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Carbon sequestration and climate change mitigation using macroalgae: a state of knowledge review

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ABSTRACT

The conservation, restoration, and improved management of terrestrial forests significantly contributes to mitigate climate change and its impacts, as well as providing numerous co-benefits. The pressing need to reduce emissions and increase carbon removal from the atmosphere is now also leading to the development of natural climate solutions in the ocean. Interest in the carbon sequestration potential of underwater macroalgal forests is growing rapidly among policy, conservation, and corporate sectors. Yet, our understanding of whether carbon sequestration from macroalgal forests can lead to tangible climate change mitigation remains severely limited, hampering their inclusion in international policy or carbon finance frameworks. Here, we examine the results of over 180 publications to synthesise evidence regarding macroalgal forest carbon sequestration potential. We show that research efforts on macroalgae carbon sequestration are heavily skewed towards particulate organic carbon (POC) pathways (77% of data publications), and that carbon fixation is the most studied flux (55%). Fluxes leading directly to carbon sequestration (e.g. carbon export or burial in marine sediments) remain poorly resolved, likely hindering regional or country-level assessments of carbon sequestration potential, which are only available from 17 of the 150 countries where macroalgal forests occur. To solve this issue, we present a framework to categorize coastlines according to their carbon sequestration potential. Finally, we review the multiple avenues through which this sequestration can translate into climate change mitigation capacity, which largely depends on whether management interventions can increase carbon removal above a natural baseline or avoid further carbon emissions. We find that conservation, restoration and afforestation interventions on macroalgal forests can potentially lead to carbon removal in the order of 10's of Tg C globally. Although this is lower than current estimates of natural sequestration value of all macroalgal habitats (61–268 Tg C $year^{-1}$), it suggests that macroalgal forests could add to the total mitigation potential of coastal blue carbon ecosystems, and offer valuable mitigation opportunities in polar and temperate areas where blue carbon mitigation is currently low. Operationalizing that potential will necessitate the development of models that reliably estimate the proportion of production sequestered, improvements in macroalgae carbon fingerprinting techniques, and a rethinking of carbon accounting methodologies. The ocean provides major opportunities to mitigate and adapt to climate change, and the largest coastal vegetated habitat on Earth should not be ignored simply because it does not fit into existing frameworks.

Key words: carbon cycle, carbon dioxide removal, CO_2, *Fucales*, Green House Gas, kelp, *Sargassum*, seaweed.

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CONTENTS

I. INTRODUCTION

Coastal vegetated ecosystems such as mangrove forests, seagrass meadows, and tidal marshes contribute disproportionally to burial and sequestration of organic carbon in the marine environment (Duarte *et al.*, 2013; Macreadie *et al.*, 2021). Conserving, managing, and restoring these so-called 'blue carbon' ecosystems is one of the most practical and cost-effective ways to contribute to climate change mitigation and adaptation (Griscom *et al.*, 2017). As a result, blue carbon contributions are being increasingly included in countries' commitments to curb their emissions (Gallo, Victor & Levin, 2017; Dencer-Brown *et al.*, 2022), and there is a rapidly growing demand for blue carbon credits amongst corporate stakeholders (Friess *et al.*, 2022). Macroalgal ecosystems are the largest and most productive coastal vegetated ecosystem on Earth (Duarte *et al.*, 2022; Pessarrodona *et al.*, 2022), and may contribute significantly to carbon sequestration (Krause-Jensen & Duarte, 2016; Ortega *et al.*, 2019; Filbee-Dexter & Wernberg, 2020) besides delivering a wide range of benefits to humans. Macroalgae have traditionally not been considered within the blue carbon framework (Howard *et al.*, 2017; Krause-Jensen *et al.*, 2018; Macreadie *et al.*, 2019; Friess *et al.*, 2022), largely due to numerous scientific, policy, and governance challenges when it comes to tracing, accounting, and verifying their carbon sequestration pathways. The need to ascertain new ocean-based pathways to mitigate the effects of climate change has recently prompted revisiting of the role of macroalgae as an actionable blue carbon ecosystem (Macreadie *et al.*, 2019, 2021), including farmed macroalgae (Duarte *et al.*, 2017; Sondak *et al.*, 2017; Froehlich *et al.*, 2019). This in turn has attracted interest from a wide range of actors in government and private industry sectors (Coleman *et al.*, 2022; Friess *et al.*, 2022; Kuwae *et al.*, 2022*a*; Ross, Tarbuck & Macreadie, 2022), catalysing research and debate about their use as a climate mitigation tool.

While recent progress has been made in providing empirical evidence and frameworks to resolve the contribution of macroalgae to carbon sequestration (Dolliver & Connor, 2022; Hurd *et al.*, 2022), their capacity to contribute to climate change mitigation remains poorly resolved. This is an important distinction, because mitigation relies on humans avoiding CO_2 emissions or increasing CO_2 removal through management interventions (e.g. protection, restoration, afforestation, improved management). Uncertainty around the climate change mitigation capacity of macroalgae ecosystems partly stems from a limited understanding of the multiple potential pathways and processes that lead to sequestration (Queirós *et al.*, 2019), which components of the pathways can be managed (Howard *et al.*, 2017; Sutton-Grier & Howard, 2018), and which might in fact cause emissions of greenhouse gases (GHGs) (Bach *et al.*, 2021; Gallagher, Shelamoff & Layton, 2022; Hurd *et al.*, 2022). There are also questions about whether human interventions to macroalgal ecosystems can generate sequestration of a meaningful magnitude, and whether robust methodologies and frameworks to measure, report, and verify sequestration generated by these actions can be developed (Howard *et al.*, 2017; Sutton-Grier & Howard, 2018; Lovelock & Duarte, 2019; Hurd *et al.*, 2022). Additionally, it is unclear whether CO_2 removals from some interventions would satisfy the set of requirements typically needed to be included in climate change mitigation policy and finance frameworks (e.g. sequestration needs to be additional, verifiable, permanent, and cause no additional harm to the environment).

This review aims to fill existing knowledge gaps by providing a robust synthesis of the potential sequestration pathways for macroalgal carbon, quantifying the potential responses of macroalgal ecosystems to management interventions, and outlining pathways for their inclusion in current carbon accounting frameworks. To do so, we conducted a systematic review of the literature and compiled unpublished estimates and expert knowledge from different macroalgal carbon working groups. The review is structured in four sections: the first presents a brief overview of the history of macroalgae carbon research; the second reviews the main mechanisms through which macroalgae might contribute to carbon sequestration; the third synthesises current efforts and outstanding uncertainties to quantify macroalgal carbon flows and storage; and the fourth evaluates whether macroalgae can provide climate mitigation benefits and be implemented as a nature-based solution in current policy and finance mechanisms. We focus on wild macroalgal ecosystems and intentionally refrain from contextualising these topics in relation to macroalgae farming. This focus arises because interventions around wild ecosystems presently have substantially higher potential abatement (NASEM, 2021), present more co-benefits (Forbes *et al.*, 2022), and the CO_2-removal capacity of macroalgae farming has been explored elsewhere (Arzeno-Soltero *et al.*, 2023; Ross *et al.*, 2022; Wu, Keller & Oschlies, 2023). Specifically, our review is largely centered on macroalgal forests formed by large brown algae (*sensu* Wernberg & Filbee-Dexter, 2019), which draw the greatest atmospheric CO_2 flux of any macroalgae habitat (Duarte *et al.*, 2022; Pessarrodona *et al.*, 2022) and whose contribution to sequestration is presumably the largest (Krause-Jensen & Duarte, 2016).

In this review, we define 'carbon sequestration' as the rate of removal of atmospheric CO_2 for >100 years (UNFCCC, 2022). The term is distinguished from 'carbon fixation', which is the drawdown of CO_2 *via* photosynthesis; from 'carbon assimilation', which is the incorporation of fixed carbon into biomass; and from 'carbon storage', which refers to the mass of organic carbon stored in a reservoir (e.g. living tissue, sediments). 'Carbon burial' refers to the incorporation of carbon into sediments for an undetermined period of time.

II. MATERIALS AND METHODS

(1) Literature searches and data compilation

We conducted systematic searches in the *Scopus* database (accessed 01/09/2022) to identify studies dealing with macroalgae blue carbon and quantify the carbon flowing through different sequestration pathways (see online Supporting Information, Table S1, for details of the searches). To minimize a bias towards English-written publications, we conducted additional searches in the following literature repositories from non-English-speaking countries (with English abstracts): *China National Knowledge Infrastructure database* (CNKI; China), *Scientific Electronic Library Online* (South America), and *J-STAGE* (Japan).

The list of potentially relevant studies meeting our search criteria was then scanned to determine if they contained relevant information and data. For the search related to macroalgae and blue carbon, studies were classified based on the focus of the study (carbon fixation, export, degradation, burial, or mapping) and on the carbon species they examined (inorganic or organic, particulate or dissolved). For the topics examining flows and sequestration pathways, we only included data that were expressed on an areal basis at sufficient time resolution (i.e. g C m^{-2} $year^{-1}$), so that studies could be compared. To be included in the study, studies had to fulfil the following criteria:

(1) Examine carbon flows on a per-area and per-time basis. This criterion excluded studies examining biomass-specific productivity rates (i.e. g C g^{-1} m^{-2} $year^{-1}$), unless those rates were applied to standing biomass or spatial cover in the field.
(2) Provide discrete estimates of primary producers (i.e. macroalgal species or assemblage) with minimal interference of other photosynthetic or heterotrophic organisms. This criterion excluded studies examining net ecosystem primary production and metabolism when the net primary productivity (NPP) of the seaweed component could not be accurately determined. These studies usually rely on diel dissolved oxygen measurements in the water column.
(3) Capture seasonal variability in carbon flows across the year. This criterion excluded studies conducted at a single time point, with the exception of studies concerning annual species where the growth or biomass accumulation was measured at the end of the life cycle (i.e. the maximum period of growth). The annual sampling frequency of each study (e.g. monthly, bimonthly, and seasonal) was noted for each study.
(4) Provide basic data not previously reported in other publications.

(2) Assessments of macroalgal forest sequestration potential

We compiled macroalgal forest sequestration potential in different countries based on studies reporting national or regional estimates (see Table S2 for references). Only estimates dealing with macroalgal forests were included. Assessments for some countries only included assessments from regions where macroalgal forests are most abundant, but may not necessarily capture the entirety of their forests and therefore the total country-level potential.

III. HISTORY AND PRESENT STATUS OF MACROALGAE CARBON SEQUESTRATION RESEARCH

Although initial blue carbon assessments did not include macroalgae (Nellemann *et al.*, 2009; Duarte *et al.*, 2013), their

role as a natural CO_2 sink in the global carbon cycle was first recognized more than 40 years ago (Smith, 1981; Ito *et al.*, 2009; Chung *et al.*, 2011). Their potential to contribute to CO_2 emission reductions by replacing fossil fuels was recognized even earlier, with the US Government funding the first pilot studies on large-scale macroalgae cultivation in the mid-1970s (Ritschard, 1992). In the early 1990s, concerns about rising atmospheric CO_2 levels led several authors to propose using such farms for direct climate mitigation purposes (Spencer, 1991; Ritschard, 1992; Alpert, Spencer & Hidy, 1992). These publications stimulated the first physicochemical models testing the feasibility of deploying large-scale macroalgal farms on the open ocean (Orr & Sarmiento, 1992), and the first efforts to synthesise evidence on the biological potential of different macroalgae for fixing carbon (Gao & Mckinley, 1994). In 2006, the first pilot project to create a coastal CO_2 removal belt using macroalgae afforestation and macroalgae farms was funded by the Korean Government (see review by Chung *et al.*, 2013). While most of the contributions of macroalgae to carbon sequestration originally focused on carbon export to the deep sea (Ritschard, 1992), it was later emphasized that macroalgae may contribute significantly to carbon burial in unvegetated and vegetated sediments at shallower depths (Krause-Jensen & Duarte, 2016; Queirós *et al.*, 2019). This recognition established macroalgae ecosystems as key 'carbon donors' in the coastal ocean (Hill *et al.*, 2015; Smale *et al.*, 2018). The first global estimate of the potential sequestration of macroalgae-derived carbon suggested that these forests may support higher carbon sequestration rates than all of the other blue carbon ecosystems combined (Krause-Jensen & Duarte, 2016).

