



**University of Dundee**

## **Forensic carbon accounting**

Hurd, Catriona L.; Law, Cliff S.; Bach, Lennart T.; Britton, Damon; Hovenden, Mark; Paine, Ellie

*Published in:*  
Journal of Phycology: An International Journal of Algal Research

*DOI:*  
[10.1111/jpy.13249](https://doi.org/10.1111/jpy.13249)

*Publication date:*  
2022

*Document Version*  
Peer reviewed version

[Link to publication in Discovery Research Portal](#)

*Citation for published version (APA):*  
Hurd, C. L., Law, C. S., Bach, L. T., Britton, D., Hovenden, M., Paine, E., Raven, J. A., Tamsitt, V., & Boyd, P. W. (2022). Forensic carbon accounting: Assessing the role of seaweeds for carbon sequestration. *Journal of Phycology: An International Journal of Algal Research*, 58(3), 347-363. <https://doi.org/10.1111/jpy.13249>

### **General rights**

Copyright and moral rights for the publications made accessible in Discovery Research Portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

- Users may download and print one copy of any publication from Discovery Research Portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain.
- You may freely distribute the URL identifying the publication in the public portal.

### **Take down policy**

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

DR. CATRIONA HURD (Orcid ID : 0000-0001-9965-4917)

MRS. ELLIE RENEE PAINE (Orcid ID : 0000-0003-2816-9521)

DR. JOHN RAVEN (Orcid ID : 0000-0002-2789-3297)

Article type : Comment

Forensic carbon accounting: Assessing the role of seaweeds for carbon sequestration

Catriona L Hurd<sup>2</sup>

Institute for Marine and Antarctic Studies, University of Tasmania, Hobart, Tasmania, Australia,  
7001

Cliff S. Law

National Institute of Water and Atmospheric Research, Wellington 6021, New Zealand

Department of Marine Science, University of Otago, Dunedin 9016, New Zealand

Lennart T Bach, Damon Britton

Institute for Marine and Antarctic Studies, University of Tasmania, Hobart, Tasmania, Australia,  
7001

Mark Hovenden

Biological Sciences, School of Natural Sciences, University of Tasmania, Private Bag 55, Hobart  
7001

Ellie Paine

Institute for Marine and Antarctic Studies, University of Tasmania, Hobart, Tasmania, Australia,  
7001

John A Raven

Division of Plant Sciences, University of Dundee at the James Hutton Institute, Invergowrie,  
Dundee, DD2 5DA, UK

This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the [Version of Record](#). Please cite this article as [doi: 10.1111/JPY.13249](#). This article may be used for non-commercial purposes in accordance with Wiley Terms and Conditions for Self-Archiving.

This article is protected by copyright. All rights reserved

Climate Change Cluster, University of Technology, Sydney, Ultimo NSW2006, Australia  
School of Biological Science, University of Western Australia, 35 Stirling Highway, Crawley.  
WA 6009, Australia

Veronica Tamsitt

College of Marine Science, University of South Florida, St Petersburg, Florida, USA  
University of New South Wales, Sydney, Australia

Philip W Boyd

Institute for Marine and Antarctic Studies, University of Tasmania, Hobart, Tasmania, Australia,  
7001

Running title: Assessing seaweed carbon sequestration

Editorial Responsibility: M. Graham (Associate Editor)

## ABSTRACT

Carbon sequestration is defined as the secure storage of carbon-containing molecules for >100 y, and in the context of Carbon Dioxide Removal for climate mitigation, the origin of this CO<sub>2</sub> is from the atmosphere. On land, trees globally sequester substantial amounts of carbon in woody biomass, and an analogous role for seaweeds in ocean carbon sequestration has been suggested. The purposeful expansion of natural seaweed beds and aquaculture systems, including into the open ocean (ocean afforestation), has been proposed as a method of increasing carbon sequestration and use in carbon trading and offset schemes. However, to verify whether CO<sub>2</sub> fixed by seaweeds through photosynthesis leads to carbon sequestration is extremely complex in the marine environment compared to terrestrial systems, because of the need to jointly consider: the comparatively rapid turn-over of seaweed biomass, tracing the fate of carbon via particulate and dissolved organic carbon pathways in dynamic coastal waters, and the key role of atmosphere-ocean CO<sub>2</sub> exchange. We propose a Forensic Carbon Accounting approach, in which a thorough analysis of carbon flows between the atmosphere and ocean, and into and out of seaweeds would be undertaken, for assessing the magnitude of CO<sub>2</sub> removal and robust attribution of carbon sequestration to seaweeds.

Keywords: Carbon cycling; carbon dioxide removal; carbon sequestration; dissolved organic carbon; ocean afforestation; ocean-atmosphere equilibrium; particulate organic carbon; seawater carbonate system; seaweed aquaculture

## Abbreviations

CDR, Carbon Dioxide Removal; FCA, forensic carbon accounting

## INTRODUCTION

Seaweeds (marine macroalgae) are primary producers from three phyla (Ochrophyta, Chlorophyta and Rhodophyta) that grow in coastal systems worldwide and provide food and habitats for invertebrates and fish (Hurd et al. 2014). In Asia, seaweeds are farmed in coastal waters on large scales for human food, alginates, agar and carrageenan, and can provide important ecosystem services (Chung et al. 2017, Hu et al. 2021). Seaweed aquaculture is being trialled by an increasing number of ‘non-traditional’ seaweed-producing countries within the Americas, Africa,



