Subsection 5B

Chapter 1

The role of ecosystems in the carbon cycle

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Key points

- Covering approximately 71% of the Earth's surface, the open ocean contributes to approximately half of annual primary production, supporting approximately 80% of global animal biomass.
- The open ocean currently sequesters a similar amount of atmospheric CO_2 to that sequestered by the whole terrestrial biosphere, and the ocean has the capacity to store 40 times more CO_2 than the atmosphere.
- In coastal systems, coastal blue carbon ecosystems , such as seagrass, mangroves and saltmarshes, are estimated to capture and store more carbon per unit area than terrestrial forests, meaning that, despite covering an area of less than 7 million km^2, coastal blue carbon ecosystems are considered globally important areas of carbon capture and storage, which contributes to their high economic and social value, together with other ecosystem services.
- Unvegetated, sea floor sediments on the continental shelf make up approximately 9% of the total marine area but hold the biggest carbon store in shelf systems, and more than 80% of organic carbon is buried in these subtidal sediments.
- The protection and restoration of coastal blue carbon ecosystems and shelf sediment seabed habitats will have significant benefits for both climate mitigation and biodiversity conservation.
- Continental shelf seas are a significant source of carbon (0.95 ± 0.25 Pg C y^{-1}) to the open ocean, although this transport is largely driven by physical and geochemical processes, rather than biological. However, horizontal carbon transport through the migration of animals is probably widespread, but largely unquantified.
- The value of carbon cycling ecosystems has been increasingly recognized, and many finance initiatives exist. However, blue carbon activities receive just 3% of total climate investment globally. This lack of financial support has been a barrier to bringing blue carbon conservation and restoration activities to scale.
- The recognition of the value of coastal blue carbon ecosystems in climate action has increased in recent years. However, at the time of publication, just over half (56%) of Parties to the United Nations Framework Convention on Climate Change have integrated coastal and marine nature-based solutions within new or updated nationally determined contributions as part of mitigation or adaptation measures.

1. Introduction

While the vast majority of the carbon in the ocean is inorganic, and many of the processes that fix, transform and transport this carbon within and through the ocean are driven by physical or chemical processes (see sect. 4, chap. 3), there are also important biological processes that contribute to significant carbon cycling, and these are directly linked to the presence, function and health of marine ecosystems. Given that these same ecosystems also provide vital services to humans, including food provision (see subsect. 5A, chap. 1), understanding and protecting the role of ecosystems in driving the carbon cycle is intrinsically linked to the health (see subsect. 5B, chap. 2) and well-being of billions of people (see subsect. 5B, chap. 3). In this chapter, we will explore the role played by biological processes of key ecosystems in cycling carbon through the two main ocean systems: the open ocean (part 2); and the near shore environment, comprising shelf, coastal, fjordic and estuarine systems (part 3). In part 4 of the present chapter we will describe the transport pathways of carbon between the near shore and the open ocean. Lastly, we will consider the potential values of these ecosystems, and the carbon cycling processes that they provide, in the context of economic and non-economic valuation (part 5).