Research effort on the carbon sequestration potential of macroalgae (both wild and farmed) soared after the concept of blue carbon was introduced to highlight the contribution of coastal ecosystems to organic carbon sequestration (Nellemann *et al.*, 2009) (Fig. 1A). Our results show that research effort to date has focused heavily on the fate of particulate organic carbon (POC; 77% of publications; Fig. 1B), even though most carbon is hypothesized to be sequestered *via* dissolved organic carbon (DOC) pathways (Krause-Jensen & Duarte, 2016). The particulate inorganic carbon (PIC) fraction cycling through macroalgae habitats remains very poorly characterized (four studies), despite the relevance of carbonate precipitation and dissolution processes to the global carbon cycle (Smith, 2013; van Dam *et al.*, 2021). The influence of macroalgae carbon sequestration on dissolved inorganic carbon (DIC) concentrations in sea water, and its effects on atmosphere–sea CO_2 exchange, remain equally poorly characterized (Fig. 1B). Of the 180 publications reviewed on the topic of macroalgae carbon sequestration, 55% investigated carbon fixation, whereas fewer studies addressed fluxes directly leading to long-term carbon storage such as export (18%) and burial (16%) (Fig. 1C).

Over the last decade, considerable discussion regarding whether macroalgae and their farming support a globally

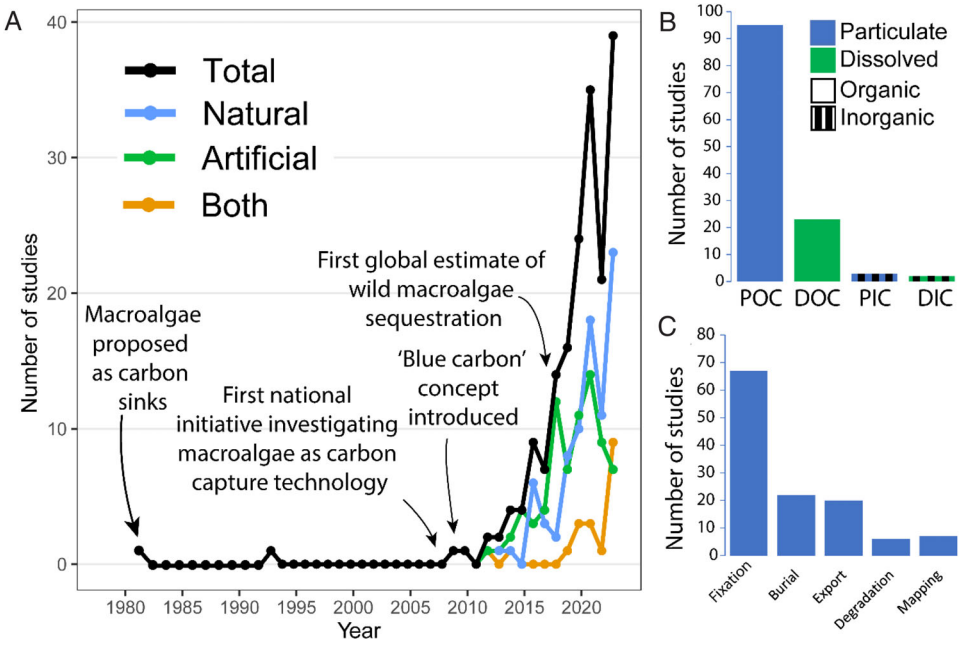

Fig. 1. Scientific research on macroalgal carbon sequestration. (A) Number of publications per year returned by the *Scopus* database (accessed 1 September 2022) using the search terms listed in Table S1. Coloured lines indicate the macroalgal habitat type considered in the study, with blue representing natural habitats, green artificial habitats, and brown representing both. The number of publications is also related to the type of carbon compound (dissolved or particulate, organic or inorganic) (B) and the carbon flux (C) examined. DIC, dissolved inorganic carbon; DOC, dissolved organic carbon; PIC, particulate inorganic carbon; POC, particulate organic carbon.

relevant (and manageable) carbon sink has played out (Krause-Jensen *et al.*, 2018; Macreadie *et al.*, 2019; Bach *et al.*, 2021; Hurd *et al.*, 2022). This has prompted a critical examination of the potential incorporation of these habitats into policy frameworks, as well as their use as a catalyst for conservation and restoration (Howard *et al.*, 2017; Smale *et al.*, 2018; Sutton-Grier & Howard, 2018; Lovelock & Duarte, 2019; Vanderklift *et al.*, 2022). It has become increasingly evident that a more refined understanding of the fate of macroalgal carbon, both at local and global scales, is needed (Krause-Jensen *et al.*, 2018; Raven, 2018), and that verifying macroalgae carbon sequestration will require a thorough accounting of all carbon flows between the atmosphere and ocean (Bach *et al.*, 2021; Gallagher *et al.*, 2022; Hurd *et al.*, 2022), as well as consideration of other GHGs (Roth *et al.*, 2022).

IV. MAIN MACROALGAL CARBON SEQUESTRATION PATHWAYS

A first-order assessment estimated the global macroalgal carbon sequestration potential to be between 61 and 268 Tg C $year^{-1}$ (Krause-Jensen & Duarte, 2016), albeit how much of that potential can contribute to climate change mitigation is not yet resolved (see Section VI). This estimate is relatively small compared to the sequestration capacity of terrestrial sinks (hundreds to thousands of Tg C $year^{-1}$; Griscom *et al.*, 2017) and of some proposed artificial forms of marine carbon sequestration (e.g. alkalinity enhancement and ocean fertilization; thousands to tens of thousands of Tg C $year^{-1}$; NASEM, 2021), but compares favourably to other blue carbon ecosystems (Krause-Jensen & Duarte, 2016). Unlike other coastal vegetated habitats, the area occupied by macroalgae forests can be extensively increased by the expansion of coastal and open ocean farms (Arzeno-Soltero *et al.*, 2023). Some of the carbon assimilated into biomass during the farming process can be lost before harvesting and buried under the farm soils under the right sedimentary conditions, potentially remaining stored long-term (Pan *et al.*, 2021). Farming also offers additional climate mitigation possibilities if macroalgae products and ingredients substitute products that have a high carbon footprint [e.g. fuels, plastics (Duarte *et al.*, 2017; Sondak *et al.*, 2017)], and those reductions outweigh the GHGs emitted along the value chain (e.g. hatchery, harvesting, manufacturing, transport).

The large sequestration capacity of macroalgal forests arises from their vast extent and high productivity, which results in large amounts of carbon fixed and, thus, available for potential sequestration. Macroalgae are the most extensive coastal vegetated ecosystem on the planet, covering at least 10, 15, and 40 times more area than seagrasses, tidal marshes, and mangroves respectively (Duarte, 2017). A systematic effort using environmental modelling estimated a global area of benthic macroalgae of $6.06–7.22 \times 10^6$ km^2, most of which is dominated by red macroalgae (for a review of existing estimates see Duarte *et al.*, 2022). Macroalgal forests dominated by kelp and *Sargassum* are estimated to cover up to 2.03×10^6 km^2 and 1.4×10^6 km^2 respectively (Gouvêa *et al.*, 2020; Jayathilake & Costello, 2021), albeit mapped areas to date are substantially smaller than modelled areas (Mora-Soto *et al.*, 2020; Table S2). By contrast, the area presently occupied by seaweed farms is several orders of magnitude lower (*ca.* 2000 km^2; Duarte *et al.*, 2017). Global NPP of macroalgae is estimated to draw 1.33 Pg C $year^{-1}$ from the water column, with macroalgal forests fixing 0.95 Pg C $year^{-1}$ alone (Duarte *et al.*, 2022).

Macroalgae can contribute to carbon sequestration *via* three well-established mechanisms: (*i*) release of DOC that is resistant to degradation; (*ii*) burial of POC in marine sediments, including those of other coastal vegetated ecosystems; and (*iii*) export of DOC and/or POC to deep sea areas with long residence times where carbon may remain sequestered even if remineralized (Fig. 2). These pathways differ in the form of organic carbon sequestered (dissolved or particulate), as well as in the physical, biological, and chemical processes with which they interact. Other pathways, such as the permanent reduction of metabolic products formed *via* alkalinity production have been proposed, but remain poorly understood in macroalgae systems (Reithmaier *et al.*, 2021; Perkins *et al.*, 2022).

(1) DOC resisting degradation

Refractory DOC (RDOC), which is the portion of DOC not accessible for biological processing or resistant to degradation, plays a central role in marine organic carbon sequestration (Hansell, 2013; Baltar *et al.*, 2021). Macroalgae are known to be important sources of DOC in coastal waters (Wada *et al.*, 2008; Wada & Hama, 2013; Watanabe *et al.*, 2020), and a large portion of their DOC production is exported to the open ocean (Bauer & Druffel, 1998; Barrón & Duarte, 2015). Average published macroalgal DOC release rates (mean ± SE = 238 ± 58 g C m^{-2} $year^{-1}$, $N = 83$, Fig. 3A) exceed the averages recorded for seagrass meadows (54 ± 13 gC m^{-2} $year^{-1}$; Barrón & Duarte, 2015), mangroves (150 ± 134 g C m^{-2} $year^{-1}$; Bouillon *et al.*, 2008), and phytoplankton (0–15 g C m^{-2} $year^{-1}$; Roshan & Devries, 2017). However, rates of release span three orders of magnitude (0–4390 g C m^{-2} $year^{-1}$), corresponding to an average of 30.4 ± 12.52% (mean ± SEM, $N = 51$) of NPP (Fig. 3B). This large variation may reflect differences in species physiology and phenology (Chen *et al.*, 2020*b*; Watanabe *et al.*, 2020; Paine *et al.*, 2021), environmental conditions (Reed *et al.*, 2015; Watanabe *et al.*, 2020; Paine *et al.*, 2021) and methodological approaches (Khailov & Burlakova, 1969; Carlson & Carlson, 1984), with short-term incubation experiments underestimating DOC (Weigel & Pfister, 2020).

Most DOC released by macroalgae is thought to be photodegraded or to enter microbial loops (Shank *et al.*, 2010; Wada *et al.*, 2015), where it is eventually remineralized back to CO_2. A smaller fraction may persist or be transformed into

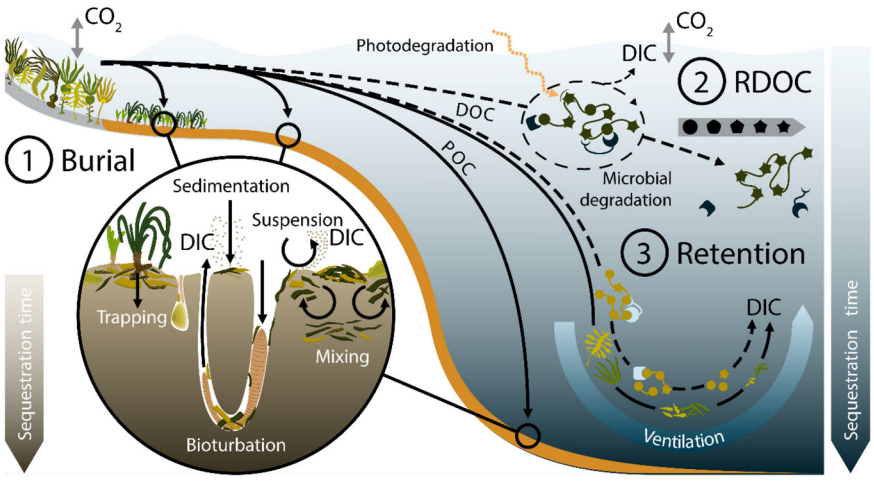

Fig. 2. Overview of established macroalgal carbon sequestration pathways. Key processes playing a role in sequestration (e.g. trapping) and remineralization (e.g. sediment resuspension) of macroalgal organic carbon into dissolved inorganic carbon (DIC) are also outlined. Other potential pathways leading to long-term carbon sinks, such as the permanent production of alkalinity, are not shown. Solid lines indicate pathways involving particulate organic carbon (POC), whilst dashed lines indicate pathways involving dissolved organic carbon (DOC). Macroalgal carbon can be sequestered in the ocean by ① burial of particulate carbon in vegetated and unvegetated sediments; ② dissolved organic carbon avoiding degradation (e.g. by sunlight or microbes) in the water column (refractory DOC; RDOC); and ③ transport of carbon to the ocean interior, where sequestration will depend on the retention time of carbon from the ocean–atmosphere interface. The intrinsic refractoriness of DOC is indicated by the scale below RDOC, and is also illustrated as a DOC molecule that loses some of its labile components as its moves down the water column.

