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The renaissance of Odum's outwelling hypothesis in 'Blue Carbon' science

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ABSTRACT

The term 'Blue Carbon' was coined about a decade ago to highlight the important carbon sequestration capacity of coastal vegetated ecosystems. The term has paved the way for the development of programs and policies that preserve and restore these threatened coastal ecosystems for climate change mitigation. Blue carbon research has focused on quantifying carbon stocks and burial rates in sediments or accumulating as biomass. This focus on habitat-bound carbon led us to losing sight of the mobile blue carbon fraction. Oceans, the largest active reservoir of carbon, have become somewhat of a blind spot. Multiple recent investigations have revealed high outwelling (i.e., lateral fluxes or horizontal exports) of dissolved inorganic (DIC) and organic (DOC) carbon, as well as particulate organic carbon (POC) from blue carbon habitats. In this paper, we conceptualize outwelling in mangrove, saltmarsh, seagrass and macroalgae ecosystems, diagnose key challenges preventing robust quantification, and pave the way for future work integrating mobile carbon in the blue carbon framework. Outwelling in mangroves and saltmarshes is usually dominated by DIC (mostly as bicarbonate), while POC seems to be the major carbon species exported from seagrass meadows and macroalgae forests. Carbon outwelling science is still in its infancy, and estimates remain limited spatially and temporally. Nevertheless, the existing datasets imply that carbon outwelling followed by ocean storage is relevant and may exceed local sediment burial as a long-term (>centuries) blue carbon sequestration mechanism. If this proves correct as more data emerge, ignoring carbon outwelling may underestimate the perceived sequestration capacity of blue carbon ecosystems.

1. Introduction

The term 'Blue Carbon' refers to the carbon captured by the world's ocean or coastal vegetated ecosystems. Blue carbon ecosystems are hotspots in the global carbon cycle, but have been destroyed at alarming rates in the last several decades (Waycott et al., 2009; Hamilton and Casey, 2016; Wernberg et al., 2019). As a result of high sediment carbon burial rates, preserving and restoring blue carbon habitats has been touted as a useful step towards sequestering anthropogenic carbon, thereby contributing to achieving United Nations sustainable development goals and meeting the Paris Climate Agreement (Kelleway et al., 2020). Increasing conservation and restoration efforts have recently lowered mangrove loss rates with positive implications to carbon sequestration (Friess et al., 2020a, 2020b).

Since the term was coined about a decade ago (Nellemann et al., 2009; McLeod et al., 2011), our knowledge about blue carbon sequestration has rapidly evolved. Initially, research emphasized blue carbon storage by determining ecosystem carbon stocks and potential CO_2

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emissions caused by habitat alteration (e.g., Donato et al., 2011; Atwood et al., 2017; Kauffman et al., 2020). Later, studies on carbon burial gained traction to quantify long term carbon storage in blue carbon ecosystems (Sanders et al., 2010; Kusumaningtyas et al., 2019; Wang et al., 2021). We now have national and global scale estimates of sediment carbon in mangrove forests, saltmarshes and seagrass meadows (e.g., Atwood et al., 2017; Serrano et al., 2019; Jennerjahn, 2020; Ouyang and Lee, 2020; Wang et al., 2021). Much less is known about aquatic pathways (e.g., outwelling), and how blue carbon is eventually stored in the ocean, the largest global reservoir of carbon. In general, blue carbon ecosystems are in constant exchange with the ocean through tides, waves and currents on diel to seasonal timescales. This exchange drives the export or import of nutrients and carbon into or out of those blue carbon habitats (Gacia et al., 2002; Jennerjahn and Ittekkot, 2002; Bouillon et al., 2007). Increasing evidence of the major role of aquatic carbon exports has triggered discussions around the need to include net carbon outwelling beyond the boundaries of coastal vegetated ecosystems in the blue carbon framework (Maher et al., 2018; Smale et al., 2018; Ortega et al., 2019; Santos et al., 2019).

Well before the emergence of blue carbon as a scientific and management concept and inspired by Teal (1962), Odum (1968; 1980) hypothesized that outwelling (i.e., lateral fluxes or horizontal exports; Fig. 1) of carbon and nitrogen supported much of the biological productivity in coastal waters off intertidal saltmarshes. Debate has appeared in the literature since then (for a review, see Lee, 1995). In an influential early review, Nixon (1980) argued there was little evidence to support the ecological outwelling hypothesis, and others found minor uptake of outwelled carbon in nearshore food webs (Rodelli et al., 1984; Fry and Ewel, 2003; Connolly et al., 2005). Some supported the outwelling hypothesis by emphasizing that coastal wetlands are a significant source of carbon and nitrogen to the coastal ocean (Alongi et al., 1992; Rivera-Monroy et al., 1995; Dittmar et al., 2006; Granek et al., 2009; Taillardat et al., 2019). Nixon (1988) also argued that physical mixing can sustain high primary productivity in the coastal ocean. Earlier outwelling investigations focused on detritus or particulate organic carbon (POC) and their uptake by consumers (e.g., Boto and Bunt, 1981; Woodroffe, 1985; Boto and Wellington, 1988) with less emphasis on dissolved organic carbon (DOC) (e.g., Twilley, 1985; Lee, 1995; Dittmar et al., 2001; Adame and Lovelock, 2011). Only recently the important quantitative role of dissolved inorganic carbon (DIC) has become clearer in coastal carbon budgets (e.g., Bouillon et al., 2007; Wang et al., 2016; Maher et al., 2017; Santos et al., 2019; Sippo et al., 2019; Saderne et al., 2020).

With a current focus on mangrove forests, saltmarshes and seagrass meadows, Lovelock and Duarte (2019) discussed scientific and management challenges that need to be overcome to include different organisms or ecosystems (such as kelp forests) into the blue carbon framework. To be considered blue carbon, an ecosystem should (1) have a significant scale of greenhouse gas emissions or removals, (2) support long term (>centuries) storage of carbon, and (3) be amenable to management actions that enhance carbon storage or avoid greenhouse gas emissions. Based on these arguments, macroalgal habitats such as kelp forests should also be part of the blue carbon framework (Krause-Jensen and Duarte, 2016; Krause-Jensen et al., 2018). Similar to mangroves, saltmarshes and seagrass meadows, kelp forests have very high primary productivity rates and may ultimately sequester large amounts of carbon in the ocean (Krause-Jensen and Duarte, 2016; Filbee-Dexter and Wernberg, 2020). In contrast to the original blue carbon systems, macroalgae/kelp forests do not have high local sedimentation rates. Therefore, to be included in the blue carbon framework, significant amounts of macroalgae carbon would have to be outwelled away from the local habitat and be sequestered in the deeper ocean as detritus or dissolved forms (Ortega et al., 2019).