Europe, and Australasia (Buschmann et al. 2008, Barbier et al. 2019, Kim et al. 2019, Kelly 2020, Msuya et al. 2022). One imperative driver of expanding seaweed aquaculture, including into the open ocean, is to increase the removal of atmospheric carbon dioxide (CO<sub>2</sub>) and sequester carbon, to help mitigate ongoing global warming (e.g., Chung et al. 2011, 2013, Ahmed et al. 2017, Duarte et al. 2017, Sondak et al. 2017, Hossain et al. 2021, UN Global Compact 2021). Carbon Dioxide Removal (CDR) from the atmosphere by seaweeds is a marine climate intervention approach that, if feasible, would remove atmospheric CO<sub>2</sub> that has been released by human activities (GESAMP 2019). This idea of growing seaweeds for CDR is attracting interest in the scientific literature (N'Yeurt et al. 2012, Duarte et al. 2017, 2021, Froehlich et al. 2019, UN Global Compact 2021), TV documentaries and the media (Gameau 2017; Figs. S1-S13 in the Supporting Information), and popular science books (Flannery 2017, Gameau, 2019, Bate 2021). However, the sequestration potential of seaweeds has also been questioned, due to logistical challenges and financial feasibility of expanding seaweed cultivation, particularly into the open ocean, efficacy and the permanence of carbon storage (Orr and Sarmiento 1992, Ritschard 1992, Howard et al. 2017, Bach et al. 2021, Gallagher et al. 2022), and the idea is considered contentious (Macreadie et al. 2019).

Sequestration is defined as the 'secure storage of a substance' and to demonstrate carbon sequestration requires proof that CO<sub>2</sub> is being removed from the atmosphere and 'locked up' in a stable form for a significant time scale, usually >100 years (GESAMP 2019, and also see Table 1 for a glossary of terms used in this manuscript). Carbon can be sequestered as living biomass such as terrestrial trees, or in an inert form such as organic carbon that has been accreted within an anoxic environment (e.g., soil). Examples of natural coastal systems known to sequester carbon are seagrass beds and mangroves: these are angiosperms with roots and rhizomes that anchor them in soft-sediment coastal systems where they create a carbon-rich soil capable of locking carbon up for millennia (Duarte et al. 2013). In the open ocean, the biological and solubility pumps are key examples of mechanisms that underpin sequestration in deep open waters or sediments. The biological pump, for example, is the vertical export into deep water of a small but significant proportion of carbon fixed photosynthetically by phytoplankton. This removal of atmospheric CO<sub>2</sub> over millennia has contributed to steady-state atmospheric CO<sub>2</sub> concentrations of ~280 ppmv during the pre-industrial Holocene epoch (Volk and Hoffert 1985). In contrast, we have relatively little understanding of the extent to which natural seaweed beds sequester carbon (Macreadie et al. 2019).

In terrestrial forests, the amount of carbon removed from the atmosphere and stored as living biomass (forests) and soil are relatively easily quantified (e.g., Hoover et al. 2000, Pan et al. 2013, Scharlemann et al. 2014, Köchy et al. 2015, Harris et al. 2021). These carbon stores are being used for carbon credits which businesses purchase to offset their carbon use and become 'carbon neutral' (Jansson et al. 2021). Similar carbon credit/offset schemes have been proposed for coastal marine systems including natural seaweed beds and aquaculture (Collins et al. 2021; Figs. S1-S3). There is also interest in growing seaweeds in the open ocean and sinking the resulting biomass to the deep ocean for carbon sequestration (D. Keller pers. comm.; Figs. S3, S4, S7, S10). In order to demonstrate CDR by seaweeds for use in carbon credit/offset schemes, the amount of CO<sub>2</sub> being removed from the atmosphere and the duration of its storage must be quantified robustly and attributed to seaweeds (GESAMP, 2019). However, demonstrating CDR and carbon sequestration by seaweeds in marine systems is much more complex than in terrestrial forests due to 1) the rapid turnover times of seaweed biomass compared to trees, 2) difficulties in tracking the fate of seaweed biomass and quantifying where and for how long it is stored, and 3) time scales of re-equilibration of CO<sub>2</sub> between the atmosphere and the low-CO<sub>2</sub> seawater that results from photosynthetic uptake of CO<sub>2</sub> by the seaweed. To unravel these complexities requires an understanding of biogeochemical cycling in a 4D context that incorporates ocean circulation and timescales of atmosphere/ocean interactions (Orr and Sarmiento 1992, Bach et al. 2021).

Forensic accounting is an investigative process used by auditors to examine business finances, to ensure that they are legitimate (Silverstone et al. 2012). As seaweeds are being proposed as a method for CDR and carbon sequestration with the potential for carbon credits, we propose an analogous approach of Forensic Carbon Accounting (FCA). In this approach, a thorough analysis of carbon flows between the atmosphere and ocean, and into and out of seaweeds would be undertaken, using a closed carbon budget adapted to the sequence of processes over relevant time scales to ensure verifiable CDR. FCA would be required for businesses that plan to use seaweeds for 'carbon credits' or 'carbon offsets' so that they can adequately account and attribute CDR and sequestration to seaweeds (Bellamy and Geden 2019). The sequence of processes centres on assessing the ocean/atmosphere carbon budget (quantification of all pools and fluxes at a single time point) in conjunction with a life cycle analysis in which all budgetary terms have annotated timescales, to provide the rigour required to demonstrate CDR and carbon sequestration. As FCA could be applied to other proposed methods for CDR, and carbon storage in the marine

environment for example shelf sediments (Luisetti et al. 2020), we use the term FCA-Seaweed (FCA-S) hereafter.

We begin our analysis of the potential of seaweeds for CDR and carbon sequestration by using the example of carbon sequestration in terrestrial forests as a counterpoint to the relative complexities of carbon accounting for seaweed beds. Next, as a baseline for discussion, we consider current knowledge of seaweed standing stocks, and the rate and fate of seaweed primary production. We then outline the physics and chemistry of CO<sub>2</sub> atmosphere-ocean interactions, and time scales of CO<sub>2</sub> influx into CO<sub>2</sub> deficient seawater (termed re-equilibration), which is critical to quantifying CDR. Finally we use FCA-S to examine three scenarios that have been proposed by which seaweeds might be used for CDR: 1) Natural seaweed beds (incorporated into Blue Carbon budgets, see later), 2) Coastal seaweed aquaculture, and 3) Ocean afforestation which is the purposeful introduction of seaweeds into the open ocean.