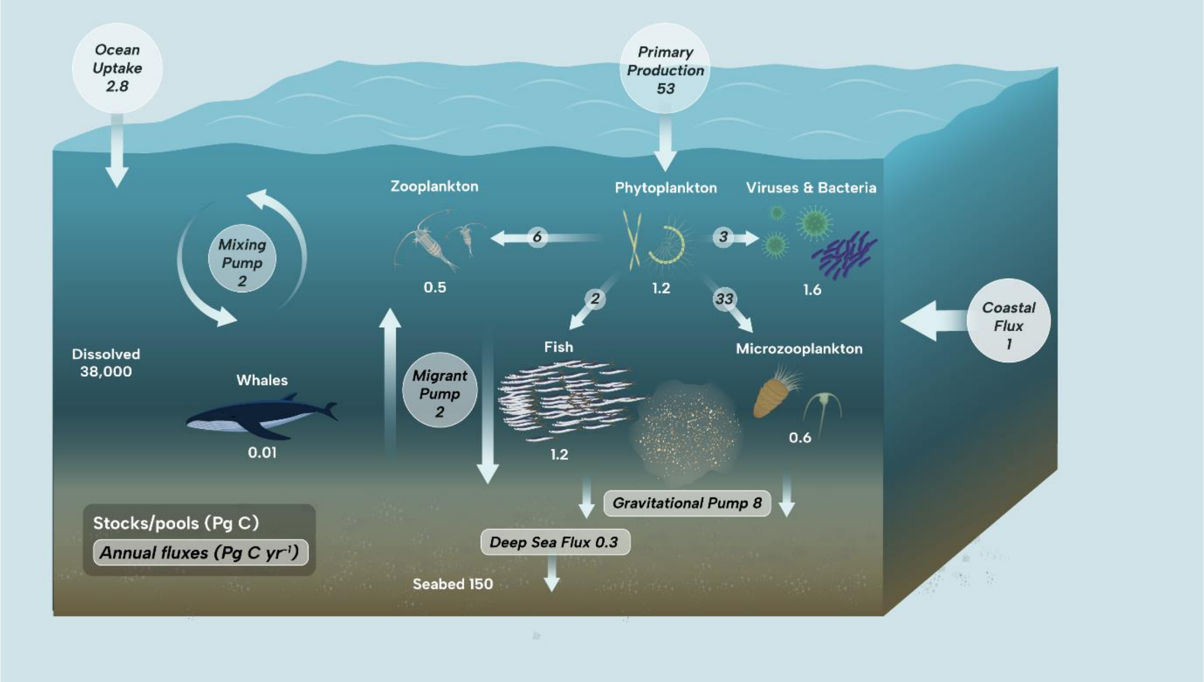
2. The open ocean

Carbon cycling in marine ecosystems

Accounting for approximately 71% of the Earth's surface, the open ocean contributes to approximately half of Earth's annual primary production (~49–56 Pg C yr^{-1}; Buitenhuis and others, 2013a; Kulk and others, 2020), despite much lower levels of photosynthetic biomass in the ocean (~0.5-2.4 Pg C) than on land (~450 Pg C) (Buitenhuis and others, 2013b; Bar-On and others, 2018). Primary production is dominated by microbial phytoplankton in the open ocean (Buitenhuis and others, 2013b; Bar-On and others, 2018), with lifespans ranging from a few days to weeks, leading to an inverted biomass pyramid from microbial primary producers at the base, up to higher trophic levels at the top, and a rapid turnover of photosynthetic biomass in the ocean (see figure I). In the wider context of the global carbon cycle, the marine biosphere represents a relatively small component; while marine biological (organic) carbon pools total approximately 5 Pg C, the ocean contains approximately 38,000 Pg C of dissolved inorganic carbon (DIC) and the atmosphere approximately 800 Pg C (see figure I; Friedlingstein and others, 2023). However, this relatively small amount of biomass, with significant fluxes between biological pools (see figure I), supports the life and productivity of the global ocean, the largest ecosystem (biome) on the planet.

Figure I

Open ocean ecosystem roles in the carbon cycle



Sources: Bar-On and others (2018); Boyd and others (2019); Friedlingstein and others (2023); Greenspoon and others (2023); Siegel and others (2022).

Significant rates of primary production and rapid turnover allow the ocean to support approximately 80% of global animal biomass and approximately half of global protist biomass, which includes significant biomass from pelagic and mesopelagic fish (0.7-1.7 Pg C), large zooplankton (e.g. copepods, krill) (0.3-0.6 Pg C) and small microzooplankton, including protists such as ciliates and dinoflagellates (0.5-0.7 Pg C) (Buitenhuis and others, 2013b; Bar-On and others, 2018; Bar-On and Milo, 2019; Bianchi and others, 2021; Drago and others, 2022). While marine mammal biomass is roughly twice the size of wild terrestrial mammal biomass, it represents a low level of biomass overall (~0.007 Pg C), with baleen whales making up the majority (Greenspoon and others, 2023). Globally, marine mammal biomass is an order of magnitude smaller than the human population (0.065 Pg C) or domesticated mammal biomass (0.1 Pg C) (Bar-On and others, 2018; Greenspoon and others, 2023).

Carbon fixed into marine biomass through photosynthesis in the open ocean is rapidly consumed by pelagic organisms, with approximately 62% lost to ingestion and respiration by microzooplankton, approximately 12% directly to larger zooplankton and approximately 2% to 10% to viral lysis and infection (Calbert and others, 2001; Schmoker and others, 2013; Gao and others, 2022). Smaller proportions of primary production are lost directly, or indirectly through grazing on herbivorous zooplankton, to fish (<3%; Bianchi and others, 2021) and marine mammals. The remaining proportion of primary production (~18% or ~11 Pg C yr^{-1}) is lost from the upper ocean through the sinking of particulate material (i.e. cells, detritus), or the downward fluxes of dissolved organic material, or through the active migration of pelagic organisms from surface waters to depth (Boyd and others, 2019; Siegel and others, 2023).

Biological carbon pump(s)

While the open ocean lacks the immense plant biomass of land ecosystems, the ocean currently sequesters a similar amount of anthropogenic atmospheric CO_2 (~2.8 Pg C yr^{-1}) to that sequestered by the whole terrestrial biosphere (Friedlingstein and others, 2023), mainly through its physical circulation and geochemical characteristics (Sabine, 2021; see sect. 4, chap. 3), although open ocean ecosystems also play a crucial role (Boyd and others, 2019; Siegel and others, 2023; Frenger and others, 2024). Marine photosynthesis draws CO_2 from the atmosphere into surface biomass, a portion of which enters the interior ocean through one of several transport pathways (see figure I), driving a gradient in CO_2 from the upper ocean into the deep sea through the collective action of ocean ecosystems, termed the biological carbon pump (Boyd and others, 2019; Siegel and others, 2023). While most of this material is typically broken down and respired by bacteria and zooplankton in the upper 1 km of the ocean, a small proportion of surface production (<2%) does reach the sea floor. So, although the biological carbon pump does not actually contribute much to the net ocean C sink, largely because its vertical fluxes (export) are balanced by the release of absorbed CO_2 (outgassing) from upwelled deep waters, it does maintain the long-term store of carbon in deep waters and sediments that would otherwise reside in the atmosphere (Frenger and others, 2024).

The timescale of ocean mixing is proportional to water depth. Some deep waters can be isolated from the atmosphere for up to approximately 1,000 years, while the upper ocean (<0.5 km) may exchange with the atmosphere seasonally, such as during winter mixing. The deeper a sinking particle reaches into the ocean the longer the carbon associated with that particle will be sequestered from the atmosphere. As a global average, particles sinking below 500 m are sequestered for 200 years or longer (Boyd and others, 2019), but this varies geographically depending on regional ocean circulation and mixing (Baker and others, 2024).

The breakdown and respiration of organic matter supplied to the ocean's interior through the biological carbon pump contributes to the ocean's capacity to store 40 times more CO_2 than the atmosphere (Friedlingstein and others, 2023; Frenger and others, 2024) and fuels deep sea bacteria and fauna at the sea floor. An even smaller proportion (<1%) of surface production ends up sequestered into deep-sea sediments through the physical activity of organisms living at the sea floor. However, the vast area of the deep sea means that this small fraction of surface production makes up a large carbon stock that contributes significantly to C cycling and sequestration on millennial timescales (150-2322 Pg C, depending on whether the upper 5 cm or 1 m is considered; Atwood and others, 2020) which is similar in size to that stored in terrestrial soils (1700 Pg C) or permafrost (1400 Pg C) (Friedlingstein and others, 2023).