Here, we argue that the blue carbon discussion needs to move beyond ecosystem types and carbon burial – it should consider all the pathways of the carbon cycle and all carbon reservoirs in the oceans and the coast. Outwelling clearly fits the blue carbon criteria. We discuss how regional and global scale estimates of blue carbon have been underestimated because they have focused mostly on storage in biomass and sediments within the respective habitats often overlooking the ocean as a major long term blue carbon reservoir. We contrast outwelling mechanisms in the different blue carbon ecosystems and discuss research questions that need to be addressed for a better integration of mobile carbon in the blue carbon framework.

2. Outwelling as a blue carbon sequestration mechanism

The oceans are the largest global active carbon reservoir, with DOC and DIC stocks that are at least one order of magnitude greater than those in global terrestrial soils (Millero, 2007). DIC concentrations in the ocean (mostly as bicarbonate) are particularly high, allowing for oceanic residence times on time scales of 100,000 years (Millero, 2007). The DOC in the oceans constitutes about ~70% of the total organic carbon present in the oceans, and the majority of DOC is found at depths >1,000 m and has an average age of 4,000-6,000 years (Druffel et al., 1992; Hansell et al., 2009). Therefore, DIC and DOC outwelling and subsequent oceanic storage is a suitable mechanism for long term carbon sequestration similar to burial in soils or sediments.

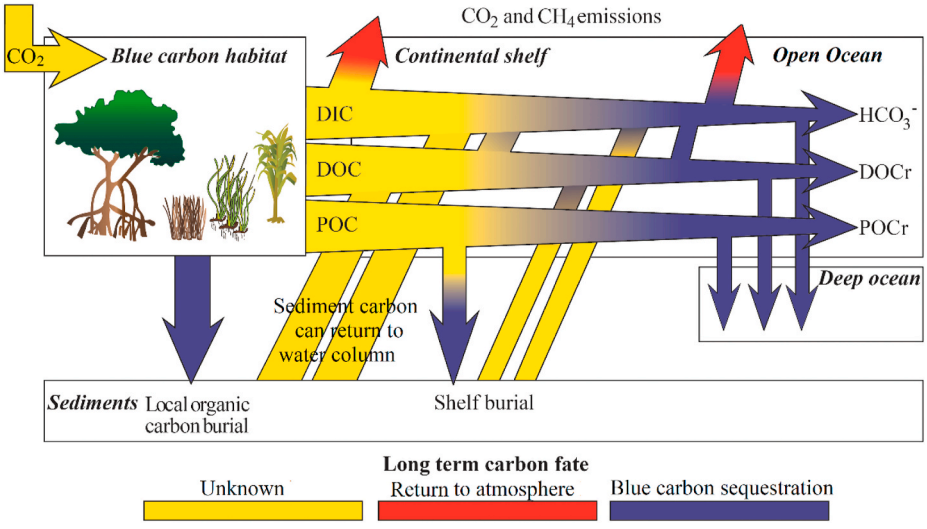


Fig. 1. Conceptual model of blue carbon pathways highlighting carbon transformations and sequestration during transport offshore. Yellow arrows represent pathways that may evolve into either sinks or sources of carbon, red arrows represent a source back to the atmosphere, and blue arrows represent long-term carbon sinks (burial and outwelling). Some of the carbon reaching the deep ocean may eventually return to the surface on time scales of ocean mixing (millennia). During outwelling across the shelf, part of the DIC pool returns to the atmosphere as CO_2, and part of the labile DOC and POC pools are oxidized to DIC. The more refractory forms of carbon (DOC_r or POC_r) have a greater chance of being stored in the ocean. Ultimately, biogeochemical reactions and transport rates will determine the net fraction of primary productivity that can be sequestered by the ocean. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

DIC corresponds to the sum of concentrations of three species: CO_{2aq} (including H_2CO_3), HCO_3^- (bicarbonate) and CO_3^{2-} (carbonate) with speciation governed by pH. Total alkalinity is defined as the sum of the concentrations of HCO_3^-, two times CO_3^{2-}, and other weak bases (mostly borate in seawater) and organic acid charge groups (i.e., organic alkalinity; Song et al., 2020). The fraction of DIC exported as alkalinity (stored in the ocean) versus CO_2 (which can more easily return to the atmosphere) will determine whether DIC outwelling becomes a long-term sink of atmospheric carbon or a short-term recycling mechanism with net zero influence on atmospheric CO_2. Key to this is the fact that when CO_2 is produced by the biogeochemical processes discussed below, it drives this reaction to the right:

$$CO_2 + H_2O + CO_3^{2-} \rightarrow 2HCO_3^- \quad (1)$$

i.e., CO_2 reacts with carbonate ions in seawater to produce bicarbonate. While this "helps" in the storage of CO_2 derived from processes such as organic carbon mineralization (see below), this reaction does not necessarily go completely to the right, and there is also an accompanying increase in aqueous CO_2 concentrations which may then result in the recycling of some of this CO_2 back into the atmosphere. The ratios between DIC and total alkalinity will ultimately determine CO_2 dynamics and the pH of the nearshore ocean (Sippo et al., 2016; Cyronak et al., 2018).

DOC has an even more complicated composition, chemistry and fate in the oceans. In its simplest sense, we can think of DOC as an intermediate pool of organic carbon produced during POC mineralization that can then be consumed along the outwelling transport pathway and eventually evolve to DIC (Fig. 1). DOC is composed of a highly diverse suite of molecules with a wide range of reactivities (Osterholz et al., 2015). "Labile" DOC (usually proteins and carbohydrates) will be rapidly consumed primarily in the surface ocean by microbes and be transformed into DIC. Refractory DOC (including lignin lipids, and other compounds that are not easily characterized) is more likely to travel to the deep ocean, where remineralization is slower and therefore longer term storage becomes possible (Dittmar et al., 2006). Ultimately, whether POC, DIC and DOC become sequestered in the ocean is a function of their chemical composition and transformations (Fig. 1). The issue is that resolving fluxes and the fate of POC, DOC, and DIC is quite challenging, yet essential to quantify the true extent of blue carbon storage.