#### *Carbon dioxide uptake and time scales of storage by terrestrial forests compared to seaweed beds*

Terrestrial forests are a critical part of the Earth's carbon cycle and are responsible for the assimilation and sequestration of a significant fraction of anthropogenically-emitted CO<sub>2</sub> (IPCC 2021; Fig. 1). Globally, terrestrial forests store around 400 Gt C in biomass (Pan et al. 2013) and ~1000 Gt C in soils (Scharlemann et al. 2014). Plant leaves take up CO<sub>2</sub> directly from the atmosphere, mostly via diffusion through stomata. In the chloroplast, CO<sub>2</sub> is fixed into organic carbon by the enzyme RuBisCO. Approximately half of the carbon assimilated by plants is rapidly re-emitted through respiration, but the remainder is stored, for various time periods, as organic carbon in above-ground biomass (woody trunks, branches, and leaves) or roots. Trees also create substantial quantities of litter, which is incorporated into soil organic matter. This soil organic matter is complex and is classified into various soil carbon pools on the basis of turn-over times (Fig. 1). Globally, soils store approximately three times as much carbon in the upper 1 m as is present in the atmosphere (FAO 2015).

The substantial capacity of forests for CDR and sequestration to offset anthropogenic emissions is due to a combination of the longevity of woody tissues and the incorporation of forest-derived soil organic matter into long-lived soil carbon pools. Individual trees can live for centuries, storing substantial quantities of carbon in timber. Fallen logs can survive for decades or centuries further extending the period of carbon storage. Harvested trees also contribute to relatively long-lived stores, particularly as structural timber in buildings (Churkina et al. 2020).

Litter and organic matter from roots (rhizodeposition) are processed by soil invertebrates and micro-heterotrophs on various timescales from days to decades but the longest-lived soil carbon stores are physically and/or chemically protected from decomposition (Dynarski et al. 2020). These organic carbon pools can persist in soils for thousands of years and are considered refractory, accumulating deep within the soil profile and contributing substantially to the sequestration potential of terrestrial ecosystems. Protecting existing forests, ‘planting more trees’ through restoring de-forested areas and afforestation, and managing tree plantations, can help in slowing the ongoing rise in atmospheric CO<sub>2</sub> (Waring et al. 2020).

Similar to terrestrial plants, seaweeds take up CO<sub>2</sub> via leaf-like structures called blades, and fix CO<sub>2</sub> via the enzyme RuBisCO at equivalent rates (Mann 1973; Fig. 2). However, seaweeds take up CO<sub>2</sub> from seawater, not from the atmosphere; this additional step adds complexity and is crucial for assessing CDR, as discussed later. Seaweeds additionally take up dissolved HCO<sub>3</sub><sup>-</sup> from seawater, which is converted to CO<sub>2</sub> prior to fixation (Raven and Hurd 2012; Fig. 2). Rates of net primary production (NPP) by seaweeds are similar to those of terrestrial plants (Mann 1973). Large (1–40 m tall) brown seaweeds (Orders Laminariales ‘kelps’ and Fucales ‘wracks’) form dense beds, often called ‘forests’, in coastal temperate regions (Wernberg and Filbee-Dexter 2019). The idea that growing more seaweeds in the coastal and open oceans will sequester more carbon is compelling in its simplicity (e.g., Flannery 2017; Figs. S4, S6, S7). However, this analogy is misplaced because of some critical differences between terrestrial forests and seaweed beds.

Most seaweeds do not have roots but instead are attached to rock surfaces with a holdfast and consequently do not accumulate organic material as soil (Duarte et al. 2013, Hill et al. 2015). Seaweeds also have no woody structures, and the many have an annual life cycle and are small (<50 cm tall) with a rapid turnover of biomass (<0.5–7 y depending on species and location; Muraoka, 2004, Howard et al. 2017). Kelp beds, however, form significant biomass in temperate coastal systems, covering ~1,469,900 m<sup>2</sup> globally (Jayathilake and Costello 2020). However, most kelps lose a substantial proportion of their biomass each year through blade erosion, being ripped off rocks in storms or through their natural life cycle that includes shedding blades, and the biomass within a kelp forest can vary substantially between years (e.g., Buschmann et al. 2006, Queirós et al. 2019, Pedersen et al. 2021). It is interesting that for terrestrial forests, carbon storage estimates largely ignore the fraction contained in leaves because of the short residence

time (months to years) and their relatively small amounts of carbon compared to that stored in timber and soil (Pilli et al. 2006, table 2d-2f of Poorter et al. 2012).

'Blue carbon is “organic carbon that is captured and stored by the oceans and coastal ecosystems” and the term is used to distinguish carbon sequestered in marine systems from that of terrestrial ‘green carbon’ systems (Macreadie et al. 2019, and see Mcleod et al. 2011). Many countries, for example China, Australia, UK, and the European Union are developing blue carbon strategies involving enhancing blue carbon stocks to assist in CDR (Zhang et al. 2017, Wu et al. 2020, Bertram et al. 2021, Frigstad et al. 2021; Fig. S12). Seaweed beds around the world have been assessed in terms of biomass, and standing stocks of carbon (e.g., Muraoka 2004, Hill et al. 2015, Aller-Rojas et al. 2020, Filbee-Dexter and Wernberg 2020, Frigstad et al. 2021). Global estimates of the amount of carbon stored as living biomass in seaweed beds are 0.0075 to 2.55 Gt C (Bar-On and Milo 2019b), 0.012 Gt C (Howard et al. 2017) and 0.4 Gt C (Bar-On and Milo 2019a), values that are orders of magnitude smaller than those of terrestrial forests and terrestrial soil (400 Gt C and 1,000 Gt C, respectively). The potential of seaweed carbon storage is therefore much lower than that of terrestrial trees, but they may contribute to the blue carbon inventory.