Sinking particulate organic carbon (POC) falls as cells and detrital material, often aggregated into particles termed "marine snow" or packaged by large zooplankton as faecal pellets, and contributes to the "gravitational pump" which is responsible for ~80% of the approximately 11 Pg C annually exported by the biological carbon pump (Boyd and others, 2019; Siegel and others, 2023). Often these sinking particles still hold nutrients usable by heterotrophs, and it is now recognized that zooplankton often fragment these sinking particles into smaller particles that slow their descent, keeping them in the upper ocean longer (Mayor and others, 2014). This strategy has been termed "microbial gardening" where zooplankton promote bacterial and protist growth on fragmented particles before consuming the enriched microbial biomass (Mayor and others, 2014) which are more nutritious than the original sinking material

(Cavan and others, 2020). This highlights the intricate ecological interactions involved in regulating carbon flow into the deep ocean.

Dissolved organic carbon (DOC), varying in form from simple metabolites such as polysaccharides and proteins to complex reworked molecules such as fulvic and humic acids, is an important component of the ocean's dissolved carbon pool (Friedlingstein and others, 2023) with microbial utilization of this pool as a carbon and nutrient source, responsible for breaking down the labile fractions of this material (Hansell and others, 2013; Jiao and others, 2014; Legendre and others, 2015). This "microbial carbon pump" recycles carbon and nutrients from the dissolved pool but also changes the nature of the pool to a more refractory one which contributes to long-term carbon sequestration, lasting from hundreds to thousands of years (Hansell and others, 2013; Jiao and others, 2024; Legendre and others, 2015). Viral infection also plays a role in the microbial carbon pump, with viral lysis of infected plankton in the upper ocean providing a "viral shunt" retaining carbon near the surface, where it is broken down by microbes (Suttle, 2007; Kranzler and others, 2019). Recent research shows that some viral infections do not cause immediate cell lysis. Instead, metabolically inactive infected cells may sink, creating a "viral shuttle" that transports organic material to the deep ocean (Kranzler and others, 2021; Poulton, 2021).

The remaining carbon exported through the biological carbon pump is pumped to depth through two distinct mechanisms, one related to the physical mixing of the water column ("mixing pump") and the other related to vertical migration by zooplankton and nekton ("migrant pump") (Boyd and others, 2019; Siegel and others, 2023). The "mixing pump" involves various oceanographic processes that transport surface water into the ocean's interior, and any dissolved and particulate carbon contained in this water thereby becomes sequestered in the deep ocean. The volume of water, and the depth to which it is transported, varies seasonally and geographically.

Many organisms in the ocean go through daily or seasonal migrations from surface waters into the ocean's interior, either driven by avoidance of visual predators during daylight or to avoid suboptimal growth conditions. These migrations carry carbon to depth, either within the organisms' bodies, to be excreted at depth as faecal pellets or respired over time and released as dissolved CO_2. This "migrant pump" transports approximately the same amount of carbon to depth (~2 Pg C yr^{-1}) as the physical mixing of the ocean (Boyd and others, 2019; Siegel and others, 2023). This behaviourally driven flux of carbon into the deep ocean is extremely important as these migrations are often down to significant depths (>1 km) where the carbon released may be sequestered away from the atmosphere for more than 500 years (Boyd and others, 2019).

Environmental controls, climate change and anthropogenic impacts

While deep remineralization of sinking material is advantageous in terms of sequestering atmospheric CO_2 in the ocean's interior, it robs the sun-lit upper ocean of nutrients and leads to widespread nutrient limitation of primary production (Moore and others, 2013). Processes by which nutrients are returned to the surface, often through stochastic or seasonal mixing, are therefore critical to support continued production. Ocean warming, as a consequence of the ocean absorbing 90% of the total energy generated by anthropogenic forcing of the climate system (Cheng and others, 2022), is likely to alter ocean circulation and mixing (Melet and others, 2022; see sect. 4, chap. 3). While the specific timing and intensity of the changes are unclear, it is likely to result in changes to the physical replenishment of essential nutrients required for primary production, growth and ecosystem health (Hutchins and

Tagliabue, 2024). Current IPCC-class global models vary considerably in their spatial projections of future changes in primary production. Although most exhibit only a modest reduction (~2%) in global marine productivity, there may be strong (>20%) increases (e.g. Arctic) and decreases (e.g. subpolar Atlantic) (Tagliabue and others, 2021) in specific regions.

Another concern is that reduced ocean mixing will reduce the replenishment of oxygen to deep waters (see sect. 4, chap. 3), essential for heterotrophic activity and higher trophic levels. The respiration of sinking organic matter requires oxygen, so there is a net oxygen consumption (deoxygenation) below the sunlit upper ocean. In shallow areas, or where there is sluggish circulation and high rates of sinking organic material and oxygen consumption, this deoxygenation can lead to hypoxic or anoxic conditions (e.g., Meier and others, 2018), the formation of oxygen minimum zones and avoidance of these areas by aerobic organisms (Schmidtko and others, 2017). Reductions in ocean mixing due to ocean warming are predicted to lead to the expansion of oxygen minimum zones and the lowering of oxygen concentrations more generally (Schmidtko and others, 2017) (see sect. 4, chap. 3), which will have a direct impact on ocean biology; for example, limiting the vertical migration of zooplankton (Abedi and others, 2022) and the strength of the migrant pump component of the biological carbon pump (Cavan and others, 2017). Reductions in oxygen availability in the ocean interior may also reduce respiration and remineralization rates, acting as feedback to the biological carbon pump through deeper depth penetration of sinking material (i.e. higher C sequestration) (Cavan and others, 2017).

