CO$_2$ and fixes it into particulate carbon. Over half of this biological carbon is removed from the atmosphere by marine organisms. However, only a small part of this so-called “blue carbon” is buried in marine sediments and thereby subtracted from the carbon cycle. A significant part of the marine organic matter is only partially decomposed and transferred to the dissolved organic carbon (DOC) pool. The DOC pool is one of the greatest reservoirs of organic matter on Earth. The amount of carbon in the DOC pool ($7 \times 10^{17}$gC) is nearly equivalent to the carbon in atmospheric CO$_2$, so the marine DOC pool is one of the greatest reservoirs of carbon on Earth. The majority of this DOC ($\sim 6.3 \times 10^{17}$gC) is recalcitrant, meaning that it is biologically non-reactive and has escaped remineralization by microbes back to CO$_2$. This recalcitrant DOC persists in the ocean for centuries to millennia (Hansell, 2012). Although the origin and cycling of this recalcitrant DOC pool remains presently unclear, it is composed of sub-micrometric carbon residues that can be stored for millennia in the water column because they are resistant to microbial degradation.

2.2 Major carbon processes in the ocean

To gain the most from the case studies provided later in this report it is necessary to introduce ocean carbon processes, to explain how the consequences of human activities are interacting with them, and why such interactions are already of unprecedented importance set in the historical perspective. This is due to the intimate relationships between ocean chemistry and marine organisms. At the simplest level organisms living in the sea are dependent on the chemistry of the water in which they live, but their biological activity also shapes and changes the chemical composition of their surrounding waters.

Marine species use carbon in sea water to build their soft tissues (organic carbon), while many of them - calcifiers - build solid skeletons made of inorganic...
2. Setting the scene: the importance of carbon in the ocean

Carbon (mineral carbon, i.e. calcium carbonate) (Figure 2.1). The planktonic and benthic organisms that live in the water column and on the ocean floor, respectively, account for the main source of particulate organic carbon\(^1\) and play a very important role in marine carbon storage (see Chapter 3).

Marine phytoplankton only represents 0.2% of the photosynthetic biomass on earth, yet they are responsible for more than half the net primary production, NPP\(^2\), (Field et al., 1998), making them as important in cycling the world's CO\(_2\) as all terrestrial plants combined (Falkowski, 2012). Uptake of dissolved CO\(_2\) by phytoplankton and the production of organic matter by photosynthesis reduces the CO\(_2\) pool in the surface ocean, and consumption of this organic matter by bacteria and zooplankton returns CO\(_2\) to the ocean pool and atmosphere (Smetacek, 1999). Particulate organic matter that escapes consumption and bacterial degradation may sink to the deep sea and become buried in the sediments, thereby sequestering carbon to the ocean interior for thousands of years or more (Falkowski, 2012). Faecal pellets of animals that graze on phytoplankton may also sink to the deep sea, thereby exporting carbon. This flux of carbon\(^3\) from the surface to deep ocean by phytoplankton and their associated food-webs is called the biological carbon pump.

Additional to this in situ production, important sources of ocean particulate organic carbon originate both from terrestrial sources and from microbial activities in the ocean. The input of terrestrial-derived nutrients from rivers exerts a major influence on coastal and pelagic primary productivity. Moreover, terrestrial organic carbon washed into the ocean is generally more efficiently sequestered in sediments than organic carbon produced in open ocean surface waters by phytoplankton. This efficiency is largely because soils and terrestrial plants contain a greater amount of substances that are relatively resistant to microbial degradation, such as humus, lignin or cellulose. In coastal marine areas where sediments accumulate much more, in comparison to pelagic areas, the discharge of terrestrial derived organic matter and nutrients from soil erosion and litter degradation sustains a high planktonic activity.

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\(^1\) Particulate Organic Carbon (POC) represents one of the main pools of organic carbon observed in the ocean. It is composed of living (phytoplankton, zooplankton and bacteria) as well as non-living materials (aggregates, faecal pellets and detritus) and is an important parameter of the global carbon cycle. POC is the main form by which organic carbon synthesized through photosynthesis in the upper layer is transferred to the deep ocean, where it can be sequestered over geological time-scales.

\(^2\) Net primary production (NPP) refers to the rate at which ecosystems accumulate biomass, excluding the energy it uses for respiration. For primary producers (plants and algae) NPP typically corresponds to the rate of photosynthesis minus respiration, and can be defined as the net flux of carbon from the atmosphere into algae/plants per unit time.

\(^3\) Carbon flux refers to the rate of movement of carbon from one reservoir to another.
The Significance and Management of Natural Carbon Stores in the Open Ocean

2. Setting the scene: the importance of carbon in the ocean

2.2.1 Microbial activity

Bacterial activity, viral infections of living microbes and planktonic organisms and algae, and oxygen conditions control the decomposition and preservation of organic matter in the water column and in surface sediments, and thereby play an important role in the burial of organic matter in oceanic sediments and, overall, in the global carbon cycle (see Section 3.6). Although the deepest regions of the ocean remain relatively unexplored, recent investigations of the very deepest sea trench (the Mariana Trench at almost 11000 m depth) reveal a surprisingly high degree of microbial activity linked to a relatively high flux of organic matter made up of dead animals, algae and other microbes originating from the surrounding much shallower sea bed. Additionally recent biogeochemical research in deep-sea ecosystems emphasizes an unusually high sediment deposition rate in these deep oceanic environments4, as well as the importance of microbial activity – the so-called microbial carbon pump - which transforms available ‘labile’ organic carbon forms, which are readily absorbed and utilized by organisms and algae, into more resistant ‘recalcitrant’ states that are non-reactive and are not used in the metabolic processes of organisms. The microbial carbon pump therefore could be a major contributor to the dissolved organic carbon (DOC) pool, which is the main reservoir of organic matter in oceanic environments.

Although most of the deep-sea floor ecosystems depend entirely on the sinking organic matter as their nutrient source, recently an exception has been discovered in the chemoautotrophic ecosystems that use organic matter produced by bacteria on the sea floor (see Section 3.7). At hydrothermal vents, microbes use the chemical energy released by the hydrothermal fluids to synthesize organic matter. Although mid-ocean ridges and the chemoautotrophic ecosystems that can inhabit such areas represent a small percentage (<1%) of the deep-sea floor, further biogeochemical research in these deep ocean ecosystems could provide important information concerning the microbial processes involved in the cycling of marine organic carbon, and the amount of organic carbon that is sequestered in these deep-water oceanic environments.

Not all the particulate organic carbon generated in surface waters reaches the deep ocean. This is because the efficiency of particulate organic carbon export from surface waters into the deeper ocean is strongly affected by the concentration of dissolved oxygen (O$_2$) in the water column that controls the oxidation of organic carbon into CO$_2$. The concentration of the sinking particulate organic carbon decreases with increasing water depth and at abyssal depths accounts for less than 1 to 5% of the production in surface waters. The oxidation of organic matter first occurs in the sunlit surface layer of the ocean, through photo-degradation by ultraviolet light in the top 200 m of water, and through the action of bacteria in the upper 1000 m of the water column.

The particulate organic carbon produced by biological activity in the pelagic realm5 is almost exclusively oxidized in the water column to liberate CO$_2$, while the remaining organic carbon that reaches the sea floor is subject to oxidation by aerobic organisms and sulphate-reducing bacteria inhabiting benthic sediments. Nutrients from soil erosion on land also constitutes an important factor influencing the marine carbon sink, by delivering the nutrients that otherwise would limit plankton growth. Similarly, coastal ecosystems (such as tidal marshes, seagrass meadows, and mangroves) represent a significant carbon sink and directly influence the productivity of remote marine ecosystems through the production and export of organic material via tides and currents from coastal ecosystems to the open ocean.

2.2.2 Carbon uptake processes

From both a physical and biological oceanography standpoint, the ocean takes up CO$_2$ from the atmosphere through two major processes that currently act to ameliorate climate change: (i) the ‘solubility pump’, and; (ii) the ‘biological pump’. The solubility pump (Figure 2.2) is so-called because CO$_2$ gas is soluble in water and its vertical draw-down and mixing within the global ocean is driven by temperature. Warm water in surface ocean currents is carried from low latitudes to high latitudes by currents - the thermohaline circulation - where the water then cools. This cold water in higher latitudes has a greater density and so then sinks down into deep ocean depths and takes with it CO$_2$ and the cycle is repeated. This continual cold-water temperature driven vertical

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5 The pelagic realm can be thought of as the open ocean - the water column that goes from the surface of the sea to the bottom. Conditions change deeper down the water column; the pressure increases, the temperature drops and there is less light. Below the pelagic zone is the benthic zone - the sea bed itself.
circulation at higher latitudes acts as an enormous carbon pump, but continued ocean warming is inhibiting sinking and reducing the efficiency of this pump.

The biological pump on the other hand (Figure 2.3), is the process by which CO₂ is converted into living matter by phytoplankton through photosynthesis. Globally, the majority of phytoplankton is consumed and recycled within food webs, but some 20% is transferred from the surface water of the ocean to deeper layers (beyond 1000 m) as dead organisms and faecal material, where it remains for decades to centuries. Increasing temperature from climate change and decreasing pH from ocean acidification have the potential to impact the primary productivity within the surface ocean, and thereby reduce the drawdown of CO₂ via this biological pump.

Approximately two-thirds of the vertical flux in carbon in the ocean is attributed to the biological pump with the rest due to the solubility pump (Passow and Carlson, 2012). The effects of the solubility and biological pumps are offset to a relatively small degree by the carbonate counter pump. Calcifiers as they grow release a small proportion of CO₂ back to the water, and potentially to the atmosphere, through the calcification process used to form calcium carbonate (CaCO₃) – thus countering processes that capture carbon into the ocean system. This process occurs as many calcifiers form – as their name suggests - heavy CaCO₃ shells made of either aragonite or calcite. These shells act as ballast for the organic carbon in their soft tissues that sinks and settles on the sea floor, providing a further avenue for carbon removal from the atmosphere and surface ocean layers. The deep ocean is, however, undersaturated with respect to CaCO₃ so that a large part of the sinking shells of calcite and aragonite dissolve when they pass through the saturation horizon⁶, or dissolve under the action of biological activity described earlier. Ultimately only carbon stored in marine sediments can be safely considered to represent a long-term (i.e. millennia timescale) ocean carbon storage solution.

2.3 Rising atmospheric CO₂ levels and consequences for ocean carbon processes

Changes in deep-sea chemistry and circulation can lead to significant differences in carbonate preservation and accumulation in oceanic sediments, but a recent overriding cause of change is ocean acidification combined with increasing seawater temperatures arising from climate change. These two

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⁶ The deeper waters of the ocean are naturally less saturated with respect to CaCO₃ minerals than the upper layers, due to the lower temperature and higher partial pressures of CO₂ at depth increasing the solubility of these minerals. The undersaturated lower layer of the ocean is separated from the upper layer by a boundary called the “saturation horizon.” Only above this boundary can the seawater chemistry support calcifying species such as coral communities and coccolithophores.
impacts are expected to have a pronounced effect on the efficiency of the ocean carbon pumps. The capacity of the ocean water column to act as a sink for atmospheric carbon is predicted to weaken in the future, and there is evidence that it may have already started (Doney et al., 2009a). This is cause for concern for the efficiency of the various carbon pumps, and the capacity of open ocean calcifiers to act as carbon pools. We do not yet know the adaptive capacity of such species over appropriate time-scales. Calcifying organisms may not be able to relocate or adapt to the rate and scale of environmental change now underway. In any event a reduction in calcification due to acidification could have a serious impact on the rates of settling out of both organic and calcareous material from ocean calcifiers with important climate feedback implications.

There is a close relationship between atmospheric CO$_2$ levels, ocean chemistry, and the role and well-being of species that are dependent on and/or play particularly significant roles in ocean carbon processes. The human impact on atmospheric CO$_2$ concentrations is altering these relationships. In 2013, and for the first time in human history, the concentration of CO$_2$ in the atmosphere reached 400 parts per million (ppm). Leading scientists and economists agree that it is essential and urgent to stabilize and subsequently reduce the atmospheric CO$_2$ concentration, and the UNFCCC set the limit of 450ppm at Cancun in 2010 (to have at least a 50% chance of stabilizing the climate at a 2°C global average temperature increase). This action is essential in order to maintain options for successful adaptation measures at globally acceptable economic, social and environmental costs.

Despite major environmental concerns for the world’s population and economy, there is still a comparative lack of knowledge about the response of marine ecosystems to the observed rapid changes in climate. Major perturbations are already affecting the biodiversity (i.e. species extinctions) and the distribution of marine species (including invasive ones), causing a reduction of the catch of some commercial fish species and affecting livelihoods in many regions. Global mean temperatures have already increased by more than 0.8°C in comparison with pre-industrial levels, and significant negative impacts can be already observed on worldwide natural ecosystems, freshwater resources and food production. According to the present state of knowledge, an increase in global mean temperature of greater than 2°C could have considerable and irreversible impacts that would certainly exceed the adaptive capacity of many systems to survive (IPCC, 2014 - AR5$^7$).

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2. Setting the scene: the importance of carbon in the ocean

2.3.1 Ocean acidification

Rising levels of atmospheric CO₂ are causing surface waters to become more acidic – the phenomenon called ocean acidification. Through a simple chemical equation the net effect of increasing CO₂ in sea water is to increase concentrations of hydrogen ions (H⁺) (thereby reducing pH), carbonic acid and bicarbonate ions (HCO₃⁻), while decreasing concentrations of carbonate ions (CO₃²⁻). A direct consequence is that sea-surface pH (a measure of how alkaline or acidic seawater is) is estimated to have already dropped by approximately 0.1 pH units over the last 150 years. Whilst this does not sound much, the pH scale is logarithmic, so this represents a 30% increase in acidity during this brief period of Earth’s history.

Why this phenomenon is both significant and of concern to current and future generations is because of its potential consequences, which it is increasingly apparent will be difficult, if not nearly impossible, to reverse even on a multi-generational timescale unless decisive action is taken now. The solubility of calcium carbonate (CaCO₃) in the surface layer of the ocean is increasing as atmospheric CO₂ concentrations rise, which makes it more difficult for calcifiers to make their carbonate shells (see Fact Box 2.2). When there are not sufficient carbonate ions in the ocean for calcifiers to manufacture shells, the water is said to be undersaturated with respect to carbonate. Open ocean calcifiers build calcium carbonate shells in one or other crystalline forms, either aragonite or calcite. Aragonite is a more soluble form of calcium carbonate.
and more readily dissolved when CO₂ levels increase compared to the less soluble form called calcite (Mucci, 1983).

This progressive change in the chemical equilibrium is likely to impact a wide range of marine ecosystems, especially calcifying organisms that use calcite and aragonite to build their shells or skeletons (e.g. species such as foraminifera, coccolithophores, pteropods, molluscs and echinoderms). Scientific research on such impacts is still at very early stages. If less calcium carbonate is produced due to ocean acidification, and more calcium carbonate dissolves, then this will tend to increase surface ocean pH and reduce surface ocean CO₂ (and therefore release less CO₂ to the atmosphere). In other words, this is a negative feedback loop. However, if you take into account the organic carbon pump driven by the photosynthetic calcifiers (e.g. coccolithophores) then the production of less shell material translates into less primary productivity, thus resulting in less CO₂ removed from the atmosphere by the ocean. Under a business-as-usual scenario for increasing CO₂ emissions, aragonite undersaturation will occur in surface Southern Ocean waters by 2050 (Orr et al., 2005) and possibly earlier in winter (McNeil and Matear, 2008), with calcite undersaturation projected to occur 50-100 years later (Orr et al., 2005) (Figure 2.4).

Organisms that are aragonite-dependent, which form important carbon pathways, and are also keystone species, such as pteropods in polar regions, are not likely to survive in waters that become undersaturated with aragonite (Bednaršek et al., 2012). Recent research in the Southern Ocean also reveals that foraminifera have thinner shells with considerably more porosity than fossilized foraminifera that lived in the pre-industrial age ocean (Moy et al., 2009). A doubling in atmospheric CO₂ concentration from current levels is projected to reduce the calcification rates of foraminifera by an additional 20 to 40 % with potentially significant impacts on the global inorganic carbon cycle (Burns, 2008).

2.3.2 Species-specific responses to climate change

Carbon processes in the ocean are complex, and our understanding is further complicated by species-specific responses to chemical change. For example, some researchers have shown that a doubling of present-day concentrations of CO₂ could result in a 20 to 40 % reduction in coccolithophore calcification, and that if CO₂ levels tripled compared to those of the present day this could result in coccolithophores losing half their protective coating (Burns, 2008). To date, however, the responses of only a few of the approximately 250-500 coccolithophore species have been studied (Young et al., 2005; Doney et al., 2009b). Whilst most studies have reported reduced calcification at elevated CO₂ levels, others have shown a doubling in calcification rates (Iglesias-Rodríguez et al., 2008), or no significant change (Langer et al., 2006). The role that these, and
other open ocean calcifiers, will play as carbon pools in a future high CO$_2$ ocean thus remains a significant research question to be addressed.

Further challenges in how species respond to elevated CO$_2$ levels are seen in fish. The increased CO$_2$ level in the ocean, which has adverse effects on the carbon mineral sequestration from the sea water, nonetheless enhances the carbonate precipitation in the intestines of fishes (see Section 3.6). Recent research suggests that fish could represent a significant source of fine-grained carbonates enriched in magnesium. These high magnesium calcite minerals produced by fish are less resistant to dissolution than calcite or aragonite precipitated in the open ocean by plankton. They are therefore more likely to dissolve quickly and restore alkalinity to the surface ocean, enhancing its ability to absorb atmospheric CO$_2$. Moreover, contrary to the trend expected for most calcifiers, excretion of gut carbonates by fish is predicted to increase as ocean CO$_2$ levels rise. This observation points to the necessity for further research on the specific responses of the different components of marine ecosystems to ongoing oceanic and biogeochemical changes (and associated organic and mineral carbon forms), in order to better assess the total net amount of atmospheric CO$_2$ that is effectively assimilated or released by marine organisms.

### 2.3.3 Implications for the ocean carbon sink

As CO$_2$ is absorbed and the carbonate concentration in the surface layers is reduced there is a feedback – a lowering of the capacity of the ocean to take up additional CO$_2$ (Figure 2.5). Climate change in itself will further reduce the ocean’s capacity to take up CO$_2$ through increased temperatures (which lowers the solubility of CO$_2$ in sea water), and the increased stratification of the water column (which will reduce the mixing and transport of CO$_2$-rich surface waters to greater depths) (Greenblatt and Sarmiento, 2004; Schubert et al., 2006). The latest scientific model predictions show that continued CO$_2$ emissions will gradually weaken the carbon sink efficiency of the ocean, resulting in a temporary, but large, increase of CO$_2$ in the atmosphere (Friedlingstein et al., 2006). However, even if the future ocean takes up a slightly smaller fraction of atmospheric CO$_2$ than presently, ocean acidification processes are likely to continue, increase in amplitude, and have an increasing effect for centuries to come (Burns, 2008).

![Figure 2.5](image)

Figure 2.5. Near past (1800 A.D.) to near future (2100 A.D.) evolution of surface pH (orange), atmospheric CO$_2$ (magenta), bicarbonate (green) and carbonate ion (blue) concentrations based on CO$_2$ emissions from historical data for the period 1820 to 2000 and considering the A2 IPCC SRES emissions scenario afterwards. Grey cloud of points shows mixed surface layer pH values in the ocean, computed from total inorganic carbon and alkalinity data (from Pelejero et al., 2010).

### 2.4 The significance of current human impacts on ocean carbon from the historical perspective

The recent increase of the concentration of CO$_2$ in the atmosphere is a consequence of human activities, particularly the combustion of fossil fuels and cement production. A quarter of the CO$_2$ released to the atmosphere year-on-year is absorbed by the ocean, giving a clear indication of the important role of the ocean in the regulation of variations in atmospheric CO$_2$. During the last million years, atmospheric CO$_2$ concentrations have shown cyclic variations closely tied to global ice volume changes. These changes follow regular periods of 100,000, 40,000 and 23,000 years (Figure 2.6) which relate to the Earth’s orbit around the sun, which in turn control the amount of sunlight received at the earth surface, and which as a result strongly influences the climate.

The reasons why the atmospheric CO$_2$ concentration reflects climate variations are not yet fully understood, but it is believed that the ocean lies at the origin of these variations. Organisms living in the sea transfer large amounts of carbon between the surface, the deep ocean and the sediments, and are therefore crucial to the carbon cycle. Nevertheless, and as described...
previously in this chapter, human activities are perturbing the biological fluxes of ocean carbon through the emission of enormous amount of $\text{CO}_2$ to the atmosphere.

It is extremely difficult to accurately predict the future state of oceanic ecosystems, and therefore the future status of the ocean’s natural carbon cycle and sink. However, by observing records of past geological time series related to environmental changes controlled by the carbon cycle it is possible to start to understand the enormity of some of the issues we now face, and it enables us to start to better predict how things may evolve in the future.

Time constants play a very important role in the carbon cycle. As described above the marine carbonate system follows the rhythms of the global climate system (Figure 2.6), but larger and longer perturbations such as tectonics, orogeny (creation of mountains), erosion and large volcanic episodes, also strongly modulate these rhythms. For example, the two best-documented previous ocean acidification events in Earth history,

Figure 2.6. The Earth’s orbital parameters are shaping the global climates: Precession is changing the seasonal pattern, eccentricity is changing the amplitude of precession and obliquity (axial tilt) changes the season intensity. The climates (e.g. atmospheric $\text{CO}_2$ recorded in ice core (EPICA) (Luethi et al., 2008), or ocean chemistry (oxygen isotopes in planktonic shells (SPECMAP) (Martinson et al., 1987), or ice ages (grey squares) are following the frequency patterns of the Earth’s orbital parameters.
the Permian-Triassic (250 million years ago) and the Triassic-Jurassic (200 million years ago) boundaries, are also the two most dramatic extinction events known. These events are contemporaneous of two significant periods of volcanic activity that emitted enormous amounts of CO$_2$ into the atmosphere over relatively long timescales (i.e. over several 100,000s of years) (Wignall, 2001; Tanner et al., 2004; Knoll et al., 2007; van de Schootbrugge et al., 2007).

The effects on marine calcifiers were dramatic, as a majority of them became extinct (Wignall, 2001). Most of the corals species for example disappeared at the Triassic-Jurassic boundary and no reefs survived and it took a couple of million years for new reef-forming coral species to evolve. The annual rates of CO$_2$ emission during those events were much slower than today, and the chemical and ecological effects at those times were certainly different from what the ocean will experience in the future (Ridgwell and Zeebe, 2005). Set against such events, the current rate of fossil carbon released to the atmosphere and the ocean by human activities is unprecedented, and it is not possible to predict all the consequences for the carbon cycle.

Over the past millions of years every variation in the atmospheric carbon chemistry has been stabilized by marine life (Figure 2.7). Challenging this equilibrium with such a rapid rate of change, as is now happening, is extremely dangerous for biodiversity and for the maintenance of marine ecosystems, and the ecosystem goods and services they currently provide, with possible catastrophic consequences for the Earth’s climate.

2.5 References


Case studies in ocean carbon

The case studies that follow illustrate the role and importance of ocean carbon from a series of different perspectives. The examples have been carefully chosen to range from microscopic organisms in the plankton that drive the biological pump which takes CO$_2$ out of the air and ultimately traps a proportion permanently in the deep ocean, through to groups of animals that hitherto have not been widely considered as very relevant in carbon management, such as krill and fish – and introduces the new concept of ‘mobile carbon units’.

The examples range from the surface waters, where carbon capture is powered by photosynthetic activities, through to the deep ocean. In the latter context case studies included in the report describe the role and importance of deep-sea microbes, and the increasingly important chemosynthetic pathways discovered, through which carbon is converted in the dark deep ocean to organic matter. In particular the report focuses on:

- **Open ocean calcifiers** (Section 3.2, page 35). These are a small group of organisms that have a very large and important role in the global climate carbon cycle. Calcifiers are organisms that manufacture shells from calcium carbonate (typically aragonite or calcite) and are key members of global marine food webs. They include both marine animals (zooplankton, e.g. foraminifera and pteropods) and marine plants (phytoplankton, e.g. coccolithophores).

- **Open ocean algal ecosystems: Diatoms** (Section 3.3, page 43). Diatoms are microscopic single-celled algae that float in the sunlit surface of the ocean, and fix dissolved CO$_2$ in their cells through the process of photosynthesis (Falkowski, 2012). Many diatom species are at the base of oceanic food webs, and indirectly influence the carbon cycles of many fauna. Diatoms export carbon to the deep-ocean via the ‘biological pump’ (Ragueneau et al., 2006), whereby dead diatom cells and faecal matter from marine consumers sink from the surface ocean.

- **Floating macroalgae: Sargassum** (Section 3.4, page 55). Large rafts of floating seaweed (macroalgae) occur in the world’s ocean, and are biodiversity hotspots that provide food and shelter to many animals. This example focuses in on floating *Sargassum natans* and *S. fluitans* (hereafter Sargassum), which occur in the Sargasso Sea and the Gulf of Mexico. Sargassum drifts thousands of kilometres at the mercy of winds and currents, and plays an important but under-studied role in the oceanic carbon cycle. Floating seaweed utilize CO$_2$ as they grow, and sequester carbon when they sink to the deep sea or when the faecal pellets of their grazers sink. Seaweed also leach dissolved organic carbon (DOC) into the sea, some of which is non-reactive (recalcitrant DOC) and is stored in the oceanic carbon pool for thousands of years.
• **Antarctic krill** (Section 3.5, page 69). Krill is one of the most abundant metazoan species on the planet and is a key species in the Southern Ocean ecosystem being the major prey for marine vertebrate predators and also a major grazer of primary production (Eversen, 2000). The krill population is a large carbon reservoir, but krill are probably more important through their control in carbon cycling processes. Krill affect the marine carbon cycle by grazing phytoplankton and producing sinking faecal pellets, and through their vertical and horizontal migrations, the turbulence their movements generate, and their role in the cycles of critical elements such as iron.

• **Fish** (Section 3.6, page 79). Fish are perhaps the most surprising addition to the list of quantitatively significant marine calcifiers and they are the only marine organisms that make calcium carbonate as an excretory by-product of gut physiological processes as opposed to the need for structural (skeletal) material. A further important distinguishing feature of fish calcification is that their gut carbonates are produced and excreted continuously throughout their lives rather than the very intermittent release associated with either death, moulting or physical erosion of traditional calcifiers. Their carbonate production rate is also expected to greatly increase as a result of environmental changes predicted for the next century.

• **Deep sea chemosynthetic carbon production** (Section 3.7, page 93). Where light is too scarce to activate photosynthetic processes or completely absent, such as in the deep sea (i.e. generally below 200m depth, although in the clearest oceanic waters some light can penetrate to around 600m depth), primary production occurs through chemosynthetic processes. Chemosynthetic (also defined “chemoautotrophic”) organisms produce organic matter through the assimilation of inorganic carbon, coupled with the use of reduced chemical compounds as an energy source. Marine microbes play a role of primary importance in controlling these processes by regulating the carbon sequestration capacity of the oceans and the ability of our planet to balance the effects of ongoing climate changes.

• **Deep-sea microbes and their role in the ocean interior** (Section 3.8, page 103). The ocean interior contains the majority of microbes inhabiting the Earth and the deep-sea floor surface sediments contain 10–10,000-fold more cells per unit volume than productive ocean-surface waters. Conversely to other biological components of the ocean, the abundance of benthic prokaryotes (i.e. microbes belonging to two domains of life: Bacteria and Archaea) and viruses (biological entities infecting living cells) does not decrease significantly with increasing water depth. This final section explores deep-sea prokaryotes and viruses and along with their interactions they play a crucial role in the decomposition processes and biogeochemical cycling of carbon, nitrogen and phosphorus at the global scale. There is increasing evidence that deep-sea microbes are key biotic components that will influence the ocean’s feedbacks to climate change.

Due to constraint on the project it was not possible to cover a larger number of case studies or indeed to go into fuller explanations in some of the current case studies. Notable gaps exist, such as the carbon role of marine mammals and of species such as echinoderms in the benthos, but it is hoped that the current case studies provide a snap-shot of this often overlooked, but nevertheless critical role, played by the open ocean and the ecosystem and species it contains.
The Significance and Management of Natural Carbon Stores in the Open Ocean

3. Case studies in ocean carbon
3.1. Summary of key findings – Ocean carbon by numbers

3.1.1 General context
There are natural CO₂ exchange fluxes between the land and atmosphere, and the ocean and atmosphere. Over the last decade (2000-2009), the ocean has taken up approximately $2.3 \times 10^{15}$ gC yr⁻¹, partially offsetting the anthropogenic CO₂ emissions ($\sim 9$ PgC yr⁻¹) from fossil fuel combustion, land use change and cement production (see Fact box 2.1). The ocean and land sinks were approximately equal at $2.3 \pm 0.7 \times 10^{15}$ gC yr⁻¹ and $2.6 \pm 1.2 \times 10^{15}$ gC yr⁻¹, respectively (Ciais et al., 2013). In this report the carbon budgets cited have mostly come from IPCC 2013 (Ciais et al., 2013). Over half of this biological carbon is captured by marine organisms. Carbon dioxide is converted into living matter by phytoplankton through photosynthesis. Globally, the majority of CO₂ (60-80%) is recycled within the food chain but some (20%) is transferred from the surface water of the ocean to deeper layers as dead organisms, faecal material and carbonate skeletons.