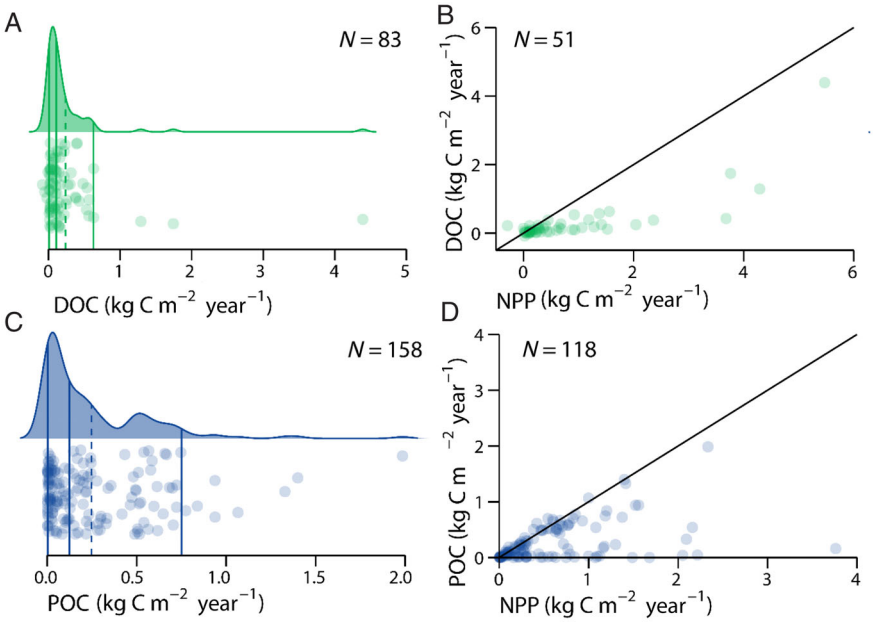

Fig. 3. Export rates of macroalgal dissolved organic carbon (DOC; in green) and particulate organic carbon (POC; in blue) in the literature (A, C) and their relationship with net primary production (NPP) (B, D). Probability distributions in A and C are based on kernel density estimates. Solid lines are quantiles (0.05, 0.5, 0.95) and dashed lines are means. Lines in B and D indicate 1:1.

RDOC that will undergo slow decomposition over years, decades, or centuries, and which contributes to long-term carbon storage (Hansell, Carlson & Schlitzer, 2012; Walker *et al.*, 2016). DOC recalcitrance exists in a wide continuum, with most DOC only resisting degradation under certain conditions (Jiao *et al.*, 2014; Shen & Benner, 2018). Specifically, DOC recalcitrance depends on its concentration in sea water, the environmental context, and its biochemical composition (Baltar *et al.*, 2021). When present in very low concentrations, DOC molecules may avoid uptake by

microbes, effectively resisting degradation and remaining in the ocean (Jiao *et al.*, 2014). Environmental conditions (e.g. temperature, nitrate, light) influence the rates and extent of DOC utilization by microbes (Zweifel, Norrman & Hagstrom, 1993), and high irradiation or temperature can physically degrade macroalgal DOC (Shank *et al.*, 2010; Lønborg *et al.*, 2018). The metabolic capabilities of the microbial communities surrounding DOC can also affect its lifetime (Chen *et al.*, 2020*a*). In this way, the fate of DOC is intrinsically linked to a range of ocean water transport and mixing processes that expose DOC molecules to microbial communities and environmental conditions. Finally, the chemical composition of DOC itself also affects its lability, and this composition is not well understood for most macroalgae. Macroalgae DOC contains high quantities of phenolic and humic-like compounds, which are typically more recalcitrant than other molecules (Wada *et al.*, 2008; Buck-Wiese *et al.*, 2022; Feng *et al.*, 2022).

Macroalgal RDOC is thought to play a central role in macroalgal carbon sequestration (Krause-Jensen & Duarte, 2016; Feng *et al.*, 2022; Li *et al.*, 2022), and evidence across a range of experimental degradation timeframes shows that a potentially relevant fraction of macroalgal DOC is – or becomes – RDOC (Table 1). Yet empirically quantifying the relative percentage of macroalgal DOC that will enter this pool is, at present, complex. From a biogeochemical perspective, RDOC is defined as the fraction of DOC remaining in water masses of varying age, but determining the original source of that fraction remains challenging (Hansell, 2013; Baltar *et al.*, 2021). Assays in the laboratory using macroalgae DOC attempt to approximate the refractory fraction using long-term incubations, but these are necessarily time constrained and are only able to study the biochemistry of RDOC in a controlled setting, which may not be representative of the natural environment. For instance, incubations to measure macroalgal DOC degradation are usually conducted under constant temperature and dark conditions (Wada *et al.*, 2008; Chen *et al.*, 2020a; Watanabe *et al.*, 2020), despite some studies showing that sunlight accelerates degradation (Shank *et al.*, 2010; Wada *et al.*, 2015; Powers *et al.*, 2020) and can affect the relative abundance of polyphenolic substances (Powers *et al.*, 2020). Additionally, the duration of experiments varies widely in the literature (from days to over a year; Table 1), even though the length of time during which DOC is allowed to degrade is known to affect its recalcitrance estimates (Watanabe *et al.*, 2020). Decay rates generally follow a negative exponential curve: the labile portion of DOC is used up relatively quickly, with a semi-labile fraction degrading more slowly and a remaining fraction (assumed to represent the refractory component) remaining stable thereafter (Chen *et al.*, 2020*a*). Yet, even the 'stable' RDOC fraction can undergo further degradation if exposed to novel conditions (e.g. light exposure after 360 days; Li *et al.*, 2022). The advent of molecular fingerprinting offers promising opportunities to bridge the gap between the geochemical and experimental perspectives of RDOC, as the production and release of macroalgae-specific molecules can be traced and matched to refractory samples (Hansell, 2013; Feng *et al.*, 2022; Li *et al.*, 2022). Coupling these tools with more realistic experimental assays will vastly improve our understanding of the fate of macroalgal DOC in the ocean. An outstanding challenge will be quantifying the labile fractions of macroalgae DOC that become refractory as they are successively utilized and transformed by microbes (Chen *et al.*, 2020*a*; Li *et al.*, 2022).

(2) Burial of POC in marine sediments

Burial of POC in marine sediments, where carbon may avoid oxidation and persist for thousands of years if left undisturbed, represents an important sequestration pathway in the ocean carbon cycle (Bianchi *et al.*, 2018). As most macroalgae grow on rocky habitats, where accumulation of organic matter is negligible, burial of macroalgal POC occurs allochthonously, that is, only after carbon has been transported to sedimentary environments.

The majority (61.28 ± 4.2%, mean ± SEM, $N = 118$) of the carbon assimilated into macroalgae biomass is eventually released as POC of a wide range of sizes, from whole plants to micrometric particles. Macroalgal POC release rates (246.85 ± 24.74 g C m^{-2} $year^{-1}$, mean ± SEM, $N = 158$, Fig. 3C) are within the range documented for other coastal vegetated ecosystems such as seagrass meadows (16–50 g C m^{-2} $year^{-1}$; Pergent *et al.*, 1994), or tidal marshes (470–670 g C m^{-2} $year^{-1}$; Bouchard & Lefeuvre, 2000). Macroalgal POC release rates vary across three orders of magnitude and are positively correlated with yearly NPP (Fig. 3D). POC release is often seasonal and variable across sites, and is generally influenced by hydrodynamic conditions (Seymour *et al.*, 1989; Hobday, 2000; Krumhansl & Scheibling, 2011), the life and reproductive cycle of a species (Walker, 1980; Pessarrodona, Foggo & Smale, 2018*a*; Kokubu *et al.*, 2019), and/or grazing and biofouling by encrusting organisms (Krumhansl & Scheibling, 2011). Macroalgal POC contributes meaningfully to the total POC in coastal areas (Fredriksen, 2003; Bode, Alvarez-Ossorio & Varela, 2006; Yorke *et al.*, 2013; Wang *et al.*, 2018) and in the deep sea (Vetter & Dayton, 1998).

The amount of macroalgal POC that reaches sediments where burial can occur depends on its degradation rate and transport time. Degradation often includes physical fragmentation by waves and currents, and biological consumption and decomposition by a variety of organisms. Decomposition will transform detrital POC into organic and inorganic carbon (Higgins & Mackey, 1987; Zhang & Wang, 2017). Herbivores also consume macroalgal detritus, interacting with the degradation process (Bedford & Moore, 1984). The biochemical composition of detritus (Smith & Foreman, 1984), as well as environmental variables (e.g. temperature, oxygen, light), are important drivers of macroalgae decomposition (Pedersen *et al.*, 2021; Filbee-Dexter *et al.*, 2022*a*; Wright, Pessarrodona & Foggo, 2022).

The transport of available POC beyond macroalgal habitats is influenced by particle size and buoyancy, as well as

Table 1. Degradation rates of macroalgae dissolved organic carbon (DOC) and remaining (recalcitrant) carbon (as a percentage of the original DOC concentration) under different experimental conditions. Values are means and standard deviations when reported. *k*, decay constant

Species	Experimental conditions	Sampling month	Duration (days)	Remaining carbon (%)	k (day^{-1})	Reference
Brown algae						
Sargassum natans, *S. fluitans*	27–29 °C (sunlight)	July, October	0.83	47–74	0.36–0.84	Powers *et al.* (2020)
Sargassum natans, *S. fluitans*	27 °C (artificial light)	June, October	2	46.56–53.98	4.74–5.9	Shank *et al.* (2010)
Ecklonia cava	20 °C (dark)	April	30	85.7 ± 5.3	0.0058	Wada *et al.* (2008)
		December	30	39.2 ± 8.1	0.0342	
		May	30	55.1 ± 25.5	0.0216	
		June	60	28.9 ± 1.0	0.0407	
		October	60	59.7	0.0182	
Ecklonia cava	23 °C (artificial light)	December	1	0.86–72.62	0.29–8.81	Wada *et al.* (2015)
		May		76.49	3.26	
Sargassum horneri	22 °C (dark)	February	150	56 ± 4	0.0042–0.0090	Watanabe *et al.* (2020)
		March	150	78 ± 27		
Sargassum tenerrimum	23–27 °C (dark)	NA	100	23.67	0.11	Manikandan *et al.* (2021)
Saccharina japonica	−1.3 to 1.7 °C	January	150	37.3	0.04	Gao *et al.* (2021)
	14.7–17.8 °C (sunlight)	April		38.2	0.09	
Saccharina japonica	20–25 °C (dark)	May	359	56.91	0.03	Li *et al.* (2022)
Saccharina japonica	20–25 °C (dark)	June	205	3.67	0.1	Feng *et al.* (2022)
Ecklonia maxima	10 °C (artificial light)	August (winter)	7	31.26	0.5	Lucas & Newell (1981)
Laminaria pallida			9	10.34	0.3	
Turbinaria ornata	23–27 °C (dark)	NA	100	13.41	0.28	Manikandan *et al.* (2021)
Padina gymnospora	23–27 °C (dark)	NA	100	23.04	0.44	Manikandan *et al.* (2021)
Fucus spiralis	11–13 °C (dark)	July, August	16	53.74	0.03	Hulatt *et al.* (2009)
	11–13 °C (sunlight)			0	0.08	
Red algae						
Chondrus crispus	4 °C (*bioturbator*)	February	17–20	0.4	0.004	Kristensen *et al.* (1992)
	4 °C (control)			0.6	0.005	
	8 °C (*bioturbator*)			0.6	0.005	
	8 °C (control)			0.7	0.004	
	16 °C (*bioturbator*)			0.4	0.005	
	16 °C (control) (dark)			0.4	0.008	
Polysiphonia spp.	15 °C (dark)	Autumn	154	0	0.01	Vichkovitten & Holmer (2004)
Green algae						
Ulva spp.	20–24 °C (artificial light)	Spring	17	28.71	0.49	García-Robledo *et al.* (2008)
Ulva lactuca	21 °C (dark)	October	70	10.41	0.1	Kristensen (1994)
Ulva rigida	20 °C (dark)	August	22	23.91	0.37	Castaldelli *et al.* (2003)
Ulva prolifera	20–25 °C (dark)	June, July	512	3.97	0.07	Chen *et al.* (2020*a*)
Ulva prolifera	25 °C (dark)	June	7	13.28	3.4	Liang *et al.* (2021)
Caulerpa racemosa	23–27 °C (dark)	NA	100	30.33	0.04	Manikandan *et al.* (2021)
Halimeda incrassata	18 °C (dark)	August	15	0	0.07	Jiménez-Ramos *et al.* (2022)
		January		14.83	0.15	
Halimeda sp.	23–27 °C (dark)	NA	100	29.44	0.05	Manikandan *et al.* (2021)

seabed morphology and oceanographic processes. Smaller, lighter particles sink more slowly and can be transported over longer distances than larger, heavier fragments such as whole plants or blades (Filbee-Dexter *et al.*, 2018*b*; Wernberg & Filbee-Dexter, 2018). Yet, small particles may be more susceptible to degradation (Smith & Foreman, 1984), and the interactive effects between these two processes remain poorly studied. Transport of neutrally or negatively buoyant macroalgal detritus is mostly influenced by wave energy or ocean currents, with higher export rates in exposed sites (Filbee-Dexter *et al.*, 2018*b*). Typically, a relatively small amount (1–3%) of the exported POC washes up ashore (Kirkman & Kendrick, 1997; Lastra *et al.*, 2014; Smale *et al.*, 2021), the rest being transported to other habitats and/or remineralized. Buoyant fragments generally travel greater distances (Kirkman & Kendrick, 1997), drifting with surface currents up to hundreds to thousands of kilometres away from their source (Harrold & Lisin, 1989; Hobday, 2000; Fraser *et al.*, 2018). Coastal geomorphological features facilitating long water residence times (e.g. fjords, estuaries) can however limit long-range transport, with most algae sinking before being exported (Ager *et al.*, 2023). Interestingly, non-buoyant algae can become intertwined with buoyant macroalgae, potentially facilitating export (Ager *et al.*, 2023). Buoyant macroalgae sink to the bottom as a result of progressive degradation (e.g. gas bladder rupture or fragmentation) and colonization by epibionts (Rothäusler, Gutow & Thiel, 2012), or by being caught in zones of convergence and downwelling (Schoener & Rowe, 1970; Johnson & Richardson, 1977). Once on the seabed, detritus can be transported by a range of oceanographic processes such as strong tidal flows, turbidity currents, or dense-shelf water cascades (Inman, Nordstrom & Flick, 1976; Canals *et al.*, 2006; Mahjabin, Pattiaratchi & Hetzel, 2020). Transport is also determined by seabed morphology. Flat areas on the continental shelf or abyssal plains contain little macroalgal detritus, while submarine canyons, fjords, and convex areas can aggregate detritus (Smith & Foreman, 1984; Filbee-Dexter & Scheibling, 2016; Krause-Jensen & Duarte, 2016; Zaborska *et al.*, 2018), and serve as rapid conduits of macroalgal POC to deeper waters (Table S3). Accumulations of macroalgal detrital fragments do not necessarily show a relationship with depth (Kokubu *et al.*, 2012, 2019; Filbee-Dexter & Scheibling, 2016; Baker *et al.*, 2018; Filbee-Dexter *et al.*, 2018*b*).

