



REVIEW

A review of existing and potential blue carbon contributions to climate change mitigation in the Anthropocene

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Abstract

1. The atmospheric concentration of CO₂ is steadily increasing and causing climate change. To achieve the Paris 1.5 or 2°C target, negative emission technologies must be deployed in addition to reducing carbon emissions. The ocean is a large carbon sink but the potential of marine primary producers to contribute to carbon neutrality remains unclear.
2. Here we review the alterations to carbon capture and sequestration of marine primary producers (including traditional 'blue carbon' plants, microalgae and macroalgae) in the Anthropocene, and, for the first time, assess and compare the potential of various marine primary producers to carbon neutrality and climate change mitigation via biogeoeengineering approaches.
3. The contributions of marine primary producers to carbon sequestration have been decreasing in the Anthropocene due to the decrease in biomass driven by direct anthropogenic activities and climate change. The potential of blue carbon plants (mangroves, saltmarshes and seagrasses) is limited by the available areas for their revegetation. Microalgae appear to have a large potential due to their ubiquity but how to enhance their carbon sequestration efficiency is very complex and uncertain. On the other hand, macroalgae can play an essential role in mitigating climate change through extensive offshore cultivation due to higher carbon sequestration capacity and substantial available areas. This approach seems both technically and economically feasible due to the development of offshore aquaculture and a well-established market for macroalgal products.
4. *Synthesis and applications.* This paper provides new insights and suggests promising directions for utilizing marine primary producers to achieve the Paris temperature target. We propose that macroalgae cultivation can play an essential role in attaining carbon neutrality and climate change mitigation, although its ecological impacts need to be assessed further.

KEYWORDS

blue carbon, carbon fixation, carbon neutrality, carbon sequestration, climate change, macroalgae, primary producer, seaweed cultivation

1 | INTRODUCTION

Given the contrasting futures for society and ocean based on different anthropogenic CO₂ emissions scenarios, in terms of changes in ocean physics and chemistry, impacts on biodiversity, ecosystem services and livelihoods (Gattuso et al., 2015; IPCC, 2018), the need to reduce emissions of CO₂ and other greenhouse gases and thereby help mitigate climate change is of considerable urgency. To achieve the Paris 1.5 or 2°C targets, many countries promised carbon neutrality by 2050. To achieve these targets, negative carbon emission technologies (NETs) must be employed in addition to efforts based on reducing carbon emissions. To limit warming to 2°C above preindustrial conditions at a global scale, a long-term carbon removal of 4 Gt CO₂/year is required in Representative Concentration Pathway (RCP) 2.6 (Sanderson et al., 2016). A variety of NETs have been proposed, among them bioenergy with carbon capture and storage (BECCS) and afforestation (AR) being the most widely modelled technologies (Bastin et al., 2019; Fuhrman et al., 2020). These two technologies are both land-area intensive and thus employment of these NETs would compete for productive agriculturally and ecologically important land and consume water resources, raising concerns about the viability of these approaches (Fuss et al., 2014; Smith et al., 2016). Recent work has focused on developing direct air capture (DAC) technology, which requires much less land, only proximity to a geological reservoir for storage (Realmonte et al., 2019). However, CO₂ concentrations in ambient air are very low and to deploy DAC is deemed to be energy intensive (Fuhrman et al., 2020).

In addition to carbon capture and storage on land, ocean negative carbon emission, an emerging field, is attracting attention. In fact, the ocean, as the largest carbon reservoir on the planet, has absorbed about one-third of CO₂ emitted to date (Gattuso et al., 2015). Marine primary producers contribute about half of global CO₂ uptake and O₂ production (Falkowski et al., 1998). Due to their large surface area (70.8% of the Earth's surface), the oceans have, in theory, the potential to contribute more to carbon capture and sequestration. Human activity has been impacting the global environment in a geologically profound way through effects in addition to the direct effect of rising CO₂ emissions. The magnitude, variety and longevity of human-induced changes, including land surface transformation and atmosphere composition changes, indicate that a new epoch, the Anthropocene, has begun (Lewis & Maslin, 2015; Mathews, 2020). The global and local environmental changes induced by human activity are affecting marine primary producers, and how climate change impacts carbon accumulation in blue carbon (BC) ecosystems is one of the key fundamental questions in BC science (Macreadie et al., 2019). To date, our understanding on this aspect and the potential of marine primary producers to contribute to carbon neutrality is still fragmentary, particularly for microalgae and macroalgae. The BC concept was introduced as a metaphor that aimed at highlighting the role of coastal ecosystems in organic carbon sequestration. Therefore, it traditionally refers to vegetated coastal ecosystems, including mangrove forests, tidal marshes and seagrass meadows (Macreadie et al., 2019). Microalgae and macroalgae, instead, have

been long neglected in terms of BC because they lack root systems, grow on rocky substrates or drift in the euphotic zone and do not accumulate carbon-rich sediments. However, more recently, there is an increasing number of studies demonstrating the potential contributions of microalgae and macroalgae to BC (Hu et al., 2021; Krause-Jensen & Duarte, 2016; Kulk et al., 2020; Raven, 2018). In this paper, we review the altering marine primary production in the context of Anthropocene (Figure 1), and evaluate and compare the potential of various primary producers for helping to achieve carbon neutrality and climate change mitigation. Therefore, the present study focuses on marine nature-based solutions in terms of NETs. Marine primary producers are, for this purpose, divided into three categories: blue carbon plants (mangroves, salt marsh species and seagrasses), macroalgae and microalgae.