The ocean's increased uptake of atmospheric CO_2, relative to pre-industrial times, is primarily driven by increasing atmospheric CO_2 concentrations (Sabine, 2021), with the ocean's role in sequestrating anthropogenic CO_2 resulting in chemical changes in the ocean (Sabine, 2021). Specifically, the dissolution of CO_2 and its reaction with seawater to form carbonic acid has dramatically decreased ocean pH (by increasing proton concentrations) and reduced the saturation state of carbonate minerals (calcite, aragonite) in the ocean over the past few decades (Lauvset and others, 2015; Jiang and others, 2019). This "ocean acidification" impacts ocean biology by making the balancing of cell pH (avoiding acidosis) more challenging for marine organisms and increasing the physiological costs of countering the increased dissolution rates of organism-associated biominerals. Ocean acidification impacts the role of marine ecosystems in the carbon cycle at multiple scales (Doney and others, 2020), for example changes in nutrient availability (e.g. Shi and others, 2010), growth, grazing and reproductive success (e.g., Keil and others, 2021), calcification, plankton diversity and community composition (e.g., Taucher and others, 2017). Despite considerable knowledge of ocean acidification impacts on specific elements of marine ecosystems and the biological carbon pump (e.g., Taucher and others, 2017), a holistic understanding of its impact on the future magnitude and efficiency of the different component pumps (gravitational, migrant, mixing) is lacking (Passow and Carlson, 2012; Wolf-Gladrow and Rost, 2014).

3. Shelf, coasts, fjords and estuaries

Moving in from the open ocean, into the shallower areas around coasts, the surface waters continue to fix and cycle carbon through many of the biological processes described in the previous part of the chapter. However, unlike open ocean environments, coastal areas are more complex and varied, often made up of different, interconnected coastal habitats (such as estuaries (see sect. 4, subchap. 5F), mudflats (see sect. 4, subchap. 5B), saltmarshes (see sect. 4, subchap. 5I), seagrass meadows (see sect. 4, subchap. 5G), lagoons and mangroves (see sect. 4, subchap. 5H)), linking the terrestrial zone to the marine through rivers which meet the ocean through deltas, estuaries or fjords (see sect. 4, subchap. 5R). This riverine connection transports organic and inorganic carbon, along with fine particles, into the coastal region, depositing carbon and fine sediment particles (mud) in the nearshore environment (Bianchi and others, 2024). The input of terrestrial carbon into the marine environment is reflected in the carbon sequestered in coastal habitats, which is often a mix of terrestrial and marine carbon, with the proportion of terrestrial carbon higher closer to the coast and marine carbon dominating with greater distance from land (Wilson and others, 2018).

In addition, in coastal zones where sufficient light can reach the sea floor, the seabed plays an additional role in carbon fixation (Legge and others, 2020; Gattuso and others, 2006). Coastal primary production is driven by photosynthesis in plants (see sect. 4, subchap. 4H), macroalgae (see sect. 4, subchap. 4I) or small single celled photosynthetic organisms (microphytobenthos), which inhabit the surface of soft sediment habitats, such as intertidal mudflats (Christianen and others, 2017). Microphytobenthos dominate carbon cycling in unvegetated coastal sediments (Underwood and others, 2022), play a role in pollutant remediation and form the basis of food webs (Hope and others, 2019). However, the complexity of coastal systems means that, currently, considerable uncertainties remain with regard to estimating the actual area covered by these vegetated coastal habitats, along with considerable variability in specific carbon flux estimates, resulting in a tenfold bracket around the estimates of their contribution to organic carbon sequestration, from 0.073 to 0.866 Pg C yr^{-1} (Duarte and others, 2017).