Once it reaches depositional sites, macroalgae POC can enter the sediment during decomposition or be buried by settling particles or bioturbating animals (Reichardt, 1987; Queirós *et al.*, 2019). Laboratory experiments have found that up to 9% of macroalgal POC decomposing on top of the sediment can become buried in it (Hardison *et al.*, 2010; Braeckman *et al.*, 2019; Ravaglioli *et al.*, 2019). On the other hand, fast-decomposing detritus may not significantly increase the sediment organic carbon content (Sundbäck *et al.*, 1989; Isæus *et al.*, 2004; Rossi, 2006). Field experiments in which macroalgae parcels were deposited on deep seafloor sediments between 1300 and 1700 m have also reported mixed results, with moderate enrichment of the top sediment layer in some locations and depletion in others (Smith, 1983; Bernardino *et al.*, 2010). This could be due to the existence of a maximum macroalgae biomass threshold that can be processed by the community in each of these areas (Sundbäck *et al.*, 1989), and to macroalgae inputs facilitating microbial or bioturbator activity.

Overall, the magnitude of POC burial will vary depending on the total macroalgal detrital flux, the accumulation rate of sediment on the seabed and its grain size, and the rate of carbon remineralization once deposited (Burdige, 2007; Leithold, Blair & Wegmann, 2016; Serrano *et al.*, 2016; Queirós *et al.*, 2019; Song *et al.*, 2022). Macroalgae detrital fluxes vary throughout the year, with burial being greater when pulses of detritus are exported outside the macroalgal habitats (Queirós *et al.*, 2019). Sedimentation rates generally decrease progressively with increasing distance from the coast and river mouths (Restreppo, Wood & Phrampus, 2020), being particularly high in coastal vegetated ecosystems, fjords, and canyons (De Haas, van Weering & de Stigter, 2002; Smith *et al.*, 2015; Leithold *et al.*, 2016; Duarte, 2017). Organic carbon also binds more effectively to fine-grained sediments, with the concentration of muds often being a good predictor of organic carbon burial (Serrano *et al.*, 2016). Macroalgal carbon that has been buried in marine sediments will, however, only contribute to carbon sequestration if it remains buried for periods of time relevant to climate mitigation (Frigstad *et al.*, 2021). Remineralization is driven by numerous physical (e.g. tidal and wave pumping, shelf currents, storm waves) and biological (e.g. bioturbation) sediment-mixing processes, and is particularly intense in the top sediment layer (Teal *et al.*, 2008; Hardison *et al.*, 2010; Braeckman *et al.*, 2019). As a result, the depth of the sediment mixed layer shows strong relationships with carbon burial (Johannessen, 2022; Song *et al.*, 2022). On the continental shelf, carbon buried on the top layer often goes through numerous oxic–suboxic cycles driven by sediment resuspension and redeposition (Bröder *et al.*, 2018), with carbon content remaining constant in deeper layers (Song *et al.*, 2022). Burial in deep sea sediments presumably leads to longer term stability (thousands to millions of years), even if oxygen is available (Estes *et al.*, 2019), with macroalgae POC having been observed in cores 1500–2200 m deep (Reichardt, 1987). Indeed, deep sea sediments experimentally enriched with kelp show little colonisation by fauna after 4.7 months (Levin & Smith, 1984), suggesting negligible remineralization as kelp may not be a trophically important resource (Smith, 1983). Although buried kelp may persist in experimental sediments, its actual long-term persistence rarely has been resolved. Continuous kelp carbon burial has been detected in Nordic fjord and shelf sediments over 120 years (Frigstad *et al.*, 2021), whilst macroalgal DNA has been found in 350-year-old loch sediments (O'Dell, 2022) Investigating the long-term permanence of macroalgal carbon in sediments remains a priority for future research.

Determining how much of the carbon stored in marine sediments is derived from macroalgae remains a key step to resolving their contribution to carbon sequestration. Improvements in carbon tracing techniques, such as stable isotope analysis and environmental DNA (eDNA) combined with quantitative polymerase chain reaction (qPCR), have recently enabled the identification of macroalgae among the potential sources of organic carbon in marine sediments, which are usually coarsely resolved. Macroalgal eDNA is commonly found in nearshore marine sediments, suggesting they contribute to carbon burial (Ortega *et al.*, 2019; Queirós *et al.*, 2019, 2022; Frigstad *et al.*, 2021; O'Dell, 2022; Ørberg *et al.*, 2022). Few studies to date have quantified their actual contribution, as finding macroalgae-specific biomarkers has remained challenging. In coastal vegetated sediments, macroalgae have been found to contribute up to 68% of the carbon buried (Kindeberg *et al.*, 2019). In other unvegetated coastal sediments (e.g. canyons, fjords, continental shelves; Table 2), average macroalgae contributions to the total organic carbon buried range from 10 to 55%. Existing macroalgae burial rates vary from 1.5 to 17 g C m^{-2} $year^{-1}$ (Table 2), representing around 9% of the macroalgal POC exported as detritus (Queirós *et al.*, 2019; Frigstad *et al.*, 2021; Zaborska *et al.*, 2018), or ∼4% of NPP (Frigstad *et al.*, 2021). A coring study conducted along a fjord and the continental shelf of Norway suggested a POC burial rate of 460 g C m^{-2} $year^{-1}$ (Abdullah, Fredriksen & Christie, 2017), but was based on multiple extrapolations and assumptions and may, therefore, be an overestimation. Burial rates of macroalgal carbon per unit area, in the continental shelf or at the bottom of fjords (Table 2), are an order of magnitude lower than burial rates in mangroves (226 ± 39 g C m^{-2} $year^{-1}$), tidal marshes (244 g C m^{-2} $year^{-1}$), or seagrass meadows (138 ± 38 g C m^{-2} $year^{-1}$) (McLeod *et al.*, 2011; Ouyang & Lee, 2014; Duarte, 2017; and references therein). Despite these relatively low burial rates, the large spatial coverage over which macroalgae carbon is exported may result in considerable carbon sequestration (Krause-Jensen & Duarte, 2016).

(3) Transport of organic carbon to the ocean interior

A first-order global estimate suggests that the transport of macroalgal organic carbon to the "deep sea", either in dissolved or particulate form, may be the main pathway through which macroalgae contribute to carbon sequestration (Krause-Jensen & Duarte, 2016). Macroalgal carbon exported below 1000 and 1500 m is often assumed to be sequestered (Krause-Jensen & Duarte, 2016; Ortega *et al.*, 2019). In reality, however, the sequestration timescales of macroalgal POC or DOC exported to the ocean interior will depend on the depth and location where it is respired back to CO_2, as the time water masses take to ventilate to the atmosphere varies spatially (Siegel *et al.*, 2021, 2023; Baker *et al.*, 2022). For example, the North Atlantic basin 'leaks' more carbon than other basins, with 33% of the carbon exported to 1000 m being returned to the atmosphere within 100 years (Baker *et al.*, 2022), whilst the Indian and Pacific Ocean have longer ventilation times (Siegel *et al.*, 2021). Future estimates of macroalgae carbon sequestration *via* this pathway should therefore explicitly consider the geographic variability in water ventilation times.

Export of macroalgal POC to the ocean interior has been documented across all major oceanographic basins (Krause-Jensen & Duarte, 2016). Oceanographic processes such as density- and turbidity-driven currents can transport macroalgal POC across the continental shelf to depths exceeding thousands of metres (Reichardt, 1987). Transport is presumably accelerated in wave-exposed locations and shelves with short water-residence times (Filbee-Dexter *et al.*, 2018*b*), but can be remarkably slower (decades to millennia) in wide and shallow continental shelves (Bröder *et al.*, 2018). Alternatively, some species may float across shelf waters and sink to the deep if caught in zones of convergence and downwelling created by winds (Johnson & Richardson, 1977) or if they lose buoyancy. For instance, *Sargassum* rafts advected below the mixed layer can sink to 5000 m in just 1 or 2 days (Schoener & Rowe, 1970; Johnson & Richardson, 1977).

Table 2. Particulate organic carbon (POC) burial rates in sediments from different depths in the continental shelf. The burial of macroalgae-derived POC (m-POC), and its equivalent fraction of the total POC burial (in parentheses) are also indicated

Location	Taxa examined	Depth (m)	POC burial (g C m^{-2} $year^{-1}$)	m-POC burial (g C m^{-2} $year^{-1}$)	Reference
NW Norway (Shelf)	Kelp	531	31.1	3.4 (11%)	Frigstad *et al.* (2021)
		515	26.8	8.6 (32%)	
		354	14.9	1.5 (10%)	
		242	49.5	10.9 (22%)	
Southern UK (Shelf)	Macroalgae	48	58.7	8.75 (15%)	Queirós *et al.* (2019)
Svalbard, Norway (Fjord)	Macroalgae	95	37.1	16.7 ± 4.3 (45%)[1]	Zaborska *et al.* (2018)
		103	38.6	17.4 ± 5 (45%)[1]	
		98	35.5	16.0 ± 4.6 (45%)[1]	
		95	15.4	8.5 ± 4 (55%)[1]	
		105	15.4	8.5 ± 4 (55%)[1]	
		103	15.9	8.7 ± 4 (55%)[1]	

[1]Based on the median contribution of macroalgae to the sediment organic matter ±95% confidence interval.

The number of macroalgal DNA reads in water samples decreases exponentially with depth (Ortega et al., 2019). Red algal DNA is the most common, which may reflect the fact that this group covers the largest geographical extent among macroalgae (Duarte *et al.*, 2022). How much carbon these DNA reads equates to is still unresolved, as it requires experimentally determined taxon-specific ratios between DNA and carbon, which are currently unknown. Once deposited on the deep seafloor, macroalgal POC can be readily used by fauna (Harbour *et al.*, 2021) or decomposed by microbes, with experimental *in situ* kelp deployments finding little material remaining after 40 days at 1300 m depth (Smith, 1983).

The export of macroalgal DOC to the ocean interior remains largely uncharacterized, but will depend on local- and regional-scale oceanographic processes, as well as degradation time. For instance, in a coral reef habitat with low water turnover, Haas *et al.* (2013) found that DOC exudates were consumed within less than a day, suggesting negligible to nil export. By contrast, 98% of DOC released in a temperate *Sargassum* bed was transported to offshore waters by tidal flushing or other hydrodynamic processes (Watanabe *et al.*, 2020). Although the contribution of macroalgae to the total DOC pool remains poorly characterized (Wada *et al.*, 2015), DOC export from the coastal to the open ocean is known to be an important flux in the carbon budget (Barrón & Duarte, 2015). Resolving ocean currents and other oceanographic processes at macroalgal DOC release sites and surrounding shelf areas could help determine the fate of this DOC and its potential to reach areas where it potentially can be sequestered.