2 | MATERIALS AND METHODS

To calculate the parameters presented in Table 1, the relevant keywords 'mangroves, salt marshes, macroalgae, microalgae, global area, net primary productivity, CO₂ sequestration' were searched through the ISI Web of Science and Google Scholar in July 2021. Recent data published after 2010 were collected and used since area and productivity of plants change with decade. For data with limited availability, such as net primary productivity (NPP) of seagrasses and global area and NPP of wild macroalgae, data collection was extended back to 1980. Total NPP and CO₂ sequestration for mangroves, salt marshes, seagrasses and wild macroalgae were obtained by the multiplication of area and NPP/CO₂ sequestration density and subjected to error propagation analysis. Data were expressed as means ± SE.

To assess the carbon pathways for cultivated macroalgae (Figure 2), the relevant keywords 'macroalgae, carbon pathway, CO₂ sequestration, particle organic carbon, dissolved organic carbon, refractory DOC, remineralization, buried carbon' were searched through the ISI Web of Science and Google Scholar in July 2021. Data used were all published after 2010 except for Wada et al. (2008). Data were expressed as means and ranges.

3 | COASTAL AND MARINE CARBON SEQUESTRATION (RESULTS SECTION)

3.1 | Mangroves

Mangrove forests inhabit tropical, subtropical and some temperate intertidal zones. More specifically, they are confined to regions between latitudes of about 35° North and about 40° South. They provide essential ecosystem services, such as fisheries production, coastal protection and climate mitigation (Barbier et al., 2011; Howard et al., 2017). Mangroves have a high CO₂ capture ($1,355 \pm 179 \text{ gCm}^{-2} \text{ year}^{-1}$) and sequestration capacity ($168 \pm 23 \text{ gCm}^{-2} \text{ year}^{-1}$), contributing $195 \pm 26 \text{ TgC/year}$ carbon capture and $24.2 \pm 3.4 \text{ TgC/year}$ carbon sequestration globally (Table 1).

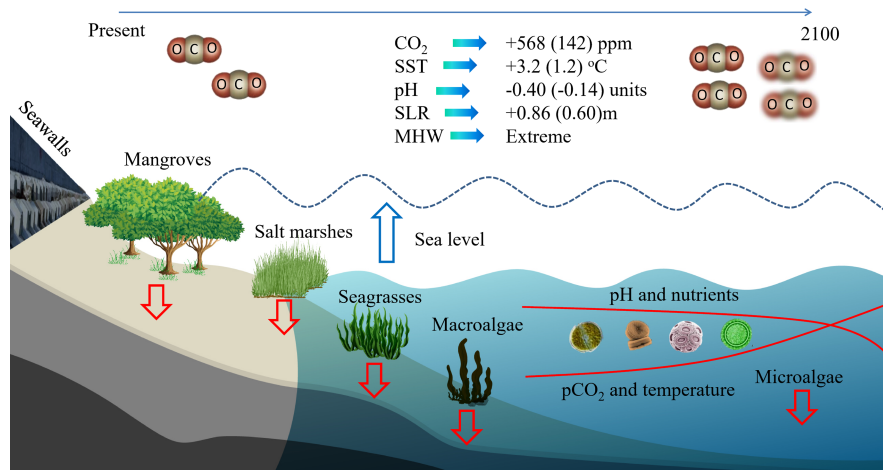


FIGURE 1 Climate changes by the end of this century according to stringent (RCP2.6) and high business-as-usual (RCP8.5) CO₂ emissions scenarios and the changes of marine primary production and carbon sequestration. The predicted changes of atmospheric CO₂, surface sea temperature (SST), surface sea pH and sea-level rise (SLR) relative to preindustrial (1870 to 1899) are based on Gattuso et al. (2015) with the values in and out of brackets representing RCP2.6 and PCR8.5, respectively. The intensity of marine heatwaves (MHW) would shift from moderate to extreme under the RCP8.5 scenario according to Oliver et al. (2019). The red arrows represent a predicted decreasing trend for marine primary production and carbon sequestration in future scenarios

By the 1980s, however, large-scale land use changes had led to the loss of mangroves and as much as 35% of the world's mangrove area was lost in the 1980s and 1990s, with deforestation rates 1%–8% per year (Friess et al., 2019; Valiela et al., 2001). The deforestation was primarily caused by anthropogenic activities, including conversion to aquaculture and agriculture, urban development and over-extraction (Friess et al., 2019). Although the loss rates (0.26%–0.66% per year) have been reduced in the early part of the 21st century due to national and international conservation policy instruments, mangroves are predicted to show further loss in future scenarios because they are susceptible to extreme climatic events and because river damming will substantially reduce fluvial sediment sources to the coast and restrict the capacity of mangroves to adjust to sea-level rise (Friess et al., 2019).