DIC and alkalinity production in many blue carbon ecosystems is primarily driven by sulphate reduction within sediments (Hu and Cai, 2011; Alongi, 2014). Denitrification and iron reduction may also be important in some cases (Kristensen et al., 2011; Alongi et al., 2012). Sulphate is far more abundant in seawater (~28 mM) than dissolved oxygen (~0.3 mM), so sulphate is often the dominant oxidant used by microbes when consuming sediment organic matter in coastal environments (Berelson et al., 1996). Organic matter mineralization follows a diagenetic reaction sequence, whereby near-surface aerobic processes are followed by anoxic processes deeper in the sediment (Fig. 2).

The production of calcium carbonate ($CaCO_3$) by calcifying organisms inhabiting blue carbon ecosystems can result in the accumulation of inorganic carbon in sediments which is sometimes perceived to represent blue carbon (Macreadie et al., 2017b). However, just like coral reef growth (Frankignoulle et al., 1994), $CaCO_3$ accumulation in blue carbon habitats is not a CO_2 sink. Indeed, $CaCO_3$ production and burial releases CO_2 to the atmosphere while consuming alkalinity:

$$Ca^{2+} + 2HCO_3^- \rightarrow CaCO_3 + CO_2 + H_2O \quad (2)$$

Here, the bicarbonate reactant is primarily derived by dissolution (weathering) of carbonate rocks on land:

$$CaCO_3 + CO_2 + H_2O \rightarrow Ca^{2+} + 2HCO_3^- \quad (3)$$

with the CO_2 that is consumed being ultimately derived from the atmosphere (Berner et al., 2003). Thus, one can think of the CO_2 produced in equation (2) as simply being recycled back to the atmosphere after uptake by weathering of carbonate rocks, and the biogenic $CaCO_3$ produced as simply being solid carbonate that has been "translocated" from land to the oceans. In other words, $CaCO_3$ production and burial in blue carbon habitats should have a net zero long term CO_2 sequestration effect. Whereas some of the $CaCO_3$ will be buried in local sediments (Saderne et al., 2019), some can be dissolved and some can be exported as particulate inorganic carbon (PIC). To date, there are no estimates of PIC outwelling from blue carbon habitats.

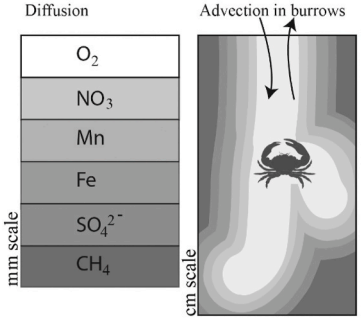
Similarly, oxic respiration in blue carbon sediments, and of POC and DOC in the water column simply returns CO_2 to the atmosphere (Fig. 1), representing net zero long term carbon sequestration:

$$CH_2O + O_2 \rightarrow CO_2 + H_2O \quad (4)$$

The key process converting sediment organic carbon to alkalinity is sulphate reduction, which is often coupled to pyrite (FeS_2) and iron monosulfide (FeS) burial (Berner et al., 1970; Reithmaier et al., 2021):

$$6CH_2O + 3SO_4^{2-} + 2FeOOH \rightarrow FeS + FeS_2 + 6HCO_3^- + 4\,H_2O \quad (5)$$

Expressing this reaction simply in terms of pyrite burial requires specifying the oxidant used to oxidize FeS to FeS_2 (e.g., O_2, SO_4^{2-}, FeOOH, "structural" Fe^{3+} in clay mineral lattice sites). While this will change the stoichiometry of reaction (5), it does not impact the fact that when reactive iron oxides (expressed as FeOOH) are present in blue carbon sediments, reaction 5 results in net alkalinity production from organic matter (CH_2O) degradation. Therefore, in contrast to $CaCO_3$ burial, FeS and FeS_2 burial results in net long term carbon sequestration



Process	Oxidant concentrations (mM)[A]	DIC produced per mole of oxidant consumed	Alkalinity produced per mole of DIC produced[B]
Aerobic respiration	0.3	+1	-0.16
Denitrification	< 0.1	+1.25	+0.8
Manganese reduction[C]	-[D]	+0.5	+4
Iron reduction[E]	-[D]	+0.25	+8
Sulfate reduction	28	+0.5	+1
Methanogenesis	-[F]	+0.5	+0

Fig. 2. Alkalinity and DIC production pathways in coastal sediments. The zonation of electron acceptors is the same in diffusion- and advection-dominated sediments, but the 3-dimensional structure created by burrows enhances the sediment area and volume where biogeochemical reactions can produce alkalinity via anaerobic processes. Modified from (Burdige, 2006).
Figure notes: [A]Approximate concentration in seawater; [B] with the exception of aerobic respiration, the alkalinity production associated with the remineralization of N and P during organic matter remineralization is generally not significant (see Burdige, 2006); [C] Assuming MnO_2 undergoes reduction; [D] In most settings the concentrations of these oxidants available for reduction are strongly controlled by internal redox cycling of these metals (Aller, 1994; Burdige and Komada, 2020); [E]Assuming $Fe(OH)_3$ undergoes reduction; [F] If we approximate methanogenesis as $2CH_2O \rightarrow CH_4 + CO_2$ then the oxidant concentration will equal the concentration of reactive organic matter undergoing methanogenesis.

via alkalinity production. In some cases, pyrite may be re-oxidized after deposition due to sediment resuspension, bioturbation or drainage of coastal wetlands (Johnston et al., 2004; Bonaglia et al., 2019; Łukawska-Matuszewska et al., 2019). This then negates the alkalinity production in reaction (5) because the acid produced by pyrite oxidation titrates alkalinity (i.e., bicarbonate) back to CO_2.