V. MAPPING MACROALGAL CARBON SEQUESTRATION POTENTIAL AND DIRECTIONS FOR FUTURE RESEARCH

Whilst blue carbon wealth estimates are available for most countries (Macreadie *et al.*, 2021), inventories of macroalgal carbon stocks and/or assessments of their carbon fixation and sequestration potential are available for only 17 countries, self-governing territories, or regions (Fig. 4A, Table S2). These assessments have been largely motivated by the need to understand the climate change mitigation capacity of macroalgal forests and whether they can be designated as blue carbon ecosystems (Filbee-Dexter & Wernberg, 2020), as well as to improve marine estate management (Bayley *et al.*, 2021; Filbee-Dexter *et al.*, 2022*b*). Efforts are starting to guide national policy actions [e.g. Chile (Vega *et al.*, 2021); UK (Bayley *et al.*, 2021; JNCC, 2021)] and, in some cases, the implementation of carbon offset projects (e.g. Japan; Kuwae *et al.*, 2022*a*,*b*), although macroalgal carbon credits are yet to satisfy any of the standards set by the major crediting organizations (Verra, GoldStandard).

Most assessments to date have focused on the carbon held within living macroalgal biomass (standing stock), which cannot be considered a long-term reservoir due to the short lifespan of most macroalgae species (Howard *et al.*, 2017). However, these are presented here as a useful proxy for the macroalgal carbon wealth held by different countries. Although some countries only have data at the regional level, available inventories reveal vast differences in macroalgal carbon stores held by each country. The Great Southern Reef, a system of interconnected rocky reefs running along the bottom third of the Australian continent, and the Eastern Canadian Arctic, appear to hold large carbon stocks (Fig. 4B). Estimates of the carbon potentially sequestered by macroalgae are less common (11 countries and/or self-governing territories), but also highlight Australia as a key contributor so far (Fig. 4C).

Importantly, assessments of carbon sequestration potential are missing from 88% of the 150 countries where macroalgae occur based on the maps of Duarte *et al.* (2022). For these areas, a useful approach may be to categorize their coastline considering the properties that can enhance or reduce macroalgal carbon sequestration (Fig. 5, Table S4). *A priori*, large spatial variations in sequestration potential can be expected because of large global variation in the fixation, transport, and burial of macroalgal carbon, and only certain contexts will likely be conducive to macroalgal carbon sequestration:

(1) Carbon fixation by macroalgae will be greatest in shallow areas with rocky habitats, with rates being greatest in temperate regions (Pessarrodona *et al.*, 2022). In the absence of good maps, the total area covered by rock, which is often available from geological surveys and habitat mapping (Wilmers *et al.*, 2012; Sondak & Chung, 2015), and the mean productivity of the most common macroalgae species might be useful proxies to derive the maximum carbon fixation in any given region.
(2) The amount of carbon buried and stored in marine sediments will depend strongly on total detrital carbon export reaching these areas, sedimentation rate (Ingall & van Cappellen, 1990), and remineralization rates of the carbon buried with the sediment (Burdige, 2007; Queirós *et al.*, 2019; Song *et al.*, 2022). Areas with high sedimentation rates such as blue carbon habitats, fjords, or canyons will have high burial rates (Smith *et al.*, 2015). Burial of organic carbon is also more pronounced in areas with fine sediment (Serrano *et al.*, 2016). Areas with shallow sediment mixed-layer depths, such as those at high latitudes and away from large river deltas or outside enclosed seas, have high carbon burial rates (Song *et al.*, 2022).
(3) Carbon transport times to deep ocean habitats where sequestration might be facilitated will be shorter in areas characterized by high flow-driven export. For example, coasts featuring dense shelf water cascades and/or short coastal water residence times (Liu *et al.*, 2019), and/or adjacent to trenches, deep cuvettes, or canyons, may transport greater amounts of carbon to the ocean interior (Canals *et al.*, 2006). Transport will be slowest in areas with long coastal residence times [e.g. polar margins, marginal seas

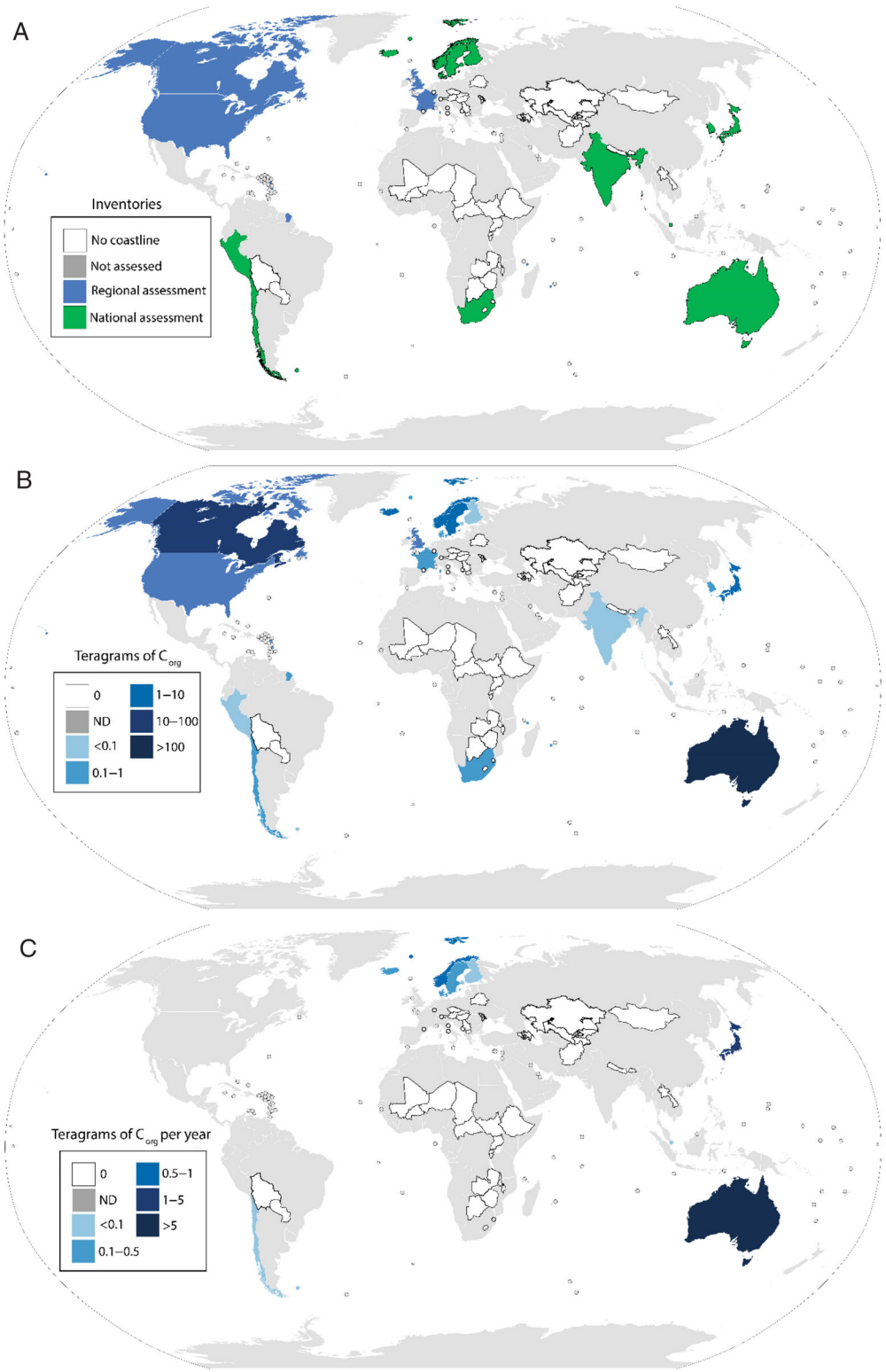

Fig. 4. Distribution of macroalgae carbon stocks and sequestration potential. (A) Absence or presence of country inventory assessments on a national or regional level is depicted as grey, green, and blue countries, respectively. (B) Mean macroalgal carbon stocks in living tissue biomass per country (teragrams of carbon). (C) Mean macroalgae carbon sequestration potential per country (teragrams of carbon per year). The small circles represent microstates or self-governing territories. Note that assessments for the vast majority of countries are lacking (not determined, ND). C_{org}, organic carbon.

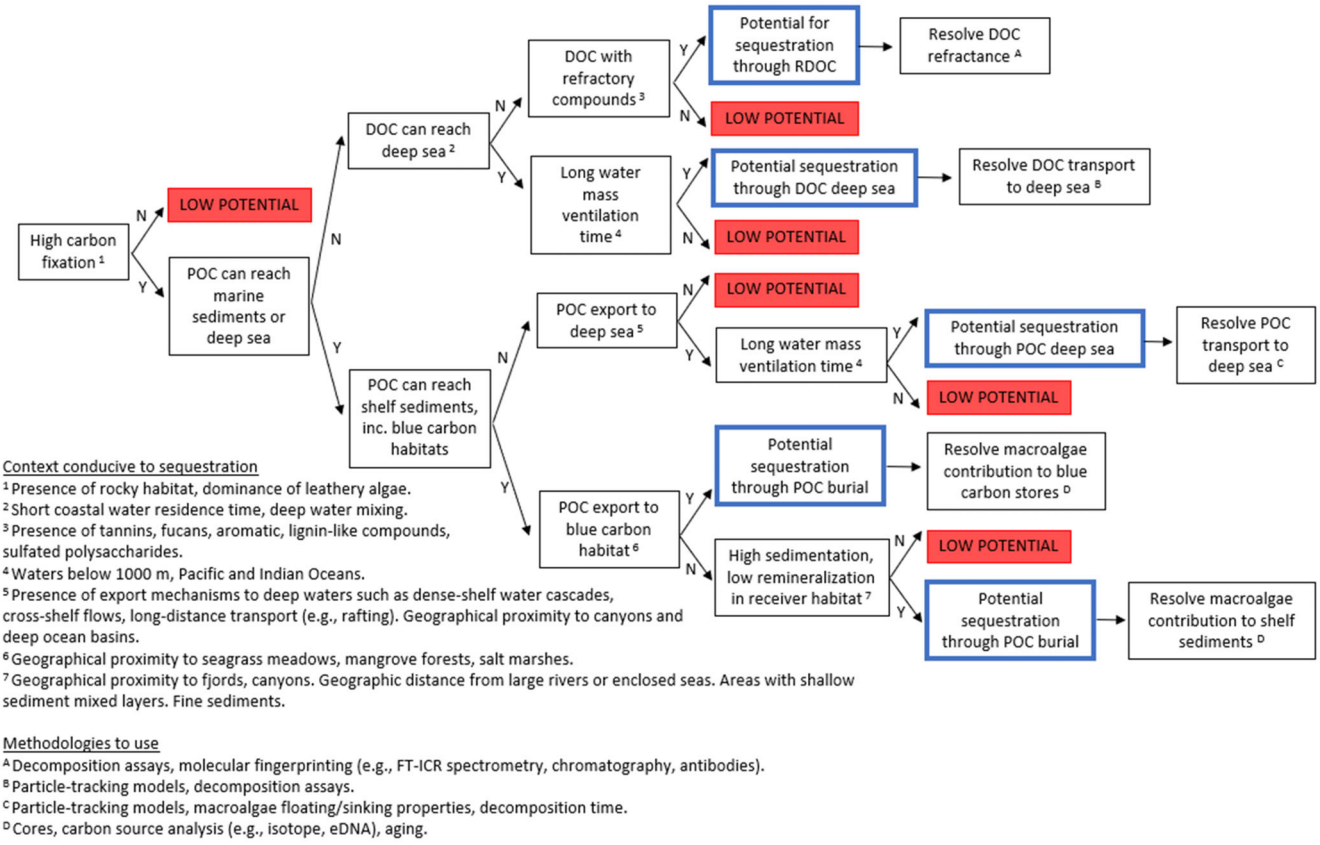

Fig. 5. Framework to determine the likelihood of macroalgae forest carbon sequestration. Pathways leading to low sequestration potential are indicated in red. DOC, dissolved organic carbon; eDNA, environmental DNA; FT-ICR, Fourier-transform ion cyclotron resonance; POC, particulate organic carbon; RDOC, recalcitrant DOC.

(De Haas *et al.*, 2002; Bourgeois *et al.*, 2016) and broad continental shelves (Bröder *et al.*, 2018)]. Decay during transport may be slower in cold waters (Filbee-Dexter *et al.*, 2022*a*), while most carbon appears to be respired in warmer tropical regions (Haas *et al.*, 2013). The presence of refractory molecules such phlorotannins, fucans, xylans, long-chain lipids, sulfated polysaccharides, aromatic and lignin-like compounds can delay degradation times (Wada *et al.*, 2007; Trevathan-Tackett *et al.*, 2015; Buck-Wiese *et al.*, 2022; Feng *et al.*, 2022).

Available evidence thus suggests that temperate and polar coastlines with large rocky areas and close to coastal carbon sinks (e.g. other blue carbon habitats, fjords, canyons) or the deep sea (narrow continental shelves) will likely have the greatest sequestration potential. This contrasts with other blue carbon ecosystems, whose sequestration capacity is largely in coastal tropical and temperate areas (Macreadie *et al.*, 2021).