A quarter of the CO₂ released to the atmosphere through the burning of fossil fuels or land-use changes year-on-year is absorbed by the ocean, giving a clear indication of the important role of the ocean in the regulation of variations in atmospheric CO₂ and the buffering of climate change.

The total carbon stocks in the ocean currently amount to ~ 40,453 PgC (DIC = 38,000 PgC, DOC = 700 PgC, marine biota = 3 PgC and ocean floor sediments = 175 PgC; Ciais et al., 2013). Terrestrial carbon stock estimates range from 3 950 - 5 450 PgC (vegetation living biomass = 450 - 650 PgC, dead organic matter in soil = 1500 - 2400 PgC, wetland soils = 300 - 700 PgC and permafrost soils = 1700 PgC, Ciais et al., 2013). Atmospheric carbon stocks amount to ~ 830 PgC (Ciais et al., 2013). Therefore, the ocean carbon stocks are currently 50 times greater than in the atmosphere, and ~ 10 times greater than on land.

3.1.2 Specific examples of ocean carbon values
Open ocean calcifiers (Section 3.2, page 33) – living organisms that use calcium carbonate to build their skeletons - lock away carbon in the form of calcium carbonate and transport it to the deep sea where the carbon is stored for decades through to geological time scales. They are also key prey for a wide range of predators including commercially important fish, and cetaceans.

Calcifiers are distributed worldwide from the surface to the deep sea and provide critical services to humans and the planet. Foraminifera, which are one of the key calcifiers in the open ocean, are single-celled calcite-shelled organisms. They have a global distribution and provide a critical link in the marine food chain, providing energy to the larger marine fauna that prey upon them including fish. Planktonic foraminifera are responsible for 32 – 80% of global deep-ocean carbon fluxes – the wide range reflecting regional and temporal scale variations, and local hydrography and dissolution. A single species of coccolithophore – another group of calcifiers - Emiliania huxleyi plays a key role in ocean carbon uptake and occurs in blooms that form vast milky turquoise patches on the ocean surface covering up to $1.4 \times 10^6$ km² (twice the size of Texas) each year.

Pteropods are small, free-swimming snails with shells of aragonite more poetically referred to as ‘sea butterflies’. They are a major food source for marine organisms with a global biomass equating to $5 \times 10^{14}$ gC (that’s more than global kelp forest biomass).

Diatoms (Section 3.3, page 43) are microscopic single-celled algae with silica cell walls, and are especially abundant in nutrient-rich surface waters at high latitudes (>40°N and S) and in coastal upwelling regions. Annual carbon production by diatoms is $10.7 \times 10^{15}$ gC, which represents ~7.4% of net primary production (NPP) on earth.

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11 In this report the carbon budgets cited have mostly come from IPCC 2013 (Ciais et al., 2013). This reports values for the decade 2000-2009. It should be noted that these carbon values are very similar (almost identical) to the more recent publication by Le Quere et al. (2013), which reports updated values for the decade of 2003 - 2012. Due to the standard error reported there is no significant difference in the updated values from Le Quere et al. (2013).

12 Net primary production (NPP) refers to the rate at which ecosystems accumulate biomass, excluding the energy it uses for respiration. For primary producers (plants and algae) NPP typically corresponds to the rate of photosynthesis minus respiration, and can be defined as the net flux of carbon from the atmosphere into algae/plants per unit time.
The Significance and Management of Natural Carbon Stores in the Open Ocean

Diatoms exhibit a seasonal carbon flux\(^{13}\) from the surface ocean to the deep via the biological carbon pump. Intense diatom blooms occur in spring and summer, after which ~ 40% of carbon fixed by diatoms (\(4.2 \times 10^{15} \text{ gC.y}^{-1}\)) sinks to >100m depth. Of this, the pelagic foodweb consumes ~90% of the carbon, and only 1-2% reaches depths > 1000m where it remains for thousands of years. The annual flux of carbon from the surface to the deep ocean (>1000m) by diatoms is \(-0.15 \times 10^{15} \text{ gC}\), which is equivalent to ~1.7 % of annual CO\(_2\) emissions from fossil fuels and ~6.5% of the annual sequestration of CO\(_2\) by the ocean (Ciais et al., 2013).

Floating Sargassum (Section 3.4, page 55), which occurs in the Sargasso Sea and Gulf of Mexico, constitutes the world’s largest biomass of pelagic seaweed. The carbon production by Sargassum is ~ 2.7 \times 10^{11} \text{ gC}, which is about 0.5% of that for phytoplankton in the entire Sargasso Sea (Carpenter and Cox, 1974), and up to 10% of the primary production in some areas (Gower et al., 2006). However, Sargassum only constitutes 0.0006% of production by all marine primary producers globally. Annual carbon sequestration by Sargassum is estimated to be > 4.3 \times 10^{11} \text{ gC}, which accounts for 0.0005% of the ~ 9 \times 10^{15} \text{ gC} emitted by fossil fuels each year (Ciais et al., 2013), and 0.002% of the annual carbon uptake by the ocean which is 2.3 \times 10^{15} \text{ gC.y}^{-1} (Ciais et al., 2013). However, these estimates do not include carbon sequestration by sinking Sargassum, which is currently unknown, and hence it is expected that total carbon sequestration by Sargassum is grossly underestimated. Although the quantity of CO\(_2\) sequestered by Sargassum appears to be of low global significance, it is likely to play a very important local role in carbon cycling within the Sargasso Sea. Rafts of floating Sargassum support a rich biodiversity of other flora and fauna, and therefore Sargassum is also likely to play an important indirect role in the carbon cycled by other organisms.

Antarctic krill (Section 3.5, page 69) is reputed to have the largest biomass of any single metazoan species (all multi-cellular animals besides sponges) on the planet, playing a key role in the structure and function of the Southern Ocean ecosystem. They display circumpolar distribution, south of the Polar Front with a distributional range of 19 \times 10^6 \text{ km}^2, which largely coincides with the extent of winter sea ice. This roughly equates to size of South America.

The circumpolar krill stock is calculated to contain approximately 3.5 \times 10^{15} \text{ gC}, which is more than the total peat-carbon stock held in the USA, and their annual carbon production is of the order of 3.1-4.9 \times 10^{13} \text{ gC}, and sequestering 2.3 \times 10^{13} \text{ gC} annually. This figure is more than the total peat-carbon stock held in the USA. Krill also play a key role in cycling elements other than carbon, some of which may limit primary production (e.g. iron).

Fish (Section 3.6, page 79) make a large contribution to oceanic carbonate production (0.04-0.33 \times 10^{15} \text{ g of CaCO}_3-C per year) in the form of high magnesium (Mg) calcite crystals excreted continuously via the gut. Their high Mg content suggests rapid dissolution near the ocean surface that would restore surface alkalinity to a greater degree than other biogenic carbonates. This would neutralize much of the CO\(_2\) released as a consequence of the calcification process.

In the deep sea, chemosynthesis (Section 3.7 page 93) is the only source of primary production. Chemosynthetic (also known as, “chemoautotrophic”) organisms produce organic matter through the assimilation of inorganic carbon coupled with the use of reduced chemical compounds as an energy source. Globally, about 52% of the chemosynthetic carbon fixation occurs by nitrifiers in the water column (37% in the euphotic zone\(^{14}\) and 15% in the dark ocean). About 48% of the total oceanic chemosynthesis occurs in sediments. Chemoautotrophic carbon fixation in the deep sea is in the order of 4.0 \times 10^{13} \text{ gC.y}^{-1}.

The ocean interior (Section 3.8, page 103) contains the majority of microbes inhabiting the Earth and deep-sea floor surface sediments contain 10–10,000-fold more cells per unit volume than productive ocean-surface waters. The prokaryotic biomass, which largely dominates over all other biotic components, is estimated in the order of 0.34 \times 10^{15} \text{ gC} in deep-sea surface

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\(^{13}\) Carbon flux refers to the rate of movement of carbon from one reservoir to another.

\(^{14}\) The euphotic zone, photic zone or sunlight zone is the depth of the ocean that is exposed to sufficient sunlight for photosynthesis to occur. It extends from the surface down to a depth where light intensity falls to one percent of that at the surface, called the euphotic depth. Accordingly, its thickness depends on the extent of light attenuation in the water column. Typical euphotic depths vary from only a few centimetres in highly locations to around 200 metres in the open ocean. It also varies with seasonal changes in turbidity.
The Significance and Management of Natural Carbon Stores in the Open Ocean

3.1.3 Consequences of human impacts on ocean carbon

In 2013, and for the first time in human history, the concentration of CO₂ in the atmosphere climbed from the 1750 pre-industrial levels of 280 parts per million (ppm) to 400 ppm which represents a 30% increase in acidity during this brief period of Earth's history.

Under a business-as-usual scenario for the growth of CO₂ emissions, aragonite undersaturation will occur in surface Southern Ocean waters by 2050 and possibly earlier in winter and undersaturation of calcite – a less soluble form of calcium carbonate – is projected to occur 50-100 years later. This is expected to have consequences for calcifiers such as pteropods. A doubling in atmospheric CO₂ concentration from current levels is projected to reduce the calcification rates of foraminifera by an additional 20 to 40 %, with potentially significant impacts on the global carbon cycle.

Calcifiers face significant challenges when exposed to lower ocean pH or ‘ocean acidification’. Lower numbers of ocean calcifiers, reduced calcification and increased shell dissolution may adversely affect the ocean's capacity to continue to act as a carbon sink. Warming of the ocean is indirectly reducing nutrient input to the surface waters, leading to a decline in diatom abundance and slowing of the biological pump, which will ultimately reduce CO₂ sequestration in the ocean and further exacerbate climate change.

More broadly with reference to mitigation, seaweed aquaculture can support long-term carbon storage and sequestration. In terms of carbon capture and sequestration, seaweed cultivated for biofuel production in 4% of the global exclusive economic zone (4x10⁶ km² or 4x10⁹ hectares) could remove 3.2 x 10¹⁵ gC from the atmosphere per year. Culture at this scale for 100 years would capture and store 10% of the carbon that is required to limit global temperature change to 2°C. However, this would require cultivating seaweed in 400 times the area currently used by aquaculture worldwide. Environmental impacts from seaweed farms are still not very well understood, and natural seaweed populations like the Sargassum should be protected.

Marine organisms are expected to be affected by ocean acidification in a number of ways and long-lived pelagic animals, such as Antarctic krill, may be especially vulnerable. The krill population is a large biological carbon reservoir, but krill are probably more important through their control of the carbon cycling processes. Declines in krill density and possible recruitment failures in the South Atlantic in recent years have been linked to reductions in sea ice area caused by global warming.

Temperature and CO₂ forecasts for the next century (±4 °C and 750 ppm) suggest fish carbonate production may be 58% higher than now, contrary to the effect predicted for many calcifiers. Warmer conditions should also increase the magnesium content in the carbonate formed in the gut, and also increases the rate of near-surface dissolution of the magnesium carbonate once it is discharged from the fish. Quantitatively, however, the fate of fish carbonates in the ocean is not yet understood well enough to be able to estimate their role as sources or sinks of CO₂.

The predicted oxygen decrease in the deep ocean interior as a result of global climate change (i.e. global warming, altered thermohaline circulation, and increased stratification) could significantly influence prokaryotic chemosynthetic processes and therefore the overall carbon storage capacity of the oceans. It is not possible yet to predict the impact of climate change on deep-sea prokaryotes and viruses, nor if this will be exacerbated by multiple stressors, such as changes in temperature coupled with acidification and shifts in salinity and oxygen concentration, or if it will be buffered by biotic interactions. However, there is increasing evidence

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16 Aragonite undersaturation is when the concentration of this relatively soluble form of calcium carbonate found in plankton and invertebrates falls to levels insufficient to allow for the building of skeletons and shells.
that deep-sea microbes are key biotic components that will influence the ocean’s feedbacks to climate change.

**3.1.4 References**


3.2 Open ocean calcifiers: Pteropods, foraminifera and coccolithophores

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Summary points:

• Calcium carbonate is the basic building block of skeletons and shells for a large number of marine organisms including corals, shellfish and open ocean plankton (both plants – coccolithophores, and animals – foraminifera, pteropods and larval stages of benthic calcifiers) that are known collectively as calcifying organisms or calcifiers.

• Calcifiers are distributed worldwide from the surface to the deep sea and provide critical services to the planet. For example:
  - Pteropods are a major food source for marine organisms with a global biomass equating to $5 \times 10^{14}$ gC (that's more than global kelp forest biomass).
  - A single species of coccolithophore, *Emiliania huxleyi*, plays a key role in ocean carbon uptake, can occur in blooms that appear as vast milky turquoise patches on the ocean surface covering up to $1.4 \times 10^8$ km$^2$ (twice the size of Texas) each year.

• The ocean currently stores 50x more CO$_2$ than the atmosphere and 20x more CO$_2$ than land plants. Open ocean calcifiers lock away carbon in the form of calcium carbonate and transport it to the deep sea where the carbon is stored for geological time scales. They are also key prey for a wide range of predators including commercially important fish, and cetaceans.

• Calcifiers face significant problems when exposed to lower ocean pH or ‘ocean acidification’. Lower numbers of ocean calcifiers, reduced calcification and increased shell dissolution may impact the ocean's capacity to continue to act as a carbon sink.
3.2.1 Introduction
Ocean calcifiers are a group of organisms that have an important role in the global climate carbon cycle. These organisms manufacture shells from calcium carbonate (CaCO₃) via a process known as bio-calcification (Fact box 3.2.1) and are key members of global marine food webs. One of the consequences of anthropogenic CO₂ emissions for the ocean is a serious threat to calcifiers’ physiology, including their ability to maintain their shells as the ocean chemistry changes. Indeed, calcifiers are now, and have always been, a barometer for how the ocean is coping with increasing CO₂ levels. Impacts on these key marine organisms, and the carbon pools they represent, are expected to be dramatic and in some cases irreversible.

Fact box 3.2.1: Bio-calcification
Bio-calcification is the process by which calcifying organisms produce shells and plates out of calcium carbonate (CaCO₃). This process is often intracellular with strong controls of the local carbonate chemistry, and is physiologically isolated from external seawater (Roleda et al., 2012). In coccolithophores, calcification occurs in vesicles using bicarbonate:

\[
\text{Ca}^{2+} + \text{HCO}_3^- \rightarrow \text{CaCO}_3 + \text{H}^+ 
\]

Foraminifera produce vesicles with elevated pH that are transported to the site of calcification. They create a zone of high pH in which calcium carbonate is precipitated (de Nooijer et al., 2009):

\[
\text{HCO}_3^- \rightarrow \text{CO}_3^{2-} + \text{H}^+ \\
\text{Ca}^{2+} + \text{CO}_3^{2-} \rightarrow \text{CaCO}_3
\]

3.2.2 Definition of the key species
Coccolithophores
Coccolithophores – microscopic, single-celled, calcite shelled phytoplankton or marine plants (Figure 3.2.1) – are found in vast numbers, sometimes in extensive blooms, throughout the surface zone of the global ocean. Phytoplankton fix 5 x 10¹⁶ gC yr⁻¹, which is equal to the photosynthetic production by land plants (Field et al., 1998), i.e. every second breath of oxygen you take is courtesy of an ocean plant. Coccolithophores play major roles in the global carbon cycle by contributing to both the production of oxygen (these calcifiers alone produces 10% of the oxygen we breathe) in addition to providing ballast through the formation of their calcite shells to transport 50 – 80% of the carbon in the surface ocean to be ultimately locked away in the deep sea carbon reservoir (Honjo, 1977; Fabry, 1989; Tanaka, 2004; Beardall and Raven, 2013).

Foraminifera
Foraminifera (Figure 3.2.2) are single-celled calcite-shelled organisms. They too have a global distribution, occurring from freshwater to marine habitats, both in the plankton (Schiebel, 2002) and the benthos (Gooday et al., 1992). These calcifiers provide a critical link in the marine food chain, consuming bacteria, detritus and plankton, harbouring aquatic symbionts such as green-, red-, and golden- algae, diatoms or dinoflagellates that meet a large portion of their daily needs (Lee, 2006), and in turn providing energy to the larger marine fauna that prey upon them including fish (Lipps and Valentine, 1970). Planktonic foraminifera are responsible for 32 – 80% of global deep-ocean carbon fluxes (Schiebel, 2002).

Figure 3.2.1: Globally distributed coccolithophore: *Emiliania huxleyi* (scale bar = 10µm). Gustaaf Hallegaeref (UTAS).
Pteropods

Pteropods are small, free-swimming snails with shells of aragonite more poetically referred to as ‘sea butterflies’ (Figure 3.2.3). Global pteropod biomass has been estimated at $5 \times 10^{14}$ gC with population densities highest in polar and sub-polar regions where, on occasion, they can swarm to more than 10,000 individuals m$^{-3}$ (Bathmann et al., 1991; Pane et al., 2004). Pteropods have been called the ‘potato chips of the sea’: contributing to the diet of other zooplankton, salmon, mackerel, herring and cod (LeBrasseur, 1966; Takeuchi, 1972). In the sub-Arctic, pteropods alone can account for up to 60% of the diet of Alaskan pink salmon (Armstrong et al., 2005).

Pteropod shell production typically accounts for between 10 and 50% of the total carbon flux to the deep sea (Berner and Honjo, 1981; Fabry, 1990; Bednaršek et al., 2012a) with the percentage increasing to > 50% in the deep Southern Ocean south of the Polar Front (Hunt et al., 2008).

Larval stages

Up to 85% of all benthic invertebrate species produce long-lived planktonic larvae that spend weeks to months in the open ocean. The duration of this planktonic phase differs between species and is usually in synchrony with species-specific needs or tolerance (presence of food, optimal environmental conditions, etc.). Many of these larvae are calcifying, including keystone and commercially important species (Figure 3.2.4). It is not possible at this time to quantify this group’s value in terms of carbon storage and transport from the open ocean to the sea floor (due to the diversity of phyla this group covers). Nevertheless, these larval stages are considered to be highly sensitive to environmental changes and a bottleneck in life cycle of some organisms. An increase by as little as 1% in mortality of their larvae has the potential to compromise future population abundance, genetic diversity, distribution, and resilience to disturbances of adult benthic organisms.

3.2.3 The marine carbon cycle

The global open ocean is the most important net sink for anthropogenic CO$_2$ from the atmosphere via the marine carbon cycle (see introductory chapter). A third of all anthropogenic CO$_2$ emissions have been absorbed by the ocean since 1959 (Le Quéré et al., 2012). This oceanic absorption of CO$_2$ reduces its accumulation in the atmosphere and so mitigates some of the negative effects of CO$_2$ emissions. Without oceanic uptake of anthropogenic CO$_2$, the relative CO$_2$ concentration in the atmosphere would be more than 55ppm above the present level (Sabine et al., 2004). However, the current absorption rate of CO$_2$, which is approximately ten times above the historical rate (Schubert et al., 2006; Feely et al., 2009), has also led to a rapid and persistent change in the carbonate chemistry of the world’s ocean – a process known as ocean acidification (Caldiera and Wickett, 2003).
As CO₂ is absorbed and the carbonate concentration in the surface layers is reduced there is a feedback – a lowering of the capacity of the ocean to take up additional CO₂. Climate change in itself may further reduce the ocean’s capacity to take up CO₂ through increased temperatures (which lowers the solubility of CO₂ in water) and increased stratification of the water column (which will reduce the mixing and transport of CO₂-rich surface waters to greater depths) (Schubert et al., 2006). Model predictions show that continued CO₂ emissions will gradually weaken the sink efficiency of the ocean, resulting in a temporary, but large, increase of CO₂ in the atmosphere (Friedlingstein et al., 2006). However, even if the future ocean takes up a slightly smaller fraction of CO₂ than presently, ocean acidification processes are likely to continue, increase in amplitude, and the effects will be felt for centuries (Burns, 2008). Only carbon stored in marine sediments can be safely considered to represent a long-term marine carbon storage solution. However, suggestions that the capacity of the water column of the ocean to act as a sink for atmospheric carbon will weaken in the future, and evidence that it may have already started to do so (Doney et al., 2009a), is cause for concern for the longevity of open ocean calcifiers as carbon pools.

As ocean acidification impacts calcifiers, the role of these key marine organisms in carbon capture, transport, recycling and storage in the global ocean is likely to change with consequences for the global marine food chain and carbon sequestration.

3.2.4 Local, regional and global significance of calcifiers as carbon pools

Calcifiers play profound roles in the way the ocean draws down CO₂ from the atmosphere and transfers carbon to the deep ocean store (Reid et al., 2009). They currently account for as much as 80% of the global marine CaCO₃ production and transport to the deep sea (Honjo, 1977; Fabry, 1989; Tanaka, 2004). Ocean acidification has the potential to reduce this transport of carbon to the deep sea. It has already been shown that small biological responses to ocean change can have large effects on these organisms’ efficiency as carbon sinks:

- Riebesell et al. (2000) reported reductions in coccolithophore calcification of 83% under high-CO₂ ocean conditions and many researchers predict declining coccolithophore calcification as CO₂ emissions continue to increase (Sciandra et al., 2003; Engel et al., 2005; Beaufort et al., 2011). To date, however, the responses of only a few of the approximately 500 coccolithophore species have been studied (Young et al., 2005; Doney et al., 2009b). And while most studies have reported reduced net calcification at elevated CO₂ levels others have shown a doubling in net calcification rates (Iglesias-Rodríguez et al., 2008), or no significant change (Langer et al., 2006).

- Similar reductions in calcification have been reported for Southern Ocean foraminifera (30 –35% reduction in calcification from pre-industrial levels (Moy et al., 2009)). Recently, Bednaršek et al. (2012b) reported a dissolution response of live juvenile southern polar pteropods within their natural environment as a result of exposure to surface aragonite-undersaturated waters, pointing to the vulnerability of polar pteropods to ocean acidification, as suggested by laboratory studies (Orr et al., 2005; Comeau et al., 2009; Fabry et al., 2009).

- The main documented impact of high ocean CO₂ on larval stages is an increased mortality (Dorey et al., 2013) and a decrease in growth rates due to additional energy costs (Stumpp et al., 2012) and physiological stresses (Stumpp et al., 2013). In addition, sub-lethal impacts on larval growth rate may have dramatic consequences for population maintenance. The cost of planktonic life can be severe because of mortality due mainly to predation and other risks such as starvation, offshore transport and exposure to intolerable environmental conditions. For example, in sea urchins, daily mortality rate has been estimated in the field and ranges between 9 and 16% per day due mainly to predation (Lamare and Barker, 1999). A slight change in larval growth rate can then translate into an important impact on survival and thus compromise adult populations’ sustainability (Dupont et al., 2010).

The exact role(s) that these ocean calcifiers play as carbon pools now, as well as their potential to continue in a future high CO₂ ocean, remains to be quantified.
However, we know that as shell calcification declines, their potential to act as ballast in the transport of organic carbon to the deep sea would be reduced (Schiebel, 2002). If CO₂ emissions continue un-checked (the so-called ‘business-as-usual scenario’ for growth of CO₂ emissions), undersaturation (the point at which there are not enough carbonate ions in the water for calcifiers to use for shell production) will start to occur for aragonite (when carbonate ion concentrations drop below approximately 66 μmol.kg⁻¹) first in the polar oceans (as early as 2020 in the Arctic Ocean (Feely et al., 2009) and by 2030 in Southern Ocean waters (McNeil and Matear, 2008). Calcite undersaturation (when carbonate ion concentrations drop below approximately 42 μmol.kg⁻¹) won’t occur as soon as aragonite undersaturation, but will start to impact the Arctic by 2095 (Feely et al., 2009).

Many challenges remain to quantify the impact of ocean acidification on the role of open ocean calcifiers as blue carbon pools, food sources or key steps in benthic organisms’ life-cycles. For example, it is not yet possible to determine the acclimation potential and adaptive capacity of open ocean calcifiers over the appropriate time-scales: these organisms may not be able to relocate or adapt to the rate and scale of change now underway.

### 3.2.5 The evolution of calcifiers

The historical record associated with previous incidents of reductions in open ocean calcifiers can serve as a warning to marine managers and policy makers. The mass extinction of huge numbers of calcifying marine species 55 million years ago (the Palaeocene-Eocene Thermal Maximum or PETM) may have been driven largely by ocean acidification and associated carbonate undersaturation (Pelejero et al., 2010). Moreover, because the release of carbon was more gradual during this era, facilitating some buffering through deep-sea carbonate dissolution, it took over 110,000 years for calcium carbonate levels to re-equilibrate (Burns, 2008). It is likely contemporary acidification will be more “rapid and intense” (European Science Foundation, 2009) with the release of CO₂ over the next 300 years too rapid to be neutralized by the dissolution of calcifiers and calcareous sediments. Consequently, the ocean acidification-induced impacts on surface ocean biota will likely be more severe than seen before (Zachos et al., 2005; Guinotte and Fabry, 2008).

### 3.2.6 The goods and services provided by calcifiers

It remains uncertain as to how open ocean calcifiers will respond to the variety of changes currently occurring in the marine realm (i.e. ocean warming, ocean acidification, and deoxygenation) and therefore whether their role as carbon pools will remain unaffected. How populations, communities and whole ecosystems will adapt is not known but what is certain is that open ocean calcifiers currently provide critical earth system services, although the importance of such services is often not fully appreciated until they are lost (Lubchenco and Petes, 2010). Just some of the services open ocean calcifiers provide include:

**Feeding the food that feeds the world**

- Potential changes in calcifier distributions and abundances could propagate through multiple trophic levels of marine food webs (Guinotte and Fabry, 2008). If high-latitude surface waters do become undersaturated with respect to aragonite by the end of the century, pteropods could eventually be eliminated from such regions, with serious consequences for food-web dynamics (Fabry et al., 2008). In the subarctic Pacific, for example, a single species of pteropod (*Limacina helicina*) comprises up to 60% of prey for juvenile pink salmon (Armstrong et al., 2005) as well as for chum and sockeye salmon, pollock and other commercially important fish. Because Pacific pink salmon have a short life cycle, prey quality and abundance during the salmon’s juvenile stage may strongly influence the pink salmon’s adult population size and biomass (Aydina et al., 2005) with follow-on effects to the consumer.

**Ocean carbon buffering system**

- Without the calcifiers that transport up to 80% of the ocean carbon to the deep sea, atmospheric levels would be much higher than they currently are: Sabine et al. (2004) estimate that without the oceanic uptake of CO₂, atmospheric concentrations would be 55 ppm higher. In effect, ocean calcifiers provide mitigation for some of the increased CO₂ emissions. However, this natural buffering service is not able to keep up with the current pace of CO₂ emissions (Caldeira and Wickett, 2003; Raven et al., 2005). If a
tipping point is reached where calcifiers can no longer maintain their shells, an important climate change dampener will be removed from the system.

Ocean carbon sink capacity
- On the time scales of several thousands of years, it is estimated that ~90% of anthropogenic CO$_2$ emissions will end up in the ocean (Archer et al., 1998). Because of the slow mixing time of the ocean, however, the current oceanic uptake fraction is only about one-third of this value (Le Quéré et al., 2012).
- On decadal time scales, there is uncertainty regarding the ocean’s ability to continue to absorb atmospheric CO$_2$ to the same extent it does now. If the efficiency of ocean (Khatiwala et al., 2009), and high latitude waters in particular (Doney et al., 2009b), absorption of CO$_2$ declines more, CO$_2$ will stay in the atmosphere (Gruber et al., 2004).

3.2.7 Recommendations for policy makers

Recommendation 1:
Atmospheric CO$_2$ levels must be reduced to alleviate the impacts of ocean acidification on open ocean calcifiers.

Recommendation 2:
Biodiversity must be protected and stressors such as overfishing and pollution reduced to buy open ocean calcifiers some time to adapt.

3.2.8 References


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3.3 Open algal ecosystems: Diatoms

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Figure 3.3.1: Electron microscope images of diatoms: Stephanopyxis sp. (x700); Thalassiosira sp. (x1080); a pennate diatom (x1080), and a chain forming diatom Odontella sp. (x370). Photo credit Cecilia Rad Menendez & Elaine Mitchell.