#### *Natural seaweed beds: Carbon fluxes and fate in food webs*

Seaweed beds are highly dynamic and the CO<sub>2</sub> that has been fixed into organic matter has many fates in the coastal carbon cycle and food webs (Fig. 2). The flux of carbon that is best quantified for seaweeds is rates of photosynthesis/NPP of both individuals and beds (e.g., Gao and McKinley 1994, Chung et al. 2011, Krause-Jensen and Duarte 2016, 2017, Raven 2017, 2018, Pessarrodona et al. 2021). Seaweed biomass enters coastal food webs as particulate and dissolved organic carbon (POC and DOC respectively; e.g., Branch and Griffiths 1988, Pedersen et al. 2020, and see review of Smith and Fox 2021). POC is lost constantly from individual seaweeds via erosion due to the large drag forces exerted by waves (Hurd et al. 2014). Seaweeds that become detached and stranded on beaches are ground down by waves and sand to progressively smaller detrital particles (Hurd et al. 2014). The resulting detrital POC ‘flakes’ support coastal filter feeders (e.g., oysters, mussels, barnacles, ascidians; Duggins et al. 1989, Elliott Smith and Fox 2021). Larger pieces of seaweed tissue (debris) are eaten by macro-invertebrates such as abalone and sea urchins (Elliott Smith and Fox 2021). DOC is defined as organic carbon molecules which pass through a filter pore size 0.22-0.7 µm (GF/F) and provide substrate for heterotrophic bacteria and micro-heterotrophic eukaryotes, which in turn support progressively higher trophic levels (Paine et al.

2021). Seaweed beds support substantial numbers of sessile and mobile invertebrates (Bué et al. 2020, Taylor and Cole 1994, Hepburn and Hurd 2005, Poore et al. 2012, Suárez-Jiménez et al. 2017), which respire – release CO<sub>2</sub> – continuously (R<sub>H</sub>; Fig. 2). The cumulative effect of heterotrophic and autotrophic respiration is that in some cases, there is net release of CO<sub>2</sub> from a seaweed bed rather than a net uptake (Fig. 2; Gallagher et al. 2022). Elliott Smith and Fox (2021) highlight the need for a better understanding of the flows of seaweed ‘energy’ throughout food webs, because in many systems they are poorly quantified at present.

A large proportion of seaweed DOC and POC is exported laterally out of seaweed beds via currents and can ‘subsidize’ (add to) the carbon available for consumption by higher trophic levels in other coastal systems such as sandy beaches, seagrass beds, soft sediments and offshore deep-water habitats (Hyndes et al. 2014, Smale et al. 2018, Pedersen et al. 2020, Cartraud et al. 2021). Seaweed beds are therefore termed ‘carbon donors’, and the export of carbon from a seaweed bed has been termed ‘carbon leakage’ and ‘carbon out-welling’ (Hill et al. 2015, Queirós et al. 2019, Santos et al. 2021). Seaweeds that have been beach stranded can enter the food webs of sandy beaches and also terrestrial systems (Mellbrand et al. 2011, Suárez-Jiménez et al. 2017).

Similarly, the carbon contained in the faeces of urchins that have consumed seaweeds can be transported via currents to neighbouring areas (Poore et al. 2012, Filbee-Dexter et al. 2020).

Tracking the fate of seaweed carbon from the system in which it was originally fixed photosynthetically is therefore challenging (Filbee-Dexter and Wernberg 2020, Watanabe et al. 2020).

One of the least understood, but crucial, aspects of seaweed’s role in CDR is the biogeochemistry of its long term (>100 y) storage. In China, preserved fragments of red seaweed were identified in oil shale ‘vitrinite macerals’, although the vast majority of macerals were formed from freshwater green algae *Botryococcus* sp. and diatoms (Xie et al. 2014). A proportion of the POC derived from seaweed tissues is refractory, including alginates, xylans and sulphated polysaccharides, and relatively resistant to microbial degradation and so is most likely to form long-term carbon deposits in sediments (Trevathan-Tackett et al. 2015, Pedersen et al. 2021). Using eDNA, seaweed material has been detected throughout water columns of the world’s oceans to 4,000 m depth, and buried in marine sediments (Zaborska et al. 2018, Ortega et al. 2019, 2020). eDNA and stable isotopes have been used to track seaweed material from temperate coastal seaweed beds into offshore (13 km) coastal sediments (45 m depth; Queirós et al. 2019). A “preliminary, quantitative estimation’ of seaweed carbon buried in sediments was obtained in Norway using

eDNA from *Laminaria hypoborea* and *Saccharina latissima* in sediments estimated at 2,000 years old (Frigstad et al. 2021). Their measurements reveal that kelp eDNA forms 0.2 to 1.6 ng · g<sup>-1</sup> sediment compared to ‘unspecified DNA’ that forms 2- 8 µg · g<sup>-1</sup> sediment, indicating that these kelps comprise < 1.0% eDNA in sediments. It is important to note that eDNA can be derived from either DOC or POC, and detection of eDNA does not directly translate into the magnitude of stored seaweed carbon although methods are being developed to use eDNA as a proxy for carbon (Reef et al. 2017). These examples indicate that sediments contain proportions of seaweed carbon, but further research is needed to quantify their contribution (Orgeta et al. 2019).

Another potential storage route for seaweed carbon is via DOC, with up to 40% of gross primary production (GPP) released into the surrounding water column in this form (Khailov and Burlakova 1969, Sieburth 1969, Brylinsky 1977, Johnston et al. 1977). DOC ranges from labile to ultra-refractory and is classified by water column residence time (Hansell 2013). Labile DOC (labile, semi-labile) is readily bioavailable to micro-heterotrophs and rapidly re-mineralised to DIC through respiration, and thus has a short life span (days, weeks) in the water column (Carlson et al. 1994, 2002). Refractory DOC (semi-refractory, refractory, ultra-refractory) consists of molecules which are comparatively resistant to micro-heterotrophic utilisation and can be transformed from labile DOC through bacterial consumption via the microbial carbon pump (Ogawa et al. 2001, Jiao et al. 2014). Refractory DOC is a route for carbon sequestration as the molecules have a long residence time (years, thousands of years) and can contribute to the deep ocean carbon pool (estimated to be 4,000-6,000 y old; Hansell 2013, Krause-Jensen et al. 2018, Watanabe et al. 2020). However, a fraction of the deep ocean refractory DOC can be upwelled and broken down photochemically into more labile forms resulting in micro-heterotrophic remineralisation to DIC (Shen and Benner 2018, Paine et al. 2021). The fate of seaweed-derived DOC in biogeochemical carbon cycles is thought to be extremely important, but we have only a rudimentary understanding of its bioavailability and fate in the oceanic food webs (Paine et al. 2021).