To enhance carbon sequestration by mangroves, rehabilitation seems a necessary step. However, rehabilitation is not a quick solution, and restoring area and ecosystem service provision is challenging and expensive to undertake at scale. In addition, the limited spatial extent of coastal habitats hinders their potential at the global scale. It has been reported that the global area of unvegetated tidal flats is 127,921 km² (Murray et al., 2019). The total carbon sequestration would be 21.50 Tg C/year if all these areas are vegetated by mangroves, which would only account for 1.97% of the CO₂ removal required to achieve limiting of warming to 2°C by the end of this century (Table 1).

3.2 | Salt marshes

Salt marshes are populated by salt-tolerant herbaceous plants or shrubs that usually inhabit the upper intertidal area of sedimentary coasts in all continents except Antarctica. They are commonly found

in temperate coastlines, but can also occur at low latitudes as a narrow fringe landward of mangroves and as more extensive stands on hypersaline flats where mangroves are excluded (Alongi, 2020). They form critical habitats for numerous aquatic and terrestrial organisms that use them as a refuge from predators and as a location to feed, shelter and spawn (Deegan et al., 2012). In addition, they deliver important ecological and economic services, such as nutrient removal, storm protection and carbon sequestration (Gu et al., 2018; Möller et al., 2014). Reports of the extent of the global area of saltmarsh range from 2.2 to 40 million hectares (Pendleton et al., 2012). A recent estimate shows the total area of saltmarsh is 5,495,089 hectares based on collation of data on 350,985 individual saltmarshes in 99 countries worldwide (Mcowen et al., 2017). Salt marshes have the highest carbon capture density ($1,226 \pm 207 \text{ g C m}^{-2} \text{ year}^{-1}$) and carbon sequestration intensity ($224 \pm 34 \text{ C m}^{-2} \text{ year}^{-1}$) among blue carbon plants, sequestering 40.6 Tg C per annum globally (Table 1).

However, a recent study shows that global wetlands have declined in area by 87% over the last 300 years and by 54% since 1900 (IPBES, 2018). This loss of wetlands was due mainly to their conversion to agriculture, urban and industrial land. In addition, a range of other human activities are also damaging wetlands, including waste tipping, pollution and eutrophication (Deegan et al., 2012; Gu et al., 2018). Furthermore, the risks for climate change-driven losses are likely to increase in the future. Due to their limited tolerance to inundation, salt marshes must gain elevation at a rate equal to or exceeding relative sea-level rise to resist drowning (Redfield, 1965). It is predicted that 60%–91% of salt marshes will be gaining elevation at a rate insufficient to keep pace with sea-level rise by 2100 (Crosby et al., 2016). On the other hand, Kirwan et al. (2016) predicted that rates of marsh migration could surpass rates of edge erosion in the scenario of accelerated sea-level rise if they are unconstrained by barriers. Wang et al. (2021) also concluded that global blue

TABLE 1 Net primary production (NPP) and carbon sequestration of marine primary producers and the potential to mitigate climate change

Type	Global area (million km ²)	NPP (g C m ⁻² year ⁻¹)	CO ₂ sequestration density (g C m ⁻² year ⁻¹)	Total NPP (Tg C/year)	Total CO ₂ sequestration (Tg C/year)	Required area to sequester 4 Gt CO ₂ /year (million km ²) ^a	Available area (million km ²)	References
Mangroves	0.14 ± 0.004	1,355 ± 179	168 ± 23	195 ± 26	24.2 ± 3.4	6.49 ± 0.90	0.128 ± 0.002	[1–15]
Salt marshes	0.18 ± 0.06	1,226 ± 207	224 ± 34	222 ± 84	40.6 ± 15.0	4.87 ± 0.73	0.128 ± 0.002	[1, 6, 10, 15–19]
Seagrasses	0.22 ± 0.04	461 ± 111	117 ± 19	102 ± 30	25.8 ± 6.0	9.35 ± 1.51	4.10 ± 0.67	[1, 5, 11, 17, 20–27]
Wild macroalgae	3.21 ± 0.74	569 ± 114	62 ± 21	1,826 ± 561	199 ± 82	17.57 ± 6.01	2.50 ± 0.58	[11, 16, 24, 27–33]
Cultured macroalgae	1.49 ± 0.30 × 10 ⁻³	1,425 ± 251	238 ± 42	2.13 ± 0.20	0.36 ± 0.03	4.59 ± 0.81	48.00 ± 9.59	[11, 34–39]
Microalgae	361.41 ± 0.38	128 ± 13	2.30 ± 0.24	46,275 ± 4759	833 ± 86	473 ± 49	0	[40–46]

Note: The recent data published after 2010 were collected and used (except for the data with limited availability) since area and productivity of plants change with decade. Data were expressed as means ± SE.