Summary points:
- Diatoms are microscopic algae with silica cell walls, and are especially abundant in nutrient-rich surface waters at high latitudes (>40°N and S) and in coastal upwelling regions.
- Annual carbon production by diatoms is $10.7 \times 10^{15}$ gC, this represents ~7.4% of net primary production on earth (earlier predictions were ~20% NPP on Earth).
- Intense diatom blooms occur in spring and summer, after which ~ 40% of carbon fixed by diatoms sinks to >100m depth, representing a carbon flux of $\sim 4.2 \times 10^{15}$ gC.y$^{-1}$ from the surface ocean. Of this, pelagic food-webs consume ~90% of the carbon, but 1-2% reaches depths > 1000 m where it remains for thousands of years.
- Carbon flux from the surface to deep ocean (>1000m) by diatoms is $\sim 0.15 \times 10^{15}$ gC.yr$^{-1}$, which accounts for ~1.7% of annual CO$_2$ emissions from fossil fuels and ~6.5% of the annual sequestration of CO$_2$ by the ocean.
- Warming of the ocean is indirectly reducing nutrient input to the surface waters, leading to a decline in diatom abundance and slowing of the biological pump, which will ultimately reduce CO$_2$ sequestration in the ocean and further exacerbate climate change.
3.3.1 General introduction and focus of section
Diatoms are microscopic single-celled algae that float in the sunlit surface layers of the ocean, and fix dissolved CO$_2$ in their cells through the process of photosynthesis (Falkowski, 2012). Several species form the base of oceanic food webs, and directly and indirectly influence the carbon cycles of many fauna. Diatoms export carbon to the deep-ocean via the ‘biological pump’ (Ragueneau et al., 2006), whereby dead diatom cells and faecal matter from marine consumers sink from the surface ocean. Once in the ocean interior, carbon fixed by diatoms circulates for thousands of years (either as POC or DOC), thereby removing carbon from atmospheric CO$_2$ cycles for that period. Therefore, diatoms and their food-webs are an important natural carbon sink. Diatoms also offer several ecosystem services, for example they support some of the most productive fisheries on earth, are of global significance in the cycling of nutrients and silica, and are used in ecological monitoring.

3.3.2 Definition of species/ecosystem
Diatoms form a major component of the phytoplankton community, and are represented by ~ 1800 different species that live in a range of habitats, from the edge of polar ice sheets to subtropical ocean gyres (Nelson et al., 1996; Leblanc et al., 2012). Diatoms are encased within heavy silica cell walls, known as ‘frustules’ (Figure 3.3.1), and are considered to be ‘large’ phytoplankton with cell sizes ranging from ~ 5 to 500 µm, and occasionally measure up to 2 mm (Leblanc et al., 2012). In addition, some diatoms form chains (Figure 3.3.1, Odontella), or clump into bigger aggregates because of a sticky substance that they secrete (Sarthou et al., 2005; Leblanc et al., 2012). The tendency for diatoms to aggregate, and their large cell size, increases their sinking rates several fold, which has a positive influence on the quantity of carbon and nutrients exported from the surface ocean (Boyd and Newton, 1999; Bopp et al., 2005; Sarthou et al., 2005; Jin et al., 2006). Silica from the cell walls of dead diatoms may accumulate on the sea floor to form deposits known as diatomaceous earth, which has various commercial uses. In some areas these deposits may be up to 1400m thick, such as on Seymour Island in the eastern Antarctic Peninsula (Sims et al., 2006).

Nutrient requirements
Diatoms are unique amongst phytoplankton because they require silica in the form of silicic acid (Si(OH)$_4$) for constructing their frustules (Ragueneau et al., 2006). Iron (Fe) is another essential element, and is important in cellular processes such as respiration and the absorption of nutrients (Sarthou et al., 2005). As such, the growth and distribution of diatoms in the world’s oceans is mainly limited by the concentrations of iron and silicic acid (Leblanc et al., 2005; Ragueneau et al., 2006). Like most primary producers, diatoms also require nitrates and phosphates, but these nutrients are generally more abundant and ubiquitous in the global ocean than iron and silicic acid.

Diatoms have a relatively high nutrient requirement because of their large cell size and small surface-to-volume ratio (Sarthou et al., 2005), therefore they are most abundant in nutrient-rich waters. However, some species have adapted unique ways to persist under low nutrient regimes. For example, several species can control their buoyancy in the water column and move from the sunlit surface ocean to deeper waters (~100m), where they absorb sufficient nutrients to keep on dividing (Villareal et al., 1999; Armbrust, 2009). Symbiotic relationships may also occur between diatoms and cyanobacteria that fix atmospheric nitrogen and supply the diatoms with essential nutrients for growth (Villareal et al., 2012).

Nutrient cycling in the ocean
The biological pump removes nutrients from the upper-ocean (between the surface and thermocline), and exports them to the deep abyss when phytoplankton and detritus sink (Sarmiento et al., 2004). Warm surface water has a lower density than cold deep water, and this density barrier traps nutrients below the thermocline where they reach high concentrations. Coastal upwelling events and strong winds induce vertical mixing of the water column, which brings nutrient-rich deep water to the surface of the ocean (Sigman and Hain, 2012). Mixing of the water column and transport of nutrients to the surface ocean is greatest in winter and at high latitudes (~40°N and S), and weakest during summer and at low latitudes (Sigman and Hain, 2012). The Southern Ocean plays a dominant role in the transport of nutrient-rich deep waters to the upper ocean in the southern hemisphere. Here, water is upwelled adjacent to Antarctica, and simultaneously a very thick winter mixed layer is formed at ~60°S (Sarmiento et al., 2004). In the northern hemisphere, a major input of nutrients to the upper ocean occurs in the NW Pacific, when intense winter mixing is combined with tidal action (Sarmiento et al., 2004).

Diatom lifecycle and seasonality
Diatoms undergo a “bloom and bust” lifecycle, with exponential growth periods in spring and summer that generally end by autumn (Sarthou et al., 2005). Nutrient
concentrations in the surface ocean increase dramatically during winter (as a result of the deep wind-induced mixing), but the light intensity and temperatures are too low to support diatom growth (Sigman and Hain, 2012). Conditions are optimal for massive diatom blooms during spring and summer, when concentrations of up to 10 million diatom cells l⁻¹ of sea water can occur (Leblanc et al., 2012). Diatoms stop reproducing exponentially and sink from the surface ocean once they have depleted essential nutrients (Leblanc et al., 2005; Sarthou et al., 2005). In addition, diatoms stressed by the lack of iron are stimulated to produce thicker silica cell walls, which reduces their buoyancy and induces greater sinking rates (Hutchins and Bruland, 1998; Sarthou et al., 2005; Ragueneau et al., 2006). This periodic sinking of diatoms is known as the ‘summer export pulse’, during which carbon is transported from the surface ocean to deeper waters (Sarthou et al., 2005).

Extent of diatom blooms
In the southern hemisphere, intense diatom blooms occur in the austral summer (November to January) around Antarctica and the polar frontal zones (~60°S) of the Southern Ocean, as shown in Figure 3.3.2A (Sarmiento et al., 2004; Alvain et al., 2008). In the northern hemisphere, diatoms are abundant in the most northerly sector of the NW Pacific and North Atlantic oceans, as shown in Figure 3.3.2B (Leblanc et al., 2005, 2012; Alvain et al., 2008). Here, blooms start at ~ 40°N between May-June, and progress to ~ 60°N by August (Alvain et al., 2008).

Diatom blooms also occur near the Angola or Namibia coasts in the Atlantic, and along the Equator and Peru coasts in the Pacific, where equatorial upwelling drives primary production (Alvain et al., 2008; Sigman and Hain, 2012). However, diatoms contribute less than 20% to the phytoplankton biomass in these equatorial upwelling regions, mainly because low iron concentrations limit their growth (Alvain et al., 2008), and favours smaller phytoplankton species that have lesser nutrient requirements (Sarthou et al., 2005). The lowest abundances of diatoms occur in the Mediterranean Sea and the Indian Ocean (Leblanc et al., 2012).

Role in food web
Diatoms form the base of oceanic food webs, and an example of their trophic role in the Southern Ocean is shown in Figure 3.3.3. Diatoms are mainly consumed by large zooplankton (macrozooplankton such as krill and copepods), and the microbial loop, e.g. bacteria (Huntley et al., 1991; Amin et al., 2012). Macrozooplankton are then eaten by larger predators including fish and squid, as well as birds and mammals such as Adelie penguins, crabeater seals and baleen whales (Figure 3.3.3; Huntley et al., 1991). Diatoms that are not consumed in the upper ocean sink rapidly, and may be eaten by deep-sea marine scavengers (Armbrust, 2009) or subjected to further bacterial degradation (Ragueneau et al., 2006). Faecal matter produced by animals in the surface ocean is assumed to sink to the deep ocean (Huntley et al., 1991). All of the animals within this food web respire CO₂ directly into the seawater, except birds and mammals that are air-breathing predators that respire CO₂ into the atmosphere (Figure 3.3.3). A model created by Huntley et al. (1991) predicted that of all the CO₂ photosynthetically fixed by diatoms in the Antarctic, ~ 12% of the carbon is returned directly to the atmosphere as CO₂ through bird and mammal respiration, ~ 54% is respired into the atmosphere. Figure 3.3.2: Global distribution of diatoms in January and June, shown in chlorophyll units, mg.m⁻³. Images taken from Gregg and Casey (2007), with permission.
Figure 3.3.3: Example of marine food-web structure in the Southern Ocean (Antarctica). Diatoms photosynthetically fix dissolved CO$_2$, and are consumed by microbial fauna and macrozooplankton, which are preyed on by fish, squid, mammals and birds. Birds and mammals respire CO$_2$ into the atmosphere, and all other fauna respire CO$_2$ directly back into the water. The numbers represent the proportion of carbon that is respired as CO$_2$ or sinks as faecal matter to the deep ocean, for every 1 unit of carbon that is photosynthetically fixed by diatoms. Adapted from Huntley et al. (1991).
water as CO$_2$ by other marine fauna, and ~34% sinks as faecal pellets to the deep sea thereby contributing to the biological carbon pump (Figure 3.3.3). These values may be different for diatom-based food webs in other locations of the world.

### 3.3.3 Biogeochemical process of carbon fixation

The net primary production (NPP) of diatoms is estimated to be $10.7 \times 10^{15}$ gC·y$^{-1}$ (Jin et al., 2006). It has been estimated that approximately 60% of the net production by diatoms...
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3.3.4 The significance of diatoms in carbon terms

Phytoplankton can be divided into two groups according to their cell size and the role they play in food webs and the biological pump, namely ‘large’ (>5 μm) and ‘small’ (<5 μm) phytoplankton (Laws et al., 2000; Jin et al., 2006). Large phytoplankton includes diatoms, which play an important role in the biological pump because their weight and size means that they have rapid sinking rates in comparison to small phytoplankton (Leblanc et al., 2012). In addition, diatom cells are ‘ballasted’ with silica frustules that enhance their sinking rates. The growth of large phytoplankton is tightly restricted by nutrient availability, and they are most abundant in nutrient-rich upwelling areas and high latitudes. Although large phytoplankton only represent 30% of NPP in the ocean (23.8 x 10^15 gC.yr^-1, Table 3.3.1), they are responsible for 74% of the POC export from the sea surface to below 100m depth, meaning they represent an important carbon sink. Small-celled phytoplankton include nano- and picoplankton and blue-green algae (cyanobacteria), as well as coccolithophores. Small phytoplankton groups contribute ~70% to net primary production in the oceans.

Table 3.3.1: Rate of net primary production (NPP), particulate organic carbon (POC) export and production-to-export ratio (POC/NPP) for large and small phytoplankton groups.

<table>
<thead>
<tr>
<th>Phytoplankton Type</th>
<th>NPP (x10^15 gC.y^-1)</th>
<th>POC export (x10^15 gC.y^-1)</th>
<th>POC/NPP</th>
</tr>
</thead>
<tbody>
<tr>
<td>Large Phytoplankton</td>
<td>23.8</td>
<td>7.2</td>
<td>0.3</td>
</tr>
<tr>
<td>Of which Diatoms contribute:</td>
<td>10.7</td>
<td>4.2</td>
<td>0.39</td>
</tr>
<tr>
<td>Small Phytoplankton</td>
<td>54.2</td>
<td>2.6</td>
<td>0.04</td>
</tr>
<tr>
<td>Of which Coccolithophores contribute:</td>
<td>1.2</td>
<td>1.1</td>
<td>0.98</td>
</tr>
<tr>
<td>Oceanic phytoplankton TOTAL</td>
<td>78</td>
<td>9.8</td>
<td>0.35</td>
</tr>
</tbody>
</table>

1(Jin et al., 2006), 2(Duarte and Cebrian, 1996), 3 (Janzen, 2004). *Diatoms and coccolithophores are used as examples of large and small phytoplankton respectively, because of the important role they play in the biological pump. *Coastal primary producers* include coastal phytoplankton, microphytobenthos, coral reef algae, macroalgae, seagrass, marsh plants and mangroves (Duarte and Cebrian, 1996).
ocean, and represent an important carbon pool (See Table 3.3.1). It was conventionally thought that small phytoplankton contribute less to the export of carbon (as POC) to the deep sea (Table 3.3.1) because they have slower sinking rates, and ~ 95% of the organic matter that they produce is remineralized and recycled in the surface ocean by herbivore grazers and bacteria (Bopp et al., 2005; Dunne et al., 2006; Jin et al., 2006). However, the carbon from small phytoplankton is effectively ‘repackaged’ in the faecal pellets of grazers, which then sink and export carbon to the deep (Lomas et al., 2010). An exception to this is coccolithophores, whose cell walls are ballasted with calcium carbonate (CaCO$_3$), which facilitates rapid sinking and carbon export from the surface ocean (Table 3.3.1), see case study on calcifiers in Section 3.2. Coccolithophores have the highest export to production ration of all oceanic algae, where nearly 98% of the carbon they fix sinks from the surface ocean (Table 3.3.1).

A simple interpretation of the data in Table 3.3.1 is that large and mineral ballasted phytoplankton (e.g. diatoms and coccolithophores) dominate carbon export (as POC) from the surface ocean. However, this is not always the case, and one needs to take the habitat area of different phytoplankton groups into account, as well as food-web interactions. Small phytoplankton are most abundant in the nutrient poor ‘oligotrophic’ waters of equatorial and subtropical regions, which represent some of the most expansive seas on Earth. These clear oligotrophic waters tend to have deeper light penetration, and hence more photosynthetic area for algae to grow (Lomas et al., 2010) than more nutrient rich waters at higher latitudes. Therefore, integrated over their entire area, most of the oceanic primary production occurs in the oligotrophic ocean gyres (Lomas et al., 2010). However, due to constraints in time and resources, only mineral ballasted phytoplankton (diatoms and coccolithophores) are considered as case studies for carbon export by phytoplankton in this report. However, the reader should bear in mind that small non-ballasted phytoplankton (e.g. picoplankton) inhabiting oligotrophic waters also play a key role in global carbon cycles (see example of Sargasso Sea, Section 3.4, page 57).

Early estimates suggest that oceanic diatoms produce ~20 x 10$^{15}$ gC.y$^{-1}$, which represents ~20% of global primary production (Mann, 1999). However, this was likely to be an overestimate. Subsequently, more accurate research placed oceanic diatom production at 10.7 x 10$^{15}$gC.y$^{-1}$ (Jin et al., 2006), which represents ~7.4% of all the primary production on earth, and ~12% of the primary production in the marine environment (Table 3.3.1). In addition, diatoms account for ~ 43% of all organic carbon exported from the surface ocean by phytoplankton (Jin et al., 2006), and therefore make the greatest contribution to the biological carbon pump. Carbon dioxide emissions from fossil fuel combustion, including cement production and gas flaring, were approximately 9 x 10$^{15}$ gC.y$^{-1}$ between 2000 and 2009 (Le Quéré et al., 2009; Ciais et al., 2013). The total uptake rates of CO$_2$ by land and the ocean were estimated to be 2.6 x 10$^{15}$ gC.y$^{-1}$ and 2.3 x 10$^{15}$ gC.y$^{-1}$ respectively (Le Quéré et al., 2009; Ciais et al., 2013). Therefore, the carbon that diatoms transfer to the deep ocean (0.11 – 0.21 x 10$^{15}$ gC.y$^{-1}$, Figure 3.3.4) accounts for ~ 1.7 % of annual CO$_2$ emissions (Le Quéré et al., 2009; Ciais et al., 2013), and is equivalent to ~6.5% of the annual total uptake of CO$_2$ by the ocean.

Deep-sea sediments are the main long-term repositories for carbon fixed by oceanic diatoms (Duarte and Cebrian, 1996). However, when compared to other marine primary producers, diatoms are remarkably inefficient at transferring carbon to storage in the sediments (Duarte and Cebrian, 1996), as shown in Figure 3.3.5. For example, all coastal primary producers store ~ 0.47 x 10$^{15}$ gC in the sediments per year, which is 10 to 20 times more than diatoms (Figure 3.3.5). Of the coastal primary producers, seagrass, marsh plants and mangroves make the biggest contribution to long-term carbon storage, as shown in Figure 3.3.5 (Duarte and Cebrian, 1996).

![Figure 3.3.5: Carbon stored in sediments by marine primary producers. Blue and orange denote oceanic and coastal primary producers, respectively. See Table 3.3.1 for relevant references.](image-url)
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Regional carbon sinks
The quantity of carbon that diatoms export from the surface ocean varies with latitude, as shown in Figure 3.3.6. The largest region of diatom-based carbon export is the Southern Ocean at ~60°S; here diatoms contribute 80% to the total carbon exported from the surface ocean by all phytoplankton (Jin et al., 2006). At latitudes northwards of ~ 50°S the concentrations of silicic acid and iron become increasingly depleted by diatoms, thereby restricting their growth. However, nitrate concentrations remain high enough to drive the biological productivity of other smaller phytoplankton species at low latitudes, as shown in Figure 3.3.6 (Sarmiento et al., 2004). The North Atlantic, the NW Pacific Ocean and the equatorial Pacific are also sinks for carbon fixed by diatoms, but they are only responsible for 30 to 50% of the carbon exported by all phytoplankton in these regions (Jin et al., 2006).

3.3.5 Evolution with time and threats to the ecosystem
Diatoms evolved approximately 250 million years ago (Sorhannus, 2007), before which phytoplankton mainly consisted of small species such as cyanobacteria and blue-green algae (Falkowski et al., 2004; Armbrust, 2009). Prior to the existence of diatoms, atmospheric concentrations of CO$_2$ were almost five times higher than today (Guidry et al., 2007); the average global temperature was significantly higher (Armbrust, 2009), and the ocean had comparatively lower oxygen concentrations (Armbrust, 2009). The emergence of diatoms initiated a major shift in global carbon cycling, whereby atmospheric CO$_2$ concentrations and temperatures decreased and oxygen concentrations increased dramatically (Katz et al., 2005), making the planet more hospitable to life. In addition, the greater sinking rates associated with large celled phytoplankton, such as diatoms, enhanced the burial of carbon in the sea floor and created most of the petroleum exploited today (Falkowski et al., 2005; Armbrust, 2009). It is the burning of these fossil fuels by mankind that is currently accelerating the release of CO$_2$ into the atmosphere, warming the earth, and causing modern-day climate change.

The greatest threat that diatom populations currently face is climate change, and there is clear evidence that marine phytoplankton abundance has declined over the last century (Boyce et al., 2010). The world’s ocean is warming, which is increasing thermal stratification between surface and deep waters, resulting in less efficient wind-driven mixing and a decline in the quantity of nutrients introduced to the surface ocean (Laws et al., 2000; Bopp et al., 2005; Cermeño et al., 2008; Falkowski, 2012). As a result, the ocean’s least productive oligotrophic (low-nutrient) waters are expanding at a rate of 0.8 to 4.3% per year (Polovina et al., 2008).

Diatom abundance is predicted to decline and there will be an increase in small phytoplankton that can tolerate low-nutrient environments (Bopp et al., 2005). A shift away from diatom communities will result in less export of organic matter to the deep, and more CO$_2$ recycled in the upper ocean by small phytoplankton (Bopp et al., 2005). Climate change simulations predict that if atmospheric CO$_2$ concentrations rise at 1% per year for 140 years (classic CMIP-II scenario; http://cmip-pcmdi.llnl.gov/, Bopp et al., 2005), reaching four times pre-industrial CO$_2$ concentrations (i.e. 4 x 286.2 ppm), then the relative abundance of diatoms will be reduced by more than 10% globally, which would decrease the export ratio (export production divided by the primary production) by as much as 25%, from 10 x 10$^{15}$ gC·y$^{-1}$ to...
Diatoms provide several valuable supporting services within ecosystems such as the cycling of nutrients between surface and deep ocean waters, provision of primary production that is the base of marine foodwebs, and supply of O₂ that is essential for most life (Sarthou et al., 2005). Diatoms also play a huge role in the cycling of CO₂ between the atmosphere and the ocean, which helps control the Earth's climate (Smetacek, 1999; Beaugrand et al., 2010; Falkowski, 2012). Diatoms have important scientific value, for example they are increasingly being used in ecological monitoring to detect changes in nutrient concentrations (Mann, 1999), and are used in palaeoecological reconstruction whereby sea-floor deposits of dead diatoms are used as historical tracers of environmental change (Mann, 1999). In terms of direct commercial value, diatomaceous earth is mined and used for a variety of applications, including use in pesticides (e.g. flea powder), insulation and toothpaste ingredients (Armbrust, 2009).

Diatoms form the base of oceanic and coastal food webs and seasonal diatoms blooms sustain some of the most productive fisheries in the world (Mann, 1999; Armbrust, 2009), such as the krill fishery in the Southern Ocean that can supply up to 11% of the current world marine fishery landings (Grant et al., 2013). Sinking dead diatoms and the faecal matter of their predators are also an important food source to deep-sea fauna and economically important demersal fish (Townsend and Cammen, 1988; Sarthou et al., 2005). Maintenance of these fisheries depends on primary production by diatoms (Grant et al., 2013), and any changes in diatom abundance will effect the provision of food to humans (Beaugrand et al., 2010). For example, a shift towards smaller phytoplankton and zooplankton species with climate warming is predicted to slow the biological pump, which would have a negative impact on demersal Atlantic cod (Gadus morhua) populations (Beaugrand et al., 2010).

One of the most crucial ecosystem services provided by diatoms is regulation of the Earth's climate, whereby the CO₂ that is photosynthetically fixed by diatoms is exported to the deep ocean via the biological pump (Falkowski, 2012). As mentioned earlier in this chapter, diatoms export more carbon from the surface of the ocean to the deep than any other phytoplankton group (Jin et al., 2006), and the evolution of diatoms more than 250 Myr ago facilitated the development of a more hospitable planet by lowering atmospheric CO₂ concentrations (and thereby temperatures) to levels that were favourable to a diversity of life (Armbrust, 2009). Without diatoms global temperature would be significantly higher than they are today. Researchers are now attempting to artificially enhance the growth of diatoms in the oceans, with the hope that it would accelerate the rate of carbon export to the deep sea via the biological pump, and thereby slow global warming caused by mankind (Boyd and Denman, 2008).

Primary production by phytoplankton (mainly diatoms) is limited by low iron concentrations in 30-40% of the world's ocean, which are known as “High Nutrient Low Chlorophyll” (HNLC) regions (Hutchins and Bruland, 1998; Moore et al., 2001; Armbrust, 2009). It has been hypothesized that if these regions were artificially fertilized with iron, then there would be an increase in diatom production, which would enhance the drawdown of CO₂ to the deep ocean. However, the results and implications of the ocean iron experiments are controversial. Experiments show that most of the organic carbon produced by fertilized diatom blooms is consumed in surface waters, and there is a relatively small increase in carbon export to the deep ocean (Denman, 2008). It is estimated that if 20% of the world's ocean were fertilized with iron 15 times per year until 2100, less than 3.2 x 10¹⁶gC would be sequestered (Zeebe and Archer, 2005; Denman, 2008). This represents ~26.6% of the carbon that must be sequestered from the atmosphere over the next century (~1.2 - 1.5 x 10¹⁷gC) in order to limit global temperature change to 2°C, and maintain atmospheric CO₂ concentrations. When diatom growth is slowed, the biological pump would reduce CO₂ sequestration, and exacerbate climate warming by increasing atmospheric CO₂ concentrations (Cermeño et al., 2008; Falkowski, 2012).
concentrations at current levels of ~400ppm (Hughes et al., 2012; Lemoine et al., 2012). However, geo-engineering the marine environment with large-scale iron fertilization is likely to result in massive ecological changes that would negatively impact other ecosystem services provided by diatoms.

There are several major threats associated with iron fertilization experiments, as highlighted by Denman (2008): 1) increased biological activity in the surface ocean will reduce O₂ concentrations and lead to the development of anoxic waters; 2) bacterial degradation of the particulate organic matter in diatom blooms may release N₂O, a long-lived greenhouse gas; 3) enhancing diatom blooms may increase nutrient export to the deep sea, and because ocean warming is slowing the return of nutrients to the surface, this will ultimately reduce total ocean primary production; and 4) accelerated CO₂ uptake by diatom blooms and recycling in the upper ocean will lead to an increase in the rate of ocean acidification, and a reduction in the pH. Therefore, large-scale iron fertilization may not be the answer to sequestering CO₂ and slowing climate change. We should rather strive to protect the healthy functioning of marine diatom ecosystems, and maintain the valuable service that they already provide.

3.3.7 References


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3.4 Floating seaweed (Sargassum)

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Summary points:
- Floating Sargassum, which occurs in the Sargasso Sea and Gulf of Mexico, constitutes the world’s largest biomass of oceanic seaweed.
- A large diversity of marine fauna is associated with Sargassum, however, its role in oceanic food-webs and carbon cycles has been under assessed up to this point.
- The annual carbon production by Sargassum is $2.7 \times 10^{11}$ gC, which is ~0.5% of the primary production in Sargasso Sea, and constitutes 0.0006% of production by all marine primary producers globally. However biological production of Sargassum is of significant importance in some areas of the Gulf of Mexico, where it may constitute up to 10% of net primary production.
- The annual carbon sequestration by Sargassum is estimated to be $> 4.3 \times 10^{10}$ gC via rDOC production and sinking faecal pellets of grazers, and accounts for ~0.002% of the $2.3 \times 10^{15}$ gC of CO$_2$ annually sequestered by the ocean (Le Quéré et al., 2009; Ciais et al., 2013). However, this estimate does not include the biomass of sinking Sargassum, which is currently unknown and is expected to make a significant contribution to carbon sequestration.
- More broadly in terms of mitigation, Sargassum occupies a small area of the sea surface, and CO$_2$ sequestration can be enhanced either by cultivating additional seaweed in the ocean, or by cultivating microalgae on land, and then converting the algae to biofuels.
- In order to limit global temperature rise to 2°C, ~ $3.2 \times 10^{15}$ gC must be removed from the atmosphere, and 10% of this goal could be met by cultivating seaweed in 4% of the oceans exclusive economic zone (EEZ) for the next 100 years.
3.4.1 Introduction

Vast rafts of floating seaweed (macroalgae) occur in the world’s ocean, and are biodiversity hotspots that provide food and shelter to many animals. The focus of this chapter is on floating *Sargassum natans* and *S. fluitans* (hereafter *Sargassum*), which occur in the Sargasso Sea and the Gulf of Mexico. *Sargassum* travels thousands of kilometres at the mercy of winds and currents, and plays an important but under-studied role in the oceanic carbon cycle. Floating seaweed utilize CO$_2$ as they grow, and sequester carbon when they sink to the deep sea or when the faecal pellets of their grazers sink. Seaweed also leach dissolved organic carbon (DOC) into the sea, some of which is non-reactive (recalcitrant rDOC) and is stored in the oceanic carbon pool for thousands of years. Because *Sargassum* forms an important food source in the open ocean, it also indirectly influences the carbon cycles of various marine fauna when it is consumed and recycle in pelagic food webs. Pioneering research is now underway to develop oceanic farms for the large-scale cultivation of seaweed (mainly kelp species), which could be used to recycle and sequester excess CO$_2$, and produce biofuel such as methane and bioethanol. If these biofuels were used as a carbon-negative substitute for fossil fuels, then floating seaweed farms would make a significant contribution to lowering global atmospheric CO$_2$ concentrations and mitigating climate change.

3.4.2 Definition of species/ecosystem

Free floating *Sargassum*, commonly known as gulf-weed or sea-holly (Figure 3.4.1), is unique amongst large algae because it undergoes its entire life cycle in the open-ocean, and floats on the sea surface using specially adapted air bladders (Ramus, 1992). The vast majority of other seaweed species in the world occur in shallow coastal areas, where they grow whilst being attached to the sea bed (Ramus, 1992). The focus of this section is on oceanic *Sargassum*, and readers are referred to Laffoley and Grimsditch (2009) for the role of coastal seaweeds in carbon cycling.

The distribution of *Sargassum* is centred on the Sargasso Sea (Figure 3.4.2); an enormous eddy located in the North Atlantic subtropical Gyre with an approximate latitude range of 20° - 40° N and longitude range of 40° - 80° W (Gower et al., 2013). The Sargasso Sea is the only sea in the world that is not bordered by land, but whose boundaries are defined by surrounding currents (Ryther, 1956; Laffoley et al., 2011). Satellite observations show that *Sargassum* starts growing rapidly in the north-western Gulf of Mexico each year in spring (June) and is transported into the North Atlantic (Sargasso Sea) in summer by the Loop Current (seen as a ‘Sargassum jet’), moving northwards with the Gulf Stream (Gower and King, 2011). The floating seaweed then moves south and west and reaches the north-east Bahamas in winter the following year where it is thought to die (Gower and King, 2008, 2011).