#### *Atmosphere-ocean equilibrium of CO<sub>2</sub>*

The critical, often overlooked, step for demonstrating CDR by seaweeds is to understand the timescales for the transfer of atmospheric CO<sub>2</sub> into the surface ocean to rebalance the atmosphere-ocean concentration gradient in CO<sub>2</sub> caused by the uptake of dissolved CO<sub>2</sub> from seawater by seaweeds during photosynthesis, which is termed re-equilibration (Bach et al. 2021). In terrestrial

plants and trees, CO<sub>2</sub> is absorbed directly from the atmosphere making assessments of CDR relatively straightforward (Fig. 1). In marine systems, however, photosynthesis is the first in a two-step process that can lead to CO<sub>2</sub> removal from the atmosphere (Fig. 2). When a seaweed takes up CO<sub>2</sub>, it results in a CO<sub>2</sub> deficit in the seawater surrounding the seaweed. This deficit alters the equilibrium of CO<sub>2</sub> between the atmosphere and ocean and may result in CO<sub>2</sub> entering the surface ocean to re-equilibrate with the seawater carbonate system. The time-scale of this re-equilibration ranges from weeks to > 12 months (Wanninkhof et al. 2009, Jones et al. 2014). Therefore, the CO<sub>2</sub> fixed by seaweed photosynthesis from seawater will not necessarily equate to the removal of CO<sub>2</sub> from the atmosphere, because the processes of photosynthesis (seconds-minutes) and the re-equilibrium of seawater CO<sub>2</sub> (weeks-months) operate at different temporal scales i.e. they are decoupled. Therefore, understanding the role of seaweed beds in CDR requires an understanding, and quantification, of atmosphere-ocean dynamics (Fig. 3). Accounting for the re-equilibration of the dissolved CO<sub>2</sub> deficit in seawater with atmospheric CO<sub>2</sub> is an essential step in assessing the role of seaweeds in CDR.

The CO<sub>2</sub> equilibrium between air and water is driven by multi-faceted factors including physical (wind stirring and tidal mixing, wave-breaking, temperature and solubility), chemical processes (sea-water carbonate chemistry), and biological processes (photosynthesis [CO<sub>2</sub> uptake], respiration [CO<sub>2</sub> release], production of organic surfactants; Wanninkhof et al. 2009; Fig. 3). The sum of these processes will determine whether a system is a net CO<sub>2</sub> source or sink; a system that is net autotrophic is likely to cause an influx of CO<sub>2</sub> from the atmosphere but a heterotrophic system will result in CO<sub>2</sub> being released back into the atmosphere (Gallagher et al. 2022). Several studies have investigated the atmosphere-ocean gas exchange in shallow nearshore environments (Edson et al. 2008, Skadberg 2008, Ikawa 2012) each using sophisticated techniques including eddy co-variance. Each study reported complex controls on atmosphere-ocean gas exchange, with the dominant drivers varying with locale (Ikawa 2012), and across temporal scales from diurnal to seasonal (Skadberg 2008). Controls in coastal systems are much more variable than in the open ocean (Edson et al. 2008, Ikawa 2012), and therefore require a comprehensive suite of detailed measurements (Edson et al. 2008). Such complex dynamics present a major challenge to interpreting signals at a single site and also in providing a baseline over longer-timescales. Furthermore, due to the long timescales of CO<sub>2</sub> equilibration (weeks to months), CO<sub>2</sub> can be exchanged between seawater and the atmosphere some distance ‘downstream’ from where it was



originally taken up by seaweeds, because of stirring and lateral advection by ocean currents and tides (Watanabe et al. 2020).

### *Forensic Carbon Accounting*

In Table 2, we provide an illustrative list of the factors that must be considered in FCA-S of natural seaweed beds (including the expansion of natural beds, e.g., Chung et al. 2013), coastal aquaculture and open ocean aquaculture systems. For each of these three scenarios, a forensic assessment needs to take into account NPP, CO<sub>2</sub> equilibration of seawater that carries the signature of carbon fixation including subsequent transport in ocean currents, the fate of organic carbon within the seaweed bed and lateral transfer of fixed carbon to the open ocean and sediments, and, finally, biological and physical processes that remineralise organic carbon into CO<sub>2</sub> and return it to the atmosphere (Figs. 2, 3; Table 2). For the purpose of this assessment, we focus mostly on the Order Laminariales and Fucales which, we collectively term ‘kelps’, as they are major habitat formers creating underwater ‘forests’ with a relatively high biomass per unit area, are extensively cultivated in Asia, and kelps have been proposed for ocean afforestation.

### FCA-S for natural seaweed beds

If a kelp bed is well established and has a constant annually-averaged biomass over >100 y (steady state), and the flux of CO<sub>2</sub> between the air and seawater is in equilibrium, then CO<sub>2</sub> may be considered sequestered as a living carbon store (assuming a net autotrophic kelp system).

However, to demonstrate CDR, the time scales over which a seaweed bed is in a long-term steady state need to be accounted for. For many kelp beds, the standing stock varies seasonally as substantial proportions of biomass are lost each year leading to the partial or complete removal of that bed which can take months or longer to re-establish (e.g., Zimmerman and Robertson 1985, Graham et al. 2007, Reed et al. 2008, 2009, Schiel and Foster 2015). These variations in seaweed standing stocks have implications for atmosphere-ocean CO<sub>2</sub> fluxes, because the influx of atmospheric CO<sub>2</sub> into seawater will occur only when the seaweed biomass is present and photosynthesising.