^aTo sequester 4 Gt CO₂/year that is required to limit warming to 2°C above preindustrial conditions in Representative Concentration Pathway (RCP) 2.6 (Sanderson et al., 2016). Data are derived from [1] Gao et al. (2016); [2] Giri et al. (2011); [3] Bunting et al. (2018); [4] Hamilton and Casey (2016); [5] Breithaupt et al. (2012); [6] Alongi (2012); [7] Duarte and Cebrián (1996); [8] Twilley et al. (2017); [9] Alongi (2014); [10] Alongi (2020); [11] Duarte (2017); [12] Mcleod et al. (2011); [13] Sasmito et al. (2020); [14] Rosentretter et al. (2018); [15] Murray et al. (2019); [16] Cai (2011); [17] Duarte et al. (2013); [18] Byrd et al. (2018); [19] Alongi (2018); [20] McKenzie et al. (2020); [21] Waycott et al. (2009); [22] Duffy et al. (2019); [23] Duarte et al. (2010); [24] Smith (1981); [25] Gattuso et al. (1998); [26] Kennedy et al. (2010); [27] Gattuso et al. (2006); [28] Krause-Jensen and Duarte (2016); [29] Duarte et al. (2005); [30] Cebrian and Duarte (1994); [31] Charpy-Roubaud and Sournia (1990); [32] Chung et al. (2011); [33] Hu et al. (2021); [34] FAO (2020); [35] Mashoreng et al. (2019); [36] CFSY 2015; [37] Buschmann et al., 2017; [38] CFSY 2020; [39] Laurens et al. (2020); [40] Eakins and Sharman (2010); [41] Costello et al. (2010); [42] Statista (2010); [43] Kulk et al. (2020); [44] Raven (2018); [45] Buitenhuis et al. (2013); [46] Gregg and Rousseaux (2019).

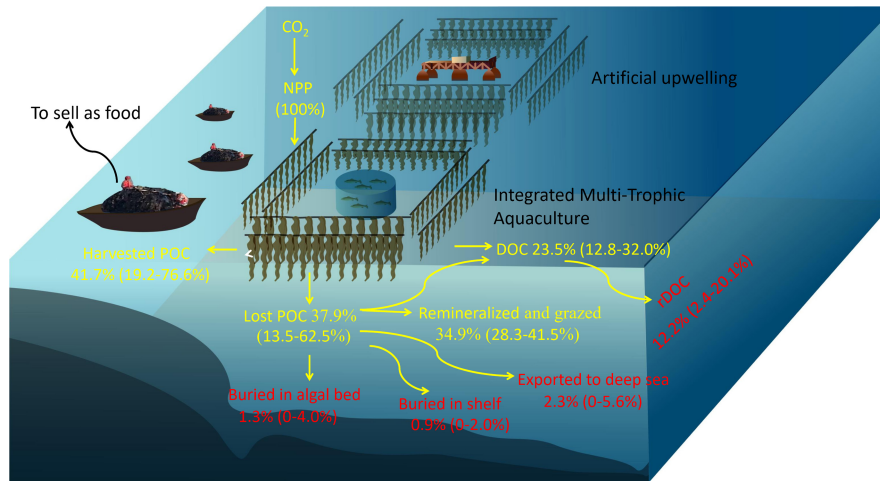


FIGURE 2 Pathways for carbon sequestration of cultivated macroalgae in open oceans where nutrients are supplied through artificial upwelling or integrated multi-trophic aquaculture. The numbers represent the corresponding proportions compared to NPP (net primary production) and sequestered carbon is marked in red. The proportions of harvested and lost POC are based on literature (Chen et al., 2020; Krumhansl & Scheibling, 2012; Zhang et al., 2012, 2017), the sequestered and remineralized POC and the proportion of DOC are based on literature (Krause-Jensen & Duarte, 2016; Zhang et al., 2017) and the transformation from DOC to rDOC (refractory DOC) is literature (Krause-Jensen & Duarte, 2016; Wada et al., 2008; Watanabe et al., 2020; Zhang et al., 2017). The means and ranges were shown. As the estimates were derived independently, their total is not necessarily the theoretical sum

carbon accumulation in tidal wetlands would increase in the changing climate context, which is mainly driven by sea-level rise in tidal marshes and global warming. However, these modellings were based on the assumption that adjacent uplands are available. The fact is that human destruction and modification of shorelines worldwide, such as through seawalls and revetments, have largely limited the area available for upland migration of salt marshes as sea level rises (Torio & Chmura, 2013). Therefore, the suitable area for salt marshes will decline in future scenarios, which threatens the carbon sequestration capacity of salt marshes. Even if all unvegetated areas in tidal zones were planted by saltmarsh plants, they would only account for 2.63% the required CO₂ removal amount to achieve a limitation of warming to 2°C by the end of this century (Table 1).