The greatest biomass of *Sargassum* is generally observed between March and June in the Gulf of Mexico, which is considered to be the *Sargassum* ‘nursery area’ (Gower and King, 2008, 2011), and satellite observations suggest that most *Sargassum* has a lifespan of 1 year or less (Gower and King, 2011). *Sargassum* is also likely to self-replicate and grow as it circulates within the Sargasso Sea. The seasonal circulation of *Sargassum* between 20° – 40° N latitude and 100° – 40° W longitude (i.e. the Sargasso Sea) is driven by prevailing surface currents and winds, and was generally consistent between the years 2003 - 2008 (Gower and King, 2011). However, in the summer of 2011 there was a major bloom of *Sargassum* at the mouth of the Amazon, after which large amounts of the seaweed were washed onto the beaches of the eastern Caribbean causing significant problems for local tourism (Gower et al., 2013). *Sargassum* also reached the coast of Africa in 2011 (Gower et al., 2013). The Amazon mouth is not an area not previously associated with *Sargassum* growth, and the reasons for this range shift are not known at present (Gower et al., 2013).
Individual Sargassum plants may be several metres long, with a highly branched stem and bushy leaf-like blades, and reproduces asexually via vegetative propagation (Ramus, 1992). Sargassum generally accumulates at the sea surface in long lines or ‘windrows’ where wind-driven currents converge in a process known as Langmuir circulation (Coston-Clements et al., 1991; Woodcock, 1993). Aerial images show that Sargassum can form continuous drift lines of at least 5 km long, which primarily consist of rafts measuring 20 - 80 m² in size, but with some aggregations measuring more than 1000 m² (Marmorino et al., 2011). At a larger scale of detection, satellite images indicate that Sargassum can form long ‘slicks’ on the ocean surface measuring 100 to 1000 m wide, and tens to hundreds of kilometres long (Gower et al., 2006). However, consolidated drift lines of Sargassum start to disintegrate at wind speed > 5 m.s⁻¹ (Marmorino et al., 2011).

Rafts of Sargassum act as floating reefs, and support more than 100 species of invertebrates (Coston-Clements et al., 1991), 54 species of fish (Dooley, 1972), four species of juvenile turtles (Witherington et al., 2012), and attracts large predators such as dolphins, jacks, barracudas and tuna, (Figure 3.4.3), (Coston-Clements et al., 1991). Many invertebrates such as hydroids, bryozoans, and barnacles are encrusted onto the surface of Sargassum, and crabs, shrimps, snails and polychaete worms live freely amongst the seaweed (Coston-Clements et al., 1991).

Sargassum that sinks to the ocean floor plays a central role in deep-sea food-webs, and is consumed by scavengers such as starfish and small crustaceans (Fleury and Drazen, 2013).

The Sargasso Sea has very low concentrations of nutrients (oligotrophic), which would typically limit the growth of seaweed (Rothäusler et al., 2012). However, Sargassum supports a unique community of epiphytes (smaller attached blue-green algae) and cyanobacteria that fix nitrogen, i.e. convert $N_2 \rightarrow \text{NH}_3$ (Hanson, 1977; Philips et al., 1986), and supply up to 44% of the nutrient requirements of Sargassum and its community (Hanson, 1977). In addition, Sargassum is able to reuse phosphates that are released by microorganisms living amongst the seaweed (Lapointe, 1986).

Despite the Sargasso Sea being considered ‘oligotrophic’, it also supports abundant growth of small phytoplankton, which tend to dominate low-nutrient environments (as described in Section 3.3). As such, the Sargasso Sea has a net primary production rate per unit area that is three times higher than the Bering Sea (Steinberg et al., 2001; Lomas et al., 2012), which is conventionally regarded as one of the world’s most productive seas (Laffoley et al., 2011). However, a large fraction (>50%) of the primary production in nutrient-rich sub-polar waters, such as the Bering Sea, is eventually consumed by larger predators (e.g. crab, shellfish and pollock), which are harvested by man, thereby removing carbon from ocean carbon sinks. In contrast, much of the carbon fixed by small phytoplankton (and possibly also by Sargassum) in the oligotrophic gyre of the Sargasso is channelled into faecal pellets of small grazers, which eventually sink as POC to the deep ocean (Lomas et al., 2011). Therefore, oligotrophic gyres that are dominated by small phytoplankton account for ~60% of global carbon export (Lomas et al., 2010), and the Sargasso Sea alone represents ~ 7% of the global net biological carbon pump (Laffoley et al., 2011).

### 3.4.3 Regional and global significance of feature in carbon terms

Early ship-based estimates for Sargassum biomass range between 4 - 11 million tons (wet weight) for the North Atlantic, the Caribbean Sea and the Gulf of Mexico combined (Parr, 1939; Stoner, 1983; Butler the recruitment success of several species (Wells and Rooker, 2004). Pelagic Sargassum is also an important nursery area for juvenile fish (Coston-Clements et al., 1991; Wells and Rooker, 2004) and has been designated as an Essential Fish Habitat (EFH) by the National Marine Fisheries Service (NMFS) (NOAA, 1996; Wells and Rooker, 2004; Laffoley et al., 2011).

Floating seaweed drifts thousands of kilometres and helps with the dispersal of plankton, juvenile fish (Kingsford, 1993) and turtles, and influences...
Sargassum Biomass: $1.6 \times 10^{11}$ gC  
NPP: $1 \times 10^{12}$ gC yr$^{-1}$

Figure 3.4.4: Fate of floating Sargassum, and pathways of carbon sequestration
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and Stoner, 1984). However, more recent estimates derived from satellite data between 2003 - 2007 found an average of ~ 1 million tonnes (wet weight) Sargassum in each of the Gulf of Mexico and the Atlantic, totalling 2 million tonnes (Gower and King, 2011). Satellite observations show a significant annual flow of ~1 million tonnes of Sargassum out of the Gulf of Mexico into the North Atlantic, which implies a carbon flux that needs to be accounted for in future carbon models (Gower and King, 2011). If Sargassum wet weight from satellite estimates is converted to its carbon value (see calculation box at end of section), then total Sargassum biomass represents approximately 8 x 10^10 gC.

The annual net primary production (NPP) of Sargassum is ~2.7 x 10^11 gC (see calculation box at end of section). Early estimates report that Sargassum productivity is ~ 0.5% of that of phytoplankton in the entire Sargasso Sea (Carpenter and Cox, 1974), and later studies suggest that Sargassum productivity can contribute nearly 10% to total productivity in the western Gulf of Mexico (Gower et al., 2006). Therefore, Sargassum can represent an important fraction of total biological productivity in areas of the ocean where it is most abundant (Gower et al., 2006). However, Sargassum only accounts for 0.0006% of the net primary production by all marine primary producers globally, which is estimated to be of 1.6 x 10^17 gC.y^-1 (Duarte and Cebrian, 1996).

More recent estimates are required for Sargassum productivity versus that of all the phytoplankton in the entire Sargasso Sea, which is now considered to be one of the most productive areas of ocean in the world (Laffoley et al., 2011). Despite being classed as ‘oligotrophic’, the high primary productivity by phytoplankton in the Sargasso Sea can be attributed to the deep euphotic zone in which algae can grow (clear sub-tropical water = deeper light penetration) and the abundance of small phytoplankton (i.e. picoplankton), which are able to reproduce very effectively in low nutrient environments because of their high surface to-volume ratio (Buitenhuis et al., 2012). Furthermore, the amount of primary production in the Sargasso Sea has been increasing over the last decade due to climate warming and changes in nutrient cycling to the surface ocean (Lomas et al., 2010; Laffoley et al., 2011; Buitenhuis et al., 2012).

3.4.4 Biogeochemical processes of carbon fixation

Floating seaweed sequester carbon via three main pathways (Figure 3.4.4): 1) algae are ‘downwelled’ or sink to the deep-ocean; 2) grazer faecal pellets sink to deep-ocean, and 3) dissolved organic carbon (DOC) leaches from growing seaweed, some of which is non-reactive (recalcitrant rDOC) and circulates in the ocean for thousands of years. A large proportion of carbon produced by floating seaweed will also be recycled in oceanic food-webs, and ultimately released as CO2 through the process of respiration (Duarte and Cebrian, 1996). The mechanisms of carbon sequestration are explained in more detail below.

Sinking seaweed

Ageing Sargassum naturally sinks to the abyssal sea floor when it loses its buoyancy, due to being heavily encrusted with epiphytic plants and animals (Stoner, 1983). In addition, winds (>4 m.s^-1) that blow over the sea surface generate circulating currents of water, and Sargassum is ‘pushed’ below the sea surface where these currents converge, (Figure 3.4.4), (Coston-Clements et al., 1991; Woodcock, 1993). It takes approximately 2 days for Sargassum to sink to 5000m (Schoener and Rowe, 1970), which is very rapid in comparison to diatoms and marine snow that take 50 to 100 days to reach 5000m (Sarthou et al., 2005). Once Sargassum reaches the sea bed it is consumed by deep-sea fauna (Schoener and Rowe, 1970; Fleury and Drazen, 2013) and/or is buried in the sediments.

Sargassum fragments have occasionally been found at depths of 1500m and 3200m in sediment traps off Bermuda (Maureen Conte, Ocean Flux Program (OFP), personal communication 2013; http://ecosystems.mbl.edu/conte/ofp/), as shown in Figure 3.4.5. It is estimated that visible Sargassum fragments (e.g. those in Figure 3.4.5) contribute less than 1% to the total mass of all particles captured in the Bermuda sediment traps each year, however, this does not mean that unidentifiable Sargassum detritus is not also present (Maureen Conte, OFP, personal communication 2013). Photographic evidence in the western North Atlantic also shows widespread occurrence of Sargassum on the sea floor (Schoener and Rowe, 1970), and therefore it is likely to play a role in carbon sequestration, and should be included in future carbon flux models (Dierssen et al., 2009).

The quantity of Sargassum that sinks to the deep ocean (1500 to 3200 m) generally increases in the late autumn
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and early-winter period, as shown in unpublished time-series data from the OFP (Figure 3.4.6 A). This seasonal trend could be attributed to the greater amount of wind-driven mixing, and a break down in the temperature-density stratification between warm surface water and cool deep water with the onset of winter (Maureen Conte, OFP, personal communication). The quantity of sinking Sargassum may also increase during this period due to natural senescence of the seaweed (Gower and King, 2008). There is considerable year-to-year variability in the quantity of Sargassum fragments that reach the deep ocean (Figure 3.4.6 B), which could be linked to natural variability in the abundance of Sargassum in surface waters (Maureen Conte, personal communication, OFP).

The data on sinking Sargassum from the Ocean Flux Program (Figure 3.4.6) are based on area measurements (mm²) of Sargassum fragments, made from image analysis of the microphotographs for each particle trap sample in the deep ocean. There are currently no data on the biomass of Sargassum-based carbon that reaches the deep ocean or abyssal sea floor. This data gap could possibly be filled by conducting geochemical studies on the Sargassum fragments captured in deep-ocean sediment traps, and thereby determine the percentage contribution of Sargassum detritus to oceanic carbon reservoirs.

Recalcitrant dissolved organic carbon (rDOC)

Marine dissolved organic carbon (DOC) constitutes one of the Earth's largest carbon reservoirs (~ 700 x 10¹⁵ gC), which is equivalent to the amount of carbon contained in the atmosphere as CO₂ (Ciais et al., 2013), and 200 times greater than the carbon content of all marine biomass (Hansell et al., 2009). As seaweeds grow, they release dissolved organic carbon (DOC) into the water, most of which are carbohydrates that are rapidly consumed by bacteria that release CO₂ as they respire (Jiao et al., 2010). These 'labile' forms of DOC play no role in carbon sequestration. However, some DOC is non-reactive small molecules that are resistant to bacterial degradation for up to 4000-6000 years, and constitutes an important but invisible carbon sink (Bauer et al., 1992). This recalcitrant DOC (rDOC) is present everywhere in the ocean, but mainly circulates at depths > 1000m (Hansell, 2013). It is estimated that Sargassum sequesters approximately 1.6 x 10¹⁰ gC.y⁻¹ as rDOC (see calculation box), which remains 'locked' in the ocean for thousands of years.

![Figure 3.4.6: Seasonal variation of sinking Sargassum fragments that reach depths of 500m, 1500m and 3200m off Bermuda, from 2001-2004, grouped per month in plot A, and per month in individual years in plot B (Unpublished data, courtesy Maureen Conte from the OFP - funded by National Science Foundation).](image-url)
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Sinking of grazer faecal pellets
Animals that live amongst *Sargassum* produce faecal pellets that contain carbon originating from the seaweed. Faecal pellets release dissolved organic matter to the ocean through dissolution and microbial decomposition (Itoh et al., 2007), which supplies nutrients for further seaweed growth. Organic matter that is not lost from the faecal pellets in the surface ocean sinks, and thereby enters deep-ocean carbon reservoirs (Itoh et al., 2007). Approximately 10% of the primary production of coastal species of *Sargassum* (e.g., *S. ringgoldianum*, *S. horneri* and *S. patens* found in Japanese waters) is vertically transported to the sea floor by faecal pellets (Itoh et al., 2007). If it is assumed that similar values occur in oceanic *Sargassum* communities, then the annual export of carbon by sinking faecal pellets would be ~2.7 x 10^10 gC (see calculation box), however, regional studies are needed to confirm this.

3.4.5 Threats to the ecosystem and evolution with time
The threats faced by *Sargassum* and its community include harvesting of *Sargassum* for fertilizer and biofuel, the toxic effects of pollutants such as oil, and changes in productivity and reproductive success as a result of climate change. *Sargassum* is a protected habitat that is not harvested at present (Laffoley et al., 2011), but there have been several proposals to extract it for biofuel production (N’Yeurt et al., 2012). No long-term changes in *Sargassum* biomass occurred between 1933 - 1983 (Butler and Stoner, 1984), but more up-to-date assessments are required.

The large amount of shipping activity within the North Atlantic is associated with the release of pollutants such as oils, tar and plastics, which accumulate in the Sargasso Sea and become trapped within *Sargassum*. Residues of oil and tar have been found in *Sargassum* and its fauna, including crabs, snails and turtles (Laffoley et al., 2011 and references therein), and the concentrations of polychlorinated biphenyls (PCBs) may be four times greater within *Sargassum* compared to the open-ocean (Bidleman and Olney, 1974). However, stricter regulations on ships’ oil discharge have recently helped to reduce the concentrations of tar and oil in the Sargasso Sea (Laffoley et al., 2011). Concerns were raised about the decline in *Sargassum* biomass as a result of pollution in the 1980s, but no effect could be shown (Butler and Stoner, 1984), however, further studies are needed to assess the current impacts of pollutants on the *Sargassum* community.

The response of floating seaweed to climate change is not well documented. Elevated concentrations of CO₂ may increase algal photosynthetic rate up to a point, but the growth of most seaweed is inhibited at atmospheric CO₂ concentrations between 500 – 1900 ppm (Gao and McKinley, 1994). Increases in solar radiation and sea surface temperature (>20°C) have negative impacts on the growth and reproduction of seaweeds found at low latitudes, such as kelp species floating off Chile (Rothäusler et al., 2012). On the contrary, *Sargassum* found in the Sargasso Sea is adapted to high levels of solar radiation and persists at temperatures between 18 – 30°C (Rothäusler et al., 2012), and thus may be more capable of dealing with elevated temperatures.

3.4.6 Goods and services: Seaweeds for bioenergy and carbon capture and storage (BECCS)
In order to limit global temperature change to the target of 2°C over the next century, there must be a significant reduction in the emissions of greenhouse gasses (especially CO₂) and removal of CO₂ from the atmosphere. To achieve this target and maintain atmospheric CO₂ concentrations near current levels (~400 ppm), approximately 1.2 - 1.5 x 10^17 gC must be sequestered from the atmosphere (Hughes et al., 2012a; Lemoine et al., 2012). It is now widely recognized that to achieve this it will be necessary to introduce sustainable and renewable alternative energies, and find additional methods of carbon capture and storage.

It was estimated that 90% of the increase in CO₂ emissions between 1990 and 2010 were attributed to the combustion of oil-based fuels for transport (Kraan, 2013), and the growing transport sector is one of the main reasons why nations are failing to meet the CO₂ emission targets set by the Kyoto protocol (Kraan, 2013). Biofuels are the most readily available substitute for fossil fuels, and can make an important contribution to restoring the CO₂ balance and reducing our dependency on non-renewable oil resources. As such, there has been a recent boom in the biofuel market, which is heavily influenced by policies that promote the production and consumption of biofuels. For example, the European Union aims to replace 10% of all transport fuels with biofuels by 2020, and of that only 5% can be supplied by food-based biofuels (EC, 2012). In the United States, the Renewable Fuel Standard (RFS) policy requires that the amount of biofuel used in national transport fuel each year must rise from 9 billion gallons in 2008 to 36 billion gallons by 2022, with a cap of 15 billion gallons for
corn-starch ethanol (Schnepf and Yacobucci, 2013). This 36 billion gallons of renewable fuel is expected to displace 13.6 billion gallons of petrol and diesel, and represent ~7% of the predicted annual fuel consumption in the US (Schnepf and Yacobucci, 2013).

A number of biofuel technologies are available, each with their advantages and challenges. Although no single biofuel may provide a total solution it seems that a combination of biofuels could substantially decrease our dependence on fossil fuels (Hannon et al., 2010). The majority of the world’s biofuels are currently produced from land-crops such as corn and sugar cane, as well as vegetable oil (OECD/FAO, 2013). However, these terrestrial sources are under scrutiny because they are associated with land degradation, conservation issues (loss of biodiversity) and place great demands on global food and water resources (Gao and McKinley, 1994; Pimentel, 2003; Hughes et al., 2012a, b). Large-scale production of marine biomass is seen as a favourable complement to terrestrial-crop biofuels, and could help contribute to a more sustainable energy future.

Marine bioenergy can be divided into two main components: cultivation of macroalgae (seaweed) for biogas production (~60% methane) or liquid fuels, and cultivation of microalgae (single celled plants such as diatoms) for biodiesel (Hughes et al., 2012b). Seaweed and microalgae utilize CO₂ to grow and the combustion of their biofuel products releases CO₂ back into the atmosphere. As such, algal biofuels may be carbon-neutral or negative, provided that the amount of CO₂ emitted during biomass production and combustion is equal to, or less than that fixed by seaweeds and/or microalgae during photosynthesis. Meaning that there would be no net build-up of CO₂ in the atmosphere (Gao and McKinley, 1994). It is difficult to compare the commercial viability of biofuel production from seaweed farms versus microalgae culture, because there is still considerable uncertainty about the levels of investment and technology required for both culture techniques (Bruton et al., 2009; Klein-Marcuschamer et al., 2013).

Bioenergy from microalgae has been a subject of considerable research and investment in recent years and shows promise as a new ‘fuel crop’ (Brennan and Owende, 2010; Shilton and Guieysse, 2010; Singh and Cu, 2010). The favourable aspects of microalgae include: their naturally high oil content; their extremely rapid growth rates compared to terrestrial crops and seaweed, with some species capable of doubling their biomass in 6 hours (Sheehan et al., 2008); the large diversity of strains to choose from to optimize oil production (> 30 000 - 1 million species (Guiry, 2012)), and; the fact that the algae can be cultivated in ponds on land that is not being used for agriculture, or can be grown in the controlled environment of photobioreactors (Hannon et al., 2010). The growth of microalgae for biodiesel can also be used for environmental remediation by culturing the algae in nutrient-rich waste-water streams, and by recycling the CO₂ released from power plants (Bruton et al., 2009).

However, the industrial commercialization of microalgal fuels faces major challenges, such as finding efficient low-cost methods for harvesting the algae and extracting the oils, and sourcing enough land, water and nutrients to cultivate algae on the scale required to substitute fossil fuels (Bruton et al., 2009; Klein-Marcuschamer et al., 2013). For example, using current technology it would be possible to replace half of the petroleum used for transport in the United States of America with microalgal biodiesel, however, this would require 5.5% of the land and nearly three times the water currently used by agriculture in the U.S. (Wigmasta et al., 2011). The massive water requirements for pond cultivation of microalgae will be one of the main factors that determine the economic feasibility of algal fuel production. Therefore, several critics argue that microalgal fuels are unlikely to be economically competitive in the biofuels market, nor logistically or environmentally feasible in the near future (Shilton and Guieysse, 2010; Hughes et al., 2012b).

Within the last 5 years there has been renewed interest in growing seaweed as a source of bioenergy (e.g. EU Biomara programme). Production of biofuels from seaweed is more cost and energy effective than for microalgae (Roesijad et al., 2010; Chung et al., 2011; Hughes et al., 2012b), and the cultivation and harvesting methods are well established. Seaweed biofuels are also a more sustainable alternative to terrestrial fuel crops because they place virtually no demand on freshwater supplies, require minimal to no fertilizer, do not compete for space on land, have a small impact on the human food chain, and may have an overall positive effect on biodiversity (Gao and McKinley, 1994; Hughes et al., 2012b). In addition, seaweed grown in eutrophic waters (e.g. next to fish farms) would help remove excess nutrients and aid environmental remediation (Kelly and Dworjanyn, 2008; Kraan, 2013). Therefore, seaweed
cultivation offers significant advantages and potential in the bioenergy market.

Seaweed aquaculture also enhances long-term carbon capture and storage (CCS) in the ocean (Hughes et al., 2012a). All seaweed fix carbon from dissolved CO\(_2\) during photosynthesis, and release some recalcitrant dissolved organic carbon (rDOC) into the water as they grow, thereby transferring carbon from atmosphere to ocean (see 3.3.4 above). This rDOC circulates in the ocean for 4000 - 6000 years, which renders the carbon unavailable to atmospheric CO\(_2\) cycles for that period (Hughes et al., 2012a). Furthermore, carbon storage can be enhanced by fertilizing land with the waste products from seaweed biofuel. A small percentage of this waste is fibrous organic material that is resistant to bacterial degradation, and will thereby enter long-term storage in the sediments (Hughes et al., 2012a).

Various estimates exist for the amount of CO\(_2\) that can be sequestered or recycled by seaweed biofuel production. In terms of carbon capture and storage (CCS) targets, seaweed cultivated for biofuel production in 4% of the global exclusive economic zone (4x10^6 km\(^2\) or 4x10^8 hectares) could remove 3.2 x 10^14 gC from the atmosphere per year (Hughes et al., 2012a). Cultivation at this scale for 100 years would capture and store 10% of the carbon required to limit global temperature change to 2°C (Hughes et al., 2012a). However, this would require cultivating seaweed in 400 times the area currently used by aquaculture worldwide (Hughes et al., 2012a). Global consumption of motor petrol in 2010 was ~ 337 billion gallons, 40% of which was consumed by the United States (EIA, 2013). To replace just 1% of the domestic supply of petrol in the US with macroalgae derived biofuels would entail cultivating ~ 10.5 times more seaweed annually than the current worldwide production, and would require ~1.0 x 10^4 km\(^2\) of ocean surface (Roesijad et al., 2010). Therefore, seaweed would have to be farmed on a massive scale to make a meaningful contribution to the biofuel and carbon capture and sequestration targets.

The best candidates for biofuel are fast growing, carbohydrate-rich brown algae, such as kelp (Gao and McKinley, 1994; Kraan, 2013). These seaweeds are traditionally cultivated in sheltered inshore areas that are already under pressure from other forms of aquaculture and fishing. In 2008, aquaculture produced approximately 15.7 million tons of seaweed globally, the majority of which was produced in coastal areas of Asia (FAO, 2010). For seaweed to contribute significantly to fuel production and carbon sequestration, without impacting the current seaweed industry, then cultivation needs to extend to the continental shelves and the open-ocean. Oceanic algae culture poses several engineering and logistical hurdles, such as developing farms that are able to withstand the strong forces during storms (Show et al., 1979; Bird and Benson, 1987; Roesijad et al., 2008) and finding sites with sufficient nutrient concentrations for mass cultivation (Orr and Sarmiento, 1992; Gao and McKinley, 1994). Additional nutrients may be supplied by: effluent and sewage waste water (Gao and McKinley, 1994); from residues of biofuel production; by artificially upwelling nutrient-rich deep sea water; or by positioning algae farms in natural upwelling areas (Gao and McKinley, 1994; Roesijad et al., 2008). Recent advancements in engineering have led to the successful cultivation of kelp in the North Sea using the ‘offshore ring system’ (Figure 3.4.7), in which seaweed was grown from a floating ring that was tethered to the sea bed (Buck and Buchholz, 2004; Roesijad et al., 2008; Reith et al., 2012). There is also potential for seaweed farms to be attached to offshore wind farms (Reith et al., 2012), thereby integrating various forms of renewable energy.

Figure 3.4.7: Offshore ring system used to cultivate kelp, Laminaria saccharina, in the North Sea. From Buck and Buchholz (2004) ©Springer, licence 3224781465077

The environmental impacts of seaweed farms are not well understood at present, but may include: removal of nutrients and trace elements by the seaweeds that are important in supporting other marine food-webs; introduction of pollution and litter associated with farms; disturbance to seabed habitats; and introduction of non-native invasive species (Reith et al., 2012). Establishment
of new seaweed farms may also result in conflict with other sea users, such as shipping, fisheries, recreation, marine reserves and the military. It is imperative to stress that harvesting wild populations of seaweed (e.g. Sargassum and coastal kelp forests) for biofuel would induce wide-scale ecosystem damage (Bruton et al., 2009). Therefore natural seaweed populations should be protected, and the seaweed for biofuel industry should focus on advancing oceanic cultivation. However, if seaweed biofuels are going to make a significant contribution to lowering atmospheric CO$_2$ concentrations and reducing the global dependence on oil, then nations must focus on developing more cost-effective methods of growing, harvesting, transporting and processing of large quantities of seaweed (Kraan, 2013).

3.4.7 References


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3.5 Antarctic krill

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Summary points

• Antarctic krill is reputed to have the largest biomass of any single metazoan species (all multi-cellular animals besides sponges) on the planet, playing a key role in the structure and function of the Southern Ocean ecosystem.

• They display a circumpolar distribution, south of the Polar Front with a distributional range of $19 \times 10^6$ km$^2$, which largely coincides with the extent of winter sea ice. This roughly is equivalent to the size of South America.

• The circumpolar krill stock is calculated to contain approximately $3.5 \times 10^{13}$ gC, which is more than the total peat-carbon stock held in the USA, and their annual carbon production is of the order of $3.1-4.9 \times 10^{13}$ gC.

• Krill sequester $2.3 \times 10^{13}$ gC annually, which offsets ~0.26% of annual global CO$_2$ emissions from fossil fuel combustion. Krill also play a key role in cycling elements other than carbon, some of which may limit primary production (e.g. iron).

• Declines in krill density and possible recruitment failures in the South Atlantic in recent years have been suggested and have been linked to reductions in sea ice area caused by global warming.

• Marine organisms are expected to be affected by ocean acidification in a number of ways and long-lived pelagic animals, such as Antarctic krill, may be especially vulnerable.

• The krill population is a large biological carbon reservoir, but krill are probably more important through their control of the carbon cycling processes.
3.5.1 Introduction
Antarctic krill (hereafter krill) may be one of the most abundant metazoan species on the planet and is a key species in the Southern Ocean ecosystem being the major prey for marine vertebrate predators and also a major grazer of primary production (Everson, 2000).

The krill population is a large carbon reservoir, but krill are probably more important through their control in carbon cycling processes. Krill affect the marine carbon cycle by grazing phytoplankton and producing sinking faecal pellets, through their vertical and horizontal migrations (Tarling and Johnson, 2006), through the turbulence their movements generate (Kunze et al., 2006), and through their role in the cycles of critical elements such as iron (Nicol et al., 2010).

A significant change in krill distribution or abundance due to human activities and/or climate change would result in a profound impact on current carbon pathways in the Southern Ocean marine system. There have been suggestions that the krill population, especially in the South Atlantic, has already decreased as a result of productivity changes caused by reduced winter sea ice (Atkinson et al., 2004).

The focus of this Section will be on Antarctic krill because its biomass dominates the pelagic zone in much of the Southern Ocean, and it plays a key role in shaping the ecosystem.

3.5.2 Definition of the species/ecosystem
Krill is a general term used to describe 85 species of free-swimming, open-ocean crustaceans, known as euphausiids, with world-wide distributions (Baker et al., 1990). Seven species occur in the Southern Ocean, and Antarctic krill (Euphausia superba) greatly outnumbers the others.

Antarctic krill display a circumpolar distribution (Figure 3.5.1), south of the Polar Front (the northern limit of the Southern Ocean). Its distributional range is $19 \times 10^6$ km$^2$ and krill distribution coincides with the extent of winter sea ice except around ice-free South Georgia, but highest densities are found in shelf-break regions. Their distribution is asymmetrical with about 70% of its stock being located in the Atlantic sector (Marr, 1962; Atkinson et al., 2008). They often form extremely large, dense aggregations, which makes krill attractive to predators as well as fisheries.