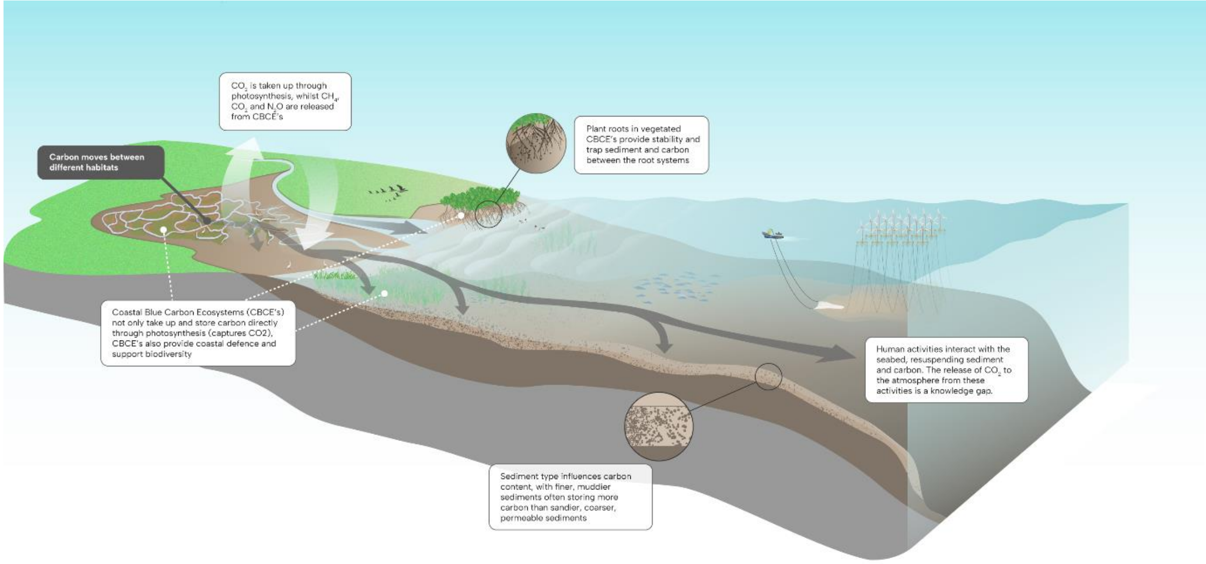
Coastal blue carbon ecosystems

Vegetated coastal habitats such as salt marshes (see sect. 4, subchap. 5I), seagrass meadows (see sect. 4, subchap. 5G) and mangroves (see sect. 4, subchap. 5H), were first described as “blue carbon” habitats in 2009 (Nellemann and others, 2009), and the term is now more generally used for biologically driven carbon fluxes and storage in marine systems that are amenable to management (IPCC, 2021; Lovelock and Duarte, 2019). It is estimated that these three coastal blue carbon ecosystems capture and store more carbon per unit area than terrestrial forests (Mcleod and others, 2011), meaning that, despite covering an area of less than 7 million km^2 (Duarte 2017), coastal blue carbon ecosystems are considered globally important areas of carbon capture and storage. The plants in these ecosystems capture CO_2 directly through photosynthesis (see figure II), and much of the carbon remains within that ecosystem, buried in the soft sediments and root systems around the plants (Macreadie and others, 2014; Saderne and others, 2019). The sediments in these plant-rich ecosystems are key for long-term carbon accumulation and storage, and this permanence (long-term storage of carbon) provides the blue carbon benefit and the potential for climate mitigation (Williamson and Gattuso, 2022). However, not all the carbon stored in coastal blue carbon ecosystems is derived from that habitat (autochthonous), and allochthonous carbon (produced outside of that habitat, e.g. terrestrial origin) can make up a significant portion of carbon stocks in sediments (Cragg and others, 2020; Kharbush and others, 2020). This can have implications for blue carbon accounting (see sect. 4). In addition, a substantial contribution to the carbon sequestration potential of coastal blue carbon ecosystems can come from the export of alkalinity that is produced by anaerobic processes (especially denitrification and sulfate reduction) in sediments and exported laterally through physical water movement (Santos and others, 2021).

The original definition of blue carbon has expanded in recent years as scientific knowledge around carbon uptake and storage in marine ecosystems has increased. Unvegetated marine sediments (coastal, shelf and offshore) store significant amounts of carbon owing to their geographical extent (Legge and others, 2020), despite low accumulation rates compared with coastal zones. The term blue carbon has broadened beyond the original coastal blue carbon ecosystems to include marine sediments (including coastal sediments such as mudflats (Brown and others, 2021) and continental shelf and offshore sediments (Graves and others, 2022)), which store carbon for climate-relevant (at least 100 years) and geological time periods (>1,000 years) but do not directly capture it like vegetated soft sediment habitats (EMB policy brief on blue carbon, 2023). Shelf sediments (see sect. 4, subchap. 5B) make up ~ 9% of the total marine area (Diesing and others, 2017) but hold the biggest carbon store in shelf systems (Legge and others, 2020) and more than 80% of organic carbon is buried in subtidal sediments (Hedges and Keil, 1995, Diesing and others, 2021). The amount of carbon stored in shelf sediments varies with sediment type, and although finer particles and muddier sediments are associated with higher organic carbon content (Bianchi and others, 2024, Legge and others, 2020, Diesing and others, 2017), most of the continental shelf is covered by permeable, sandy sediment, or a mix of mud and sand (Diesing and others, 2021). Sandy sediments hold less organic carbon but a large amount of inorganic carbon, which is generally not considered as part of blue carbon.

Figure II

Major carbon pathways and stores in coastal marine ecosystems



CO_2 is taken up through photosynthesis, whilst CH_4, CO_2 and N_2O are released from CBCE's

Carbon moves between different habitats

Plant roots in vegetated CBCE's provide stability and trap sediment and carbon between the root systems

Coastal Blue Carbon Ecosystems (CBCE's) not only take up and store carbon directly through photosynthesis (captures CO2), CBCE's also provide coastal defence and support biodiversity

Human activities interact with the seabed, resuspending sediment and carbon. The release of CO_2 to the atmosphere from these activities is a knowledge gap.

Sediment type influences carbon content, with finer, muddier sediments often storing more carbon than sandier, coarser, permeable sediments

Source: Prepared by the writing team.

As shown in figure II, carbon is directly captured by plants (as carbon dioxide (CO2)) through photosynthesis in coastal blue carbon ecosystems, while methane (CH4), nitrous oxide (N2O) and CO2 are released by coastal blue carbon ecosystems. Carbon may become stored in coastal blue carbon ecosystems, particularly in the sediment around the root systems, or may flow between the different but connected coastal ecosystems and out onto the shelf (as indicated by the arrow). The largest carbon stores are in the sediments, and carbon stocks vary with sediment type. Human activities (such as fisheries activity or energy infrastructure) that interact with the seabed resuspend sediment and carbon.

Macroalgae and calcifiers

Other organisms play a major role in the coastal biological carbon cycle, such as macroalgae (see sect. 4, subchap. 4I) and calcifying organisms. Macroalgae (such as kelp and seaweed) take up CO_2 through photosynthesis and release it at the end of a growing season when much of the algal biomass dies. Since this vegetation is not rooted in sediment, much of this biomass goes through degradation and remineralization (microbial breakdown into CO_2). Up to 40% may be released into the coastal and open ocean (Krause-Jensen and Duarte, 2016), and a small proportion may be buried in marine sediments (Queirós and others, 2023). Calcifying organisms, such as corals (see sect. 4, subchaps. 5D and 5E) and bivalves (e.g. mussels or oysters), produce solid calcium carbonate in the form of skeletons and shells. While it may seem counter-intuitive, the process of calcification actually emits CO_2 (Pernet and others, 2024), and many calcifiers additionally produce CO_2 through respiration. However, calcifying organisms do play a vital role in the biological carbon cycle, even though they are not considered to be blue carbon, or a nature-based solution for climate change. They are also important for many other species and provide a number of co-benefits, such as habitat provision, supporting biodiversity and improved water quality (see sect. 4, subchaps. 5D and 5E). Recently, coralline algal beds found in sediments have also been suggested to be blue carbon habitats, because the carbon captured and stored through photosynthesis may exceed the carbon released by calcification (James and others, 2024).