Finally, another alkalinity generating process in some blue carbon systems is seagrass-mediated carbonate dissolution (Burdige and Zimmerman, 2002). By transporting some of their photosynthetically produced O_2 below ground to support aerobic respiration of roots and rhizomes, seagrasses stimulate oxidative mineralization of organic matter buried in the sediment (Equation (4)). The CO_2 that is then produced dissolves the sedimentary carbonates, a process that is particularly relevant in some tropical and sub-tropical regions (also see Burdige et al., 2010) and can be expressed as:

$$CH_2O + O_2 + CaCO_3 \rightarrow Ca^{2+} + 2HCO_3^- \quad (6)$$

The bicarbonate produced in the sediments by this reaction eventually escapes to the overlying waters as a diffusive or advective benthic flux (Cyronak et al., 2013). Since much of the organic matter mineralized in these sediments is seagrass-derived detritus (Hu and Burdige, 2007), this process represents another way in which blue carbon-derived organic matter is transferred to the oceanic alkalinity pool.

The biogeochemical reactions discussed here continuously take place in blue carbon ecosystems and other marine sediments, but the conventional one-dimensional view of organic matter mineralization becomes more complex in systems that have three-dimensional sediment structures such as crab burrows (Fig. 2). Tidally-driven porewater or groundwater flushing in intertidal sediments transports the products of those biogeochemical reactions to the coastal ocean. This exchange process is often referred to as tidal pumping (Stieglitz et al., 2013; Chen et al., 2018; Call et al., 2019; Taniguchi et al., 2019). When oxic surface waters infiltrate burrows, they encounter organic-rich sediments, potentially speeding up sediment respiration processes, rapidly exhausting the available oxygen, and triggering anaerobic reactions that produce DIC and alkalinity (Equation (5)). This process enriches porewater with by-products of anaerobic organic matter degradation. In many mangroves and saltmarshes, porewater exchange becomes the essential link between the coastal sediment and oceanic carbon reservoirs (Bouillon et al., 2007; Maher et al., 2017; Call et al., 2019; Xiao et al., 2021). The extent of tidal inundation, tidal range, vegetation, and microtopography will mediate tidal pumping and where these biogeochemical reactions occur, highlighting the importance of physical characteristics in mediating outwelling.

The large amounts of burrows and roots (Ouyang et al., 2017) in mangroves, saltmarshes and some seagrass meadows create conduits for water flow in otherwise impermeable muddy sediments, allowing for extremely high intertidal sediment flushing rates (Xin et al., 2009; Stieglitz et al., 2013). As a result, tidal pumping can be considered equivalent to flushing the entire continental shelf water column volume through mangrove sediments on time scales of centuries (Tait et al., 2016). Porewater exchange delivers seawater oxygen, sulphate and other electron acceptors deeper into organic-rich sediments than the surface region of sediments where diffusive benthic fluxes are often quantified (Huettel et al., 2014). Indeed, burrows increase the sediment area available for sediment-water biogeochemical exchange by a factor of two or more (Stieglitz et al., 2000; Agusto et al., 2020), while simultaneously increasing sediment permeability (Guimond et al., 2020), making the transport of solutes via tidal pumping (advection) to be much faster than molecular diffusion (Bouillon et al., 2007; Santos et al., 2014; Robinson et al., 2018).

It remains unclear how much of the outwelled carbon is processed in nearshore regions or gets stored in the deep ocean over the long-term. Oceanic carbon sequestration will depend not only on biogeochemical processing (decomposition rates), but also residence times and physical processes (waves, tides, currents) driving carbon transport from the blue carbon habitat to the long-term oceanic reservoir. Part of the DIC will return to the atmosphere as CO_2, and part will travel to the open ocean as bicarbonate for long-term storage, effectively becoming blue carbon. Part of the DOC will be oxidized to DIC, and part will travel offshore and be stored in the ocean as refractory DOC (Fig. 1). The proportion of bicarbonate alkalinity relative to labile DOC and CO_2 will dictate how blue carbon habitats contribute to the coastal ocean's capacity to absorb atmospheric CO_2 (Santos et al., 2019), and also whether they can partially buffer coastal ocean acidification. The removal of CO_2 by primary production in seagrass beds (Hendriks et al., 2014) and the export of porewater-derived bicarbonate in mangroves (Sippo et al., 2016; Liu et al., 2021) and saltmarshes (Wang et al., 2016) can create detectable effects on seawater pH.

Outwelling from coastal vegetated habitats has often been perceived to be mostly in the form of POC (Lee, 1995; Dittmar et al., 2001; Duarte et al., 2005) that can accumulate both nearshore and offshore (Jennerjahn and Ittekkot, 2002; Luisetti et al., 2020). However, the fate of this POC in the ocean also remains poorly understood. If part of this POC accumulates in marine sediments, is transformed to refractory DOC, or eventually gets respired by anaerobic processes into bicarbonate, then this POC export will also represent a blue carbon sink.

Outwelling from blue carbon ecosystems and carbon burial in continental margin sediments largely depends on the environmental setting (Woodroffe et al., 2016). For example, the portion of mangrove POC found off the Brazilian tropical coast was negligible despite dense mangrove vegetation due to limited connectivity (Jennerjahn et al., 2010). In contrast, high rates of POC export and mangrove-derived POC burial were observed 20–30 km off an open Australian shoreline (Boto and Bunt, 1981). High carbon accumulation rates (194–658 g C m^{-2} yr^{-1}) with 10–50% mangrove carbon contribution were measured off tide- and river-dominated mangroves in Java, Indonesia (Kusumaningtyas et al., 2019; Hapsari et al., 2020). The significant amount of mangrove-derived POC buried offshore is often not accounted as blue carbon and remains poorly quantified (Jennerjahn, 2020). POC export from saltmarshes is dependent upon geomorphic stability, such that erosive marshes export POC, while stable marshes import POC (Ganju et al., 2019). Further research on the long-term fate of this POC is required. Quantifying these biogeochemical transformations as carbon travels across the continental shelf is challenging, but essential for determining the ultimate contribution of blue carbon to carbon sequestration in the ocean.