3.5.3 Global and regional significance of krill in terms of carbon and carbon pathways, biomass and production of Antarctic krill
Estimates of the total biomass of Antarctic krill vary between 60-500 million tonnes depending on the method of estimation (Ross and Quetin, 1988; Nicol et al., 2000; Siegel, 2005). This wide range reflects the difficulties inherent in measuring abundance in an open-ocean species that occurs over such a large range,
the difficult nature of the seasonally ice-covered habitat and the uncertainties in the estimation techniques. A recent re-examination of krill biomass using a variety of methods ranged between 117-379 million tonnes, with 379 million tonnes as probably the best estimate of mean total biomass, with a circumpolar annual krill production of 342-536 million tonnes (Atkinson et al., 2009). Krill body carbon is approximately 40% of its dry weight (Huntley et al., 1994), and the dry weight of krill as 23% of wet weight (Nicol et al., 1992), so the total circum-polar krill stock is calculated to contain ~3.5 x 10^{13} gC and their annual carbon production would be of the order of 3.1-4.9 x 10^{13} gC (Table 3.5.1). This compares to or more than the total peat-carbon stock of 2.9 x 10^{13}gC in the USA (Kaat and Joosten, 2008). It is also important to note that the circumpolar stock size and its production described here are averages over the period 1926-2004 and therefore will certainly fluctuate substantially between years (Atkinson et al., 2009).

### Carbon pathways mediated by Antarctic krill

Krill is primarily a herbivore during the spring to early summer period when phytoplankton blooms occur, but exhibits omnivory and carnivory throughout most of the year (Pakhomov et al., 2002). During winter krill also rely on the sea-ice microbrial community and sea-ice algae in early spring for a substantial part of their diet before the phytoplankton bloom occurs (Nicol and Allison, 1997; Fach et al., 2002; Meyer, 2012). An individual krill (mean wet weight of 0.486 g during summer period; Atkinson et al., 2009) consumes up to 15% of its body carbon weight per day (Pakhomov et al., 2002). Total annual food consumption is estimated 1.3 x 10^{15} gC (Table 3.5.2). Of this, 30% is egested and 70% is assimilated (Tarling and Johnson, 2006). However, food intake and defaecation rates could be even higher when digestion is incomplete during periods when phytoplankton is especially abundant (Schmidt et al., 2012).

The contribution by Antarctic krill to the vertical flux of carbon by grazing primary producers and defaecating is extremely variable regionally due to the patchy nature of krill distribution (Clarke et al., 1988). Sediment trap data suggest that the vertical flux of krill faeces can range from 0.01-15.6 gC.m^{-2}.d^{-1}, contributing up to 80% of the total carbon flux to deep water in the high Antarctic regions. (Pakhomov et al., 2002).

Antarctic krill also have an important role in sourcing dissolved organic carbon (DOC). Experiments conducted around the Antarctic Peninsula area have demonstrated, on average, the combined krill + phytoplankton production equates to 73% of DOC production in the ecosystem. The contribution of krill varied from 10-98% within the combined DOC (krill + phytoplankton) release rate (Ruiz-Halpern et al., 2011).

Predation by vertebrates is considered as the most important cause of natural mortality of adult Antarctic krill (Siegel and Nicol, 2000), which means that most of the carbon assimilated by krill is consumed by higher predators. The total amount of circumpolar carbon annually channelled into a long-lived vertebrate carbon pool may range from 3.1-4.9 x 10^{13} gC by assuming that long-term annual predator consumption equates to mean annual krill production (Table 3.5.2).

Antarctic krill’s key role in transferring carbon from the mixed layer is enhanced through their behaviour of feeding near the surface then sinking to deeper waters and defaecating when satiated. This behaviour may result in the sequestering of 2.3 x 10^{13} gC annually in the Southern Ocean (Tarling and Johnson, 2006) which offsets ~0.26% of annual global CO_2 emissions from fossil fuel combustion (8.7 x 10^{15}gC.yr^{-1} according to Le Quere et al. (2009)) , adding a further 8% to previous estimates of global active carbon flux (Tarling and Johnson, 2006) (Table 3.5.2).

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<tr>
<th>Wet Weight</th>
<th>Carbon Assumption</th>
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<tr>
<td>Biomass 379 million tonnes (Atkinson et al., 2009)</td>
<td>3.5 x 10^{13} gC</td>
<td>DW/WW=0.23 (Nicol et al., 1992), C/DW=0.4 (Huntley et al., 1994)</td>
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<tr>
<td>Production 342-536 million tonnes (Atkinson et al., 2009)</td>
<td>3.1-4.9 x 10^{13} gC.y^{-1}</td>
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3.5.4 Evolution with time

Antarctic krill occur in regions undergoing rapid environmental change with loss of winter sea ice, ocean warming and other environmental stressors that are thought to act in concert to modify the abundance, distribution and lifecycle of krill (Flores et al., 2012). Warming, sea ice, and primary production

The life history of Antarctic krill is strongly linked to sea ice and they therefore mainly inhabit the seasonal ice zone (Kawaguchi et al., 2007). During winter, the physical topography beneath the sea ice provides a habitat and the algae growing on the underside of the ice provides a nursery ground for larval krill which they utilize to survive their first winter. Ice algae production in early spring also boosts growth of adult krill after the long food-limited winter period. As the sea ice retreats in late spring and early summer, a phytoplankton bloom seeded from decaying sea ice fuels krill growth and ovarian maturation for the summer reproduction period. The sequence and the timings of these processes occurring within the seasonal ice zone are the key determinants for successful krill recruitment and subsequent abundance (Kawaguchi and Satake, 1994; Siegel and Loeb, 1995). Recent suggestions of declines in krill density and possible recruitment failures in the South Atlantic have been associated with reductions in sea ice area (Loeb et al., 1997; Atkinson et al., 2009) attributed to global warming. Annual mean sea ice extent in the western Antarctic Peninsula region, believed to be a key factor for krill population productivity in the South Atlantic (Hofmann et al., 1998), has been declining at a rate of almost 7% per decade between 1979 and 2008. However, the overall circumpolar annual mean extent of Antarctic sea ice has increased at a rate of 0.97% per decade since the late 1970s (Turner et al., 2009). Climate change is also considered to cause changes in ocean currents that may affect their distribution (Murphy et al., 2007).

It has been projected that by 2100 there will be an up to 20% reduction in area of the habitat that can support growth of krill due to direct effects of warming (Hill et al., 2013). This reduction of favourable habitat for krill would arise as a consequence of rising seawater temperatures that would cause an increase in metabolic demand and therefore negatively affect their ability to grow without increasing their energy intake (Wiedenmann et al., 2008). This reduction in growth potential is unlikely to be compensated for even if future primary production increased by 50%.

Ocean acidification

The ecosystems of the Southern Ocean are expected to be those most severely affected by ocean acidification (OA) due to the higher solubilities of CO₂ and CaCO₃ in cold waters and because of regional upwelling of hypercapnic (CO₂ rich) deepsea water (Sabine et al., 2004; Doney et al., 2009). Increases of pCO₂ levels in Southern Ocean surface waters over the last decades have already been observed (e.g. Midorikawa et al., 2012). Marine organisms are expected to be affected by OA in a number of ways and long-lived pelagic animals, such as Antarctic krill, may be especially vulnerable. Antarctic krill lay sinking eggs that hatch at a depth of 700-1000m where CO₂ levels are currently much higher than the levels in surface waters (Kawaguchi et al., 2013).

Table 3.5.2. Fate of carbon channelling through Antarctic krill.

<table>
<thead>
<tr>
<th>Carbon pathway</th>
<th>Amount</th>
<th>Assumptions and references</th>
</tr>
</thead>
<tbody>
<tr>
<td>Food consumption by krill</td>
<td>$1.3 \times 10^{15}$ gC·y⁻¹</td>
<td>Biomass 379 million tonnes (WW) (Atkinson et al., 2009), DW/WW=0.23 (Nicol et al., 1992), C/DW=0.4 (Huntley et al., 1994) Daily consumption of 15% BodyC during spring-summer and 5% during autumn-winter (Pakhomov et al., 2002).</td>
</tr>
<tr>
<td>Krill consumed by predators</td>
<td>$3.1-4.9 \times 10^{13}$ gC·y⁻¹</td>
<td>Major cause of mortality is due to predation (Siegel and Nicol, 2000)</td>
</tr>
<tr>
<td>Sequestration into deep layers</td>
<td>$2.3 \times 10^{13}$ gC·y⁻¹</td>
<td>Tarling and Johnson (2006)</td>
</tr>
</tbody>
</table>
Recent experimental studies have revealed a sharp decline in embryonic development rates at CO₂ levels of 1200 ppm and above, with complete interruption at very early stages of their development when krill were reared in seawater with 2000 ppm CO₂ (pH 7.4) (Kawaguchi et al., 2011, 2013). Based on these experimental data and on ocean carbon cycle models forced by IPCC emission scenarios it is suggested that the important krill habitats of the Weddell Sea and to the east are likely to become high-risk areas for krill recruitment within 100 years. Furthermore, unless CO₂ emissions are mitigated, the entire Southern Ocean krill population could collapse by 2300 (Kawaguchi et al., 2013). Post-larval krill also respond to the elevated CO₂ levels expected within a century by increasing ingestion rates, nutrient release rates, and metabolic activity, reflecting enhanced energetic requirements which may compromise their physiological performance (Saba et al., 2012). If elevated CO₂ concentrations persist, these physiological disturbances would retard their growth and reproduction, and affect their behaviour.

### 3.5.5 Values - goods and services provided by krill

Although there are other ecological pathways in the Southern Ocean, the dependence of so many of the upper level vertebrate predators on a single species results in a “wasp-waist ecosystem” (Bakun, 2006) (wasp-waist control occurs when one of the intermediate trophic levels is dominated by a single species). Hence any perturbations to krill populations will have ramifications throughout the Southern Ocean ecosystem. For these reasons krill is the “keystone species” of the Southern Ocean ecosystem; the effects of variations in the life cycle, annual production, and recruitment success of Antarctic krill can be traced throughout the ecosystem (Quetin et al., 2003).

### Role of Antarctic krill in the marine geochemical cycle

The Antarctic krill population is a large biological carbon reservoir, but krill are probably equally important through their control of the carbon cycling processes. In marine bio-geochemical studies the major research efforts have focused on smaller organisms at the base of the food chain (i.e. microbes, primary producers). There is, however, growing evidence to suggest that the role of larger animals in structuring marine ecosystems has been underestimated (Nicol et al., 2010). The processes of nutrient cycling have largely been explained by physical forces (e.g. upwelling, vertical mixing due to wind), but recent studies suggest that vertically migrating animals can significantly mix and transport nutrients through the water column (Dewar et al., 2006; Katija and Dabiri, 2009). Observations of vertically migrating krill indicate that such mass movements may enhance biological productivity through the transport of deep nutrients to the surface layer (Kunze et al., 2006).

There is increasing evidence that adult krill may regularly migrate from the surface to the sea floor where they forage on organic material associated with the sediments (Schmidt et al., 2011). The vertical fluxes involved in this behaviour may have fundamental implications for nutrient transfer from deep water contributing to enhanced primary production in the surface layer.

Krill also play a key role in cycling elements other than carbon some of which may limit primary production. Krill contains iron at a concentration that is ten million times higher than surrounding seawater and the Antarctic krill population has been estimated to contain approximately 24% of the total iron in the surface waters of the Southern Ocean (Nicol et al., 2010). This iron can be made available to primary producers, which are often iron limited, when baleen whales prey on krill and defaecate iron-rich faeces (Nicol et al., 2010; Roman and McCarthy, 2010).

The contributions of krill and other larger animals to marine biogeochemistry may be significant thus climate change is likely to impinge on the effect that these marine organisms have on the nutrient cycles of the Southern Ocean and hence its productivity.

### The commercial value of Antarctic krill

The fishery for Antarctic krill has been operating for over 35 years, and it has been highlighted many times as one of the world’s last under-exploited fisheries (Nicol and Endo, 1997). The total annual catch peaked in the early 1980s (over half million tonnes) and rapidly declined thereafter to around 120 000 tonnes following the break-up of the USSR, which was the main nation fishing for krill. Recently, the catch level has increased and in 2009/10 was 211 180 tonnes (Kawaguchi and Nicol, 2007; Nicol et al., 2012). Currently Norway, Korea, and China are the major nations fishing for krill (SC-CAMLR, 2012). Krill catches have been reported from all around the Antarctic continent, however, the majority of catches have been from the south-west Atlantic sector, and currently all the krill fisheries are operating in this area (Kawaguchi and Nicol, 2007). The reported
catch of krill in 2011/12 was 181,000 tonnes, whereas the total precautionary catch limit is 8.6 million tonnes, and the krill standing stock is of the order of 215 million tonnes. The value of the current krill catch is of the order of $US 241 million, whereas the value of the catch at its sustainable limit would be ~$US 11.4 billion, and that of the entire stock ~ $US 286 billion based on the current market value of whole krill (obviously, should the fishery expand then the economics would also change). The high value of the krill stock compared to the global fish catch ($US 85 billion) illustrates the significance of this resource (Grant et al., 2013).

A wide variety of products have been produced from krill, and there is an expansion in the range of products being extracted from krill. The main krill products are for aquaculture, but pharmaceuticals and health food products made of krill oil are also rapidly expanding due to new developments in harvesting and processing technologies, and the emergence of new markets (Nicol et al., 2012). The fatty acid profile of krill oil makes it effective in the treatment of various medical conditions. Such oils with high levels of Omega-3 command a premium price in complementary medicine markets, and the use of krill oil in pharmaceutical and nutraceutical products will continue to drive investment in the krill industry (Hill, 2013). However, this interest may result in greater extraction of chemicals from existing catches rather than increased catches (Nicol et al., 2012). There is considerable research into alternative supplies of feed for the rapidly growing aquaculture sector because of dwindling fish stocks traditionally used for meal.

**Krill fishery management under a changing climate**

Krill is one of the few marine resources with the potential for a large but sustainable increase in catches. It is likely that changes in the Southern Ocean may negatively affect krill populations and also make them more accessible to the fishery (Kawaguchi et al., 2009, 2013; Hill et al., 2013). The krill fishery in the Southern Ocean is regulated by CCAMLR that sets precautionary catch limits for the krill fishery in the Southern Ocean in large statistical management areas (Figure 3.5.2). The sum of the precautionary catch limits established for the Antarctic

![Figure 3.5.2. Precautionary catch limits on the krill fishery in the CCAMLR Area. Statistical areas are outlined and surveyed areas outlined and labelled.](image-url)
krill fishery in the South Atlantic and the South Indian Oceans is equivalent to 11% of the current total tonnage of all wild-caught marine fish (FAO, 2012; SC-CAMLR, 2012), indicating a huge potential for this fishery, and it is essential that an appropriate management scheme is in place before this fishery fully develops. These catch limits are set based on simulations using a generalized yield model and an estimate of the unexploited biomass derived from acoustic surveys (Constable and de la Mare, 1996).

Although precautionary catch limits are currently set for large statistical areas this does not take account of potential fishery impacts on the ecosystems at smaller scales. Therefore CCAMLR has also set “trigger levels” that cannot be exceeded as a safeguard until a more elaborate management strategy is established (Constable, 2011). Because CCAMLR is mandated to take into account the needs of dependent and related species, the CCAMLR Ecosystem Monitoring Program (CEMP) was established to detect and delineate signals of fishery impacts from natural variability and trends and designed to inform management of the krill fishery (SC-CAMLR, 1995).

Current CCAMLR management approaches do not take the effects of climate change into account. To allow a robust projection of krill status in the future, management models must be responsive to climate change scenarios including warming and ocean acidification. Some of CCAMLR’s priorities for the management of the krill fishery are the development of krill life history and ecosystem models that allow robust assessment and projections of the rate of change of krill populations and the uncertainties under various climate change scenarios.

As indicated in the previous sections, there is an increasing number of studies indicating the critical role that krill play in the ecosystem, not just as a key species in the food web but also through their important role in biogeochemical cycles as well as their importance as a fishery resource. Krill provide critical ecosystem services in the Southern Ocean, and this underscores the importance of careful management of the krill resource for the health of the Southern Ocean ecosystem.

3.5.6 References


3. Case studies in ocean carbon


3. Case studies in ocean carbon


3.6 Fish

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Summary points

- Fish make a significant contribution to oceanic carbonate production (0.04-0.33 x 10^{15} \text{ g of CaCO}_3) per year) in the form of high Mg calcite crystals excreted continuously via the gut.
- The high Mg content suggests rapid dissolution near the ocean surface that would restore surface alkalinity to a greater degree than other biogenic carbonates. This would neutralize much of the CO_2 released as a consequence of the calcification process.
- Temperature and CO_2 forecasts for the next century (+4 °C and 750 ppm) suggest fish carbonate production may become 58% higher than today, contrary to the effect predicted for many calcifiers. Warmer conditions would also increase their Mg content and near-surface dissolution.
- Conversely, there is evidence for preservation of fish carbonates in shallow, tropical sediments. Mid-Cretaceous marine conditions would have massively enhanced production of fish carbonates with much lower Mg content, enhancing their potential for preservation in carbonate sediments and geology.
- Quantitatively, the fate of fish carbonates in the ocean is not yet understood well enough to estimate their role as sources or sinks of CO_2.
**3.6.1 Introduction**

Marine biogenic calcification has traditionally been attributed solely to those marine organisms that make skeletal material from inorganic calcium carbonate. The major calcifiers in the open ocean are phytoplanktonic coccolithophores, representing about half of global calcium carbonate production (Beardall and Raven, 2013). Microscopic animals such as foraminifera and pteropods also make key contributions (Schiebel, 2002). The role of these species in the open ocean C cycle is discussed in Section 3.1 by Roberts, Hopcroft and Dupont. Of the shallow marine calcifiers, corals are perhaps the most charismatic and well known. However, due to their limited distribution their quantitative significance globally is actually small (<10%; Ware et al., 1992; Milliman and Droxl, 1999). More recently the carbonate budget of benthic calcifiers, specifically echinoderm, has been updated and recognized as another major calcifier on a global scale (Lebrato et al., 2010). However, fish are perhaps the most surprising addition to the list of quantitatively significant marine calcifiers (Wilson et al., 2009), and they are the only marine organisms that make calcium carbonate as a by-product of gut physiological processes as opposed to the need for structural (skeletal) material. A further important distinguishing feature of fish calcification is that their gut carbonates are produced and excreted continuously throughout their lives rather than the very intermittent release associated with either death, moulting or physical erosion of traditional calcifiers.

Fish may turn out to be a major player in both the net production of calcium carbonate minerals and subsequently the control of surface ocean chemistry. In particular the more rapid dissolution of fish carbonates is likely to have a more immediate impact on surface alkalinity and buffering of seawater, enhancing the ability of the ocean to absorb CO$_2$ from the atmosphere. This chapter will provide the current, though still limited, understanding of the role fish play in the marine inorganic C cycle.

**3.6.2 Definition of the key species**

Only teleost fish (i.e. those with a bony skeleton) produce gut carbonates, not elasmobranchs (sharks and rays that have a cartilaginous skeleton). However, teleost fish make up ~95% of the global marine fish biomass ($8.99 \times 10^{10}$ t), the remaining 5% being elasmobranchs (Jennings et al., 2008). To our knowledge all teleosts produce gut carbonates, as a by-product of their physiological strategy of drinking sea water for osmoregulation (see below for details), whereas elasmobranchs do not drink sea water in significant amounts. The need for drinking sea water is present throughout the lives of teleost fish from hatching to fully mature adult (Tytler and Blaxter, 1988). The production of gut carbonates from this ingested sea water has not yet been explicitly measured across the full size range of teleost fish (<1 mg to > 1000 kg). However, the mass-specific gut carbonate production rate (i.e. µmol-C/kg$^{-1}$ of fish.h$^{-1}$) has been shown to follow a consistent scaling relationship over a wide range of body sizes and species in tropical teleosts (1 g to 13 kg; Perry et al., 2011) in which it doubles for every 10-fold decrease in body mass. This relationship is linked to the overall mass-specific metabolic rate of animals, which is similarly higher in smaller animals (Clarke and Johnston, 1999).

Production and release of gut carbonates by teleost fish is thought to occur throughout their lifecycle and therefore wherever they are found within the oceans. The vast majority of fish biomass occurs around the continental shelves, and this is why Jennings et al. (2008) reported that 50% of fish biomass is restricted to only 17% of the total area of the ocean. More specifically, high densities of teleost fish biomass are mainly restricted to upwellings and coastal shelves in the mid-latitudes. However, this does not mean that the open ocean is devoid of significant biomass of fish and their carbonate production, just that the density is lower in these regions. It is worth noting that the mesopelagic fish (e.g. lanternfish - small deepwater fish of the Myctophidae family) dominate the global biomass of fish and are the most widely distributed and populous of all vertebrates, let alone fish. Furthermore, Irigoien et al. (2014) suggest that their biomass has been previously underestimated by at least an order of magnitude. So despite a much lower density of fish in the open ocean, the potential total contribution of such species to the global production of carbonates should not be ignored, even though it is yet to be measured directly.

**3.6.3 The biochemical processes of calcium carbonate production by fish**

Teleost fish, unlike other calcifiers, do not produce significant amounts of CaCO$_3$ as part of their skeleton; the bones of vertebrates are made up of the mineral apatite, which is primarily calcium phosphate. The CaCO$_3$ discussed here is produced continuously within the intestines of marine teleosts as a waste product.
that is excreted on an almost daily basis. For most species examined so far, the crystals of CaCO$_3$ formed in fish guts conform to the mineral type known as high magnesium calcite (Wilson et al., 2009). The reason for this high Mg content (up to 40 mole %; Perry et al., 2011; Salter et al., 2013) relates to the Mg$^{2+}$ concentration at the site of production (the intestine) and will become clear below.

Teleost fish need to drink substantial quantities of sea water to avoid dehydration. This is because their blood-salt content is approximately one third that of the ambient sea water, resulting in substantial osmotic loss of water across their permeable outer surfaces (Marshall and Grosell, 2005). For example, a typical seawater ingestion rate in marine fish is equivalent to an adult human drinking about 7 litres of fluid per day. Drinking a fraction of this volume of sea water would be lethal to most vertebrates, due to the high concentrations of salts, particularly the dominant sodium and chloride ions. Such high intake of Na$^+$ and Cl$^-$ ions would exceed the salt-excretion capacity of human kidneys and actually lead to even worse dehydration, but teleost fish have evolved extra-renal mechanisms to exclude the ingested and absorbed Na$^+$ and Cl$^-$ ions, primarily via the gills. Sea water also has high levels of divalent ions, specifically calcium (Ca$^{2+}$), magnesium (Mg$^{2+}$), and sulphate (SO$_{4}^{2-}$) that may also be absorbed once ingested and require additional mechanisms of regulation (Wilson et al., 2002; Wilson and Grosell, 2003; Marshall and Grosell, 2005). To limit their dehydration problem, marine fish produce very little urine that consists almost entirely of Mg$^{2+}$ and SO$_{4}^{2-}$ ions. Excretion of excess Ca$^{2+}$ ions via the kidney of marine fish is limited, as this would risk the precipitation of kidney stones (Wilson et al., 2002; Wilson and Grosell, 2003). The majority of ingested Ca$^{2+}$ actually remains within the intestinal fluid and, after passage through the (usually acidic) stomach, it is precipitated within the intestine as carbonate crystals.

The cause of gut precipitation is the highly alkaline (pH 8.2-9.2) and bicarbonate-rich (30-100 mM) nature of intestinal fluids (Grosell, 2011). To put this into perspective the bicarbonate concentration/alkalinity of the intestinal fluids is 15 to 50 times higher than the ambient sea water (~2 mM). Intestinal epithelial cells use metabolic CO$_2$ to generate bicarbonate ions that are transported at very high rates into the intestinal fluid (Figure 3.6.1).
This creates super-saturated conditions with respect to \( \text{CaCO}_3 \), resulting in at least 80% of ingested \( \text{Ca}^{2+} \) ions being precipitated prior to their ultimate defaecation in mucus-coated pellets (Wilson and Grosell, 2003). Precipitation occurs along the entire length of the intestine with the transit time for intestinal fluid ranging from a few hours to days, decreasing as temperature (and metabolic rate) increases. Ingested sea water has about 52 mM \( \text{Mg}^{2+} \) which becomes more concentrated (i.e. >150 mM) as fluid is absorbed along the intestine (Wilson and Grosell, 2003). This explains why the gut carbonate crystals of fish often incorporate such high proportions of magnesium giving rise to the collective description as high Mg calcite (Wilson et al., 2009; Perry et al., 2011; Salter et al., 2012; Woosley et al., 2012). It is worth highlighting that although these carbonates pass via the guts of marine fish, they are produced \textit{de novo} from calcium ions in the ingested sea water rather than representing undigested food items. Indeed, marine fish produce gut carbonates at very high rates even when starved (Wilson et al., 2002, 2009).

As pointed out in Section 3.2 of this report, the role of biogenic \( \text{CaCO}_3 \) producers in carbon cycling is complicated by the fact that the calcification reaction is simultaneously a sink for carbon and a source of \( \text{CO}_2 \) gas (Figure 3.6.2), with ~0.6 mol of \( \text{CO}_2 \) being generated for each mol of \( \text{CaCO}_3 \) precipitated (Ware et al., 1992). At first glance this is counterintuitive and it is therefore important to make clear the distinction between carbon sinks and \( \text{CO}_2 \) gas sinks. The latter are the most relevant regarding our understanding, and potential management, of atmospheric \( \text{CO}_2 \) levels.
3.6.4 Local, regional and global significance of calcifiers as carbon pools

Global CaCO$_3$ production by fish

Laboratory based physiological studies of marine fish have produced data on mass-specific calcium carbonate excretion rates (i.e. quantity of HCO$_3$ - C excreted per kg of fish per unit time) in a variety of fish species over a wide range of temperatures (Wilson et al., 1996, 2002, 2009; Perry et al., 2011). Walsh et al. (1991) were the first to raise the possibility of fish as an environmentally relevant source of carbonates. However, until 2008 no models of global fish biomass were available such that a global estimate of fish CaCO$_3$ production was previously impossible. Then two separate approaches using ecological computer simulations of fish populations provided the first ever models of fish biomass across the full range of body sizes and habitats globally (Jennings et al., 2008; Christensen et al., 2009). By combining the physiological data from lab experiments with population modelling a conservative estimate of the global contribution of fish to the marine inorganic carbon cycle yielded values between 40 and 110 million tonnes (0.04 to 0.11 x 10$^{15}$ g) of CaCO$_3$ - C per year (Wilson et al., 2009). This represents 3 to 15 % of the previous estimates of new calcium carbonate production in the surface ocean globally. To put this into perspective, 0.11 x 10$^{15}$ gC.y$^{-1}$ is equivalent to the carbon emissions in the surface ocean globally. To put this into perspective, 0.11 x 10$^{15}$ gC.y$^{-1}$ is equivalent to the carbon emissions in the surface ocean globally. To put this into perspective, 0.11 x 10$^{15}$ gC.y$^{-1}$ is equivalent to the carbon emissions in the surface ocean globally. To put this into perspective, 0.11 x 10$^{15}$ gC.y$^{-1}$ is equivalent to the carbon emissions in the surface ocean globally. To put this into perspective, 0.11 x 10$^{15}$ gC.y$^{-1}$ is equivalent to the carbon emissions in the surface ocean globally. To put this into perspective, 0.11 x 10$^{15}$ gC.y$^{-1}$ is equivalent to the carbon emissions in the surface ocean globally.

The key assumptions within the model centre around the influences of temperature, body size, feeding, activity and lifestyle on the individual rates of carbonate production by fish. Current research is providing more precise data on these influences and will lead to a refinement of the estimates of global production by fish. The suggestions so far are that the influence of the most important variables, temperature and body size, on fish carbonate production are much greater than previously assumed in Wilson et al. (2009). The estimate of global CaCO$_3$ production by fish therefore seems likely to increase as a proportion of the global inorganic carbon cycle.