Microbial carbon cycling

As in the open ocean, microbial communities make up a significant proportion of the carbon biomass (see part 2 of the present chapter) and drive sedimentary carbon dynamics on the seabed (balance between sequestered and respired). Organic carbon reaches the seabed and is either remineralized through microbial breakdown or consumption of the carbon, releasing CO_2 and nutrients (Middelburg, 2018) or a small proportion may become buried in the sediment and eventually sequestered. The proportion of carbon buried rather than respired is driven not only by microbial activity, which favours aerobic respiration (Glud, 2008), but also by environmental parameters such as temperature and water depth (Diesing and others, 2017) and presence of macrofauna (Middelburg, 2018). Generally, warmer waters stimulate more microbial activity, and a greater proportion of carbon is converted to CO_2 while less is buried. This has implications for reducing carbon sequestration as ocean temperatures warm. Microbial processing of organic carbon determines the flux of oxygen and carbon dioxide (CO_2) at the sediment-water interface (and the sea surface-air interface) and methane in coastal sediments (LaRowe and others, 2020).

Carbon is microbially mineralized in the surface oxic layers of the sediment, the depth of which varies with sediment type and season (Hicks and others, 2017), as muddy sediments with smaller grain size have a shallower oxic depth and have higher organic carbon content than sandy sediments (Bianchi and others, 2024). Below the oxic layer in sediments, the carbon is less easily broken down by microbial communities owing to the hypoxic or anoxic conditions. However, hypoxic or anoxic microbial breakdown of carbon can lead to the release of other metabolites such as ammonium, hydrogen sulfide or methane, another greenhouse gas (Middelburg and Levin, 2009), although a greater proportion of carbon becomes buried in sediments under low-oxygen conditions. This has implications for warming of coastal and marine ecosystems, leading to an increase in the occurrence, duration and frequency of hypoxia (Diaz and Rosenberg, 2008).

Coastal microbial carbon cycling in coastal blue carbon ecosystems is influenced by the presence of plant roots, which provide a route for oxygen to penetrate the sediment layers beyond the oxic zone (Trevathan-Tackett and others, 2023), and microbial communities differ between the coastal blue carbon ecosystem habitats. The origin of the carbon (allochthonous rather than autochthonous) is also important for microbial processing, as marine microbes are less efficient at breaking down land-derived (allochthonous) carbon than marine-derived (autochthonous) carbon (Cragg and others, 2020; LaRowe and others, 2020).

Knowledge gaps and uncertainties

The protection and creation of coastal blue carbon ecosystems are seen as nature-based solutions for marine climate change mitigation (Pörtner and others, 2023) and may contribute to nationally determined contributions under the Paris Agreement 2015, for climate mitigation (Macreadie and others, 2021). Recent estimates suggest that, with full restoration of coastal blue carbon ecosystems, the total contribution to climate mitigation is approximately 2% globally. In temperate regions, the small geographical area of these ecosystems means that it is unlikely that they will play a significant role in meeting mitigation targets. For small island nations, which have a larger geographical extent of coastal blue carbon ecosystems, their relative contribution may be significantly higher. For example, mangroves are found in more than 100 countries, but more than a fifth of global mangroves are located in Indonesia (Macreadie and others, 2019; Giri and others, 2011). The huge global variability of carbon stocks in the same habitat makes it difficult to accurately assess carbon sequestration and climate change mitigation potential, and studies are often underrepresented in the global South (Wasserman and others, 2023).

Recent research has been focused on different approaches to restoration and conservation of coastal blue carbon ecosystems for climate mitigation, particularly as they are vulnerable to sea level rise in the next few decades. Restoration efforts could include intentional breaching of sea defences or embankments in North-West Europe (called "managed realignment") (Burden and others, 2013; Mossman and others, 2012). Restoration approaches for coastal blue carbon ecosystems, such as realignment, provide a nature-based solution for increasing carbon capture and storage, as well as providing coastal protection from floods and storm surges. However, the role of greenhouse gases in carbon cycling, particularly in coastal blue carbon ecosystems, is not yet fully understood (Williamson and Gattuso, 2022; EMB policy brief on blue carbon, 2023), and the climate benefit of salt marshes (natural and restored) is variable (Mason and others, 2023; Mason and others, 2024; Williamson and others, 2024). Studies have shown that coastal wetlands can be emitters of greenhouse gases such as methane and nitrous oxide (Megonigal, 2004; Mason and others, 2023; Roth and others, 2023), although this may be linked to the health and age of the coastal wetland.

Restoration of coastal blue carbon ecosystems for climate mitigation (ability to store carbon) would lead to co-benefits such as coastal protection, increased biodiversity and improved water quality (Williamson and Gattuso, 2022). This is important to recognize, because the climate benefits of restoration, or rewilding, efforts are not likely to be immediate, and it will take time for climate mitigation objectives to be met through the transition of other habitats into coastal blue carbon ecosystems (Burden and others, 2013; Pétillon and others, 2014; Williamson and others, 2024). Coastal blue carbon ecosystems will also need to be climate resilient, in the face of warming and rising sea levels (Macreadie and others, 2019).