3.3 | Seagrasses

Seagrasses, marine flowering plants forming underwater meadows that include the widely distributed genera *Zostera*, *Thalassia* and *Posidonia*, represent some of the most productive ecosystems on earth.³² They are distributed over most of the Earth, from the tropics to the subarctic regions, and are absent only in polar regions. They are usually confined to areas shallower than 20 m. Most seagrasses are found in subtidal zones and only some species, in the genera *Zostera*, *Phyllospadix* and *Halophila*, can survive in intertidal zones (Hemminga & Duarte, 2000). They play an important role in supporting fisheries production, coastal protection, sediment stabilization and climate change mitigation (Ondiviela et al., 2014; Orth et al., 2006; Unsworth et al., 2019). Seagrass has a total CO₂ net primary production of 102 ± 30 Tg C/year, of which 25.8 ± 6.0 Tg C is sequestered (Table 1). However, seagrasses and the services they

provide are being threatened by eutrophication and habitat loss due to dredging, anchoring and coastal infrastructure as well as by the impacts of climate change and extreme events such as storms and marine heat waves (Arias-Ortiz et al., 2018; Marbà & Duarte, 2010; Orth et al., 2006; Strydom et al., 2020). It has been found that approximately 30% of seagrass beds worldwide have disappeared, with a loss rate of 110 km²/year since 1980. Furthermore, the rates of decline have accelerated from 0.9% year⁻¹ before 1940 to 7% year⁻¹ since 1990 (Waycott et al., 2009). Apart from the reduced carbon sequestration associated with the decline in seagrass beds, seagrass losses can lead to CO₂ emissions from soil carbon stocks that are exposed to hydrodynamic forces and erosion and consequently suffer more rapid remineralization in bare areas (Salinas et al., 2020). Seagrass has been predicted to suffer a further decline in future due to cumulative stressors (Adams et al., 2020). On the other hand, loss rates of seagrass in Europe have slowed down since the 1980s and the net rate of change in seagrass area experienced a reversal in the 2000s, with density metrics improved or remaining stable in most sites (de los Santos et al., 2019).

In spite of the global loss of seagrass, the causes of seagrass loss are manageable to a large extent and threats can be reduced with effective management. In fact, seagrass restoration is increasingly successful, although it is expensive and many large projects have failed historically (success rate: 38%; Bayraktarov et al., 2015; Cullen-Unsworth & Unsworth, 2016; Duarte et al., 2020; Unsworth et al., 2018; van Katwijk et al., 2016). On the other hand, seagrasses can only grow in shallow waters, which constrains the upper limit of their carbon sequestration. Thus although some seagrass species occur as deep as 90 m (Duarte, 1991), the seagrass meadows that can contribute significantly to carbon capture and sequestration are mostly confined to depths of 20 m or less, even under very

transparent waters (Tanaka & Kayanne, 2007). The global total area suitable for seagrass growth was estimated at 4.32 million km² and there are 4.10±0.04 million km² available for replanting since the present distribution area is only 0.22±0.04 million km² (Table 1). This available area is 43.8% of the required space for the CO₂ removal by seagrasses to achieve the limitation of warming to 2°C by the end of this century (Table 1). In addition, the most cost efficient and feasible conservation strategy is to preserve wild seagrass meadows rather than having to rebuild or recreate them (Unsworth et al., 2018).

3.4 | Macroalgae

Macroalgae occur along the coasts of all continents, from the intertidal zone down to depths receiving about 0.01%–0.5% of the light incident in the surface, dominate rocky shores, and form the most extensive vegetated coastal habitats in the world (Gattuso et al., 2006; Krause-Jensen et al., 2018). Macroalgae play an essential role in sustaining coastal ecosystems, serving as refugia, as foraging and nursery habitat for marine animals and supplying food, medicine and biofuels for humans (Gao et al., 2018, 2020). In addition to the anchored forms in the coasts, some macroalgae can drift in the surface of open oceans, such as pelagic *Sargassum* in the Atlantic Ocean, Gulf of Mexico and Caribbean Sea. Macroalgae in the genera *Ulva* and *Sargassum* are also the causative species that form macroalgal blooms drifting in the surface of oceans in many areas of the world (Smetacek & Zingone, 2013). Although defining macroalgae in terms of blue carbon is still debatable (Macreadie et al., 2019), an increasing number of studies have shown their important contribution to oceanic carbon sequestration (Krause-Jensen et al., 2018; Krause-Jensen & Duarte, 2016; Ortega et al., 2019; Trevathan-Tackett et al., 2015). They cover an area of about 3.21±0.74 million km² and support a global net primary production of about 1,826±561 Tg C/year, of which 199±82 Tg C is sequestered (Krause-Jensen & Duarte, 2016).