The shallow dissolution of fish carbonates in the ocean

Perhaps equally important to the quantity of high Mg calcite produced by fish is the fate of this carbonate material once excreted by the fish. Its high magnesium content compared to most biogenic calcite or aragonite is thought to increase the rate of dissolution within sea water (Morse et al., 2003). This suggests that fish carbonates may go into solution at shallower depths (< 1000 m) than carbonates from better-studied planktonic calcifiers (especially coccolithophores, the dominant producers of calcite) (Wilson et al., 2009). Dissolution of pelagic calcite and aragonite particles is only expected to occur once they sink below the chemical lysoclines for these carbonate minerals (i.e. depth where undersaturation becomes critical and the rate of dissolution increases dramatically; Milliman et al., 1999). The lysocline for calcite ranges from 750 to 4,300 m in the north Atlantic and Pacific oceans, respectively. The equivalent lysocline depths for the more soluble aragonite mineral are 500 and 1,500 m, respectively. However, even the latter cannot explain consistent reports of dissolution of the majority of exported surface carbonates at depths much shallower than 500 m (Milliman and Droxl, 1996; Lee, 2001; Sabine et al., 2004), resulting in a parallel and striking increase in total alkalinity between the surface and 500 m depth (Feely et al., 2002; Chung et al., 2003; Millero, 2007). This contradiction has been the source of a long-standing debate (Milliman, 1999). The simplest explanation is a significant source of much more soluble carbonates in the surface ocean. High Mg calcite excreted by fish would fit this scenario, and Wilson et al. (2009) suggested fish may therefore explain at least a quarter of the observed alkalinity-depth profile phenomenon, based on the original conservative estimates of fish production. A key factor in this being a correct hypothesis lies in the solubility of high Mg calcite from fish being much greater than that of calcite and even aragonite. The only published estimate of the solubility of fish gut carbonates suggests this is the case (Woosley et al., 2012) with the value for high Mg calcite from the Gulf toadfish (Opsanus beta) being twice that of aragonite. However, it is worth noting that the method used by Woosley et al. (2012) did not actually measure dissolution, but instead measured the precipitation of new carbonates in super-saturated sea water stimulated by the presence of toadfish excreted carbonates. Direct measurements of the dissolution of fish carbonates remain unpublished, but certainly their consistently high Mg content should favour the potential for rapid dissolution at relatively shallow depths. The phenomenon of rapid dissolution of sinking carbonates is clearly important to understand because it reverses the original calcification reaction (which is a CO$_2$ source). In doing so it helps replenish the surface ocean alkalinity (Figure 3.6.2) which both buffers against further ocean acidification and enhances the absorption of further atmospheric CO$_2$ (Feely et al., 2002).
Preservation of fish carbonates in shallow marine sediments

In warm shallow areas of the ocean, like the Bahamas, fish have recently been established as a significant source of carbonate sediment (Perry et al., 2011; Salter et al., 2012), suggesting that their dissolution is not always rapid. The potential for preservation of fish carbonates in such habitats is most likely explained by the high carbonate saturation states of surface waters. Based on lab experiments and ecological surveys of 11 fish species across a variety of different habitat types, Perry et al. (2011) estimated that fish contributed 14% to the total quantity of carbonate mud (i.e., particles <63 µm) across the Bahamas, with values as high as 70% of the fine-grade CaCO₃ particles produced in specific areas such as mangrove habitats. Perry et al. (2011) also identified identical crystals to those excreted by fish in sediments from all seven habitats surveyed in the Bahamas. Thus, in contrast to the potential for rapid dissolution of fish carbonates in the open ocean, at least in warm, shallow habitats (i.e., resulting in high carbonate saturation states) burial and preservation of high Mg calcites from fish is also a plausible fate.

Carbonate sediments generally provide important records of changes in ocean chemistry and climate throughout Earth’s history (Elderfield, 2002; Riebesell, 2004; Ridgwell and Zeebe, 2005). Despite the occurrence of seemingly fish-derived crystals in modern shallow sediments, key questions remain about their long-term preservation potential. Specifically, how long do fish carbonates last in the sedimentary record before either dissolving or undergoing a chemical transformation to more stable mineral forms (i.e., diagenesis) within sediments. Revealing these unknowns is important to understanding the long-term fate of fish carbonates. However, it is too early in this field of research to provide a truly quantitative analysis of the global role of fish in both the calcification and dissolution fluxes of the marine inorganic carbon cycle. Nevertheless, the size of the estimated global carbonate production by fish, together with their global distribution, suggests that this information will be vital to accurately predict the impact of fish on the surface chemistry and potential of the oceans as a sink or source of atmospheric CO₂.

In essence, fish appear to be a big player in the fluxes of marine inorganic carbon but at present it is not possible to be confident of the quantification of their short and long-term impacts.

3.6.5 Evolutionary aspects of fish as calcifiers – Lessons from the geological past and predictions for the future

Cretaceous marine fish carbonates?

Given that fish-derived carbonates are significant components of modern carbonate production it is of interest to consider how this source of carbonate production may have varied in the geological past. Modern marine bony fish (Osteichthyes) evolved from freshwater bony fish in the Jurassic (Fyhn et al., 1999) and are considered to have undergone several major radiations that began in the early Cretaceous ~150 My ago (Benton, 2005) and include a particularly spectacular radiation during the Cretaceous that is unprecedented in its rapidity amongst the vertebrates (Finn and Kristoffersen, 2007). The precipitation of CaCO₃ in the intestine provides a key advantage in the osmoregulation of marine bony fish. It is an adaptation that probably arose very early in the evolution of vertebrates, even prior to the emergence of marine bony fish. This is because it can be induced in chondrostean and chondrichthyan fishes (sturgeon and sharks) when they are experimentally manipulated to drink seawater by transfer to a hyper-osmotic medium (Taylor and Grosell, 2006). So it seems likely that marine bony fish were excreting gut carbonates from very early in their evolutionary history. A key question therefore concerns how the prevailing environmental conditions over this timescale may have influenced the quantity produced, its mineralogy and fate, and hence the inorganic carbon cycle through Earth’s history.

The effects of past marine conditions on fish carbonate production

The ocean environmental conditions have varied greatly during the ~200 million years of marine teleost inhabitation. From the current understanding of the physiology of gut carbonates it is likely that many of these variables would have resulted in major differences in CaCO₃ production by marine fish and its fate compared to today. In the mid-Cretaceous period, environmental conditions should have been particularly favourable for fish carbonate production and its preservation in sediments. In some cases the predicted effect of individual seawater variables are as great as an order of magnitude increase (see below). The combined effects of several of these variables have never been tested, but additive and possibly synergistic effects on CaCO₃ production can be hypothesized. The warmer temperature, higher Ca²⁺ and CO₂ levels,
but lower Mg$^{2+}$, SO$_4^{2-}$ and potentially O$_2$ in sea water, suggest that during the mid-Cretaceous fish may have peaked in terms of a truly massive contribution to the inorganic carbon cycle of the ocean. Its preservation was also much more likely given the considerably lower magnesium content under such conditions (see below). Thus Cretaceous fish could have been a major sink of inorganic carbon and a major source of CO$_2$ via the calcification process.

The effects of the above environmental variables on fish carbonate production are all linked to how they affect the delivery of seawater divalent ions (Ca$^{2+}$, Mg$^{2+}$ and SO$_4^{2-}$) to the gut via ingestion, and/or the supply of secreted HCO$_3^-$ ions from the intestinal epithelial cells. The variables known or predicted to affect these processes are discussed below:

A: Factors affecting seawater drinking rate in marine fish – salinity, temperature and oxygen

Gut carbonate production in fish is directly linked to the rate at which they drink sea water in order to osmoregulate. Ultimately this depends on the rate of osmotic water loss via their permeable outer surfaces. Obviously ambient salinity affects this directly by changing the osmotic gradient between the blood and external environment. Seawater drinking rate increases in proportion to this osmotic gradient, and gut CaCO$_3$ production actually increases exponentially with ambient salinity (Genz et al., 2008; Cooper et al., 2010). This is because as salinity rises, so do all the individual ion concentrations being ingested. So if salinity doubles, the ingestion of seawater Ca$^{2+}$ ions would increase ~4-fold (double the volume x double the concentration) and could subsequently all be precipitated by the supersaturated conditions within the intestine (Cooper et al., 2010). Palaeo-salinity proxies suggest that Cretaceous surface oceans were saltier than today’s mean salinity of 35 (Rohling, 2007) with some suggesting values in the low 40s (Wagner et al., 2008) not dissimilar to the current Red Sea. Based on the above relationships a salinity of 40 in mid-Cretaceous should have generated CaCO$_3$ production rates that were 40-50% greater than today.

Temperature and oxygen affect seawater ingestion rate indirectly; rising environmental temperature or falling O$_2$ cause fish to increase gill ventilation so the osmotic loss of water via the gills increases in parallel. Gut CaCO$_3$ production increases at least 2.3-fold for every 10°C rise in temperature (i.e. Q$_{10}$ = 2.3; Wilson et al., 2009), which compares well with the Q$_{10}$ of 2.5 for drinking rate in marine fish (Takei and Tsukada, 2001). Cretaceous temperatures were substantially warmer than today, the global average sometimes by as much as 10°C and deep ocean at least 10°C warmer (Huber et al., 2002) with the mid-Cretaceous being one of the best examples of “hot greenhouse” climate conditions. Although the precise temperature differences relative to today are debated, fish in a Cretaceous surface ocean that was 7-8°C warmer on average (Friedrich et al., 2012) would be expected to produce at least two thirds more CaCO$_3$ based on a Q$_{10}$ of 2.3 (Wilson et al., 2009).

Similar to temperature, atmospheric O$_2$ (currently ~21%), and hence dissolved O$_2$ in the surface ocean, is known to have undergone major changes over geological time. Most fish maintain normal metabolic rates (i.e. O$_2$ uptake) in the face of hypoxia. This is achieved by increases in gill ventilation (Perry et al., 2009) that in turn induce proportional changes in passive water fluxes across fish gills (Wood and Randall, 1973; Loretz, 1979). To compensate for the dehydrating effect of hypoxia-induced hyperventilation, marine fish must increase their drinking rate. Preliminary data on European flounder exposed to half the current atmospheric O$_2$ levels suggest that gut CaCO$_3$ excretion also increases more than 2-fold under such chronic hypoxic conditions (Rogers and Wilson, unpublished). Commonly cited scenarios for early-Cretaceous (~145 Mya) based on chemical proxies suggest that atmospheric O$_2$ was around 15% and subsequently rose to the modern level of 21% (Falkowski et al., 2005; Berner, 2006; 2009). Under the mild hypoxia of early-Cretaceous it is estimated that gut CaCO$_3$ production would have been 50-60% higher than today.

Of additional relevance is the impact of the above variables on the mineralogy of biogenic carbonates. Magnesium content typically increases with temperature in marine calcifiers (Dickson, 2002) that in turn should enhance its solubility and thus reduce its preservation potential in carbonate sediments. However, the effects of salinity and oxygen on the carbonates produce by fish are not known and not obvious to predict.

B: Seawater Ca$^{2+}$, Mg$^{2+}$ and SO$_4^{2-}$ variations over geological time - influence on CaCO$_3$ precipitation and mineralogy

Modern oceanic sea water has a molar Mg/Ca ratio (mMg/Ca) of 5.2 (Mg$^{2+}$ = 52 mM, Ca$^{2+}$ = 10 mM). However, this has varied greatly during the Phanaerozoic
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Eon (i.e. the last 542 My) between about 1.0 and the present value (Horita et al., 2002; Lowenstein et al., 2003; Brennan et al., 2004; Hönisch et al., 2012). These secular variations in marine mMg/Ca are considered responsible for major changes observed in the mineralogy of marine carbonates throughout this timeframe (Sandberg, 1983). A particularly low mMg/Ca (<2) overlapped with the Cretaceous explosion of marine bony fish when the predominant form of abiotic carbonate mineral produced in shallow seas was low Mg calcite. Stanley and Hardie (1998) reported that the carbonate mineralogy of calcifying organisms correlates well with changes between “aragonite-sea” (when high seawater mMg/Ca ratios >2 were prevalent) and “calcite-sea” conditions (low seawater mMg/Ca ratios) throughout the Phanerozoic. Ries (2009) provides a thorough review of lab studies that explore the effects of experimental manipulation of seawater mMg/Ca on extant marine calcifying organisms, although notably this did not include fish.

Preliminary studies with various seawater-acclimated fish species have revealed some remarkable responses to experimental manipulations of marine chemistry that mimic those within the Cretaceous period (Wilson, Rogers, Bill, Whittamore and Reardon, unpublished). For example, tripling seawater Ca²⁺ concentration alone from 10 to 30 mM (by addition of CaCl₂) produces a predictable 3-fold increase in CaCO₃ excretion by the gut of European flounder. However, a more realistic Cretaceous scenario is elevated Ca²⁺ concentration but with simultaneously reduced Mg²⁺ and SO₄²⁻ concentrations. Both latter ions are individually known to inhibit CaCO₃ precipitation (Morse et al., 2007), and so Cretaceous seawater conditions should enhance CaCO₃ precipitation. The most extreme variation occurred around 130-100 Mya, when Ca²⁺ concentration was at least 3x higher than today (≥30 mM), with Mg²⁺ and SO₄²⁻ concentrations approximately half their current levels (about 26 and 9 mM, respectively; Lowenstein et al., 2003; Ries et al., 2009; Bots et al., 2011). When these conditions were recreated in the lab, gut CaCO₃ excretion by three different species of fish (flounder, rainbow trout, sheepshead minnow) increased by 4- to 10-fold, i.e. much more than predicted simply by 3-fold greater Ca²⁺ ions available. This enhanced CaCO₃ excretion may be partly due to the lower Mg²⁺ and SO₄²⁻ levels in gut fluid and hence less inhibition of CaCO₃ precipitation. However, these lower seawater Mg²⁺ and SO₄²⁻ levels may also increase the osmotic permeability and water loss via the gills (Isaia and Masoni, 1976). In turn this would require elevated drinking rates to restore water balance thus supplying even more Ca²⁺ to the gut for precipitation.

As well as producing far more carbonate in total, the above three fish species exposed to Cretaceous seawater conditions all produced crystals with a much lower Mg content (half to a quarter of their carbonate crystals produced in modern seawater carbonates). Although warmer Cretaceous temperatures alone would yield higher magnesium content, the much lower availability of Mg²⁺ ions in Cretaceous sea water is likely to have much greater influence on the gut products from fish at that time. So the chances of being preserved, and so acting as both a carbon sink and a CO₂ source, would have been much higher during the Cretaceous period.

C: Factors affecting intestinal HCO₃⁻ secretion - seawater pCO₂

The permeability of fish gills to all respiratory gases is obviously essential and means that blood pCO₂ parallels external pCO₂ in fish (Heisler, 1984). Increased seawater pCO₂ therefore raises blood pCO₂ and causes an initial blood acidosis. However, fish are very good acid-base regulators and undergo compensatory accumulation of HCO₃⁻ ions in the blood to restore normal blood pH within 10-24 hours (Meizner et al., 2009). The combined elevation in blood pCO₂ and HCO₃⁻ ions fuels further HCO₃⁻ production and secretion by intestinal cells (Esbaugh et al., 2012). Unpublished data (Cobb, Whittamore and Wilson) shows that increasing seawater CO₂ from 470 to 4600 ppmv doubled the excretion of precipitated carbonates in European flounder, with no effect on their magnesium content. Atmospheric and marine CO₂ was elevated during the Cretaceous relative to today, but estimates of by how much vary from 1500 to 3000 ppmv during the peak at around 110 Mya (Royer et al., 2007; Zeebe, 2012). Gut carbonate production is expected to respond to rising CO₂ in a linear manner, for the reasons explained above. So ocean CO₂ values of 1500 to 3000 ppmv would be expected to increase production by about 30 to 60%, but with no effect on its magnesium content and hence dissolution potential.

3.6.6 Predictions for the fish CaCO₃ production in the near future

Marine conditions during the Cretaceous will not be repeated in the near future. In particular no major changes in salinity, individual seawater ion concentrations, alkalinity or oxygen that are likely to affect fish carbonate production are predicted. However,
both temperature and CO$_2$ are rising exponentially and at an unprecedented rate, and both these factors individually are known to accelerate CaCO$_3$ production in fish by different means (seawater ingestion rate and intestinal HCO$_3^-$ supply, respectively). Based on the assumption of simple additive effects of these climate change variables in fish a 58% increase under a +4°C and 750 ppmv scenario would be predicted with a 40% increase being due to temperature alone (assuming a Q$_{10}$ of 2.3 for carbonate production; Wilson et al., 2009).

This contrasts with many other calcifiers that are predicted to decrease carbonate production at higher levels of seawater CO$_2$. Thus, if global fish biomass and distribution remain the same, their role in CaCO$_3$ production seems likely to increase as a proportion of all marine calcifiers. In addition the effect of warmer temperatures increasing the magnesium content suggests that their high Mg calcite products will have higher dissolution potential than today. However, precise data on solubility and magnesium content of fish carbonates are not yet available, and so the relative contribution of fish carbonates to future near-surface dissolution (i.e. neutralizing the effect of calcification) versus long-term preservation in sediments (i.e. a net carbon sink but CO$_2$ source) is currently impossible to predict.

Marine fish biomass is declining through over-fishing and there may be good reason to consider how this will also affect their role in carbonate production and subsequently ocean chemistry (Jennings and Wilson, 2009). This issue is complicated by the fact that fishing tends to remove larger individuals, leaving fewer predators for smaller fish, and these smaller individuals have a much larger contribution to global CaCO$_3$ production than larger fish (Jennings and Wilson, 2009; Wilson et al., 2009). Predicting the future ocean carbon budget therefore becomes difficult when considering both the population effects of over-fishing, and the expected effects of climate change on individual fish highlighted above. Thus fish carbonate production in the future is difficult to forecast, and there are not enough data currently to allow confirmation of the combined effects of population restructuring by overfishing together with rising temperatures and CO$_2$. Further research into how the interaction of these various factors affects the role of fish in the global inorganic carbon cycle is therefore important, given the quantitative significance of fish as a major source of marine calcium carbonate.

3.6.7 Values - goods and services provided by fish

Management recommendations to maintain or enhance feature's ocean carbon role

The study of fish with respect to their quantitative role in the ocean's carbon cycle is in its infancy, having only been recognized as significant global producers of carbonates five years ago (Wilson et al., 2009). The estimates of global carbonate production are in the process of being revised, based on more precise information on the influences of various biotic and environmental factors. However, little is yet known, quantitatively at least, about the fate of fish carbonates within the ocean. Yet this is the most vital component regarding our understanding of their influence on surface ocean chemistry and their net effect as a sink or source of CO$_2$. Without a better appreciation of the fate of fish carbonates, it is currently not possible to judge or recommend how to influence their role in the ocean carbon cycle. Nevertheless, a number of anthropogenic factors are already influencing fish populations globally, and with these undoubtedly global carbonate production by fish.

The direct impact/responsibilities of human activities on biogenic carbon sink

The only available global estimates of gut carbonate production by fish conservatively suggests a 3-15 % contribution to newly formed surface ocean carbonate, and this could be up to 45 % based on realistic rather than the most conservative assumptions (Wilson et al., 2009). Furthermore, Irigoien et al. (2014) have very recently suggested that mesopelagic fish (quantitatively the largest group of fish by biomass) may be 10-30 times more abundant than previously estimated - including the biomass data used by Wilson et al. (2009) to estimate global fish carbonate production. So the upper figure of 45 % of surface ocean carbonate production looks likely to be even higher than previously suggested. This would potentially make fish the largest contributor globally. Perhaps more importantly, unlike the calcite and aragonite minerals produced by the better known ocean calcifiers (see Section 3.2), the high Mg calcite produced by fish is thought to dissolve rapidly enough whilst sinking to restore alkalinity to the surface ocean within a timescale of years rather than centuries (Wilson et al., 2009; Woosley et al., 2012). Thus fish carbonates may be a quantitatively substantial offset to the net CO$_2$ release by other sources of calcification currently, and likely to increase in this role.
in response to future warming and rising CO₂ levels (see above). Anthropogenic changes in fish populations and biomass therefore have the potential to diminish this neutralising role of fish carbonates in the surface ocean. The most obvious human activity in this respect is over exploitation through fishing.

Wild capture fisheries have already altered fish populations with regard to both total biomass (reduced) and their size distribution being shifted from larger to smaller individuals (Bianchi et al., 2000; Shin et al., 2005). Jennings and Wilson (2009) considered how fishing could influence the carbonate production by fish as a potential “ecosystem service”. Fisheries managers often aim to take the largest catch that can be removed from a species stock over an indefinite period, i.e. the “maximum sustainable yield” (MSY). Jennings and Wilson (2009) applied modelling of fishing impacts on carbonate production to a North Sea herring population and a coral reef fish community. This modelling suggested that even at exploitation rates that were lower than those deemed sustainable for the fish populations, their carbonate production would be substantially reduced. Thus, if fish carbonate production were to be considered by fisheries managers as an ecosystem service simply on the basis of their production of marine carbonates, then lower rates of fishing mortality (than currently considered to be sustainable) would be required to viably maintain this service (Jennings and Wilson, 2009).

**Multiple ocean stressors**

Rising temperature and CO₂ are the most obvious combined stressors that are known to influence fish carbonate production, and its potential for dissolution. However, the third major chemical change to the ocean concerns oxygen, with the incidence of hypoxia increasing in coastal regions and the expansion of the oxygen minimum layer (OML) as a result of eutrophication and climate change (Diaz and Breitburg, 2009). As discussed above, any reduction in available oxygen is likely to accelerate the production of carbonates by fish (due to the link between gill ventilation, osmotic water loss, and compensatory drinking of sea water). Thus, all three of the most serious environmental changes afflicting the ocean (warming, carbonation, and deoxygenation) are expected to enhance global carbonate production by fish, with the interactions likely to be additive.

**Unknown unknowns**

Increasing temperature and CO₂ are predicted to increase gut CaCO₃ production by individual fish. In addition, fish are thought to be pre-adapted to coping with the increases in CO₂ forecast for the next century given their very good acid-base regulation capabilities (Melzner et al., 2009). However, surprising and unpredictable effects have been reported for such small elevations in CO₂ on fish sensory systems and behaviour of fish early life stages in particular. Specifically, the ability to smell, hear and respond appropriately to ecologically relevant stimuli such as predators and settlement habitat cues may be severely impacted in juvenile fish (Munday et al., 2009; 2012; Simpson et al., 2011). The negative implications of such behavioural changes for survival and population stability are obvious. So far most of these observations have been on coral reef fishes, but if the same applies to fish in other habitats, and acclimation or adaptation were limited, then this could be a major concern for fish populations as a whole.

**3.6.8 Recommendations for policy makers**

Fish represent a major source of protein for human populations globally, as well as providing a number of specific dietary health benefits via their oil content (particularly omega-3 fatty acids). In terms of harvesting fish, aquaculture currently provides just under half and continues to expand so will soon outweigh wild-caught fisheries production (FAO, 2012). Of course, the biodiversity loss due to over-fishing has already had an important impact on ecosystem services that fish provide (Worm et al., 2006). Although aquaculture is often heralded as the solution to over-fishing its dependence on wild-caught fish as a source of fishmeal therefore means it is currently still contributing to the problem and is therefore not yet a totally sustainable answer. Fish also provide vital ecosystem services across all their life stages and via a wide range of both fundamental ecological and human “demand-driven” processes (Holmlund and Hammer, 1999). Examples of these services include maintaining healthy habitats (Mumby et al., 2007), and nutrient cycling (Deegan et al., 1993; Meyer and Schultz, 1985). Additional socio-economic values of fish include the aquarium trade (Wood, 2001) and tourism (Vianna et al., 2012). It is therefore not the intention of this review to make recommendations for policy makers regarding how we may wish to influence fish populations specifically based on their production of marine carbonates. However, the quantitative significance of fish within the inorganic carbon cycle has only recently been highlighted (and may be even larger). In addition, their carbonates appear to
have a very different dissolution potential relative to most other calcifiers, with significance for the chemistry of the surface ocean and its ability to absorb atmospheric CO₂. This suggests that we currently do not fully understand this half of the ocean’s carbon cycling and cannot appreciate it properly without substantially more basic information on the role and fate of fish carbonates.

3.6.9 Acknowledgements

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3.6.10 References


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3.7 Deep-sea chemosynthetic carbon production

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Summary points:
• In the deep sea, chemosynthesis is the only source of primary production. Chemosynthetic (also known as, “chemoautotrophic”) organisms produce organic matter through the assimilation of inorganic carbon coupled with the use of reduced chemical compounds as an energy source.
• A large variety of microbes synthesize organic matter through chemoautotrophic pathways, including sulfur oxidizers, ammonia oxidizers and methanogens.
• Habitats/ecosystems based on chemosynthetic primary production include hydrothermal vents and cold seeps (including whale carcasses), that deliver reduced chemical species, which are used by microbes and transferred to the food chain.
• Archaea in deep-sea sediments are the major contributors to chemosynthetic production, and chemosynthetic processes in the deep ocean interior are quantitatively more important than previously thought.
• Globally, about 52% of the chemoautotrophic carbon fixation occurs as a result of the activity of nitrifiers in the water column (37% in the euphotic zone and 15% in the dark ocean).
• About 48% of the total oceanic chemoautotrophy occurs in sediments.
• Chemoautotrophic carbon fixation in the deep sea is in the order of 4.0 \times 10^{13} \text{ gC.y}^{-1}.
• The predicted decrease in oxygen in the deep ocean interior as a result of global climate change (i.e. global warming, altered thermohaline circulation, and increased stratification) could significantly influence prokaryotic chemoautotrophic processes and therefore the overall carbon storage capacity of the ocean.
3.7.1 General introduction
Organisms capable of autotrophic production are usually defined as “primary producers”. These organisms can assimilate inorganic carbon (i.e. CO₂) and convert it into organic carbon (i.e. living biomass). Fixation of CO₂ to produce living biomass in marine systems can occur by photosynthesis or by chemosynthesis. In the ocean, phytoplankton and macroalgae are the most important photoautotrophic organisms. They depend on light to gain energy and on inorganic C for the bio-synthesis of organic matter. The organic carbon produced is consumed by the “secondary producers” (i.e. heterotrophic organisms), which release CO₂ by respiration processes (Figure 3.7.1). However, a net distinction between autotrophic and heterotrophic metabolism can be sometimes difficult due to the existence of microorganisms able to either act as autotrophs or heterotrophs (the so called “mixotrophs”).

In the ocean, the balance between autotrophic and heterotrophic processes (i.e. assimilation or release of CO₂) might contribute to either increase the carbon sequestration efficiency of the biological C pump, or to the release of carbon from the ocean to the atmosphere (depending on whether autotrophy or heterotrophy prevails, respectively). Marine microbes play a role of primary importance in controlling these processes by regulating the carbon sequestration capacity of the ocean and the ability of the planet in balancing the effects of ongoing climate change.

3.7.2 Definition of chemosynthetic processes
Where light is too scarce to activate photosynthetic processes or completely absent, such as in the deep sea (i.e. below 200m depth), primary production occurs through chemosynthetic processes. Chemosynthetic organisms produce organic matter through the assimilation of inorganic carbon, coupled with the use of reduced chemical compounds as an energy source (i.e. electron donor). The concept of chemosynthesis was initially developed towards the end of the 19th century, following the discoveries of the metabolism of sulfur-oxidizing and nitifying bacteria by Sergei Winogradsky (Dworkin, 2012). Before that, the only fixation pathway of CO₂ in the ocean was assumed to be the Calvin-Benson-Bassham (CBB) cycle. Ecological, biochemical and genomic studies carried out over the last decade have, however, provided evidence of new pathways of inorganic carbon fixation. Presently, five different alternative CO₂ fixation pathways to CBB have been described in microorganisms. These pathways include: a) the reductive tricarboxylic acid (rTCA), b) the reductive acetyl-CoA, or Wood-Ljungdahl (WL), c) the 3-hydroxypropionate (3-HP), d) the 3-hydroxypropionate/4-hydroxybutyrate (3-HP/4-HB), and e) the dicarboxylate/4-hydroxybutyrate (DC/4-HB) cycles (Hügler and Sievert, 2011).

A large variety of microbes are able to perform chemosynthesis, including:

![Figure 3.7.1. Schematic representation of the differences between autotrophic and heterotrophic organisms, their carbon sources and processes in the photic zone and in the dark portion of the oceans (deep sea) (image by Michael Tangherlini).](image-url)
• **Sulfur oxidation:** \( H_2S + CO_2 \rightarrow S + H_2O + \text{Biomass} \)

• **Aerobic ammonia oxidation:** \( NH_3 + O_2 + CO_2 \rightarrow NO_2^- + H_2O + \text{Biomass} \)

• **Anaerobic ammonia oxidation:** \( NH_4^+ + NO_2^- + CO_2 \rightarrow N_2 + H_2O + \text{Biomass} \)

• **Methanogenesis:** \( H_2 + CO_2 \rightarrow CH_4 + H_2O \)

In particular, among CO\(_2\) fixation pathways, the rTCA cycle prevails in deep-sea hydrothermal vents (at high temperatures). The 3-HP/4-HB cycle of nitrifying Archaea prevails in oxygenated deep-sea systems, while the WL-pathway of methanogenic Archaea and potentially bacteria able to perform the anaerobic ammonium oxidation (ANAMMOX) is the most important CO\(_2\) fixation pathway in anaerobic deep-sea systems.

### 3.7.3 Deep-sea chemosynthetic ecosystems

The discovery of deep-sea hydrothermal vents in 1977 on the Galápagos Rift (Lonsdale, 1977; Corliss et al., 1979) provided the first evidence of an ecosystem where chemosynthesis—and not photosynthesis—was the predominant form of organic carbon production (Jannasch and Wirsen, 1979; Jannasch and Mottl, 1985). This profoundly changed our view of life on Earth, showing that deep-sea environments could host unexpected oases of primary production and biodiversity in the complete absence of light (Van Dover, 2000; Cavanaugh et al., 2006; Baker et al., 2010). These ecosystems were demonstrated to have much higher biomasses and C production rates than the surrounding deep waters.

The hydrothermal fluids that characterize hot vents originate from high-temperature seawater-rock interactions, such as in mid-ocean ridge and back-arc spreading centres. These geothermal processes enrich the bottom water with reduced chemical species (e.g. \( H_2, H_2S, Fe^{2+}, CH_4 \)) and have a strong influence on the metabolism and diversity of microbes inhabiting these systems (Takai et al., 2006; Amend et al., 2011). The impressive progress in deep-sea hydrothermal vent research during recent years has resulted in the discovery of new chemosynthetic bacteria, which are free living, forming mats or living in symbiosis with macro- and megafaunal organisms (Dubbilier et al., 2008). The first symbiotic relationship that has been described from the hydrothermal vents was the giant tubeworm *Riftia pachyptila* (Siboglinidae) and its chemosynthetic bacterial endo-symbionts (Figure 3.7.2). Many other chemosynthetic associations have since been discovered, such as in whale and wood falls, cold seeps, mud volcanoes, continental margins and shallow-water coastal sediments (Tunnicliffe et al., 2003; Figure 3.7.3).