Coastal and shelf soft sediments are a significant repository for carbon, and shelf sediments are often highly productive systems with intensive seabed activity. Despite concerns that these carbon stocks could be remineralized into CO_2 through disturbance of the sedimentary carbon stores (Sala and others, 2021), there is limited empirical evidence on the vulnerability of this carbon to anthropogenic activity (Epstein and others, 2022; Hiddink and others, 2023). This includes trawling, dredging, installation and removal of energy structures and associated infrastructure and deep-sea mining. The uncertainty around the vulnerability of the carbon, and limited knowledge on carbon accumulation rates and burial, makes it challenging to effectively manage the seabed.

4. Exchange between coastal and open ocean systems

In previous parts of the chapter the open ocean and the coastal environment have been considered separately. However, these two systems are tightly coupled when it comes to carbon transport, with continental shelf seas being a source of 0.95 ± 0.25 Pg C yr^{-1} to the open ocean (Regnier and others, 2022). This flux consists chiefly of dissolved inorganic carbon, dissolved organic carbon and particulate organic carbon (DIC, DOC and POC, respectively) and is mainly driven by physical processes. The net transport of DIC is largely driven by enhanced physico-chemical dissolution of atmospheric CO_2 into shelf waters. Shelf seas also typically have higher concentrations of DOC and POC than the open ocean, because of high biological productivity and inputs of DOC and POC from land. Moreover, movement of nektonic animals to and from shelf seas contributes a carbon flux, although this remains very poorly quantified. Quantifying these carbon fluxes is challenging, in part because of the high spatial and temporal variability of shelf seas.

The purely physico-chemical mechanism of shelf-to-ocean DIC flux is mainly driven by winter-time cooling of shelf waters at temperate and higher latitudes, which lowers the partial pressure of CO_2 (pCO_2) in the water and results in uptake of atmospheric CO_2. This cold, dense shelf water can then flow off the shelf and below the oceanic thermocline, a process called the “continental shelf pump” (Tsunogai and others, 1999; Cossarini and others, 2015). Conversely, in tropical shelf seas the opposite can occur: cooler oceanic water can warm up on the shelf, leading to an increase in shelf sea pCO_2 and promoting CO_2 flux to the atmosphere (Lacroix and others, 2021).

Biological production contributes to the continental shelf pump by converting CO_2 into POC and DOC. However, to become part of the continental shelf pump this POC and DOC must either be transported below the open-ocean thermocline or be transformed into refractory DOC, so that the carbon is not remineralized back into CO_2 and exchanged with the atmosphere over short timescales (Lee and others, 2022; Holt and others, 2009). However, most of the POC and DOC produced in shelf seas is remineralized before it can become part of the continental shelf pump, and net biological production rates are not correlated with the strength of the CO_2 sink when comparing globally across shelf seas (Lacroix and others, 2021). Moreover, there can be seasonal and even inter-annual lags between biological production and physical transport, such that shelf sea carbon budgets are not necessarily balanced over a year (Chaichana and others, 2019; Humphreys and others, 2019). The production of biologically refractory DOC, which can accumulate and be exported off the shelf during episodic flushing events, mass transportation of both DOC and POC from shelf to the deep sea by tectonic triggers such as big earthquakes and tsunamis (Kioka and others, 2019), is therefore important for the continental shelf pump; since this carbon is refractory it does not matter whether this material is exported above or below the thermocline (Chaichana and others, 2019; Humphreys and others, 2019). Part of the POC and DOC that is transported from shelf seas to the open ocean is terrestrial in origin. The fate of this terrestrial carbon remains poorly quantified, but approximately 50% appears to be transported off shelf seas (Lacroix and others, 2021), including below the permanent thermocline (Medeiros and others, 2016). Turbidity currents are an important vector transferring shelf sea sedimentary POC below the oceanic thermocline (Ren and others, 2024; Gibbs and others, 2020; Talling and others, 2024). A distinct increase in coastal to upper slope temperatures gives rise to unstable conditions in the organic rich sediments found under the oxygen minimum zone. The high rate of organic carbon deposition can introduce slope failures by the dissolution of gas hydrates. These non-tectonic slope failures may be an important starting point for the lateral transportation of organic carbons to the deep ocean in the form of turbidites (Kitazato, 2024).

Some organic matter enters the open ocean above the permanent thermocline. Unless it is in the form of refractory DOC, this carbon is not sequestered from the atmosphere, but it can be recycled and fuel primary production off the shelf, and also contribute to the biological carbon pump in the open ocean (Frischknecht and others, 2018). This contribution is partly directly by POC and DOC originating from the shelf, and partly by POC and DOC produced from recycling of organic matter that originated from the shelf.

Horizontal carbon transport through animals is probably widespread but largely unquantified, unlike the vertical flux from animal migrations (see part 2 of the present chapter). For example, fish contribute 16% ± 13% of downward POC flux out of the euphotic zone, but the horizontal carbon flux from fish migrations is unknown (Saba and others, 2021). Physical transport of zooplankton across the shelf break can be significant (Keister and others, 2009) and is even part of the ontogenetic migrations of some commercially important species such as rock lobsters (Phillips and others, 2006). Horizontal fluxes have been estimated in only a few instances. For example, the spawning migration of the squid *Illex argentinus* on the Patagonian Shelf transfers approximately 0.09 Gg C yr^{-1} ($0.09x10^{-6}$ Pg yr^{-1}) to the shelf slope (Arkhipkin, 2013), using biomass-to-carbon conversions from Hoving and others, 2017). This is approximately 0.7% of the Patagonian Shelf's net biological production (Lacroix and others, 2021), although it is partly balanced by on-shelf migration of other squid species. Horizontal carbon transport via nektonic animals is likely to be impacted by fishing practices and potentially by climate-induced changes in seasonal and ontogenetic migration patterns.