Current assessments must be viewed only as a first step towards inventories of macroalgal carbon stocks and sequestration potential. A major constraint is their reliance on a pre-determined range of fixed carbon that was proposed to be ultimately sequestered (11–23% depending on the pathway; Krause-Jensen & Duarte, 2016), values which remain largely unconstrained by empirical field studies (Queirós *et al.*, 2019). The only exception can be found in estimates of carbon sequestration in Norway, which relied on carbon burial rates estimated from sediment cores, and whose values were used for other Nordic countries (Frigstad *et al.*, 2021). The development of model-based approaches to estimate carbon sequestration has been useful in established blue carbon ecosystems (Lovelock *et al.*, 2022*a*,*b*), and is particularly promising for macroalgae given the complexity of their flows and the amount of parameters that require measurement (Hurd *et al.*, 2022). Building simple, robust, evidence-based, and conservative models of the relationship between carbon fixation, export and sequestration will necessitate advances in macroalgae bio-tracing.

Although the importance of oceanographic processes in shaping the fate of POC and DOC exported from coastal habitats is widely recognized, oceanographic models are still rarely used to investigate the transport of macroalgal carbon outside of source habitats. Fortunately, hydrodynamic models are rapidly becoming available for many coastal regions, allowing tracing of macroalgae-derived carbon (Broch, Hancke & Ellingsen, 2022; Queirós *et al.*, 2022). Parametrizing these models with realistic values will require

a better understanding of the size distribution of detritus particles, their floating and sinking velocities, and decomposition rates. Model outputs should then be ground-truthed with presence/absence data of macroalgae in sediment cores or seawater samples. Advances in numerous fingerprinting techniques offer promising prospects in that regard. For example, eDNA analysis can be used to verify the presence of macroalgae carbon in sediments or deep-water samples (Ortega *et al.*, 2019; Frigstad *et al.*, 2021; Ørberg *et al.*, 2022), while the increasingly widespread use of Fourier-transform ion cyclotron resonance mass spectrometry (FT-ICR MS) or antibody-based techniques can enable the detection of specific recalcitrant molecular species derived from macroalgae (Buck-Wiese *et al.*, 2022; Feng *et al.*, 2022; Li *et al.*, 2022). Ultimately, verifying sequestration of macroalgae carbon will require dating of sediments or water masses, whose sampling and analysis is often costly.

Improved mapping efforts are required to produce robust global and national estimates of macroalgal forest sequestration potential, as there are currently substantial gaps between the mapped (70,000–110,000 km^2; Table S2) and potential (1,500,000–2,000,000 km^2, Jayathilake & Costello, 2021; Duarte *et al.*, 2022) distribution of macroalgal forests worldwide. Improvements in the resolution of predictive environmental layers can help close that gap. For instance, predicted macroalgal forest extent at 1 km resolution is twice that predicted at 25 m resolution (Frigstad *et al.*, 2021). Some of the discrepancies may also arise from inconsistencies in mapping methodologies among countries, which either rely on satellite imagery, visual surveys, estimates of suitable rocky area and macroalgae cover, or modelled distributions based on presence/absence data and environmental variables (Table S2). Developing remote-sensed high-resolution maps may help standardize those differences. A good starting point to estimate the global sequestration potential may be to map floating or shallow subsurface macroalgal forests, which will have the highest carbon fixation rates (Pessarrodona *et al.*, 2022). These approaches have been successfully implemented for other shallow underwater habitats (e.g. seagrass beds, coral reefs) and are rapidly gaining traction for macroalgal forests (Mora-Soto *et al.*, 2020). For deeper subsurface forests, high-resolution modelling may be the most cost-effective alternative to estimate their carbon sequestration potential (Gorman *et al.*, 2013; van Son *et al.*, 2020; Frigstad *et al.*, 2021; Gundersen *et al.*, 2021). Resolving what fraction of the world's macroalgal forests can be captured remotely or through modelling will thus be an important direction for future research.

The majority of assessments to date rely on extrapolating region- or continental-scale averages, masking considerable variability in the amount of carbon fixed and stored in macroalgal standing stocks at fine spatial scales (Gorman *et al.*, 2013; van Son *et al.*, 2020; Gundersen *et al.*, 2021). The amount of data available and methods to estimate carbon flows vary widely within each jurisdiction, which will likely affect the confidence of the estimates. For example, Australian carbon fixation estimates are derived from >1500 individual growth rates surveyed along the distribution of the most dominant species. Those from France, Japan, and Korea are based on extrapolations of the productivity-standing stock ratio from a few species spanning a few locations, whereas those from the UK are derived from a pan-Atlantic compilation of mean growth rates (Table S2). Assessments also vary in the form of carbon considered, with few estimates including DOC (but see Frigstad *et al.*, 2021). Developing standard methodologies and models to map and quantify macroalgae carbon stocks and fluxes (e.g. fixation, export, burial) should thus be a priority for future research.

Accurately assessing the contribution of macroalgae forests to carbon sequestration will also require further investigation of the direct effects of macroalgal forests on radiative forcing (e.g. cloud formation, albedo), and consideration of other biogeochemical processes that regulate CO_2 fluxes, such as those producing or consuming alkalinity. These are only just receiving attention, as showing additionality and permanence of these processes is more challenging than for those already discussed (Reithmaier *et al.*, 2021). The production and export of alkalinity is increasingly viewed as a significant CO_2 sink that complements the previously described organic carbon sequestration potential of blue carbon ecosystems (Reithmaier *et al.*, 2021; Perkins *et al.*, 2022). For instance, alkalinity produced *via* carbonate dissolution, denitrification, or sulfate reduction can enhance the carbon sink capacity of blue carbon sediments, as long as those metabolic products are permanently prevented from being re-oxidized (Reithmaier *et al.*, 2021). By contrast, the consumption of alkalinity can offset the carbon sequestration capacity of blue carbon ecosystems (Bach *et al.*, 2021; Buapet & Sinutok, 2021; van Dam *et al.*, 2021).

Carbonate precipitation by calcifying organisms is a major consumer of alkalinity in blue carbon ecosystems (Saderne *et al.*, 2019), and could also play an important role in macroalgae ecosystems (Bach *et al.*, 2021). Although generally lower than that of other environments (O'Mara & Dunne, 2019), carbonate precipitation in macroalgae forests is not necessarily negligible (Smith, 1972; Canals & Ballesteros, 1997). Calcifying groups such as coralline algae are often important carbonate producers (Smith, 1972) and are therefore potential CO_2 emitters if that CO_2 is released back to the atmosphere (Kalokora *et al.*, 2020). Our understanding of the magnitude of calcification-driven CO_2 fluxes and potential emissions in macroalgae forests is hampered by the paucity of empirical measurements. Decreases in alkalinity inside some macroalgal forests have been suggested to be indicative of increased calcification (Delille *et al.*, 2000). Yet, the majority of studies have not found significant differences in alkalinity or pH between the interior of macroalgal forests and open waters, nor between the benthos (where most calcifiers live) and canopy compartments (e.g. Watanabe *et al.*, 2020). This suggests that other processes may be responsible for changes in alkalinity within macroalgal forests (Koweek *et al.*, 2017), or that CO_2 released by calcification can be immediately fixed. This would constitute a positive feedback whereby

macroalgae favour calcification which, in turn, provides CO_2 for photosynthesis (Kalokora *et al.*, 2022). The ultimate effect of carbonate precipitation on CO_2 emissions will depend on whether the dissolved CO_2 is released to the atmosphere, as well as on the long-term fate of the carbonate retained in sea water. Available air–sea flux measurements show that, even when dominated by calcifying organisms, macroalgae forests are strong CO_2 sinks (Bensoussan & Gattuso, 2007). More research in this field is needed to unravel the importance and drivers of calcification and alkalinity in macroalgae forests, and in which contexts it may offset blue carbon potential.

VI. MACROALGAL FORESTS AND CLIMATE CHANGE MITIGATION

Although there is still considerable uncertainty in the magnitude of carbon that is sequestered globally by macroalgae (Krause-Jensen & Duarte, 2016; Hurd *et al.*, 2022), protecting, managing, and restoring macroalgae forests is increasingly viewed as an important step in efforts to mitigate climate change (Pidgeon *et al.*, 2021; Vanderklift *et al.*, 2022). As a result, macroalgae are currently included or being considered for inclusion in several climate mitigation policy and carbon market frameworks (Kuwae *et al.*, 2022*a*; Ricart *et al.*, 2022; Vanderklift *et al.*, 2022). To contribute to climate change mitigation, interventions targeting macroalgae must (*i*) modify the emissions or removals of GHGs associated with forests in addition to what would happen naturally (additonality); (*ii*) create permanent GHG gains, at least as defined by carbon accounting methods, which are typically at least 25 years (Richards & Huebner, 2012) but often 100 years (UNFCCC, Verra) (permanence); and (*iii*) reside within jurisdictional areas eligible for policy and management action (governability). For instance, even though macroalgal forests may naturally remove relevant fractions of a country's annual emissions (e.g. 4.4% of Norway's CO_2 emissions; Frigstad *et al.*, 2021), only emissions or removals beyond that natural baseline can be formally recognized within climate mitigation frameworks.

This section will explore these three criteria from the perspective of macroalgal-driven changes in CO_2 fluxes. Information on their emissions of other GHGs such as methane, nitrous oxide, or halocarbons is scarce, precluding an assessment of their potential importance. Methane emissions within macroalgae forests are likely to be low, as macroalgae occur mostly on exposed rocky substrates and most coastal methane emissions result from anaerobic methanogenesis in sediments (Rosentreter *et al.*, 2018, but see Roth *et al.*, 2022, 2023), being particularly high in eutrophic and meso- and hyposaline waters. The decomposition and burial of macroalgae-derived carbon in beaches and anoxic sediments, however, can stimulate methane production (Björk *et al.*, 2023), and requires further investigation. Large macroalgal aggregations have also been found to increase the sediment production of nitrous oxide (Wong *et al.*, 2021), which could potentially offset carbon sequestration. Finally, the release of halocarbons like bromoform by macroalgae may also contribute to the heating effect of GHGs in the atmosphere (Goodwin, North & Lidstrom, 1997; Leedham *et al.*, 2013), albeit release rates are largely variable between species and its global significance requires further investigation (Leedham *et al.*, 2013). Importantly, these macroalgae-driven GHG emissions will only counteract carbon sequestration if the dissolved gases are exchanged with the atmosphere. For example, methane released from sediments below 100 m depth rarely has any GHG effects (Pohlman *et al.*, 2017).

Most studies to date have found macroalgae forests to be strong net CO_2 sinks (Delille *et al.*, 2000; Ikawa & Oechel, 2015; Watanabe *et al.*, 2020; Kim *et al.*, 2022), with the intensity of CO_2 drawdown being related to forest area and productivity (Ikawa & Oechel, 2015). Evidence linking human actions in macroalgae ecosystems to CO_2 drawdown is mostly available for POC pathways, as tracking the fate of macroalgae-derived DOC presents numerous challenges as discussed above.

(1) Actionability and additionality

The responsiveness of macroalgal carbon fluxes to human interventions (actionability) is key to satisfying the principle of additionality, which ensures that interventions generate net GHG abatement that would not have occurred if they were not implemented. Within carbon markets, additionality also refers to actions that would not have taken place unless carbon finance was provided. For example, government-owned protected areas managing kelp harvesting can potentially generate additional carbon sequestration. However, that additional benefit would not necessarily meet the additional criteria for carbon crediting as it may have happened regardless of a carbon finance incentive (was government led). Below we provide a brief overview of evidence of human-driven changes in macroalgal carbon fluxes, outlining several interventions that could result in additional CO_2 emission reductions, and discuss challenges in measuring additionality. Interventions can be broadly grouped based on whether (*i*) CO_2 emissions to the atmosphere or decreases in carbon sequestration capacity resulting from habitat degradation can be avoided *via* improved management or conservation, or (*ii*) CO_2 removals can be enhanced by either restoring previously degraded forests or creating additional ones *via* afforestation (Macreadie *et al.*, 2017). Collectively, the reduction of net emissions achieved through either avoiding emissions or enhancing removals is known as abatement (Vanderklift *et al.*, 2022).