![Figure 3.7.2](image)

**Figure 3.7.2.** A. A diagrammatic representation of the deep-sea hydrothermal vents and their associated fauna, showing giant tubeworms (such as *Riftia pachyptila*), bivalves and shrimps in proximity of the black smokers. B. The zonation of organisms along with the properties of the fauna and associated prokaryotes moving from the vent emission (left) to areas far from the vent (right). The extent of the area depends on the thermal flow gradient, but typically the shift from one zone to another is in the order of metres. (Image by Michael Tangherlini).

Cold seep communities were first discovered in the 1980s (Paul et al., 1984) and are characterized by seepage through the sediment of cold fluid with high concentrations of reduced compounds such as sulfides or methane (Sibuet and Olu, 1998; Tunnicliffe et al., 2003; Levin, 2005). As in vents, free-living and symbiotic chemoautotrophic microorganisms use the reduced compounds to produce organic matter...
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(Tunnicliffe et al., 1996; Sibuet and Olu, 1998) and this sustains the development of dense faunal communities, similar to those reported from hydrothermal vents. The major faunal groups found in cold seeps include bivalves (mytilids, vesicomyids, lucinids and thyasirids) and siboglinid tubeworms, decapod crustaceans (shrimp and crabs), gastropods and sponges (Levin, 2005). In 1989, the discovery of a whale skeleton during a dive of the submersible *Alvin* led to the identification of another type of chemosynthetically-driven community (i.e. the so called "whale falls", see Smith et al., 1989). Smith and Baco (2003) described three main successional whale falls stages. The first one ("scavenger stage") involves megafaunal organisms, mainly sharks, fish and crabs that are attracted by the sudden input of organic matter. After the flesh of the whale is eaten, an "opportunistic stage" follows, where small polychaetes and crustaceans clean up the bones. The sediments surrounding the whale skeleton become highly enriched in organic matter, leading to the third phase (the "sulphophilic stage"), in which the skeleton of the whale (containing a large fraction of lipids) is decomposed by anaerobic bacteria to produce reduced chemicals (e.g. sulfides), which are in turn used by chemosynthetic bacteria to produce organic matter. Because the environmental conditions can be very similar to those found in other reducing deep-sea ecosystems such as vents and cold seeps, the organisms described from whale falls also have many phylogenetic similarities at the genus and family level with fauna from those systems (Smith and Baco, 2003; Tunnicliffe et al., 2003). Interestingly, more than 50 new species have been recently discovered in whale falls in the North Pacific alone.

Chemosynthetically-driven processes were also found particularly in oxygen minimum zones (OMZ, O$_2$ concentrations <0.5 ml l$^{-1}$) of the ocean interior. In these areas the high inputs of organic matter produced by intense photosynthetic processes due to upwelling significantly enhance heterotrophic microbial respiration on the sea floor. The increased microbial oxygen consumption forms severely oxygen-depleted zones that vary in thickness from 200 to 1000 m (Wyrtki, 1962; Levin, 2003; Levin and Dayton, 2009). This process was reported along the eastern Pacific Ocean, northern Indian Ocean and in the southern part of western Africa, covering cumulatively more than 1 million km$^2$ (Helly and Levin, 2004). These zones of permanent hypoxia may last for thousands of years (Reichart et al., 1998) and are major sites of carbon burial. Studies initiated in the early 1960s showed that OMZs, despite severe oxygen depletion, support extensive autotrophic bacterial mats (Gallardo, 1977; Fossing et al., 1995; Gallardo and Espinoza, 2007). In some cases, chemosynthetically-based trophic adaptations similar to those found in vents and seeps have been described (Levin, 2003). Mats of sulfide-oxidizing bacteria (*Thioploca, Beggiatoa, Thiomargarita*) are commonly found in the lowest-oxygen core regions of OMZs.

Beside this, it has been shown that chemoautotrophic processes are not only confined to specific ecosystems but are widespread in oxygenated deep-water masses of the oceans (Herndl et al., 2005; Ingalls et al., 2006; Hansman et al., 2009; Tamburini et al., 2009; Reinthaler et al., 2010). Photosynthetic C production in the oceans is ca. 48.5–54.0 x10$^{16}$gC.y$^{-1}$ (Field et al., 1998; Burdige, 2007; Dunne et al., 2007). Only ~1% of the organic matter produced reaches the deep sea floor.
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(Duarte et al., 2005), and only ~0.4% of the carbon fixed by phytoplankton at the ocean surface is buried in oceanic sediments (Middelburg and Meysman, 2007). The combination of direct measurements of organic C (OC) supply versus consumption and various modelling approaches have revealed that the OC input to the ocean interior is not sufficient to fulfill the metabolic requirements of the deep-sea biota (Smith and Kaufmann, 1999; Danovaro et al., 2001; Reinthaler et al., 2010). This apparent paradox of the imbalance between the OC supply and its consumption has been explained on the basis of potential underestimation of the allochthonous inputs of OC (Aristegui et al., 2009; Burd et al., 2010) and/or that of additional sources of OC that are produced in situ through chemoautotrophic processes (Gasol et al., 2008; Herndl et al., 2008; Reinthaler et al., 2010). While the lateral inputs of OC (i.e. OC horizontally transported by currents and advection processes) and the presence and fluxes of peculiar aggregates of organic matter are still a question of debate (Herndl and Reinthaler, 2013), it is now evident that heterotrophic metabolism produces metabolites, by-products and inorganic nutrients (e.g. ammonia, sulphide) that can be used to sustain chemoautotrophic metabolism.

Reduced inorganic compounds are used in light-independent processes ruled by deep-sea chemoautotrophs, thus obtaining energy for inorganic carbon fixation and fresh biomass production also in the dark (Howarth, 1984; Raven, 2009). In this way, high amounts of new organic matter are synthesized in the dark ocean in the form of microbial biomass, potentially fuelling the heterotrophic food web (Baltar et al., 2010; Yakimov et al., 2011; Herndl and Reinthaler, 2013). While the reactivity of the exported primary production declines with water depth as a consequence of heterotrophic activities, prokaryotic chemoautotrophy represents a source of newly fixed carbon in the deep ocean. Therefore, it might be a far more important carbon source for the deep-water microbial food web than previously hypothesized. However, the vertical and lateral inputs of organic carbon plus the organic carbon produced by chemosynthesis are apparently insufficient to satisfy the energy demands of heterotrophic microbes inhabiting the deep sea (Herndl and Reinthaler, 2013). Thus, future investigations are needed to identify the processes and energy sources able to complement and sustain heterotrophic metabolism in the dark ocean.

3.7.4 The biochemical processes

Evidence is accumulating that a variety of reduced inorganic compounds may be used as an energy source by chemosynthetic microbes in the oxygenated water column of the dark ocean, with high complexity for niche differentiation processes (Swan et al., 2011; Herndl and Reinthaler, 2013). Aerobic ammonia oxidation through nitrification is believed to be the main process responsible for dark CO₂ fixation in the ocean interior (Herndl et al., 2005; Wuchter et al., 2006; Middelburg, 2011). Nitrifying prokaryotes belong to both the bacteria (i.e. the β-subgroup and γ-subgroup of Proteobacteria, Kowalchuk and Stephen, 2001; Arp and Stein, 2003) and Archaea (Venter et al., 2004; Könneke et al., 2005; Hallam et al., 2006a, b; Martens-Habbena et al., 2009). Different studies have shown that chemoautotrophic processes involving aerobic ammonia oxidation in marine ecosystems are mainly due to archaeal rather than bacterial assemblages (Francis et al., 2005, 2007; Wuchter et al., 2006; Santoro and Casiotti, 2011; Santoro et al., 2011; Yakimov et al., 2011; Mulari et al., 2013). Indeed, Archaea represent a key component of the prokaryotic assemblages at benthal and abyssal depths (Karner et al., 2001; Teira et al., 2006). In this regard, the amoA genes encoding the subunit A of the ammonia monooxygenase, a key enzyme in the oxidation of ammonia, are 10 times more abundant in Archaea than in bacteria (Francis et al., 2005; Schleper et al., 2005; Wuchter et al., 2006).

While the inorganic carbon fixation by heterotrophic bacteria (i.e. CO₂ fixation through anaplerotic reactions (i.e. that replenishes the concentration of an intermediate in a metabolic pathway) involving carboxylation reactions in central and peripheral metabolism) is well known from laboratory studies (Gottschalk, 1986), its quantitative relevance in deep-sea ecosystems is expected to be low. Indeed, inorganic carbon utilization through an anaplerotic pathway declines with decreasing concentration in laible organic substrates, which are generally very low in the deep ocean. In contrast, inorganic carbon use through chemoautotrophic processes is far more important than previously thought (Herndl et al., 2005; Ingalls et al., 2006).

If the mechanisms and microbial components that are responsible for inorganic C use in deep water masses of the oceans remain to be quantified, information on the quantitative importance and ecological role of dark inorganic C fixation in surface and sub-surface deep-sea sediments is practically nonexistent. Pioneer
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3.7.5 Global significance of chemosynthetic primary production in the deep sea

Diagenetic models of the chemical energy potentially released upon mineralization of organic matter give global estimates for chemoautotrophy of 0.37 - 0.77 x 10^16 gC·y^(-1) (Middelburg, 2011). The primary production originating through oceanic photosynthesis (Field et al., 1998; Dunne et al., 2007) is certainly far more relevant on the global scale. However, it is noteworthy that reported global chemosynthetic C production rates are similar to those of riverine organic carbon delivery (0.4-0.5 x 10^16 gC·y^(-1); Cole et al., 2007) and organic carbon burial in marine sediments (0.2-0.79 x 10^16 gC·y^(-1); Duarte et al., 2005; Burdige, 2007; Dunne et al., 2007). This implies that chemoautotrophy should be accounted for in future oceanic carbon budgets and cycling models.

Globally, about 52% of the chemosynthetic carbon fixation is due to microbial nitrification processes occurring in the water column (37% in the euphotic zone and 15% in the dark ocean). Chemoautotrophy in sediments is estimated to contribute about 48% of the total oceanic chemoautotrophy (ca. 0.37 x 10^16 gC·y^(-1)), and in deep-sea sediments it is currently thought to be very limited (0.004 x 10^16 gC·y^(-1)). Here, chemoautotrophy is mainly due to nitrifiers (i.e. ammonia oxidation), given that the oxidation of other reduced compounds, such as sulfides in hydrothermal vents and iron, sulfide and hydrogen in basaltic ocean crust has been estimated to support lower inorganic carbon fixation rates, in the order of 3.0 x 10^15 gC·y^(-1) (Bach and Edwards, 2003; Raven, 2009). Recent studies determined experimentally the rates of chemoautotrophic C production and reported values much higher than those predicted by diagenetic models (Middelburg, 2011; Molari et al., 2013). This suggests that chemosynthetic processes can be quantitatively more important than previously thought, providing new clues for a better understanding of ecosystem functioning and biogeochemical cycles at the global scale.

3.7.6 Goods and services related to deep-sea chemoautotrophy

The deep-sea ecosystems host diverse and unique microbial communities, which are fundamental in preserving the global ecosystem and the environmental conditions permitting human life on Earth. The chemosynthetic processes occurring in the dark ocean interior significantly influence the global budgets of production and utilization of organic matter, by supplying an important fraction of the organic carbon that can enter the oceanic food web (Middelburg, 2011). In this way, the deep-sea microbial chemoautotrophic communities play a significant role in the biogeochemical cycles, supporting the food webs and contributing to the productivity of the ocean. Moreover, a body of evidence is accumulating of the importance of chemosynthetic microbes involved in symbiotic relationships with organisms of high scientific, ecological, and possibly biotechnological/industrial interest (Dubilier et al., 2008). The importance of the microbes involved in the chemosynthetic processes thus extends beyond their relevance in the organic carbon budgets and the carbon storage capacity of the oceans. Indeed, a significant portion of the high biodiversity that deep-sea ecosystems were recently demonstrated to host, is strictly dependent on the activity of such unique and peculiar microbes.

3.7.7 How climate change can influence deep-sea chemoautotrophy

Pelagic prokaryotic chemoautotrophy increases with decreasing oxygen concentrations in the water column (Taylor et al., 2001; Hannig et al., 2007; Lam et al., 2007; Woebken et al., 2007). Consequently, highest pelagic prokaryotic CO₂ fixation rates have been reported for suboxic and anoxic water bodies such as the Black Sea, the Cariaco Basin and the twilight zones of upwelling areas (Taylor et al., 2001; Kuypers et al., 2005; Hammersley et al., 2007). By the end of the century, a loss of ca. 25% of the current oxygen content of the global ocean is predicted to occur due to changes in thermohaline circulation patterns and the accompanied warming and increased stratification (Bopp et al., 2002). This also implies that areas with suboxic conditions will expand in the future, with substantial consequences for the global carbon and nitrogen cycle (Francis et al., 2007). The predicted spread of oxygen minimum zones will likely lead to increasing prokaryotic chemoautotrophy, particularly in the mesopelagic waters of the global ocean. Hence, it is likely that deep-water pelagic food webs might be based on prokaryotic chemoautotrophy.
to a larger extent in the future ocean than at present. Therefore, including deep-water chemosynthesis into general oceanic carbon flux models will surely help in better forecasting of future trends in oceanic biogeochemical cycles.

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3.8 Deep-sea microbes and their role in the ocean interior

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Summary points:
• The ocean interior contains the majority of microbes inhabiting the Earth and deep-sea floor surface sediments contain 10–10,000-fold more cells per unit volume than productive ocean-surface waters.
• Conversely to other biological components of the ocean, the abundance of benthic prokaryotes (i.e. microbes belonging to two domains of life: Bacteria and Archaea) and viruses (biological entities infecting living cells) does not decrease significantly with increasing water depth.
• The prokaryotic biomass, which largely dominates over all other biotic components, is estimated in the order of $0.34 \times 10^{15} \text{ gC}$ in deep-sea surface sediments.
• Deep-sea prokaryotes and viruses along with their interactions play a crucial role in the decomposition processes and biogeochemical cycling of carbon, nitrogen and phosphorus at the global scale.
• The global heterotrophic carbon production of deep-sea microbes could be estimated in the order of $0.6-1.5 \times 10^{15} \text{ gC.y}^{-1}$, contributing significantly to overall heterotrophic carbon production in the oceans at all depths.
• Viruses in the deep sea have the potential to affect all microbial-driven processes, thus influencing material and energy transfer and fluxes. Viral-induced mortality in the deep sea can convert a large part of the prokaryotic biomass into detritus, releasing on a global scale $0.4-0.6 \times 10^{16} \text{ gC.yr}^{-1}$.
• It is not possible yet to predict the impact of climate change on deep-sea prokaryotes and viruses, nor if this will be exacerbated by multiple stressors, such as changes in temperature coupled with acidification and shifts in salinity and oxygen concentration, or if it will be buffered by biotic interactions. However, there is increasing evidence that deep-sea microbes are key biotic components that will influence the ocean’s feedbacks to climate change.
3.8.1 Introduction
The “Deep Sea” includes the waters and sediments of the ocean interior beneath approximately 200 m depth, representing more than 65% of the Earth’s surface and more than 95% of the global biosphere. The deep ocean is the world’s largest biome and the deep sea contributes constantly to the discovery of both new habitats and species. Indeed, the exploration of new deep-sea areas in the last few decades has resulted in the discovery of more than 30 previously completely unknown deep-sea habitats and ecosystems, along with a great many new species inhabiting these peculiar systems. However, despite the huge scale and ecological importance of deep-sea habitats, the knowledge of the deep-sea microbiology and implications on ecosystem functioning is still limited. Current estimates report that only 5% of the deep ocean has been explored in detail so far, and that less than 0.001% has been sampled and described in terms of microbiological and biodiversity variables. Even less is known of their functioning and on the interactions between biodiversity and ecosystem functioning. The development of advanced instrumentation for observing, mapping and sampling the sea bed and all of its features has now enabled scientists to develop a picture of the deep-sea environment as a highly dynamic geo- and biosphere.

Besides the vast deep-sea flat and muddy plains and their subsurface, the ocean sea floor is characterized by high habitat heterogeneity. A variety of highly diverse landscapes have been described recently, including canyons, seamounts, ridges, furrows, deep-water coral reefs, cold seeps, pockmarks, mud volcanoes, carbonate mounds, brine pools, gas hydrates, fractures and trenches that host rich and diverse landscapes have been described recently, including canyons, seamounts, ridges, furrows, deep-water coral reefs, cold seeps, pockmarks, mud volcanoes, carbonate mounds, brine pools, gas hydrates, fractures and trenches that host rich and diverse microbial assemblages (Ramirez-Llodra et al., 2010).

Organisms inhabiting the deep sea have to cope with severe food limitation, depending mostly on the carbon export from the surface ocean and on peculiar primary production processes previously neglected, such as chemoautotrophy based on the use of chemical compounds as an energy source. Along with the export of organic material from the photic zone, geological processes transport chemical energy (hydrogen, methane, hydrogen sulphide and iron) up to the sea floor from the subsurface below. At the sites on the sea floor where chemical energy is particularly high, rich and diverse microbial communities thrive, such as in hydrothermal vents and cold seeps (Cavanaugh, 1985; Jørgensen et al., 2007). However, most subsurface micro-organisms live in conditions of extreme energy limitation, with mean generation times of up to thousands of years.

Deep-sea microbiology is a young branch of marine biology and ecology research. Although the scientific discovery of the ubiquitous and enormous abundance of micro-organisms dates back to the 1860s, microbes inhabiting the deep sea started to be studied in detail only in the 1950s, along with the appearance of the first historical monographs on marine microbiology (e.g. Benecke, 1933). In the 1950s, deep-sea samples that were gathered on the Danish Galathea Deep-Sea Expedition from depths of more than 10,000 metres were shown to host millions of viable bacteria per gram of sediment, confirming that pressures up to 1100 times higher than atmospheric pressure do not exclude the possibility for life to evolve (ZoBell and Morita, 1959). Subsequent studies conducted in the 1980s and 1990s aimed at quantifying the microbial assemblages, demonstrated their activity in the deep ocean interior (Jannash and Taylor, 1984; Alongi, 1990; Deming and Baross, 1993; Yayanos, 1995).

Most deep-sea micro-organisms are extremely difficult to cultivate, due to their slow in situ growth rates and their probable strict adaptation to extreme environmental conditions (oligotrophy, low temperatures and high in situ pressure conditions or anaerobiosis). The number of pure cultures that are available is limited to a few hundred species, and the cultivation of micro-organisms under high pressure has been achieved only in a limited number of cases.

3.8.2 The ecological role of microbes in the deep sea
In the last few years enormous progress has been made in the investigation of deep-sea microbes and their functional role, and an increasing portion of the deep sea floor has been sampled (Figure 3.8.1). The analysis of these samples has revealed that deep-sea floor surface sediments, at all depths, contain 10–10,000-fold more cells per unit volume than productive ocean-surface waters. It is thus now evident that microbes play a key role in deep-sea ecosystems, by fundamentally contributing to the total fresh biomass (Rex et al., 2006; Wei et al., 2010), with prokaryotes representing the largest pool of biomass and biomass production in the world’s ocean (Whitman et al., 1998). All of this evidence confirms the microbes as the most important players in the biogeochemical cycles on a global scale.
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(Nealson, 1997; Mason et al., 2009). Prokaryotes and other tiny micro-organisms such as viruses (Figure 3.8.2), heterotrophic flagellates and other protists, play key roles in organic matter remineralization, in nutrient cycling and in the transfer of energy to higher trophic levels. Early studies hypothesized that microbial enzymatic activity and settling particle decomposition during their descent, was so strong as to be able to limit the input of organic material to the deep-sea floor (Cho and Azam, 1988; Arndt et al., 2013). But subsequent studies proved that the downward flux of organic material to the sea floor was in some cases, extremely rapid (Billett et al., 1983; Lochte and Turley, 1988). As a consequence, recent studies suggest that the microbial components are controlled by a combination of factors (top down-predation and bottom up- resources) rather than by food supply alone.

Being unable to self-replicate, viruses invade other organisms and use the host cell’s machinery to propagate. They can infect all known life forms in the ocean, from the smallest marine microbes to the largest mammals. Since the prokaryotes are the predominant life forms in the deep oceans in terms of biomass, the interactions between viruses and the members of the prokaryotes are considered one of the most relevant processes driving the ecosystem functioning on the global scale (Proctor and Fuhrman, 1990; Fuhrman, 1999). The huge, nitrogen- and phosphorus-rich, prokaryotic biomass represents a potentially enormous and high quality food source for higher trophic levels in

Figure 3.8.1. Sampling sites of deep-sea surface sediments analysed so far and considered in the present study (data are from Rex et al. (2006), Danovaro et al. (2008b), along with unpublished datasets from Danovaro and colleagues)

Figure 3.8.2. Some examples of viruses and of prokaryotes (microbes belonging to the two prokaryotic Domains of Life: Bacteria and Archaea) from sea water and sediments as revealed by microscopic analysis using different epifluorescence techniques to stain the DNA contained inside viruses or inside cells. Illustrated are: a) green fluorescence is produced by staining DNA with SYBR Green I or with Acridine Orange. Both these dyes make the detritus appear orange-red, allowing DNA-containing objects to be distinguished from detrital particles; b) Archaea appear as red dots in sediment samples following CARD-fish analysis, which selectively identifies Archaea, excluding Bacteria, or vice versa. This enables an evaluation of the relative contribution of Archaea and Bacteria in benthic prokaryotic communities. Since CARD-fish analysis targets RNA, coloured cells are usually considered as having an active metabolism; c) the high efficiency of the stain SYBR Green and Gold allow the discrimination of the viruses (virus-like particles), which can be distinguished from the prokaryotes from their dimensions as they are mostly in the range of 0.02-0.2 μm, while Bacteria and Archaea have a cell size ranging usually from 0.2 to 2 μm; d) the DNA stain DAPI results in a blue fluorescence. This stain is now much less frequently used given the high background fluorescence.
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Deep-sea food webs (Dell’Anno and Danovaro, 2005). However, since heterotrophic consumers decrease exponentially with increasing water depth, the potential role of viruses in controlling other microbial components increases in the deep ocean interior. Deep-sea viral ecology is a crucial field in deep-sea microbiology, so far largely neglected, which is only now starting to be included in global models of carbon, nitrogen and phosphorus cycling and nutrient fluxes. By killing their hosts, viruses can transform the living biomass into organic detritus (mostly dissolved organic matter -DOM), which can then be used again by other microbes stimulating their growth. This process was defined as the “viral shunt” (Suttle, 2005, 2007) and, depending on the balance between the abatement of living cells and the stimulation of the metabolism of the survivors, it can either fuel prokaryotic heterotrophic and autotrophic production by the release of DOM and enhancing nutrient regeneration pathways, or it can decrease the efficiency of the carbon transfer to higher trophic levels. The debate on this topic is still on-going among marine ecologists.

3.8.3 Microbial abundance biomass and distribution in the ocean

Whitman et al. (1998) made a global estimate of the number of prokaryotic cells that are present in the oceans, from the surface to subsurface sediments, up to temperatures of approximately 110°C, which are now considered to represent the thermal limit for microbial life. They concluded that deep-sea microbes represented the ‘hidden majority’ of all life forms, comprising between 50 and >80% of the Earth’s total microbial biomass and between 10 and 30% of the Earth’s total living biomass. Archaea have been assumed for a long time to be a minor portion of the total microbial community in the surface ocean and in seafloor sediments. Subsequent work has indicated that archaeal abundance, not only in deep-sea waters beneath 1000 m depth but also in subsurface sediments, can equal bacterial abundance or even dominate (Karner et al., 2001; Schippers et al., 2005; Biddle et al., 2006; Schippers and Neretin, 2006; Lipp et al., 2008; Xie et al., 2013). Finally, recent data based on integrated estimates from the ocean surface to the deep-sea subsurface sediments, indicate that the abundance of Bacteria and Archaea could be roughly equivalent (Lloyd et al., 2013).

Studies conducted on sediment cores, within the frame of the Integrated Ocean Drilling Program (IODP) expeditions revealed the presence of metabolically active microorganisms several hundred metres below the sediment surface (Parkes et al., 2000; D’Hondt et al., 2002, 2004; Teske, 2005). Recently, a meta-analysis of these studies has indicated that the average cell numbers and metabolic activities decrease exponentially with depth in the sediment, highlighting the possible quantitative importance of Archaea in the prokaryotic communities and in the functioning of deep-sea ecosystems, especially in the subsea floor (Lloyd et al., 2013).

The first investigations of global trends in the distribution and abundance of microbial cells showed that the abundance of cells in surface sediments is usually related to the input of fresh detritus, rather than to any other oceanographic parameter (Deming and Baross, 1993; Smith et al., 1997; Boetius and Damm, 1998). It is generally accepted that the abundance and biomass of the microbial components is controlled by the quantity and quality of the available organic substrates. This applies to most biological components in the deep sea (e.g. meiofauna macrofauna, megafauna) and since the availability of food and resources typically decrease with increasing water depth, consequently the biomass of all faunal components decreases exponentially.

Viruses inhabiting the deep-sea ecosystems are quantitatively far more important than was thought only two decades ago. It is accepted that viruses are the most abundant biological entities in the biosphere, with current estimates of the global viral abundance in the order of 10^{30}-10^{31}, outnumbering prokaryotes by at least one order of magnitude (Suttle, 2005, 2007). The analysis of the spatial patterns of the different microbial components, however, indicates that the distribution of prokaryotes and viruses in surface deep-sea sediments does not show a trend similar to those of other benthic components (megafauna, macrofauna and meiofauna) and does not significantly decrease with increasing water depth (Rex et al., 2006, and further implementation of the dataset, Figure 3.8.3). Data reported here indicate that prokaryotic and viral abundances are high at all depths in the deep sea, from the shelf-break down to the ultra-abyssal or hadal depths (i.e. from 6000 to 11000m depths) sediments with values similar to those reported for coastal areas (Danovaro et al., 2008a; Siem-Jørgensen et al., 2008).
3.8.4 Deep-sea microbial activity

Deep-sea microbes occur at depths where the light intensity is too low for photosynthetic primary production and the temperatures are constantly low (from ca –2°C to 4°C). These conditions together with the low availability of organic matter set the limits to benthic secondary microbial activity and production. Nonetheless, emerging evidence from different studies using different approaches is confirming that the microbial components inhabiting deep-sea ecosystems are more dynamic than previously thought (Dell’Anno and Danovaro, 2005; Danovaro et al., 2008b; Luna et al., 2012; Moliari et al., 2013), with deep sea planktonic particles and sediments both considered as “hotspots” for microbial growth and organic matter remineralization (Cho and Azam, 1988; Turley and Mackie, 1994; Turley and Stutt, 2000; Arndt et al., 2013). Little is still known about how prokaryotes respond to changes in the distribution, composition, and flux of organic matter in the oceanic food webs (Azam, 1998), or which microbial species are responsible for most of the carbon, nitrogen and phosphorous cycling in deep waters and sediments (Jørgensen et al., 2007; Aristegui et al., 2009).

Viral abundance is also strongly and positively correlated with prokaryotic abundance in deep-sea surface sediments (Figure 3.8.4), so that the ratio between the two abundances seems not to be directionally affected by depth or by pressure. A high viral abundance in the deep-sea sediments could be due to both the supply of viruses adsorbed onto particles sinking down from the upper water column (Mari et al., 2007) and/or to the high in situ viral production rates (Danovaro et al., 2008a; Siem-Jørgensen et al., 2008). However, the downward flux of viruses associated with settling particles to the deep sea was demonstrated to be extremely low (Danovaro et al., 2008b). When the abundance of prokaryotes and viruses per m² of surface sediment is multiplied by the extent of the deep-sea sediments at different bathymetric ranges, the overall abundance of these microbial components in surface sediments shows a marked increase with water depth, with viruses outnumbering prokaryotes also at abyssal depths (Figure 3.8.5).

Recent attempts to derive estimates of carbon cycling in the global ocean suggest that about one-third of the biological production of CO₂ in the ocean is due to the microbial activity from the dark pelagic layers (del Giorgio and Duarte, 2002; Aristegui et al., 2005). This evidence has been further confirmed by investigations conducted in hadal trenches, where hot spots of biomass and heterotrophic activity were found at the deepest depths (up to 11000 m) of the ocean interior (Yayanos, 1995; Danovaro et al., 2003; Blankenship-Williams and Levin, 2009; Glud et al., 2013).
Lochte (1992) found that the bacterial biomass in the top 10 cm of abyssal deep-sea sediment increased rapidly in response to the sedimentation of a spring plankton bloom, showing that deep-sea microbial life can be potentially very (re)active. The input of phytodetritus and other labile organic materials to deep-sea sediments is known to trigger the production of enzymes useful for organic matter degradation, such as proteases, agarases, alginases, esterases, β-glucosidases, phosphatases, succinate dehydrogenases, amylases and chitinases. Approximately 1–2% of the organic carbon supplied from the ocean surface and reaching deep sea sediments, is oxidized by benthic micro-organisms within a few days, but remineralization rates slow down if the organic material ages, becoming richer in compounds which are refractory and difficult to degrade (Lochte and Turley, 1988; Turley and Lochte, 1990).