Macroalgal communities, particularly laminarian kelp forests, are declining worldwide. Over a time-scale of 20–50 years of monitoring, declines (61%) of kelp forests are observed much more commonly than increases (5%; Wernberg et al., 2019). This decline is caused by the combination of multiple stressors such as ocean warming, marine heatwaves, pollution by heavy metals and organic chemicals and harvesting for food and the phycocolloid industry. Furthermore, losses of canopy-forming macroalgae are predicted to further increase with rising global temperatures and more frequent extreme weather events (Oliver et al., 2018). On the other hand, there is a trend for mat-forming macroalgae to replace canopy-forming macroalgae in many regions over the past two decades (Benedetti-Cecchi et al., 2001; Filbee-Dexter & Wernberg, 2018). There are multiple drivers causing these transitions, among which warming and eutrophication may play a critical role (Filbee-Dexter & Wernberg, 2018; Strain et al., 2014). Furthermore, the return to the dominance by canopy-forming macroalgae is difficult to achieve as

community states dominated by mat-forming macroalgae are often maintained by complicated and interlaced feedbacks, suppressing the recovery canopy-forming macroalgae (Benedetti-Cecchi et al., 2015; Filbee-Dexter & Wernberg, 2018; Rindi et al., 2017). In addition, it is predicted that green and golden macroalgal tides are also showing a rising trend in the climate change scenarios (Gao, Clare, et al., 2017; Smetacek & Zingone, 2013; Xu et al., 2017).

Despite the increasing occurrence of mat-forming and drifting macroalgae, carbon sequestration by wild macroalgae may decline in future scenarios due to the significant loss of kelp forests (Wernberg et al., 2019). In addition, the modification of natural rocky coasts and coastal urbanization (e.g. seawalls, breakwaters, artificial islands) are negatively affecting the attachment and development of macroalgae (Lai et al., 2018). Therefore, the most effective approach to enhance biomass and carbon sequestration of macroalgae is to culture them. Compared to 'conventional' blue carbon plants, wild macroalgae have much lower CO₂ sequestration density (Table 1); however, cultivated macroalgae have comparable values (Table 1). Gattuso et al. (2006) calculated the potential coastal area suitable for macroalgae as being 5.71 million km². Assuming the current distribution area of macroalgae to be 3.21 million km² (Krause-Jensen & Duarte, 2016), the remaining area (2.50 million km²) seems inadequate for macroalgae to sequester 4 Gt CO₂, which would require an area of 4.59±0.81 million km² (Table 1). However, the estimate of Gattuso et al. (2006) is based on the light reaching the seafloor, while seaweed cultivation is usually carried out in surface seawater via using bamboo poles or floating buoys, thus overcoming the issue of light limitation. It has been estimated that the area suitable for macroalgae farming is approximately 48 million km² (Froehlich et al., 2019). Therefore, there is enough space for a large expansion of macroalgae cultivation and in fact offshore culture has been successfully conducted in many countries in the world thanks to the development of related techniques, such as improvements in both tensile strength and weight of materials that can be used at sea and development of flexible and submersible offshore aquaculture structures (Fernand et al., 2017; Golberg et al., 2020). For instance, an offshore cultivation (106 days) of *Saccharina latissima* off the Atlantic coastline of northern Spain had a yield of 45.6 t fresh weight/ha (Peteiro et al., 2014). One challenge for offshore cultivation is the low nutrient availability. This could be solved by artificial upwelling that transports deep nutrient-rich water to surface. Recently, a solar-powered and air-lifted artificial upwelling device was deployed in an oligotrophic area of the Yellow Sea in China, which more than doubled the biomass and carbon removal of cultivated kelp (Fan et al., 2020). One concern regarding artificial upwelling is that the cool CO₂-rich water from depth may be released to the atmosphere when it is transported upwards. This may be managed through pumping seawater with minimal temperature difference from the surface seawater at a very slow speed at which additional CO₂ can be fixed by macroalgal photosynthesis. Another solution to supply nutrients is integrated multi-trophic aquaculture (IMTA) in which species from two or more trophic levels grow in one farm and where the waste of one feeds another (Ashkenazi et al., 2019). This system can significantly increase

system sustainability and productivity which has been conducted in a project scale worldwide (China, Europe, USA and South Korea; Buck et al., 2017; García-Poza et al., 2020). The selection of suitable seaweed species that can grow well in different environments (nutrient availability, temperature, currents, etc.) is also an essential prerequisite for globally expanded seaweed cultivation.

3.5 | Microalgae

Microalgae are ubiquitous in the oceans, from coastal zones to open oceans, from equatorial to polar regions and from the surface waters to the deep ocean (more than 200 m; Pierella Karlusich et al., 2020; Zechman et al., 2010). Although the carbon capture and sequestration capacities of microalgae on an areal basis are very low, particularly in oligotrophic oceans, microalgae contribute the most carbon capture and sequestration globally due to their wide coverage (Table 1). However, the ratio of carbon sequestration to carbon capture for microalgae (1.2%–2.4%) is the lowest compared to blue carbon plants and macroalgae, indicating a high carbon turnover rate, which may be attributed to the high grazing rate by herbivores (Duarte & Cebrián, 1996). Some studies have shown that ocean acidification or warming could stimulate primary production (Gao, Jin, et al., 2017; Schippers et al., 2004), but the combination of these factors or interactions with other environmental drivers may reduce ocean primary productivity (Gao et al., 2012; Gao, Jin, et al., 2017). In fact, the primary productivity of phytoplankton shows a decreasing trend in recent decades, with a rate of -0.8 PgC/year ($-2.1\% \text{ decade}^{-1}$; Gregg & Rousseaux, 2019; Kulk et al., 2020). The main reason for this is likely to be the reduced nutrient availability caused by ocean warming and consequently enhanced stratification. Furthermore, ocean warming could also stimulate fixed carbon remineralization by heterotrophic micro-organisms and thus reduce the strength of the ocean carbon sink (Cavan et al., 2019).