Importantly, the fate of the seawater that carries the CO<sub>2</sub> deficit that resulted from photosynthesis needs to be tracked as the parcel of seawater may be rapidly transferred laterally in the tidally stirred, dynamic coastal system adjacent ecosystems, where it will mix with other water parcels that bear the signature of the resident ecosystem (Watanabe et al. 2020; Fig. 4). For example, if

the seafloor which the transported water parcel overlies is net heterotrophic (e.g., an mussel or oyster bed), then respiratory production of CO<sub>2</sub> may reduce the CO<sub>2</sub> deficit and so the net influx of CO<sub>2</sub> from the atmosphere (Fig. 4). Further, if the seawater parcel remains in a highly-dynamic wave impacted region, physical processes will lead to the seawater CO<sub>2</sub> rapidly re-equilibrating with the atmosphere (Fig. 4). As highlighted by Siegel et al. (2021) for marine carbon sequestration, there are also myriad pathways regulated by complex interactions of biology and physics that will determine the CO<sub>2</sub> deficit at any point in time and space. The complexities of tracking the fate of the seawater are also discussed by Watanabe et al. (2020), and Figure 4 shows a conceptualization of how different dynamic and biological factors may alter CO<sub>2</sub> re-equilibration with the atmosphere.

The CO<sub>2</sub> deficit in seawater that results from seaweed photosynthesis has been measured in several diverse systems, using changes in the seawater carbonate system and estimates of the resulting CO<sub>2</sub> flux (e.g., Delille et al. 2000, Chung et al. 2013, Han et al. 2021), but there are fewer studies directly measuring the effects of coastal seaweed beds on atmosphere-ocean CO<sub>2</sub> fluxes (Ikawa and Oechel 2014, Watanabe et al. 2020). Each study demonstrated that photosynthesis resulted in a sustained dissolved CO<sub>2</sub> deficit and so a flux of CO<sub>2</sub> from the atmosphere into the seawater, but there was substantial flux variation over time related to seaweed biomass per unit area, and other factors such as seasonal rates of photosynthesis and growth. For *Macrocystis* in La Jolla, California, a 7-y time series (2006-2011) revealed a correlation between canopy cover and annual CO<sub>2</sub> flux: the flux ranged from zero (i.e., no influx of atmospheric CO<sub>2</sub>), during 2006 when an El Niño event led to a temporary loss of the kelp bed, to -600 g C · m<sup>-2</sup> · y<sup>-1</sup> in 2008, at which time the surface area of this *Macrocystis* bed was maximal at 4.2 km<sup>2</sup> (Ikawa and Oechel 2014). Similarly, for *Ecklonia cava* and *E. stolonifera* beds in Korea, the seawater CO<sub>2</sub> deficit was evident only during the growth period of the seaweeds, in this case for ~ 1 y (Chung et al. 2013). Both studies illustrate the impermanence of seaweed canopies over time and the need for steady state for long term CDR and carbon sequestration as living biomass (Fig. 4). The importance of including atmosphere-ocean CO<sub>2</sub> fluxes in estimations of carbon sequestration is also highlighted for seagrass systems, which are considered to be important blue carbon stocks: Measurements of atmosphere-ocean CO<sub>2</sub> fluxes indicate that seagrasses may sequester much less CO<sub>2</sub> than previous estimates based on sediment accretion rates alone (Van Dam et al. 2021). In summary, natural kelp beds are probably not in steady state for timescales relevant to CDR and carbon sequestration, and this needs to be carefully accounted for when calculating carbon offsets or credits.

## FCA-S for coastal aquaculture

The expansion of kelp aquaculture in coastal systems has been considered for carbon sequestration, with an example being the 'CO<sub>2</sub> removal belt' in Korea (Chung et al. 2013). The rates of growth and NPP for kelps in aquaculture are likely to be comparable to those growing in a natural seaweed bed, but there will be a much more rapid turnover of biomass, because all biomass is harvested every 3-6 months, depending on species (e.g., Redmond et al. 2015, Hwang and Park 2020). Also, for aquaculture there will be a comparatively low standing stock for much of the cultivation cycle as the seaweeds are typically out-planted from nurseries as small (< 2 cm) juveniles with a low biomass per unit area, then harvested at maximum biomass (Hwang and Park 2020). The shorter time-scales of seaweed cultivation in aquaculture compared to natural seaweed beds will reduce loss and recycling of carbon via grazing, blade erosion and storm damage. However, the rapid turnover of an aquaculture system, and the relatively short time frame of maximum biomass prior to harvesting, means that it may not reach the necessary equilibrium between atmosphere and water required for observable CDR.

In seaweed aquaculture, seaweeds farmed on fabricated structures in monocultures in surface waters up to ~5 m depth in regions that are naturally occupied by diverse assemblages of phytoplankton (primary producers that support natural coastal food webs including zooplankton; e.g., Utto et al. 1997). Seaweed and phytoplankton compete for the same limiting resources of light, nitrogen and phosphorous (Hurd et al. 2014). Intensive seaweed aquaculture could therefore alter the trophodynamics of the coastal food web. For FCA-S, there is a need to demonstrate that CDR by cultivated seaweeds would be of a greater magnitude than that of the existing phytoplankton system, which means that a baseline assessment of the natural ecosystem is required. This comparison was undertaken by Jiang et al. (2013) who used seawater carbonate system parameters and constant values of atmospheric  $p\text{CO}_2$  to estimate the flux of CO<sub>2</sub> in a seaweed farm consisting of either *Laminaria japonica* or *Gracilaria lemaneiformis* and a nearby phytoplankton system. Primary production by phytoplankton, based on Chl *a*, was similar in both systems. In spring and summer the CO<sub>2</sub> influx to seawater where seaweeds were grown was over twice that of the phytoplankton system, but there was no difference in CO<sub>2</sub> influx between the two systems in autumn, and the influx was ~30% higher for the seaweed system in winter. This study illustrates that the natural phytoplankton are a CO<sub>2</sub> sink that can be as effective as seaweeds, at some times of year, at generating a CO<sub>2</sub> deficit in surface waters and an influx of atmospheric

CO<sub>2</sub>. Further, growing more macroalgae in coastal waters could increase resource competition with phytoplankton which may result in less phytoplankton carbon fixation (Boyd et al. 2022). Additionally, the cultured seaweeds provide a substrate for 'fouling' heterotrophs such as bryozoans which would not otherwise grow in surface waters with associated CO<sub>2</sub> losses due to respiration and calcification (DeLille et al. 2000, Bach et al. 2021): each of these factors need to be accounted for.