3. State-of-the-art estimates of outwelling from blue carbon systems

Odum's outwelling hypothesis has an ecological connotation and has remained somewhat dormant for a few decades. The hypothesis is now being tested from a blue carbon perspective in different habitats. A rapidly growing number of local-scale investigations have quantified outwelling of DIC, alkalinity, POC and DOC in mangroves, saltmarshes, seagrass beds, and kelp forests. While those coastal vegetated habitats tend to behave differently (Table 1) in the limited datasets available to date, it seems that outwelling exceeds burial as a long-term carbon sink in the four major blue carbon habitats (Fig. 3).

Mangrove forests. Mangroves cover 0.3% of the global coastal zone, but contribute 14% of global organic carbon burial and 28% and 13% of DIC and DOC global outwelling (Alongi, 2020b). Mangrove outwelling estimates initiated with POC and DOC observations in Australia (Boto and Bunt, 1981) and the USA (Twilley, 1985). Molecular markers and stable isotopes revealed significant DOC outwelling potentially exceeding regional river inputs off Brazil (Dittmar et al., 2001). By measuring all the major carbon species over a diel cycle in a mangrove tidal creek, Bouillon et al. (2007) observed a strong porewater-derived DIC signal. Large carbon outwelling was implied by alkalinity enrichments near blue carbon habitats in New Caledonia (Leopold et al.,

Table 1
A conceptual comparison of carbon outwelling in the four major blue carbon habitats.

Blue carbon ecosystem	Type of substrate	Relative contribution of outwelling to burial *in situ*	Carbon species	Key mechanism triggering outwelling	Comments and major uncertainties in global estimates in Fig. 3
Mangroves and saltmarshes	Intertidal organic rich muds or peats	Outwelling>burial	DIC>DOC>POC	Sulphate reduction in sediments followed by tidal flushing in burrows, macropores and buried plant material (marshes)	Short term datasets and geographical bias against the tropics (Bouillon et al., 2008; Alongi, 2020b, a). Saltmarsh data mostly from the USA East coast.
Seagrass meadows	Intertidal and subtidal sands or muds	Outwelling»burial	POC>DOC DIC?	Tides and storms transporting detritus offshore, leaching of DOC	DOC and POC outwelling derived from manipulative experiments, a global summary and averages (Duarte, 2017). DIC not quantified.
Macroalgae forests	Subtidal hard substrates	Outwelling»>burial	POC>DOC>DIC	Tides and storms transporting detritus offshore, leaching of DOC	Geographical bias (Caribbean). No data from the Indian Ocean and only one in the South Atlantic (Krause-Jensen and Duarte, 2016).

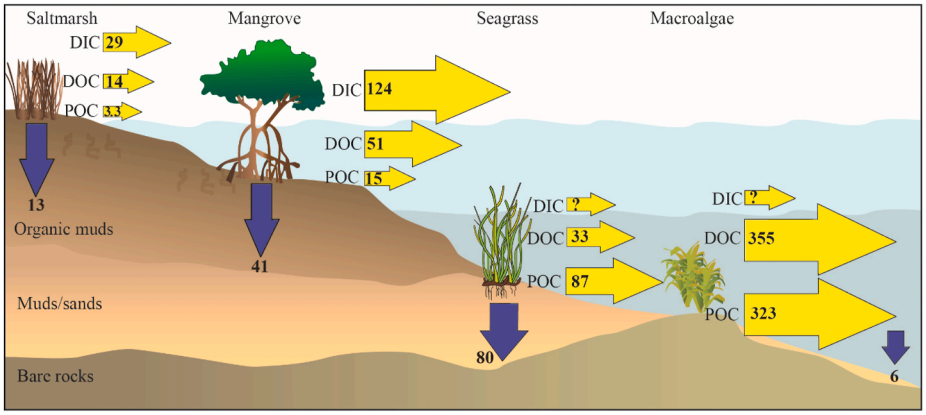


Fig. 3. Global scale estimates of carbon outwelling and burial as compiled by literature summaries in saltmarshes and mangroves (Alongi, 2020a, b; Wang et al., 2021), seagrass meadows (Duarte and Krause-Jensen, 2017), and macroalgae (Krause--Jensen and Duarte, 2016) habitats. All fluxes in Tg C yr^{-1}. The number of studies on the topic are limited and uncertainties are unavailable. Carbon outwelling seems to exceed burial for the four major blue carbon habitats, but whether the outwelled carbon is stored in the ocean over long time scales remains to be quantified and will be a function of transformations along the transport pathway that are often unquantified. Arrow colors follow Fig. 1. Greenhouse gas emissions from blue carbon habitats are summarized elsewhere (Rosentreter et al., 2021). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

2017), and in the Andaman Islands (Linto et al., 2014), but no outwelling rates were estimated because the focus was on CO_2 emissions. DOC exports from mangroves may be equivalent to 10% of river fluxes into the oceans (Dittmar et al., 2006; Sippo et al., 2017), but it remains poorly understood whether this DOC is labile or refractory, and whether it is exported off the continental shelf and should therefore be thought of in terms of long-term sequestration.

DIC outwelling rates were 3-fold greater than total carbon burial in an Australian mangrove/saltmarsh dominated estuary (Santos et al., 2019). Estimates of significant DIC outwelling from Australian mangrove systems (Maher et al., 2013; Sippo et al., 2016) demonstrate that considering DIC outwelling may help resolving mangrove carbon budget imbalances identified in earlier literature reviews (Bouillon et al., 2008). On a global scale, mangrove outwelling contributes to ~60% of the DIC discharged from the worlds tropical rivers (Alongi, 2020b), and porewater fluxes of carbon can exceed river carbon transport to the ocean (Chen et al., 2018). These high porewater fluxes are unlikely to reach the ocean due to transformations within mangroves and estuaries. These recent studies have shown that tidally-derived porewater exchange from the mangrove sediment to the adjacent ocean is a considerable outwelling source of carbon (Taillardat et al., 2018). However, most of these studies are concentrated in few locations, especially in Australia (Alongi, 2020b), making it difficult to build reasonable global budgets due to geographical biases and short-term observations. While sulphate reduction is usually the major source of DIC in mangroves, carbonate dissolution was an order of magnitude greater than organic carbon burial as a CO_2 sink in carbonate sediment mangroves in the Red Sea (Saderne et al., 2020).