Given the large coverage but low biomass density, some geoengineering solutions have been proposed to stimulate primary productivity of phytoplankton. One of the most well known is ocean iron fertilization, which considers that low iron availability limits primary productivity in high-nutrient, low-chlorophyll regions. Therefore, 13 ocean iron fertilization experiments have been performed since 1990 in high-nutrient, low-chlorophyll regions. These field experiments showed that iron fertilization stimulated primary production but did not significantly affect carbon export flux (Boyd et al., 2000; Buesseler et al., 2008; Yoon et al., 2018). Furthermore, nutrient enrichment can enhance organic carbon production but reduce the activity of the microbial carbon pump (MCP), leading to more CO_2 release and less refractory DOC production (Jiao et al., 2018). Therefore, considering the complexity of ocean biological pump and MCP and the changing environmental conditions, there is a long way to go before we might be able to enhance carbon sequestration by phytoplankton through iron fertilization or other technologies. In addition, there are concerns about the potential negative impacts of ocean fertilization and geoengineering (Dixon et al., 2014; McGee

et al., 2018). Alternatively, due to their high growth rates under nutrient-replete conditions, mass cultures of microalgae in open ponds or closed photobioreactor (PBR) systems have been proposed as a tool for carbon sequestration (Paul et al., 2020; Singh & Ahluwalia, 2013). However, to date, the land occupation and culture cost hinder its application at scale.

4 | ANALYSIS AND DISCUSSION

In the Anthropocene, human activity has transformed local environments and, in addition, has profoundly influenced the global environment (Lewis & Maslin, 2015; Mathews, 2020). The combined changes to global and local environments are affecting marine primary producers. The human occupation and destruction of habitats, combined with coastal eutrophication, extreme weather events (storms, drought and heatwaves) and climate change (e.g. warming and sea-level rise), are leading to a decreased biomass of coastal plants (mangroves, salt marsh species, seagrasses and macroalgae; Figure 1). Meanwhile, the primary productivity of phytoplankton also demonstrates a decreasing trend due mainly to a reduced nutrient supply in the upper layer of the oceans that is caused by intensified stratification driven by global warming (Gao, Gao, et al., 2022; Gregg & Rousseaux, 2019). These findings suggest a decreasing carbon sequestration capacity of marine primary producers. Therefore, measures must be implemented to restore and enhance the role of blue carbon in mitigating climate change. Rehabilitation and growing more traditional blue carbon plants (mangroves, salt marsh species and seagrasses) are certainly important for restoring their ecological function. However, although these plants have high carbon sequestration densities (Table 1), these restoration/rehabilitation actions can only play a limited role in mitigating climate change due to inadequate availability of suitable areas for expansion. In terms of microalgae, there is huge potential to improve their carbon sequestration density since the current sequestration density is quite low (Table 1). However, the possible negative impacts of geoengineering approaches hinder their application in oceans to enhance the efficiency of ocean biological pump (Dixon et al., 2014; McGee et al., 2018). On the other hand, the existence of sufficient available area, higher carbon sequestration density and operability, along with lower negative impacts make macroalgae cultivation promising in mitigating climate change.

Apart from carbon sequestration by particulate organic carbon (POC) burial and dissolved organic carbon (DOC) transformation into refractory DOC (Figure 2), the harvested macroalgae (41.7% NPP) can be used as food, animal feeds and raw materials for the hydrocolloid and pharmaceutical industries (Ferdouse et al., 2018; Gao et al., 2018). There is a mature market for the macroalgae industry that is worth more than USD 6 billion/year (Ferdouse et al., 2018). Taking kelp as an example, kelp cultivation can sequester 4 Gt CO_2 with the production of 2.34×10^{10} tonnes/year, given a carbon content of 28% (Gao, Gao, et al., 2022). With a current kelp price of $\sim \$11 \text{ kg}^{-1}$ (dry weight), this can potentially