Prokaryotic heterotrophic production and viral production were demonstrated to be potentially high at all water depths in surface sediments and are significantly correlated (Figure 3.8.6). This is in line with the theoretical dependence of viral replication on the host abundance and metabolism. The impact of viruses on benthic prokaryotic production, determined by monitoring the abundance of viruses and their prokaryotic hosts over time, led to the estimation of a viral-induced abatement of 80% of the total prokaryotic heterotrophic production in deep-sea sediments. Virus-induced prokaryotic mortality increases with increasing water depth, and beneath a depth of 1,000m nearly all of the prokaryotic heterotrophic production is transformed into organic detritus (Figure 3.8.7), indicating that viruses are the main agents of mortality for prokaryotes in deep-sea sediments worldwide (Danovaro et al., 2008b). The implications on food web functioning and biogeochemical processes in deep-sea ecosystems are that viruses, by killing most of the prokaryotes produced, determine the shunt of most of the prokaryotic carbon production into organic detritus, drastically reducing the microbial biomass potentially available to higher trophic levels. These results can help in explaining the paradox of deep-sea ecosystems in which prokaryotic biomass is largely unused by deep-sea fauna, despite severe food limitation (Witte et al., 2003).

Epifluorescence microscopy analyses specifically developed for sediment samples, allow for the direct measurements of viral abundance during time-course experiments, and indicate that viral production rates in deep-sea sediments are consistently high, and that viruses are produced in situ. Several studies reported the predominance of the lytic viral cycle (viral replication strategy resulting in the lysis of the infected cells and consequent release of virus progeny and other intracellular components) both in deep-sea sediments and in deep-sea waters (Danovaro et al., 2008b). However, new viral replication strategies also can be observed from the study of new host systems, as was recently demonstrated for some viruses infecting Archaea (Prangishvili et al., 2006; Bize et al., 2009). Analyses of viral and prokaryotic production in deep-sea sediment samples in situ, and at decompressed (at 0.1 MPa), and repressurized conditions demonstrated that production rates are not significantly influenced by deep-sea sample recovery (Danovaro et al., 2008b).
Unfortunately, only a limited number of studies have been conducted under deep-sea in situ conditions so far (Jannasch and Wirsen, 1973; Tamburini et al., 2009), and it is still difficult to derive universal conclusions on how pressure affects, directly or indirectly, the metabolism and dynamics of microbial communities in the deep ocean. However, it is clear that deep-sea viruses, and especially viruses in the sediments, are a highly dynamic and active component of deep-sea ecosystems, with high turnover, comparable to, or even higher than, that reported for coastal aquatic ecosystems (Danovaro et al., 2008a; Siem-Jørgensen et al., 2008).
of this organic matter is not consumed by metazoans (multicellular animals), but is remineralized into CO₂ and DOC by microbial degradation within the top 500 m of the water column, becoming available for further primary production processes. Only a small proportion and quantity of the particulate organic carbon produced in the ocean surface reaches the ocean sea floor (on average, 1 g C m⁻² y⁻¹, Jahnke and Jackson, 1992). Assuming the typical average prokaryotic abundance of 10⁸ cells cm⁻³ in deep-sea sediments and a carbon content of 20 x 10⁻¹⁵ g per cell, the top 10 cm of sediment (per m²) contains 0.2 g of carbon as microbial biomass. Hence, each year, the amount of fresh organic matter available to sustain the metabolism of deep-sea prokaryotic cells is likely limiting microbial growth in these systems.

A much larger potential source of organic carbon for energy and growth could be the refractory organic material buried in the sediments, which comprises approximately 0.1–1% of the sediment by dry weight. This total sedimentary organic matter is the equivalent of approximately 1–10 x 10¹⁵ g C m⁻³ at the sea floor, but is typically composed of recalcitrant organic substrates undergoing extremely slow microbiologically driven degradation processes (Mayer, 1993; Hedges and Keil, 1995). On the contrary, there is evidence to suggest that intracellular material released by viral lysis can be an important and readily bioavailable source of labile organic carbon for prokaryotes (Noble and Fuhrman, 1999; Corinaldesi et al., 2007).

As evident from the comparative analysis of the biomass patterns of the different biological components with increasing water depth (Figure 3.8.8), the relative importance of prokaryotes increases progressively in the deep ocean surface sediments. At abyssal depths, prokaryotic biomass is estimated to be in the order of 0.34 x 10¹⁵ g C in surface sediments at the global scale (Whitman et al., 1998) and is typically composed of recalcitrant organic substrates undergoing extremely slow microbiologically driven degradation processes (Mayer, 1993; Hedges and Keil, 1995). On the contrary, there is evidence to suggest that intracellular material released by viral lysis can be an important and readily bioavailable source of labile organic carbon for prokaryotes (Noble and Fuhrman, 1999; Corinaldesi et al., 2007).

The viral lysis, on the one hand, kills an important fraction of benthic prokaryotes and reduces the competition for available resources, but on the other, generates labile, highly bioavailable material and stimulates the metabolism of uninfected deep-sea prokaryotes. This process has important implications for carbon cycling and nutrient regeneration and, on a global scale, can release 0.4-0.6 x 10¹⁵ g C y⁻¹ (Danovaro et al., 2008b). Therefore, it represents an essential source of labile organic compounds to deep-sea ecosystems, contributing to around 35% of the metabolism of benthic prokaryotes, increasing their turnover and promoting the recycling of key elements (including nitrogen and phosphorus associated with prokaryotic biomass). Viral infections play important roles in the functioning of the largest ecosystem of the biosphere, by controlling benthic prokaryotic biomass (top-down, predatory control), by stimulating prokaryotic metabolism (bottom-up mechanism), and by accelerating biogeochemical processes.

Figure 3.8.9. Estimate of the possible relative contribution of deep-sea prokaryotes, meiofauna (including foraminifera), macrofauna and megafauna to the heterotrophic carbon production in deep-sea surface sediments worldwide.

### 3.8.6 Goods and services provided by deep-sea microbes

The dark portions of the ocean represent the most remote biome on Earth, they are potentially characterized by a huge microbial diversity, which is still largely unexplored (Sogin et al., 2006), representing one of the last frontiers of scientific research. The deep-sea microbes play crucial roles in the ecosystem at the global scale, and their ecological and physiological functions are fundamental to preserve the Earth and human life as we know it. As well as the microbes inhabiting the ocean surface, the deep-sea microbial communities significantly contribute to the biogeochemical cycles and in the regeneration of organic matter and nutrients that support the food webs and keep the ocean healthy and productive. Moreover, the significance of the value of these almost invisible but essential components of the biosphere extends way beyond ecological aspects. Indeed,
deep-sea ecosystems have an enormous potential in the discovery and development of new products of microbial origin, such as pharmaceuticals, molecular probes, enzymes, cosmetics, nutritional supplements, and agrichemicals.

Deep-sea microbes, and particularly those inhabiting extreme ecosystems such as hydrothermal vents, have been fundamental in the discovery of new bioactive molecules employed for technological and industrial purposes (Ohta and Hatada, 2006; Wu et al., 2006; Cavicchioli et al., 2011). Different enzymes such as DNA polymerases, enzymes involved in ethanol production and with antioxidant properties derived from deep-sea bacteria are already commercially available. Several secondary metabolites with novel structures and specific bioactivities, which have promising potential benefits for medical therapy, have been discovered from deep-sea microbes including alkaloids as therapeutic agents, bone-healing materials and exopolysaccharides with anticoagulant properties (Colliec Jouault et al., 2001; Zanchetta et al., 2003; Yang et al., 2013). Increasing evidence is also accumulating on the involvement of microbes in the origin, biomineralization and transformation processes of deep-sea polymetallic nodules and metal crusts, whose economic value is currently of great industrial and technological interest (Wang et al., 2011). Thus, the deep-sea ecosystems are important not only because they are essential for the existence and life on Earth, but also because they provide unique goods and services which can be exploited for human activities, profit and health.

The enormous value of deep-sea ecosystems in terms of ecology and as reservoirs of exploitable resources highlights the need to establish shared criteria governing their sustainable use and their preservation. Human activities such as trawling, deep-sea mining, drilling and dumping profoundly threaten the deep-sea ecosystems. Moreover, if not properly regulated, recent developing research fields such as deep-sea bioprospecting (i.e. the screening of deep-sea microbes in search of new products of possible economical interest) could potentially generate impacts, similar to any other kind of exploitation of the deep sea. To date, there is no legal framework for the management, benefit sharing and resource access in areas beyond national jurisdiction but this appears to be of fundamental importance to preserve deep-sea ecosystems, their astonishing microbial biodiversity and their role in their response to global climate change.

3.8.7 Deep-sea microbial response to global climate change

It is not possible to predict how climate change will impact deep-sea prokaryotes and viruses. However, there is increasing evidence that deep-sea microbes interact actively with the present climate changes, being affected, adapting, and coping with these, but also influencing the biological and physico-chemical responses of marine ecosystems to these ongoing changes (Danovaro et al., 2011). Notably, most of the limitations currently hampering the modelling and understanding of the functioning of the deep-sea ecosystems are due to the insufficient evidence of the biological and physiological processes that are driven by deep-sea microbes, and especially a lack of measurements conducted in situ.

Temperature is known to increase the metabolism and thus respiration of the heterotrophic microorganisms. But an increased metabolic activity could result in an increase of viral infections. Thus it is not predictable yet whether climate change (e.g. rise of deep-water temperature) will result in an increase or in a decrease (depending on the ultimate cascade effect of the biological interactions) in the ability of deep-sea ecosystems to store carbon. Moreover, the paucity of data relating to the contribution of deep-sea Archaea to primary production through chemosynthesis is still a question of debate, especially for the benthic realm. The continuous discovery of new processes mediated by the different microbial components can help in the understanding of the functioning of the deep-sea ecosystems.

The success in the unveiling of the secrets of the carbon budgets and of the microbial diversity and activity in the deep oceans will thus depend on our ability to increase the economic and technological efforts, but also maximize and optimize the efficiency of the ongoing research projects dedicated to these topics, possibly creating global monitoring networks in key areas. The direct impact of human activities on biogenic carbon sinks in the deep sea are still relatively limited, although the increasing pressure derived from deep-sea drilling for oil extraction, methane and gas hydrates exploitation, and deep-sea mining can certainly directly and indirectly alter the functioning of deep-sea ecosystems and their ability to sequester carbon (Barbier et al., 2014; Van Dover et al., 2014).
3.8.8 References


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4.1 Introduction

In 2009 IUCN released a report\textsuperscript{11} on coastal carbon sinks that stimulated a world-wide debate on the value and importance of coastal ecosystems such as mangroves, saltmarshes and seagrass beds for climate change mitigation. This was undertaken to directly tackle gaps in carbon management and address the policy and management issues. The key issue the 2009 report tackled was that if we manage ecosystems for carbon on land, why don’t we do the same for ecosystems along the coast?

The perspective we offered in that report was new to many, and stimulated much discussion and debate globally which ultimately led to recognition of coastal and marine carbon sinks – the so called ‘blue carbon’ perspective. This work led to the development of many projects and programmes on coastal climate change mitigation and ultimately to a greater overall respect for these ecosystems. It helped explain to a much wider audience why ‘mud matters’ and added a new tangible ecosystem service that many policy advisers and decision makers could more readily relate to than perhaps other less financially quantifiable values placed on these coastal habitats such as biodiversity importance and aesthetic values etc.

This new report on ocean carbon seeks to be just as ground breaking as the coastal one. In the report we expand the ocean perspective by once again promoting the work of key scientists who are studying carbon, but this time in the open ocean. We tell the story of the role and importance of the ocean in the carbon cycle, and the importance of specific oceanic carbon pools and sinks and their potential role for climate change mitigation.

The overall premise is the same – that if we manage and value ecosystems for carbon on land and now at the coast, why don’t we take a similar view for carbon in the open ocean? Once again we have illustrated this report through case studies on selected ocean ecosystems and key species. In this report we have documented their carbon role as well as exploring the value of such carbon services. Where known we also explore the implications of how we use the ocean for the continued persistence or otherwise of such carbon services.

4.2 Significance of ocean carbon

What is evident from the work documented in this report is that globally and regionally ocean carbon services are important and now need to be factored into...
agreements, actions and the decision making process. Actions to address ocean carbon should not be just through climate change policy discussions, but also through the management decisions of industrial sectors that currently exploit ocean resources - such as krill and capture fisheries.

The case studies help illustrate the scale and nature of how ecosystems and species form fundamental elements of the mechanisms in the ocean that move carbon, and ultimately sequester a proportion permanently in the deep ocean. Whilst there are gaps and uncertainties in what we understand we know enough about carbon to start to appreciate the importance of ecosystems and species in the ocean for climate change mitigation. The scale and roles are impressive and important in their own rights, as well as some being comparable to carbon values from nature-based solutions to carbon sequestration on the terrestrial side.

- The annual carbon production by diatoms represents ~7.4% of net primary production on earth. Diatom carbon sequestration to the deep ocean (>1000m) per year accounts for ~1.7% of annual CO₂ emissions from fossil fuels and ~6.5% of the annual uptake of CO₂ by the ocean.
- A single species of coccolithophore, *Emiliania huxleyi*, which plays a key role in ocean carbon uptake, each year occurs in blooms forming vast milky turquoise patches on the ocean surface that cover an area twice the size of Texas (up to 1.4 x 10⁶ km²).
- Pteropods, tiny citizens of the surface waters and so essential to the food chain, especially in polar regions, exist in such abundance that they have a global biomass that is more than the total biomass of kelp forests in the world ocean.
- Krill, essential to food chains where they live, have a distribution that roughly equates to the size of South America. Their role in carbon sequestration offsets ~0.26% of annual global CO₂ emissions from fossil fuel combustion.
- If fisheries managers considered fish as an ecosystem service simply on the basis of their carbonate production, then rates of fishing mortality would need to be lower (than rates currently considered sustainable) to viably maintain this service.

The predicted oxygen decrease in the deep ocean interior as a result of global climate change (i.e. global warming, altered thermohaline circulation, and increased stratification) could significantly influence prokaryotic chemoautotrophic processes and therefore the overall carbon storage capacity of the oceans. This issue clearly matters in terms of climate change mitigation and adaptation but is rarely if ever considered. Deep-sea

Table 4.1: Rate of net primary production (NPP), particulate organic carbon (POC) export and production-to-export ratio (POC/NPP) for large and small phytoplankton groups.

<table>
<thead>
<tr>
<th>Type</th>
<th>NPP (x10¹⁵ gC.y⁻¹)</th>
<th>POC export (x10¹⁵ gC.y⁻¹)</th>
<th>POC/NPP</th>
</tr>
</thead>
<tbody>
<tr>
<td>Large Phytoplankton</td>
<td>23.8</td>
<td>7.2</td>
<td>0.3</td>
</tr>
<tr>
<td><em>Of which Diatoms contribute:</em></td>
<td>10.7</td>
<td>4.2</td>
<td>0.39</td>
</tr>
<tr>
<td>Small Phytoplankton</td>
<td>54.2</td>
<td>2.6</td>
<td>0.04</td>
</tr>
<tr>
<td><em>Of which Coccolithophores contribute:</em></td>
<td>1.2</td>
<td>1.1</td>
<td>0.98</td>
</tr>
<tr>
<td>Oceanic phytoplankton TOTAL</td>
<td>78</td>
<td>9.8</td>
<td>0.35</td>
</tr>
<tr>
<td>2Coastal primary producers</td>
<td>10</td>
<td></td>
<td></td>
</tr>
<tr>
<td>3All terrestrial vegetation</td>
<td>69</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sum of global NPP</td>
<td>157</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

(Jin et al., 2006), (Duarte and Cebrian, 1996), (Janzen, 2004). *Diatoms and coccolithophores are used as examples of large and small phytoplankton respectively, because of the important role they play in the biological pump. *Coastal primary producers* include coastal phytoplankton, microphytobenthos, coral reef algae, macroalgae, seagrass, marsh plants and mangroves (Duarte and Cebrian, 1996)
prokaryotes and viruses along with their interactions play a crucial role in the decomposition processes and biogeochemical cycling of carbon, nitrogen and phosphorus at the global scale.

In terms of absolute comparative values to terrestrial carbon ecosystems more work is required in this area to provide definitive statements. The most recent analysis at a broad strategic scale is provided in Section 3.3 on diatoms.

In terms of net productivity, figures given elsewhere in this report compare favourably to the ones quoted in Table 4.1. Coccolithophore figure from Jin et al. (2006):

- Coccolithophores $1.1 \times 10^{15}$ gC yr$^{-1}$
- *Sargassum* $\sim 1 \times 10^{15}$ gC yr$^{-1}$
- Krill $3.1-4.9 \times 10^{13}$ gC yr$^{-1}$
- Deep sea chemoautotrophy $4 \times 10^{13}$ gC yr$^{-1}$
- Deep sea microbes $0.6 - 15 \times 10^{15}$ gC yr$^{-1}$

For fish, the situation is more complex. This is because the figures for fish of $0.04 - 0.33 \times 10^{15}$ gC yr$^{-1}$ represent carbon within CaCO$_3$ excreted via fish guts. Firstly, not all of this carbon may be sequestered into sediments (in fact most might not). Secondly, the production of CaCO$_3$ generates CO$_2$ rather than removing it from the ocean. Therefore, the impact of fish CaCO$_3$ production has the opposite effect on atmospheric CO$_2$ to NPP; and also we don’t yet know whether this impact will be neutralized (perhaps completely) by the rapid dissolution of fish carbonates.

Aside from the complex situation for fish, additional data from other case studies in this report show similar, but an order of magnitude lower, values for sequestration effects estimated to be achieved through the actions of krill $(2.3 \times 10^{13}$ gC yr$^{-1}$) and *Sargassum* $(1.6 \times 10^{11}$ gC yr$^{-1}$). It should be noted, however, that both species occupy distinct regions of the world ocean. The figures are therefore comparable with those associated with more globally distributed species groups such as diatoms, and at a regional scale their carbon roles are likely to represent significant issues to be addressed through relevant policy and management routes. Indeed even with globally distributed groups such as diatoms the work cited here shows regional variations on distribution and abundance. More work is required to define this further.

### 4.3 Policy and management implications

Action is needed to include ocean carbon considerations across all relevant policy approaches and sectoral management areas. This is in the knowledge that any actions are likely to be positive in contributing, however small, to ameliorating climate change impacts and the progression of ocean acidification. Actions on ocean carbon are needed alongside taking the existing practical actions underway to address carbon emission and management issue for forests, peatlands, soils and coastal ecosystems.

We often recognize the ocean is the largest carbon sink on Earth but we have failed to act on this perspective so that no sectorial management currently addresses carbon issues – the case studies in this report should be food for thought in changing that perspective, in stimulating discussion and more research, and in triggering debate and policy development at all levels. From a strategic perspective there are clearly two routes through which action can be taken on ocean carbon:

- **Policy frameworks and agreements:**
  - For carbon emissions this should be addressed through the United Nations Framework Convention on Climate Change (UNFCCC). The UNFCCC is of relevance because ultimately, only the reduction of atmospheric CO$_2$ levels will alleviate the impacts of ocean acidification on open ocean calcifiers. In addition, warming of the oceans, which has been linked to CO$_2$ emissions, is altering nutrient cycling in the ocean and leading to a decline in diatom abundance and productivity, which in turn has massive negative impacts on the biological pump and export of carbon from the atmosphere to the deep ocean. Only by lowering CO$_2$ emissions can we hope to slow the rate of rise in sea surface temperature and thereby prevent the loss of ocean biodiversity that is essential for maintaining the global carbon balance. These concerns justify a call for overall action on climate change and ocean acidification.
• For improvements in ocean management this should be addressed through the United Nations Convention on the Law of the Sea (UNCLOS). The call for action under UNCLOS is because without a framework to manage activities that might affect the open ocean biodiversity (the so called Implementing Agreement) managing carbon stocks and pools will be impossible.

• **Sectoral management of ocean resources:**
  • Incorporating the implications for ocean carbon cycling of undertaking specific ocean activities into sectoral regulation and management (e.g. fisheries, deep sea mining).
  • Incorporation of carbon management through regional sea management organizations that cover multiple sector management considerations such as the Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR).

The reasoning is that management of ocean activities should now factor in the carbon role of ocean habitats and species subject to exploitation or extraction due to ongoing impacts. This is also to be consistent with carbon management policies and actions from governments on land and at the coast. This will be essential in order to protect biodiversity and better manage stressors such as overfishing and pollution. By incorporating carbon considerations into current sectoral management we may buy some time whilst policy actions gear up globally.

### 4.4 Taking policy actions on ocean carbon

Alongside actions under UNCLOS to provide a modern management framework within which to manage ecosystems and species on the High Sea, the other most significant route is under the UNFCCC. The UNFCCC, the relevant international convention to deal with anthropogenic CO$_2$ emissions, has the aim to reduce anthropogenic CO$_2$ and other greenhouse gas emissions. It also addresses the impacts arising from human activities on natural environments that lead to emissions, or sequestration. It does this through the programme known as land use, land-use change and forestry (LULUCF) activities of the Kyoto Protocol. For terrestrial, and now recently for some coastal activities, the UNFCCC has developed financial incentive mechanisms on one hand (e.g. REDD+, CDM, see also Herr et al., 2012) and technical guidance for national carbon accounting on the other hand (via the IPCC, e.g. IPCC, 2014).

Following the consideration of forest and coastal ecosystems, ocean carbon considerations are to be taken “on board” on the basis of Art 4(d) of the Convention. Article 4 of UNFCC notes that Parties shall:

> ‘Promote sustainable management, and promote and cooperate in the conservation and enhancement, as appropriate, of sinks and reservoirs of all greenhouse gases not controlled by the Montreal Protocol, including biomass, forests and oceans as well as other terrestrial, coastal and marine ecosystems’

The article talks about “oceans” and “other marine ecosystems”. As pointed out already in the previous IUCN report (Laffoley and Grimsditch, 2009) on coastal carbon sinks only greenhouse gas emissions and sequestration that occur as a direct result of human activity can be counted towards national greenhouse gas inventories and therefore qualify as projects under the UNFCCC (and also as part of projects for the voluntary carbon market). Any natural sequestration (or emissions) from unmanaged/pristine habitats cannot count towards a country’s greenhouse gas emission reduction commitments. Carbon credits cannot be earned for sequestration from unmanaged habitats.

Clearly more work is required moving forward from this report to define which aspects of open ocean ecosystem and species might qualify under this article of the UNFCCC, but an initial analysis might conclude that those ocean ecosystem and species that have a significant carbon role (sequestration) that could be deleteriously impacted through human exploitation would qualify. This would include activities that impact carbon sequestration rates such as krill extraction, harvesting of natural floating algae (e.g. Sargassum) and exploitation of fish stocks. Such activities also cause significant emissions (e.g. from large ocean-going fishing boats often equipped with freezer systems) and which up to now appear not to be factored into any emission management frameworks. It could also be argued that impacts on calcifiers as a result of excess
anthropogenic carbon emissions would similarly qualify, thus creating more support for actions through the UNFCCC on ocean acidification. Such activities are currently not debated, nor accounted for by UNFCCC.

Thinking towards the future, actions under the UNFCCC should be expanded to include the open ocean. The furthest actions currently go is the consideration of “draining and rewetting” under LULUCF, and the recently provided wetland guidance under LULUCF (IPCC). Open ocean could be included through the introduction of a new concept of ‘Ocean Use and Ocean Use Change (OUOUC)’. The IPCC has already defined several carbon pools for the LULUCF section and additional action to now include the ocean would need significant input from policy and science specialists to define the carbon pools associated with OUOUC. As documented in this report these carbon pools could usefully include:

- biomass, such as pteropods, seaweed, fish etc.;
- Dissolved Organic Carbon (DOC) (via the biological pump); and
- maybe ocean sediments?

The logic here is that such elements are directly influenced by human actions. For example ocean carbon biomass that sequesters CO₂ through natural processes into the deep ocean is being impacted by emissions from human activities. Extractive industries are removing the biological assets (ecosystems and species) that provide the natural sequestration capability (e.g. the fish and krill) without any assessment of such impacts. DOC is similarly impacted by anthropogenic emissions, whilst deep-sea carbon reported in Sections 3.7 and 3.8 will be impacted by future deep-sea mining operations. The latter is a good case in point where enthusiasm for licensing the mining of deep-sea habitats has bypassed any effective regulation and management framework (UNCLOS Implementing Agreement). This will mean that the carbon role of areas subject to deep sea are unassessed and ignored in the decision-making process. On land digging up peatland and cutting down forests is closely scrutinized with protective policy frameworks and legislative measures in place. The same approach new needs to occur for activities in the open ocean.

This vision of the future that includes ocean carbon within international policy frameworks such as the UNFCCC and UNCLOS will need considerable development, but it should not prevent the real issues of ocean carbon implications from being recognized now. The brief analysis provided in this report shows that it is not a trivial undertaking.

### 4.5 The need to act now

The discussion here is a first attempt at connecting all the carbon and climate dots under the UNFCCC, and to fill current accounting gaps. Clearly significant issues remain to be addressed including how to measure ocean carbon emissions and the impacts of particular human uses. Debate around the release of this report may hopefully help quantify this faster than might be imagined given the scope of relevant work being undertaken by scientists around the world. Issues will also emerge over who to attribute the ocean carbon emissions or sinks to - which countries would take responsibility for ‘global ocean carbon units’ and make them part of their national carbon inventory? This is, however, not an unfamiliar debate as it has already arisen before in a different context in relation to sea-level rise and the future fate of Pacific Islanders.

Finally what the report also shows through the section (Section 3.4) on algal cultivation and ocean fertilization to stimulate diatom growth is that it is far better to work with nature, and to protect and better manage the impacts we have on the systems that in turn keep our world healthy, than to try to mimic nature. Not only is the area needed for such algal cultivation vast, but when factoring in direct carbon enhancement measures, including ocean fertilization, the downstream effects are both unpredictable and often undesirable.

The report has been developed to challenge current thinking – that all aspects of carbon management, not just on the land and at the coast but now in the ocean, are critical. Evidence in this report shows the impacts and possible future implications for ocean systems of not addressing them in ongoing climate change adaptation and mitigation discussions. Addressing the management of natural carbon pools and sinks in the open ocean may appear (and doubtless is) technically and attribution-wise more complex, but this complexity is no longer a reason for not doing so. The ocean has been a major buffer for the rate of atmospheric CO₂ increase, shielding us from more rapid climate change impacts, albeit with the “side-effect” of ocean acidification. It is now time that the ocean gets more prominent recognition, both as an impacted ecosystem as well as solution provider, in the climate change debate.
4.6 References


This report has, through its case studies, demonstrated the need to address ocean carbon issues in international policy and sectoral management approaches. It demonstrates the overall need for mitigation of CO$_2$ and other greenhouse gases in order to limit the impacts on the ocean, including ocean acidification and ocean warming, and the effects that this in turn is having on key components of the ocean ecosystem that play essential roles in the carbon cycle.

We already know that these impacts will act on the overall role of the ocean in the global carbon cycle, e.g. altering the capacity to buffer climate change and the uptake of CO$_2$ as well as the side effects of shifting species range and impacts on shell forming organisms. There are a number of recommendations that therefore naturally flow from this report:

- Urgent action is needed to address ocean carbon and protect the systems that regulate planetary processes – the essential role of mitigation of CO$_2$ is demonstrated through the case studies in this report, and the urgency illustrated by views across all case studies that our use and abuse of the ocean will alter the status quo in carbon management.
- Further analysis and research is needed to develop the analysis presented in this report - just like IUCN’s original report in 2009 on coastal carbon sinks this report is only the beginning, and further work both technically and politically is needed. Limits on time and resources meant that issues such as the carbon role of large vertebrates or echinoderms in the benthos could not be covered. More research is also needed to understand how ocean acidification not only affects calcification, but how it (perhaps in turn) affects photosynthesis, and hence primary production in the ocean. The focus in this report is mainly on calcification processes in calcifiers, whilst research on these other impacts is needed to help clarify the current uncertainties around open ocean carbon pool quantification.
- Ocean carbon issues need to be addressed through international climate policy routes such as the UNFCCC to develop new processes and strengthen relevant existing measures.
- An Implementing Agreement is needed under the UN Convention Law of the Sea to secure a proper conservation and management framework for the High Seas – through which relevant supporting measures for ocean carbon could be taken.
- Sectoral ocean management bodies need to recognize and address ocean carbon budgets and undertake full environmental assessments of their activities – for example regional agreements such as CCAMLR and entire extractive industries such as capture fisheries and krill fisheries and the algal harvesting sector need to include carbon into their day-to-day decisions and activities.
To conclude it is hoped, overall, that this report will stimulate debate and action on those hidden carbon processes that are not only so essential at the global and regional scales, but that also, without intervention through policy and management, will become further impacted whilst remaining out of sight and out of mind.
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