Empirical data from mangrove-rich tropical regions (e.g., South America, Indonesia and Africa) are needed to reduce the uncertainties of global estimates of carbon outwelling (Fig. 3). The existing datasets imply that mangroves export three times more POC and DIC and twice more DOC to the adjacent coastal waters than saltmarshes (Alongi, 2020a). However, these rates might be underestimated due to the lack of outwelling data in highly productive equatorial and tropical mangroves, areas that hold the largest sediment carbon stocks and above ground biomass (Sanders et al., 2016; Atwood et al., 2017).

Saltmarshes. Observations in marsh-dominated estuaries and saltmarsh tidal creeks (Raymond et al., 2000; Neubauer and Anderson, 2003; Wang and Cai, 2004) on the USA East Coast revealed high DIC outwelling that may rival local riverine fluxes. Similar to mangroves, saltmarsh DIC outwelling has been suggested to be sustained by porewater and/or groundwater inputs (Cai, 2011; Diggle et al., 2019) though DIC outwelling from shallow porewater exchange appears to be at least an order of magnitude greater than DIC outwelling associated with fresh groundwater discharge (Czapla et al., 2020; Tamborski et al., 2021). Saltmarsh DIC outwelling is seasonally variable (Wang et al., 2016), highly episodic (Chu et al., 2018) and partially controlled by hydrogeology (Tamborski et al., 2021).

A recent synthesis of carbon flux measurements for eastern North America identified 12 studies for total organic carbon outwelling and only 4 for DIC (Najjar et al., 2018). This summary revealed that the saltmarsh uptake of atmospheric CO_2 is comparable to regional riverine carbon fluxes to the ocean. About ~80% of this atmospheric CO_2 uptake is exported from the wetlands as a lateral flux to adjacent estuaries. There was roughly a 50:50 split between organic and inorganic carbon export, although there was not an explicit attempt to characterize whether these fluxes result into permanent versus temporary storage in the ocean, i.e., whether the exported POC and DOC are refractory, and whether the exported DIC occurs as bicarbonate or CO_2. Carbon burial in these saltmarsh sediments represented ~20% of the atmospheric CO_2 uptake by vegetation, and virtually all of this burial was in the form of

organic carbon (i.e., POC). Saltmarsh flux estimates are concentrated along the east coast of the USA, creating not only a latitudinal but a locational bias in saltmarsh carbon outwelling understanding.

Lateral DIC exports from intertidal saltmarshes have been assessed via high-frequency tidal creek measurements (Chu et al., 2018; Bogard et al., 2020) and radium isotope mass balance models (Tamborski et al., 2021). At the ecosystem-scale, lateral DIC fluxes can be indirectly inferred as the difference between atmospheric carbon exchange and sediment burial (Forbrich et al., 2018) and modeled from respiration chamber experiments and tidal water depth (Czapla et al., 2020). Further, POC export may be modeled as a function of elevation and the ratio of unvegetated-to-vegetated marsh area (Ganju et al., 2019). Recent experiments suggest that fertilization of the marsh surface enhances lateral carbon outwelling (Czapla et al., 2020). Despite high sulfide concentrations, there is emerging evidence that salt marshes generate CH_4 (Seyfferth et al., 2020) and thus reduce blue carbon potential when CH_4 escapes to the atmosphere (Schutte et al., 2020).

While carbon budget calculations such as the one by Najjar et al. (2018) reveal the general behavior of saltmarsh carbon budgets, they generally do not examine alkalinity fluxes and budgets as a part of the overall analysis (Song et al., 2020). Indeed, no direct quantifications of lateral transport of alkalinity seem to be available for saltmarshes. Thus, it can be difficult to specifically look at the importance of many of the alkalinity-generating processes such as a sulphate reduction (equation (5)) as they relate to carbon outwelling from saltmarshes.

Seagrass. Seagrass meadows are some of the most productive ecosystems in the world and can be found within inter- to subtidal habitats up to 40 m depth (Duarte et al., 2005). Early observations of seagrass detritus in the deep-sea floor in the 1960's revealed the importance of POC (detritus) export beyond seagrass habitats (Moore, 1963; Menzies et al., 1967). Since then, several studies have assessed how seagrasses release DOC and POC to ambient seawater (Barrón et al., 2004; Apostolaki et al., 2010). Seagrasses release DOC directly via leaching from the leaves and roots (Ziegler and Benner, 1999; Barrón and Duarte, 2009) and during the decomposition of detritus and sediment carbon (Vichkovitten and Holmer, 2005). The perennial nature of seagrasses contributes to the export of biomass offshore (Menzies et al., 1967). About 24% of seagrass net primary production (NPP) can be exported beyond their habitats as DOC and POC, and >2% may end up exported and sequestered in the deep sea (Duarte and Krause-Jensen, 2017). This contribution can be relevant at global scales since the proportion of NPP exported is about double that accumulating locally in seagrass sediments (Duarte and Cebrián, 1996).

The process of $CaCO_3$ production and dissolution within seagrass meadows remains poorly understood (Mazarrasa et al., 2015). Seagrass meadows provide habitat to calcifying organisms that bury $CaCO_3$ and release CO_2 (equation (2)). Indeed, CO_2 emissions via $CaCO_3$ burial in global seagrass meadows may offset ~30% of carbon sequestered via organic carbon burial (Saderne et al., 2019). The release of oxygen from seagrass roots enhances aerobic respiration within sediments, affecting both the organic and inorganic carbon pools as shown by equation (6) (Burdige and Zimmerman, 2002). Organic carbon respiration results in the release of CO_2 and a decrease in pH, driving carbonate sediment dissolution that represents a CO_2 sink (Frankignoulle et al., 1994; Burdige et al., 2010). The outwelling of alkalinity and DIC from seagrass meadows can contribute to carbon sequestration, but further studies are required to understand the interplay of multiple processes releasing or consuming CO_2 within seagrass sediments (Macreadie et al., 2017b). While we have initial global estimates of POC and DOC outwelling from seagrass meadows (Fig. 3), there are no global estimates focusing on DIC or alkalinity (Fig. 3).