As macroalgae-driven carbon sequestration most likely occurs in habitats different from those where carbon was fixed, most human activities will affect either the carbon source or the sink. For example, increased harvest of wild stocks will only decrease the carbon donor capacity of a

Table 3. Human interventions with potential to modify macroalgal forest carbon fluxes. The column 'Certainty' denotes the confidence that a given intervention would lead to an alteration of the flux, based on available knowledge

Intervention	Examples	Certainty	Relevant literature
Avoid decreases in carbon sequestration capacity			
Directed at the carbon source			
Avoidance of direct habitat loss	Manage macroalgae harvest, decrease reef mining, land reclamation and coastal development	Medium–High	Dahl *et al.* (2016); Steen *et al.* (2016); González-Roca *et al.* (2021)
Avoidance of indirect habitat loss from overgrazing	Grazer management (e.g. sea urchin removal, protection of sea urchin predators like sea otters and sustainable management of coastal fish stocks like wolffish, cod and reef fish)	Medium–High	Gundersen *et al.* (2011); Wilmers *et al.* (2012); Williams *et al.* (2021); Miller *et al.* (2022)
Avoidance of indirect habitat loss from poor water quality	Catchment area management to reduce nutrient inputs, sedimentation	Medium	Airoldi (2003); Gorman *et al.* (2009); Mayer-Pinto *et al.* (2020)
Directed at the carbon sink			
Avoidance of marine sediment disturbance	Management of coastal vegetated sediments, management trawling or dredging activities	Low	Sala *et al.* (2021); Epstein & Roberts (2022); Epstein *et al.* (2022)
Increase carbon sequestration capacity			
Directed at the carbon source			
Management of wild habitats to increase carbon sequestration	Catchment area management to increase macroalgal productivity	Low	Fujita (2011)
Re-establishment of previously lost habitat	Macroalgal forest restoration (including enabling natural recolonization by reversing drivers of decline)	Medium	Eger *et al.* (2020, 2022)
Creation of new habitat	Coastal afforestation, expansion of coastal aquaculture	Medium	Sondak & Chung (2015); Hwang *et al.* (2020)

macroalgal forest (González-Roca *et al.*, 2021), but the past carbon stores originating from this habitat may remain unaffected. For this reason, we also distinguish whether human actions affect the carbon sources (i.e. macroalgal forest) or the carbon sinks (e.g. sediment) (Table 3). Most evidence for the effects of human interventions on carbon fluxes to date has been focused on POC pathways.

(*a*) *Avoiding decreases in carbon sequestration capacity from habitat degradation*

The harvesting of macroalgae forests, or destruction of their rocky habitat, has obvious negative effects on their standing stock and carbon donor capacity. Wild macroalgae are harvested mostly for human consumption (Ferdouse *et al.*, 2018), with Chile being the largest producer (~0.01 Tg C year^{-1}; Vega *et al.*, 2021). Unless done in a sustainable manner, overharvesting can lead to reductions in forest carbon stocks (Steen *et al.*, 2016; González-Roca *et al.*, 2021). For instance, Chilean kelp forests not subjected to harvest management have 50% lower standing stocks compared to forests that are sustainably harvested (González-Roca *et al.*, 2021). The total amount of illegally harvested kelp confiscated each year in Chile represents ~0.2% of the legal harvest, although the actual amount removed is unknown (SERNAPESCA, 2022). An upper limit estimate of the avoidable standing stock losses from all harvesting globally can be obtained from the global production and average carbon and dry mass contents of kelps (Ferdouse *et al.*, 2018; Vega *et al.*, 2021), yielding ~0.04 Tg C year^{-1}. Besides harvesting macroalgae itself, the localized removal of stones and boulders for use in construction has led to the total destruction of macroalgal habitat in some areas (Dahl *et al.*, 2016). Similarly, extensive losses in macroalgal habitat have occurred during the past 50 years due to land reclamation and industrialization, although these losses are poorly mapped (Kang, 2010; Wu *et al.*, 2020). Creating sustainable management plans and regulating destructive activities could therefore avoid further losses and have a positive effect on macroalgae carbon stocks.

Changes in the local biological community and in species interactions can also lead to widespread habitat losses. Grazing by sea urchins or fishes can cause persistent losses of macroalgae over large areas of coastline, with grazers playing an important role in determining the global distribution of macroalgae forests (Filbee-Dexter & Scheibling, 2014). For example, loss of macroalgal forests due to urchin grazing in

Norway is estimated to have caused the release of ~5.5 Tg C (Gundersen *et al.*, 2011; Verbeek *et al.*, 2021). As a result, grazer management is a widespread practice to avoid losses and preserve kelp carbon stocks (Eger *et al.*, 2022). A recent meta-analysis found that removal of sea urchins led to increases in macroalgae in 70% of cases (Miller, Blain & Shears, 2022), although scaling up to larger areas can become difficult without financial incentives (Cresswell *et al.*, 2019), and often requires continued culling efforts (and funding) to achieve long-term success (Shears & Babcock, 2002). Existing management actions to reduce overgrazing include protecting or reintroducing predators or sustainably managing grazer fisheries (Salomon *et al.*, 2008). Introduction of predators to control sea urchin populations in the northeast Pacific, for example, could potentially lead to increases of 4.4–8.7 Tg C in kelp carbon stocks (Wilmers *et al.*, 2012).

Land use changes and their effect on water quality are also an important global driver of macroalgal forest decline. Excess of nutrients and sediments around urban coastlines often result in coastal eutrophication and decreases in light availability, respectively. These, in turn, lead to decreases in, or total loss of, macroalgal standing stocks, carbon fixation, and export, as well as to contraction of their depth distribution (Tegner *et al.*, 1995; Gorman, Russell & Connell, 2009; Shepherd *et al.*, 2009; Blain, Hansen & Shears, 2021). For example, coastal pollution around the Adelaide Metropolitan Area (Australia) resulted in an estimated annual loss of 0.02 Tg C in macroalgal forest standing stock and of 3×10^{-3} Tg C in sequestration capacity (Filbee-Dexter & Wernberg, 2020). Globally, many macroalgae forests have been replaced by low-lying algal turfs as a result of urbanization and habitat destruction (Filbee-Dexter & Wernberg, 2018; Pessarrodona *et al.*, 2021), leading to decreases in standing stocks and carbon fixation (Copertino, Connell & Cheshire, 2005). Finally, the release of pollutants such as metals into waterways can impair the photosynthetic capabilities of macroalgae and lead to a decrease in their carbon fixation rates (Mayer-Pinto *et al.*, 2020). Management actions to improve water quality and reduce nutrient loads can stall declines and reverse them by allowing natural recolonization (de los Santos *et al.*, 2019), and should be effective in restoring the carbon sequestration potential of macroalgal forests.

Ocean warming is also a main driver of changes in macroalgal carbon fluxes, and addressing it may hold substantial benefits. Besides reducing carbon emissions to limit the effects of ocean warming, some management interventions such as reductions in harmful interactions driven by warming (e.g. herbivory), and genetic fortification of wild populations with warm-adapted individuals or beneficial microbes, may offer opportunities to maintain or prevent carbon stock losses (Wood *et al.*, 2019). In temperate regions, warming is expected to decrease kelp carbon fixation, increase detrital remineralization, and ultimately diminish carbon sequestration potential (Pessarrodona *et al.*, 2018*a*,*b*; Filbee-Dexter *et al.*, 2022*a*; Wright *et al.*, 2022), especially in warm range-edge populations (Pessarrodona *et al.*, 2018*b*). In Australia, marine heatwaves have resulted in 120,000 ha of macroalgal forests being lost in just two decades, which represents an estimated loss of 0.4 Tg C in standing stock and of 0.05 Tg C $year^{-1}$ in sequestration capacity (0.2–0.6% and 0.6–1.1% of the total stock and capacity, respectively) (Filbee-Dexter & Wernberg, 2020). Further climate change-related losses could reduce the sequestration potential by an additional 1–1.4 Tg C $year^{-1}$ by the year 2100, depending on the degree of future warming (Filbee-Dexter & Wernberg, 2020). On the other hand, warming and changes in ocean currents will likely drive macroalgal forest expansion and increases in carbon stocks in some regions like South Africa or the Arctic (Bolton *et al.*, 2012; Krause-Jensen *et al.*, 2020). For example, warming has limited sea urchin activity and mediated the partial recovery of macroalgal forests in northern Norway, leading to an increase in standing stocks of *ca.* 2 Tg C (Gundersen *et al.*, 2011). In some tropical regions, macroalgae are becoming the primary habitat providers following the decline of reef-building corals (De Bakker *et al.*, 2017). Shifts towards macroalgae dominance can result in drastic changes in ecosystem primary productivity, calcification and DOC fluxes, all of which can impact the net metabolic state of reefs (Roth *et al.*, 2021). In polar regions, the majority of predictive models and long-term data sets available show macroalgae forest expansions and increases in productivity, suggesting polar CO_2 fixation and sequestration by macroalgae is likely to be enhanced in the future (Krause-Jensen *et al.*, 2020). The latter can, however, be countered by melting permafrost and increased run-off in some regions, which may lead to increases in wind-driven resuspension of sediments and reductions of light and benthic primary productivity (Bonsell & Dunton, 2018; Filbee-Dexter *et al.*, 2018*a*).

Compared to macroalgal carbon sources, the effects of interventions targeting macroalgal carbon sinks are far less understood. The protection, management, and restoration of mangroves, saltmarshes and seagrasses likely secures the macroalgae carbon that is buried in these environments (Macreadie *et al.*, 2022), including those that are macroalgae derived. A range of human activities (e.g. shipping, dredging, deployment of cables) impact the carbon stored in shelf sediments, with fish trawling and shellfish dredging having the most widespread impacts by far (Pusceddu *et al.*, 2014). The disturbance of sediments by fishing gear is often expected to lead to carbon emissions due to remineralization of the organic carbon stored in shelf sediments (Pusceddu *et al.*, 2014; Paradis *et al.*, 2021; Epstein & Roberts, 2022). Global demersal fisheries have been estimated to cause 600–1400 Tg C to be released from sediments to the water column every year (Sala *et al.*, 2021). There is, however, still considerable uncertainty about the amount of carbon in the sediments that is contributed by macroalgae, the magnitude of organic carbon exposed during demersal fishing, and whether remineralized carbon contributes to atmospheric emissions (Epstein & Roberts, 2022). A review of 49 studies

found that 29% and 10% of studies reported decreased and increased organic carbon storage in sediments due to fishing activities, respectively, with the majority (61%) reporting no effect of fishing on carbon sediment stocks (Epstein *et al.*, 2022). Regulating fishing activities in areas with high carbon stocks (including high macroalgal carbon burial) and high fishing disturbance represents a sensible precautionary policy to avoid seabed carbon remineralization (Epstein & Roberts, 2022). Restrictions may have to be implemented for long periods of time, as short-term bans of fishing activities do not restore lost carbon stocks (Paradis *et al.*, 2021).

(*b*) *Increasing carbon sequestration capacity via habitat restoration and afforestation*

Globally, macroalgal forests have declined at a rate of 1.8% $year^{-1}$ since the 1950s (Krumhansl *et al.*, 2016), with at least 1.5 million hectares being lost this century alone (Filbee-Dexter *et al.*, 2022*c*). Restoration offers an opportunity to re-establish the carbon donor capacity of macroalgal forests, along with other valuable ecosystem services. This potential recovery could likely increase standing stocks by tens of Tg C, and sequestration capacity by several Tg C (Filbee-Dexter & Wernberg, 2020; Verbeek *et al.*, 2021). The number of macroalgae forest restoration initiatives is still substantially lower than that of other coastal blue carbon habitats, albeit efforts are rapidly scaling up (Duarte *et al.*, 2020; Morris *et al.*, 2020; Eger *et al.*, 2022). The majority of projects are small in scale (<1 ha) and short in duration (<2 years), typically being conducted scientifically to test best practices for restoration (Morris *et al.*, 2020; Eger *et al.*, 2022). It is clear that most restoration projects conducted so far cannot match the scale of degradation or loss already experienced by these habitats (56% of all projects are <100 m^2; Morris *et al.*, 2020) and are, therefore, far from realizing the full potential carbon abatement. Restoration projects have generally been motivated by the value that macroalgae provide as a habitat for coastal species, especially for commercially important ones (e.g. abalone; Unno & Hasegawa, 2010), and not for the value of macroalgal carbon *per se*. This has been the case for all of the large-scale restoration efforts conducted to date (Eger *et al.*, 2020).

Operationalizing macroalgae restoration at larger scales will be crucial if this tool is to be employed to increase carbon sequestration capacity. The upscaling of underwater restoration initiatives will largely rely on the elimination or amelioration of drivers of decline and improvements to restoration cost effectiveness. Currently project success and feasibility tend to be low (Morris *et al.*, 2020) while costs are generally high – typically tens to thousands of dollars per hectare (Bayraktarov *et al.*, 2015; Eger *et al.*, 2020). Some cost-effective technologies exist however. The recent development of 'green gravel' as a restoration tool, during which small rocks previously seeded with macroalgae are later out-planted in the field, also offers promising prospects for conducting cost-effective restoration at large scales (Fredriksen *et al.*, 2020). Establishing robust links between intervention actions and sequestration represents an additional challenge, particularly when interventions are not directed at the habitat itself and will rely on robust experimental designs. Given that the restoration of macroalgal habitats is a costly activity, avoiding losses by conserving and protecting existing wild habitats may offer a more effective way to achieve carbon abatement at scale.