5. The value of carbon cycling ecosystems

Ocean natural capital accounting (encompasses the systematic measurement and reporting of the status or "health" of ocean natural capital, as well as the contributions these assets make to society and the blue economy. Through monetary quantification, the ocean natural capital accounting enables decision makers to make trade-offs and assess impacts associated with various development scenarios and policies for ocean environmental sustainability and human well-being. Marine and coastal ecosystems form natural capital stocks that provide numerous benefits – such as food, climate regulation and air quality control – collectively known as ecosystem services. The value of coastal blue carbon ecosystems can be understood as the total economic value of conserving, restoring and sustainably managing marine and coastal ecosystems, while the concept of total economic value comprises the use and non-use values (Zarate-Barrera and Maldonado, 2015). The valuation of the ecosystem services provided by marine and coastal ecosystems clearly evidences the links between humans and the oceans, informs policymakers for improved ocean management/planning and advance policies and motivates the investment in ocean conservation.

Recently, a country-level blue carbon wealth assessment showed that coastal blue carbon ecosystems have an average value of \$190.67±30 billion. Australia, Indonesia and Cuba were the three countries that contributed the most benefits from blue carbon wealth and India, China and the United States are the largest beneficiaries (Bertram and others, 2021). Of the different types of coastal blue carbon ecosystems, the most extensively studied are mangroves (see sect. 4, subchap. 5H) and salt marshes (tidal marshes). For instance, all the ecosystem services provided by all mangroves worldwide have been valued at \$69.9 billion (Sanford, 2009). Regulation services of various coastal wetlands (see sect. 4, subchap. 5I) have an average value of \$369.7 and a total economic value of \$3,184 ha^{-1} yr^{-1}. Mangroves have an average of \$806 ha^{-1} yr^{-1} for provision services, \$1,446 ha^{-1} yr^{-1} for regulation services, \$113 ha^{-1} yr^{-1} for support services, \$1,721 ha^{-1} yr^{-1} for cultural services, and a total economic value of \$6,553 ha^{-1} yr^{-1} (Lopez-Rivas and Cardenas, 2024). Seagrass meadows (see sect. 4, subchap. 5G) are less studied but have an average \$3,226.5 ha^{-1} yr^{-1} for provision and \$871.7 ha^{-1} yr^{-1} for regulation (Lopez-Rivas and Cardenas, 2024). A study examined the ecological and economic potential of three key ecosystem services – fishery production, nutrient cycling, and carbon removal – provided by six kelp genera (*Ecklonia, Laminaria, Lessonia, Macrocystis, Nereocystis* and *Saccharina*) The results show that the potential value of each genus was between \$64,400 and \$147,100 ha^{-1} yr^{-1} (Eger and others, 2023). There are still gaps in valuation of blue carbon ecosystems. For example, Arkema and others (2024) found that only a third of papers quantify societal benefits of coastal ecosystems within marine protected areas (MPAs), and these tend to focus mainly on corals and mangrove ecosystems.

The value of carbon cycling ecosystems has been increasingly recognized and many finance initiatives exist i.e. voluntary and compliance carbon markets, public funding, philanthropic and other alternatives, such as payment for ecosystem services, ocean natural capital accounting and blue bonds. Blue Carbon activities are one type of climate mitigation solution, which currently receives just 3% of total climate investment globally.[1] This lack of financial support has been a barrier to bringing Blue Carbon conservation and restoration activities to scale.[2]

The recognition that marine ecosystems, other than coastal blue carbon ecosystems, also have the power to fix and transport large quantities of carbon has increased interest in using them as marine CO_2 removal measures (see subsect. 5A, chap. 10). It should be noted that great uncertainty remains regarding the efficacy, scalability or financial viability of many of these proposed nature-based marine CO_2 removal approaches. For example, the estimated costs for ocean iron fertilization vary widely, with best-case values of \$7 per net ton carbon captured, compared with worst-case values of \$1,500 per net ton carbon captured depending on oceanographic factors. Ocean iron fertilization aerial delivery ranges between \$21 and \$2,033 per net ton carbon captured inclusive of verification costs; up to 30%–40% more cost-effective than ship-based ocean iron fertilization (Emerson and others, 2024).

While seaweed aquaculture is not considered as either blue carbon or geoengineering (see subsect. 5A, chap. 10), the additional value of such activities to carbon storage, over and above the commercial value of the seaweed product, has been noted. The levelized unit costs (LCOC) of CO_2eq sequestration (LCOC; \$tCO_2eq^{-1}) for kelp aquaculture at baseline were estimated at \$17,048 tCO_2eq^{-1}, with only a 39% true sequestration "additionality" rate. However, by process improvement and decarbonization of production

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[1] See https://verra.org/two-new-biosequestration-working-groups/.

[2] See https://verra.org/first-blue-carbon-conservation-methodology-expected-to-scale-up-finance-for-coastal-restoration-conservation-activities/.

supply chains LCOC were reduced to \$1,257 tCO_2eq^{-1} and the additionality rate increased to 91% (Coleman and others, 2022). Froehlich and others, (2019) analysed global production data and determined that the cost of producing carbon credits from macroalgae ranged from \$71 to \$27,222 tCO_2eq^{-1}.

More generally, the recognition of the value of coastal blue carbon ecosystems in climate action has increased in recent years. However, while a total of 81% (158) of Parties to the Paris Agreement have included an adaptation component in their nationally determined contributions, only 31% (49) identified ocean ecosystems as a priority sector for adaptation. Of the 21% of Parties that included information on ocean or blue carbon as a priority sector for reducing greenhouse gas emissions, 71% mentioned specific ocean-based mitigation measures (UNFCCC, 2024).

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