Macroalgae. Unlike other blue carbon habitats that occur on soft sediments, kelp and other macroalgal forests generally occur on subtidal rocks, and therefore do not directly bury much carbon locally. Macroalgal forests have exceptionally high rates of primary production per unit area, often replacing their entire canopy annually (Pessarrodona et al., 2018). Much of this carbon production (40–80%) is exported as POC or DOC (Krumhansl and Scheibling, 2012; Krause-Jensen and Duarte, 2016). The POC can take the form of entire plants, whole blades or fragments of all sizes, and once they break off either float at the surface due to gas vesicles (Rothausler et al., 2012), travel with ocean currents in the water column and slowly sink (Wernberg and Filbee-Dexter, 2018), or move laterally along the seafloor into deeper habitats (Filbee-Dexter et al., 2018).

The fate of outwelled macroalgal POC depends largely on where in the ocean it ends up. POC mineralization rates determine residence time and transport distance, and are influenced by many factors, such as grazers, sea temperature, and fragmentation (Wernberg and Filbee-Dexter, 2018). Because the surface ocean is oxic, mineralization of floating macroalgae turns organic matter into CO_2 (equation (4)) returning much of the POC to the atmosphere (Fig. 1). However, macroalgae can remain in the water column for weeks to months, and many species have structural components that are not easily broken down or grazed (Trevathan-Tackett et al., 2015). For example, a portion of kelp detritus (~15%) largely escapes from further decomposition under anoxic conditions in deep shelf habitats (Watanabe et al., 2020; Pedersen et al., 2021). Some species of macroalgae have refractory components that escape mineralization in sediments (7–68%) (Pedersen et al., 2005). Although the ultimate fate of macroalgal detritus is not well understood, there is strong evidence that some of this material ends up in the deep ocean. Macroalgal detritus have been observed in the deep sea below 1000 m (Krause-Jensen and Duarte, 2016), and eDNA signals from kelp are found throughout the global ocean and increase in relative abundance from 3,000 to 4,000 m (Ortega et al., 2019).

Another source of outwelling from kelp forests is DOC, which can make up 12–42% of the total kelp carbon production (Wada et al., 2008; Rassweiler et al., 2018; Watanabe et al., 2020). DOC is produced as exudates from living tissue, as well as from detritus (POC) as it is broken down. Less is known about the fate of kelp-derived DOC compared to POC, which is composed of a range of compounds (e.g., fucoidan, alginates and laminarin) that are unique to macroalgae, and more common metabolites. Much of the macroalgae-derived DOC is labile, and rapidly consumed by bacteria to produce DIC in the process (Wada et al., 2008). But some kelp DOC can be recalcitrant and have long turn over times, with a portion lasting months to 100s–1000s of years (Wada et al., 2008; Watanabe et al., 2020).

Kelp forests typify the challenges associated with accounting for outwelled carbon. The relatively large amount of kelp-carbon detrital export, and lack of direct burial in local sediments may have prevented the initial inclusion of kelp as 'blue carbon' habitats. There are challenges with incorporating these processes, such as the spatial disjunction between the source of production and sink for kelp carbon. Yet, the available estimates suggest kelps and other macroalgae can transport more POC and DOC to the ocean (Krause-Jensen and Duarte, 2016) than all other blue carbon ecosystems combined (see Fig. 3). If we do not consider kelp carbon outwelling and storage in the ocean, we would not account for sequestration by a habitat that cover about 25% of the world's coasts, that are declining globally, that hold some of the highest rates of per area primary productivity on Earth, and are amenable to management actions to enhance carbon sequestration (Krause-Jensen et al., 2018; Raven, 2018; Wernberg et al., 2019).

4. The way forward and research needs

The flurry of recent outwelling work has built momentum and added value to blue carbon science and management. Carbon outwelling estimates remain spatially and temporally limited, but they have now been put in perspective (Fig. 3) in a coastal carbon budget context. A series of research questions remain. Here, we briefly discuss 10 major research needs or questions related to blue carbon outwelling:

1. *Are different methods used to estimate physical transport and carbon outwelling comparable?* Quantifying outwelling requires an understanding of physical transport. Methods of estimating transport include radium isotope transects across the shelf (Sippo et al., 2019), tidally-integrated water flows in and out of creeks (Maher et al., 2013; Santos et al., 2019), dye tracers (Rypina et al., 2016) and physical models (Rühs et al., 2018). Each approach has advantages and disadvantages, represents different spatial and temporal scales (Tamborski et al., 2021), and may capture different transport mechanisms such as tides, waves, currents and eddy diffusivity. How (or even if) results obtained from different approaches can be compared remains a challenge.
2. *What are the natural drivers of carbon outwelling?* Rainfall, temperature, tidal range and hydrodynamic energy, geomorphology, and sediment types influence sediment carbon stocks (Kelleway et al., 2016a; Sanders et al., 2016) and POC exports from mangroves (Adame and Lovelock, 2011), but it is unclear if they drive DIC and DOC outwelling. Also unclear is the relative importance of physical drivers of water exchange versus the ecosystem's biogeochemical characteristics and sediment carbon stocks in mediating the quantity and form of carbon outwelling. An attempt to correlate DOC outwelling to potential environmental drivers revealed no patterns (Sippo et al., 2017), perhaps due to the small number of sites studied (n = 6) over short time scales (one diel cycle).
3. *How will climate change and sea-level rise modify carbon outwelling?* Marine heat waves have impacted seagrass (Arias-Ortiz et al., 2018), mangrove (Sippo et al., 2020), and kelp forest (Wernberg et al., 2019) carbon stocks, burial and/or biomass. Sea-level rise is also having a major impact on blue carbon habitat composition, extent, and sediment carbon (Lovelock et al., 2015; Kirwan et al., 2016; Rogers et al., 2019), but there are no empirical data linking climate change and sea level rise to carbon outwelling. Sea level rise will also impact flooding frequency and thus the magnitude of porewater exchange that may ultimately drive lateral carbon exports (Tamborski et al., 2021).
4. *How will anthropogenic disturbance of blue carbon habitats modify outwelling?* A number of case studies have revealed how carbon stocks or burial respond to eutrophication (Sanders et al., 2014; Jiang et al., 2018; Liu et al., 2020), habitat destruction (Macreadie et al., 2015), aquaculture development (Ahmed and Glaser, 2016), and drainage of coastal wetlands (Brown et al., 2019). However, there are only local-scale, initial datasets contrasting outwelling in disturbed versus undisturbed habitats (Davis et al., 2020; Wadnerkar et al., 2020). With increasing pressures on blue carbon habitats, it is essential to assess how habitat modification will affect carbon outwelling.
5. *Geographical bias against the tropics and high latitude regions.* We lack data from the tropics where high rates of primary productivity are often observed. For example, ~30% of the world's mangroves occur in macrotidal regions near the equator between 5° N and 5° S (Giri et al., 2011), the largest seagrass meadows are found in the tropics (Coles et al., 2015), and the largest macroalgae habitats are found near polar areas (Ortega et al., 2019). However, outwelling estimates are quite rare for these areas. With ongoing kelp expansion towards the poles with retreating sea ice (Wernberg et al., 2019) and mangrove expansion away from the tropics (Kelleway et al., 2016b), shifts in carbon outwelling are also expected.
6. *Long term datasets are needed.* The few available outwelling estimates are often based on short term datasets. For example, a continental-scale assessment of DOC and DIC outwelling in Australia relied on 24 hour time series observations at six sites to estimate outwelling (Sippo et al., 2016). For saltmarsh habitats, discrete sampling over individual tidal cycles is unlikely to capture the "true" carbon flux (Chu et al., 2018). It is unlikely that one day of observations is sufficiently representative for a full annual cycle and resolve natural and anthropogenic drivers.
7. *How refractory is the DOC and POC exported from blue carbon habitats?* Organic carbon will be consumed and modified as it travels away from blue carbon habitats. For example, photodegratation destroys aromatic molecules (Dittmar et al., 2006) and leads to more aliphatic DOC signatures away from mangroves (Mori et al., 2019). Only the refractory components of DOC and POM can escape short-term mineralization (Fig. 1). Therefore, quantifying DOC and POC reactivity is essential for constraining long-term blue carbon outwelling.
8. *How do burrows, bioturbation and macrofauna modify carbon outwelling?* Crabs and shrimps modify the sediment structure (Berkenbusch et al., 2007; Kristensen, 2008), enhance advective porewater exchange (Xin et al., 2009, 2012), and seem to ultimately reduce the potential for blue carbon storage via burial (Thomson et al., 2019; Xiao et al., 2021). However, the extent to which these processes also enhance alkalinity production and carbon outwelling should also be better constrained.
9. *What is the contribution of alkalinity (bicarbonate) to carbon budgets?* Processes that produce aqueous CO_2 or HCO_3^- (i.e., alkalinity) will appear "similar" in a total carbon or DIC budget but will have very different impacts on blue carbon sequestration (Fig. 1). While most CO_2 will return to the atmosphere on short-time scales, alkalinity will likely remain in the ocean. The differences between DIC and alkalinity budgets need to be better quantified in future blue carbon studies.
10. *How should outwelling be managed to maximize blue carbon?* Blue carbon management interventions include restoration of water flows, replanting of original species, pollution prevention, reinstating ecological functions, and the creation/enforcement of laws that protect original habitats (Macreadie et al., 2017a; Kelleway et al., 2020). Some of these interventions are known to increase sediment carbon sequestration over decadal time scales (Burden et al., 2019), but there is no related data on how outwelling will be modified following intervention. Documenting how management modifies outwelling should help to strengthen arguments to preserve and restore coastal vegetated habitats.

Addressing these major questions is essential to refining existing global upscaling exercises (Fig. 3) that are often based on averages taken from datasets too limited to allow for relevant spatial upscaling, and contain large and poorly constrained uncertainties. In spite of increasing attention to blue carbon ecosystems, we lack integrated ecosystem scale budgets that account for all the pathways of the coastal carbon cycle and we lack insight about the real carbon connectivity across ecosystems (Najjar et al., 2018; Webb et al., 2019). We now have the tools and expertise to estimate all terms of the coastal carbon budget, including outwelling and carbon storage beyond ecosystem boundaries (Luisetti et al., 2020).

5. Summary, conclusions and outlook

The blue carbon concept has helped to develop coastal carbon sequestration science. It has long been recognized that mangroves and saltmarshes release carbon and nutrients via tidal exchange, though the effects of such export on coastal ecosystems and its contribution to carbon budgets remain poorly resolved. The outwelling hypothesis is not new, but its original construction had an ecological connotation. With growing interest in resolving carbon budgets, the outwelling hypothesis can now be reframed in a climate change mitigation context.

A small awareness of outwelling in the blue carbon scientific and management communities may be related to traditional disciplinary silos. Many of us in the blue carbon community have an ecological/conservation background that may naturally overlook the complex geochemical mechanisms that result in the type of outwelling discussed

here (see section 2) as well as physical mechanisms driving exchange. One can see and feel carbon in muds or vegetation, but outwelled dissolved carbon is essentially invisible. After decades of progress, sampling sediment cores for carbon stock assessment has become relatively straightforward, widespread and comparatively cheap. Estimating outwelling often requires more sophisticated and expensive analytical approaches and expertise that are still being developed and are not as widely available.

The currently available local-scale, short-term estimates as well as global summaries (Fig. 3) all suggest that outwelling followed by ocean storage can be a quantitatively relevant blue carbon sequestration mechanism, and may exceed local burial in blue carbon habitats. If this suggestion proves true as more compelling datasets emerge, the estimated carbon sequestration capacity of blue carbon ecosystems will have been greatly underestimated and will therefore need to be revised. As a consequence, carbon outwelling should be considered as a blue carbon term in future earth system climate models. The renaissance of the outwelling hypothesis could thus create new, stronger arguments for preserving and/or rehabilitating highly threatened blue carbon habitats to maximize global carbon sequestration. The development of an interdisciplinary blue carbon scientific community as well as new analytical tools open up opportunities to push the outwelling hypothesis forward.

Over the past decade we have mainly been looking down into sediments to develop the foundations of blue carbon. To further strengthen the argument for preservation and give blue carbon ecosystems their due credit, we should also look out to sea.

Authorship statement

Isaac R. Santos prepared the original draft. All authors contributed to conceptualization, investigation, writing, reviewing and editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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