To date, only afforestation projects, which deployed artificial structures for macroalgae to colonise (Lee *et al.*, 2020), have been conducted at the hundred to thousand hectare scale. However, they do not qualify as 'true' restoration, as they create additional habitat rather than restorinng previously lost habitat (Eger *et al.*, 2022). Afforestation projects rely heavily on cement manufacturing, an activity that generates substantial CO_2 emissions (Ali, Saidur & Hossain, 2011). Manufacturing the cement necessary to afforest a hectare of macroalgal habitat generates ~4–5.7 tons of CO_2: an average of 2.5 cement blocks are deployed per hectare (Eger *et al.*, 2020), with each block containing 2.5 tons of cement (a conservative estimate; Lee *et al.*, 2020) and each ton of cement manufactured emitting 0.65–0.92 tons of CO_2 (Ali *et al.*, 2011). Assuming that afforested habitats could fix a maximum of 7.97–11.01 tons of CO_2 ha^{-1} $year^{-1}$ (Sondak & Chung, 2015), and that 8% of that carbon reaches long-term sinks (Queirós *et al.*, 2019), the potential sequestration value of 1 ha of afforested habitat would equate to 0.6–0.9 tons of CO_2 $year^{-1}$. The largest afforestation projects to date have created 21,489 ha of habitat in Korea and 870 ha in Japan (Eger *et al.*, 2020; Hwang, Choi & Kim, 2020), which would yield an approximate sequestration potential of $\sim 5.2 \times 10^{-3}$ and 0.2×10^{-3} Tg C $year^{-1}$, respectively. Thus, it would take a minimum of 4.5–13.3 years before carbon sequestration from the artificial habitat could offset the emissions associated with concrete manufacturing alone, even without accounting for any of the emissions associated with transport and deployment of cement blocks.

(*c*) *Challenges when measuring additionality*

Central to the principle of additionality is the definition of a baseline scenario with which comparisons are benchmarked. Although simple in principle, determining that baseline in practice may prove challenging for macroalgae forest ecosystems, which often show large spatial and temporal natural variability in carbon fluxes. For example, forest areal extent and carbon fixation can vary several-fold across time and space, particularly amongst the surface-floating macroalgal species (Rassweiler *et al.*, 2018; Vega *et al.*, 2021), whilst export and burial may vary greatly depending on prevailing oceanographic conditions (Harrold & Lisin, 1989; Canals *et al.*, 2006). The use of regional means to stabilize variability may not solve this issue, as it has been shown to lead to systematic overestimation of climate benefits in other systems (Badgley *et al.*, 2022). Another challenge encountered when evaluating the net benefits of these activities include assessing

'leakage': unintended increases in emissions, either directly from unanticipated increases in GHG emissions or due to indirect decreases in other forms of carbon sequestration. For instance, large-scale kelp afforestation could lead to increases in GHG emissions from increased beach wrack (Björk *et al.*, 2023), whilst decreasing the sequestration capacity of phytoplankton due to nutrient reallocation (Bach *et al.*, 2021). The mitigation value of macroalgal forests restoration actions will thus depend on the net difference between the original ecosystem and its likely replacement state. Consequently, understanding carbon storage and sequestration in collapsed ecosystem states of macroalgal forests, such as turf reefs and sea urchin barrens, is required (Filbee-Dexter *et al.*, 2023). Finally, it is important to note that evidence linking human activities with carbon fluxes is mostly documented at the carbon stock level, and measuring and verifying whether they translate into permanent sequestration may be challenging and expensive (Coleman *et al.*, 2022).

(2) Permanence

Permanence refers to the net reduction in GHGs not being reversed for long periods of time, with 100 years often being used. Although this timescale is adopted by the United Nations Framework Convention on Climate Change (UNFCCC, 2022), it is important to note that the climatic effects of CO_2 release are likely to persist for longer timescales. An important consideration is that the drawdown of dissolved inorganic carbon species (CO_2 and HCO_3^-) from the water column by macroalgae during photosynthesis does not immediately remove CO_2 from the atmosphere (Bach *et al.*, 2021; Hurd *et al.*, 2022). As opposed to oceanic waters however, many of the coastal waters that macroalgal forests occupy are in close atmospheric equilibrium (Delille, Borges & Delille, 2009; Watanabe *et al.*, 2020). Carbon stored in the living biomass of macroalgae cannot be considered permanent, as most macroalgae are short-lived (<20 years; Howard *et al.*, 2017), but forests and their stocks, if protected and consistent in species and minimum size, can be accounted as permanent provided that loss and regrowth are in balance (e.g. persistent sub-Antarctic macroalgal forests 1829–2020; Mora-Soto *et al.*, 2021). Macroalgal carbon stored in marine sediments or the deep sea satisfies the principle of permanence, although obtaining and dating sediment cores is logistically challenging and analytically expensive, and there are still obstacles in resolving the sources of organic carbon in sediments. Both barriers hamper progress in research and in actioning macroalgae-related climate change mitigation actions. Still, continuous burial of carbon derived from kelp has been detected over centuries in Norwegian shelf sediments and Scottish Lochs (Frigstad *et al.*, 2021; O'Dell, 2022), and over several decades near macroalgae and abalone farms in China (Pan *et al.*, 2021). The carbon donor capacity of macroalgae can be recovered relatively fast after disturbance sources are removed (Tegner *et al.*, 1995), as long as negative feedback loops have not become established (Bennett *et al.*, 2015). For example, the full recovery of standing stocks after macroalgae were harvested from Norwegian forests took less than 5 years (Steen *et al.*, 2016).

(3) Governability

The carbon pools and flows of blue carbon ecosystems often do not fall neatly into existing carbon accounting and verification mechanisms (Friess *et al.*, 2022), which were originally developed for land-based ecosystems where carbon sequestration occurs autochthonously (i.e. in the same habitat where it is produced). In particular, the spatial decoupling of carbon sources and sinks is poorly captured in existing carbon mitigation policy frameworks, which may present accounting and governance challanges for macroalgae forest carbon. Despite efforts to address lateral carbon flows in carbon accounting, challenges remain associated with governance and attribution. For example, macroalgae carbon fixation can be easily attributed to forests within a specific country, but if the carbon is sequestered in the high seas or outside of national jurisdictions (e.g. outside Exclusive Economic Zones; EEZs) it cannot currently contribute to national GHG inventories or GHG reduction targets (Sutton-Grier & Howard, 2018; Gitarskiy, 2019). This could apply to refractory DOC stored in the open ocean or the POC exported beyond EEZs, neither of which are accounted for in established blue carbon ecosystems (Duarte & Krause-Jensen, 2017). Another governance challenge may include carbon flows that cross national boundary lines, where, for example, carbon being fixed in one country or project is sequestered in another. Some accounting methods (e.g. Verra methodologies) deal with this challenge through allochthonous deductions. More holistic 'seascape scale' approaches are being developed to account for carbon transport across habitats, as well as independent activities affecting carbon sources (e.g. kelp restoration) and sinks (e.g. seagrass conservation) (VERRA, 2022). Accounting for transboundary carbon flows may require new resource governance frameworks, such as those used in management of migratory fish stocks (Luisetti *et al.*, 2020). These will be crucial to ensure that activities enhancing carbon fixation by one nation (e.g. marine forest conservation, restoration) will not be counteracted by degradation of stocks in another (e.g. bottom trawling). Transboundary carbon flows may be common where continental shelves are shared between multiple countries (e.g. NW European Shelf), but may represent less of an issue in large or isolated countries (e.g. Australia, Japan, South Africa, Chile, island states). Developing novel accounting takes a significant amount of time (Sutton-Grier & Howard, 2018), and will rely on robust empirical evidence of macroalgal carbon flows.

Carbon finance is most often done at a project scale and relies on cost–benefit analysis (Coleman *et al.*, 2022), leveraging the costs of operation and benefits of carbon credits. Field sampling to quantify sequestration can represent a significant cost and a corresponding barrier to project implementation. The costs of field measurements are likely

to be higher for macroalgae forests, particularly if they need to be performed in deep water (Coleman *et al.*, 2022). To encourage investment into macroalgae forest protection and restoration through carbon markets, simpler and more cost-effective solutions are needed. Possibly, one of the most promising ways forward is developing indicator measures and models that predict the amount of sequestration generated by a given activity. Such models already exist for mangrove, tidal marsh and seagrass ecosystems (Needelman *et al.*, 2018; Lovelock *et al.*, 2022*a*,*b*), and could be adapted for application to a macroalgal forest context. Conservative estimates could then be used when models are applied with little validation required, which is likely to be the case for most regions where macroalgae forests occur. Developing parameters for such models is a worthy task for ecologists, biogeochemists and oceanographers. It is hoped that data presented in this review can serve a basis for the development of some of these products.

It seems apparent, then, that while macroalgae carbon sequestration may well be relevant at the global scale, macroalgae-derived carbon remains largely unacknowledged or unaccounted for and is presently invisible to existing climate mitigation frameworks.

VII. CONCLUSIONS

(1) Three potential sequestration pathways yielding long-term carbon storage have been reliably established in macroalgae by multiple studies, which suggests that macroalgae forests likely contribute to the natural global carbon sequestration baseline in a manner that is relevant to local, regional, and/or national scales.

(2) Scientific understanding of macroalgal forest carbon flows is centred around particulate organic carbon pathways, with several key fluxes leading to carbon sequestration (e.g. air–sea CO_2 flux, carbon burial in sediments, production of refractory compounds) still remaining poorly quantified.

(3) Macroalgae forests may make a meaningful contribution to climate change mitigation in certain contexts. Available evidence suggests that several management actions (conservation, restoration, and afforestation) have the potential to lead to additional carbon removal in the order of tens of Tg C, albeit their net effect on the radiative balance will ultimately depend on the emissions or removal of all greenhouse gases to/from the atmosphere.

(4) To date, preventing the loss of macroalgae forests would appear to be the most cost-effective strategy to avoid losing any carbon removal capacity from these habitats as well as safeguarding the numerous benefits they provide. Recovering this capacity from areas where forests have been lost will necessitate increases in the scale and improvements in the cost effectiveness of the restoration actions. Interventions to protect/enhance the amount of carbon sequestered in marine sediments may yield substantially higher (up to 1000 Tg C) climate benefits, but the relative contribution of macroalgal carbon to the overall sedimentary record is currently unknown.

(5) Incorporating macroalgae in blue carbon frameworks or carbon offsetting schemes will require resolving the spatial and temporal complexity of the fluxes leading to carbon sequestration with more locally relevant data (Table S4), assessing the removals/emissions of other greenhouse gases, as well as meeting the numerous specific rules and requirements of carbon accounting.

(6) Regions relatively close to each other may have starkly different sequestration potential, and methods to establish reliable links between the carbon fixed by marine forests in coastal environments and the carbon sequestered in marine sediments or the ocean interior are needed. This will likely require the use of particle-tracking models and carbon-source analysis of sediment cores or deep-water samples, tools that are not yet widely used.

(7) There are currently no frameworks that consider DOC in carbon accounting, but resolving the fate and contribution of macroalgae RDOC to the oceanic DOC pool, which is posited to be the largest carbon sequestration pathway, is an important scientific challenge.

(8) Carbon finance strongly relies on leveraging the costs of operation and benefits of carbon credits. The costs of management actions, carbon monitoring, reporting, and verification remain poorly quantified for macroalgal forests, but will likely be high. Developing robust, evidence-based and conservative models of macroalgal sequestration offers a promising solution to aid project implementation.

(9) The fact that sequestration may occur beyond EEZs or within other countries' jurisdictions can present challenges to carbon accounting in national GHG inventories. The low carbon burial intensity per unit area in continental shelves or in the "deep sea" may require that relatively large areas of ocean be protected from disturbance to guarantee the permanence of carbon stocks. This can be a benefit in relatively isolated areas where protection may safeguard significant carbon stocks with low stakeholder impact (e.g. southern Australian shelf), but can also be an obstacle in heavily transited areas with intense resource use (e.g. NW European shelf).

(10) Although developing the methods to measure and verify carbon flows in macroalgal forests presents several challenges (Table S5), the largest coastal vegetated habitat on Earth should not be ignored simply because it does not fit into existing frameworks.

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X. SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Search queries conducted using the *Scopus* database.
Table S2. Compiled estimates of net primary production (NPP), standing stock, area and sequestration rates for different species or groups of macroalgae within different countries or regions.
Table S3. Macroalgal particulate organic carbon (POC) on shelf sediments.
Table S4. Summary of the key drivers of main carbon fluxes and stores associated with macroalgae.
Table S5. Principal knowledge gaps regarding macroalgae-driven carbon fluxes and stores, the relative uncertainty (very low to very high) and the spatial coverage of available data.

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