In aquaculture scenarios (coastal and open ocean), all 'carbon costs' in a balance sheet must be accounted for, such as those for fabricating, deploying and maintaining infrastructure needed to grow seaweeds, in the nearshore or open ocean, and using automated machinery and vessels to harvest seaweeds (Viser and Obi 2020). Seaweed biomass may be used for various products that have been considered as carbon off-sets such as biochar (e.g., Gao and McKinley 1994, Bird et al. 2010, Hughes et al. 2012, Duarte et al. 2013, Singh et al. 2021) and the carbon costs of processing and transport also need to be accounted. In cases where seaweeds are harvested for human food or animal feed, the seaweed-carbon is transformed into another form and this does not equate to sequestration since both human and animal carbon cycles ultimately return seaweed-carbon to the atmosphere as a mix of gases including CO<sub>2</sub> and methane (CH<sub>4</sub>) which must be accounted for, particularly as CH<sub>4</sub> is a much more potent greenhouse gas than CO<sub>2</sub> (C2ES).

#### FCA-S for ocean afforestation

Ocean afforestation for CDR and sequestration is receiving substantial interest from scientists, governments and businesses interested in blue carbon, carbon offsetting or carbon credits (Figs. S1-S4, S6, S13). It has been suggested that 'planting' ~9% of the global ocean surface, an area of ~36 million km<sup>2</sup> equivalent to a land area of China + USA + Canada + Brazil, with floating or underwater seaweed farms would assist in CDR (N'Yeurt et al. 2012). Based on a seawater dissolved inorganic nitrogen concentration threshold, Froehlich et al. (2019) further suggest that 48 million km<sup>2</sup> of the global ocean is suitable for growing seaweeds. Melara et al.'s (2020) life cycle analysis of a Bioenergy with Carbon Capture and Storage (BECCS) open ocean cultivation system suggested by Hughes et al. (2012) indicates that 17% of the global ocean would need to be cultivated with seaweeds for carbon sequestration on a global scale. These values are orders of magnitude greater than those of 1,600 km<sup>2</sup> estimated for current seaweed farming (Duarte et al. 2017). At such expanded and vast scales, seaweeds will interact with the Earth System in various

ways, many of which are not understood or even considered (Bach et al. 2021). The Earth System is multi-faceted and finely balanced, with many feedbacks between atmosphere, land and oceans that are not fully understood (IPCC 2021), which makes projecting the cumulative effects of seaweeds on the climate system very challenging (Bach et al. 2021).

As for coastal aquaculture, FCA-S in the open ocean would need to demonstrate that CDR and sequestration by seaweeds is greater than that of the existing natural system. The open ocean is not an unproductive 'desert' as has been claimed (see Maruyama et al. 2004), but a highly-complex functioning ecosystem with phytoplankton forming the base of food webs that underpin food security from the open ocean (UN SDGs; Boyd et al. 2022). Furthermore, each ocean basin is different biogeochemically, and in some regions NPP is limited by nitrogen, in others iron (Moore et al. 2013). Nutrient limitation of seaweed growth is a critical factor that needs to be considered in assessing the feasibility of macroalgal occupation of the open ocean (Orr and Sarmiento 1992, Bach et al. 2021). A discussion of how seaweeds, purposefully released on rafts, may fare in the open ocean, and their potential interactions with the natural phytoplankton community, including nutrient competition, macroalgal DOC release, and allelopathy, are detailed in an accompanying perspective paper (Boyd et al. 2022).

NPP in the subtropical North Atlantic is naturally limited by nitrogen (Moore et al. 2013) and pelagic *Sargassum* spp. has been resident in this area (Sargasso Sea) for centuries (Wang et al. 2019). Seemingly, inadvertent fertilization since the early 2000's from riverine transport of excess fertilisers from the Amazon (soyabean crops) has resulted in a massive increase in the extent of floating *Sargassum* biomass, termed the Great Atlantic Sargassum Belt (Wang et al. 2019). Pelagic *Sargassum* spp. has extended and created substantial environmental problems as tonnes of seaweed wash onto beaches as far north as Florida (Wang et al. 2019). It has been suggested for the GASB that rates of sequestration via the export of refractory DOC to the deep ocean will be greater than that of the biological pump of the natural phytoplankton community (Hu et al. 2021). However, neither study considers key elements of the FCA-S approach we advocate in terms of atmosphere-ocean exchange and consideration of time scales of equilibrium influenced by transport. Provisional estimates indicate that, following CO<sub>2</sub>-fixation by *Sargassum*, the influx of atmospheric CO<sub>2</sub> would take 2.5–18 times longer than the CO<sub>2</sub>-deficient seawater remains in contact with the atmosphere (Bach et al. 2021), potentially hindering CDR verification.

It has been proposed that seaweeds growing on (biodegradable) structures in the open ocean could be sunk, which would sequester seaweed carbon at depth beneath the seasonally or

permanently stratified density layer and out of communication with the atmosphere for time periods (up to millennia) dependent on the depth to which the carbon penetrates (Fig. S3, a and b): the open ocean contrasts with the coastal ocean as there is strong seawater density stratification between the upper ocean and deep and abyssal waters below (Fig. 3). However, the long time-scales of re-equilibration in the open ocean (3-4 months global average; Jones et al. 2014) may decouple the processes of seaweed NPP and CDR; for example, in the event that the surrounding surface water is subducted and isolated from the atmosphere, the CO<sub>2</sub>-deficit will not be replenished by influx from the atmosphere (Fig. 4). The sequestration potential of sinking seaweeds will also depend on the density (i.e., rafts · km<sup>-2</sup>) of the aquaculture system. If seaweeds are free-floating in small scale patches, as has been proposed (Fig. S3b), the scale cannot be sufficient for a substantial CO<sub>2</sub> influx from the atmosphere (Boyd et al. 2022).