yield $\$ 2.57 \times 10^{14} \text{ year}^{-1}$ (Zhang & Thomsen, 2021). However, such costings are approximate as the price is likely to decrease with any increase of production. Seaweed cultivation can certainly sequester more CO_2 if the harvested macroalgae are buried or transformed to biochar rather than being sold as food, but macroalgae cultivation would be economically unfeasible in that case. Assuming the current price per tonne of CO_2 is $\$25$, this is far from enough to cover a moderate cultivation cost of $\$278$ per tonne dry weight (equal to $\$244$ per tonne CO_2) even if all CO_2 in harvested POC is sequestered (Greene et al., 2020). On the other hand, the net income for macroalgae farmers would be $\$ 2.51 \times 10^{14} \text{ year}^{-1}$ if harvested macroalgae are sold as food using the cultivation cost of $\$278$ per tonne dry weight. Therefore, macroalgae cultivation seems a feasible solution to mitigate climate change both technically and economically when a large proportion of seaweed biomass (including lost POC and excreted refractory DOC) is sequestered while some harvested POC is sold as food (Figure 2). To maximize carbon sequestration, the proportion of seaweeds sold as food should be determined based on the cost and market price of seaweed products and CO_2 in future study. In coastal oceans, seaweed biomass dropping to the seafloor can be remineralized and most of the fixed carbon can return to the atmosphere through turbulent mixing. The strengthened mixing in future coastal oceans would speed up the turnover rate of CO_2 (Falkowski & Oliver, 2007). On the other hand, the fixed carbon in the seaweeds that sink below 1000 m in open oceans can be sequestered for a long time (around 1,000 years; Bach et al., 2021). The intensified stratification in future open oceans would further hinder CO_2 transport from the seafloor to surface and enhance carbon sequestration in deep oceans (Falkowski & Oliver, 2007). However, it should be recognized that enhanced transfer of organic matter to depth and its subsequent mineralization could stimulate oxygen consumption leading to a risk of hypoxia and enhancement of oxygen minimal zones, though the outcome is subject to debate (Lønberg et al., 2020).

It is worth noting that spatial planning of macroalgae cultivation to mitigate climate change should also seek to minimize life cycle CO_2 emissions during farming and processing. It has been estimated that about 14%–25% of all current cultured seaweed production is required to neutralize the CO_2 emissions of the whole aquaculture industry (Froehlich et al., 2019). However, this estimation was based on aquaculture on land and in coastal areas. As mariculture extends to open oceans, CO_2 emissions will increase, which needs to be reassessed in future study. In addition, nutrient reallocation, calcification by encrusting marine life and altered ocean albedo should also be considered because they may counteract the effect of ocean afforestation on climate intervention (Bach et al., 2021). Meanwhile, the shift from coastal to offshore areas would increase the cultivation cost, which may constrain global macroalgae cultivation, particularly in developed countries where the cost is relatively high (Froehlich et al., 2019). Ecological influences of large-scale seaweed farming are often

benign. Cultivated seaweeds can interact with wild organisms and thus alter local ecosystems, but seaweeds can also attract marine animals from several trophic levels by providing them with habitat, protection, nursery sites and food (Hasselström et al., 2018). Although nutrient addition to support macroalgal cultivation could potentially lead to localized phytoplankton blooms, it has been reported that kelp farming could appreciably increase phytoplankton diversity (Jiang et al., 2020). It has also been demonstrated that macroalgae can release short-lived volatile halocarbons that can increase radiative forcing and UV flux by O_3 destruction (Raven, 2017), although the potential production of halocarbons by cultivated seaweeds remains unknown and needs to be addressed in future studies.

5 | CONCLUSIONS

Climate change and extreme weather events driven by human activities are impacting the marine ecosystem and our planet, and the ocean plays an essential role in modulating climate change by absorbing CO_2 and heat. However, the reduced biomass and productivity of marine primary producers in the Anthropocene indicate that the capacity of ocean as a CO_2 sink is decreasing (Figure 1). While it is still necessary to promote restoration of blue carbon plants for their ecological services, the available areas restrict their contributions to achieving carbon neutrality. In terms of microalgae, more work is needed to enhance the efficiency of biological pump and microbial carbon pump and reduce the cost for large-scale cultivation. On the other hand, offshore macroalgae cultivation seems a promising way to strengthen carbon sequestration of the ocean and achieve the Paris target (Table 1). Furthermore, a portion of the harvested macroalgae can be sold as food which ensures culturing macroalgae for carbon neutrality can be economically feasible (Figure 2). To further understand and enhance the potential of seaweed cultivation for climate change mitigation, future study needs to be conducted in several directions: (a) to select or breed seaweed species that can grow well in the open ocean environments, (b) to estimate and minimize life cycle CO_2 emissions and the cost of seaweed cultivation in open oceans, (c) to enhance societal preferences and market demand for seaweed products, (d) to determine the proportion of seaweeds sold as food for maximal carbon sequestration in an economically feasible way, and (e) to quantify the ozone-destroying substances released by cultivated seaweeds.

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CONFLICT OF 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.

AUTHORS' CONTRIBUTIONS

G.G.: Conceptualization, Methodology, Formal analysis, Visualization, Writing—Original draft preparation, Writing—Reviewing and Editing, Supervision, Funding acquisition; J.B.: Conceptualization, Writing—Original draft preparation, Writing—Reviewing and Editing; P.J.: Writing—Original draft preparation, Writing—Reviewing and Editing; L.G.: Writing—Original draft preparation, Writing—Reviewing and Editing; S.X.: Writing—Original draft preparation, Writing—Reviewing and Editing; K.G.: Writing—Original draft preparation, Writing—Reviewing and Editing.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.x95x69pm2> (Gao, Beardall, et al., 2022).

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