The idea of ocean afforestation for climate mitigation has been considered since 1974, focussing on growing *Macrocystis pyrifera* offshore (see Ritschard 1992), and more recently as Ocean Macroalgal Afforestation (N'Yeurt et al. 2012). Early ocean modelling illustrated that ocean afforestation led to limited enhancement of CDR, and the efficacy of such offshore systems has been questioned (Orr and Sarmiento, 1992). In contrast, others project that ocean afforestation would result in significant CDR across the global ocean (D. Keller, pers. comm.). Further, artificial upwelling of nutrient-rich seawater from below the thermocline has been proposed as a method to overcome nutrient limitation of seaweed growth in the open ocean, and hence to increase seaweed NPP and potentially CDR and carbon sequestration (Ritschard 1992, GESAMP 2019). This idea has gained popularity as 'marine permaculture' (Flannery 2017, Gameau 2017, 2019; Figs. S5, S9). A factor sometimes neglected in the analyses of marine permaculture is that artificially upwelled seawater needed to fuel seaweed growth offshore is not only rich in inorganic nitrogen, but also has high dissolved CO<sub>2</sub> concentrations (see Karl and Letelier 2008, Oschlies et al. 2010). Moving CO<sub>2</sub>-rich seawater to the ocean surface will affect the atmosphere-ocean CO<sub>2</sub> equilibrium which may result in the out-gassing of CO<sub>2</sub> to the atmosphere (GESAMP 2019), and this needs to be accounted for within the concept of FCA-S. There are additional challenges for undertaking FCA-S in the open ocean which include the financial and energy costs of verifying that seaweed carbon is sequestered in the deep ocean and tracking the lateral transport or subduction of the seawater that carries the CO<sub>2</sub> deficit.

## CONCLUSIONS

Natural seaweed beds are without doubt extremely important for the health and well-being of coastal systems, marine biodiversity, and the people who rely on them for fisheries, aquaculture, and recreational activities (Smale et al. 2013). Terrestrial systems are extremely important in global carbon sequestration, and rates and fates of CO<sub>2</sub> assimilated directly from the atmosphere and sequestered in woody biomass and soil are well quantified and can therefore be used reliably for carbon credits and offsets (Mappin et al. 2021). In contrast, the complexities of atmosphere-ocean CO<sub>2</sub> interactions, the rapid turnover of seaweed biomass, and potential for lateral export to other systems of POC and DOC, means that quantifying CDR and carbon sequestration will be very challenging. A thorough FCA-S of natural seaweed beds, coastal and open ocean aquaculture in various biogeographic regions system will require multi-disciplinary teams of biogeochemists, algal physiologists and ecologists, chemical and physical oceanographers, modellers and expertise on atmosphere-ocean interactions and ocean dynamics (Table 2). As seaweed eDNA has been detected in various global locations such as the deep ocean and marine sediments, it is likely that on a geological time scales (millennia) they have contributed to sedimentary carbon stores, although this contribution is yet to be quantified. However, the time scale to mitigate anthropogenically produced CO<sub>2</sub> by 2050 is short. Given the immediate and urgent need of removing CO<sub>2</sub> from the atmosphere, the concept of FCA-S must be developed as soon as possible if we are to explore in detail the concept of using seaweeds to sequester carbon.

#### ACKNOWLEDGEMENTS

We are extremely grateful to Albert Pessarrodona for his critical feedback on an earlier version of the m/s, and that of three anonymous reviewers. This study was funded by an Australian Research Council (ARC) Discovery Project DP200101467 to CLH, ARC Future Fellowship FT200100846 to LTB, and ARC Laureate Fellowship FL160100131 to PWB. The University of Dundee is a registered Scottish Charity No SC015096.

#### REFERENCES

Ahmed, N., Bunting, S. W., Glaser, M., Flaherty, M. S. & Diana, J. S. 2017. Can greening of aquaculture sequester blue carbon? *Ambio* 46:468-77.

Aller-Rojas, O., Moreno, B., Aponte, H. & Zavala, J. 2020. Carbon storage estimation of *Lessonia trabeculata* kelp beds in Southern Peru: an analysis from the San Juan de Marcona region. *Carbon Management* 11:525-32.

Bach, L. T., Tamsitt, V., Gower, J., Hurd, C. L., Raven, J. A. & Boyd, P. W. 2021. Testing the climate intervention potential of ocean afforestation using the Great Atlantic *Sargassum* belt. *Nat Commun* 12:2556.

Bar-On, Y. M. & Milo, R. 2019a. The biomass composition of the oceans: a blueprint of our blue planet. *Cell* 179:1451-54.

Bar-On, Y. M. & Milo, R. 2019b. The global mass and average rate of rubisco. *Proc. Natl. Acad. Sci. USA* 116:4738-43.

Barbier, M., Charrier, B., Araujo, R., Holdt, S., Jacquemin, B., Rebours, C. & Chopin, T. 2019. Pegasus - Phycomorph European Guideline for a Sustainable Aquaculture of Seaweeds. In Barbier, M. & Charrier, B. [Eds.] *COST Action FA1406* Roscoff, France.

Bate, M. 2021. *With a Little Kelp from Our Friends*. Thames & Hudson Australia Pty Ltd, Melbourne, Australia, 64 pp.

Bellamy, R. & Geden, O. 2019. Govern CO<sub>2</sub> removal from the ground up. *Nat. Geosci.* 12:874-76.

Bertram, C., Quaas, M., Reusch, T. B. H., Vafeidis, A. T., Wolff, C. & Rickels, W. 2021. The blue carbon wealth of nations. *Nat. Clim. Chang.* 11:704-09.

Bird, M. I., Wurster, C. M., de Paula Silva, P. H., Bass, A. M. & de Nys, R. 2010. Alga-biochar--production and properties. *Bioresour. Technol.* 102:1886-91.

Boyd, P.W., Bach, L.T., Hurd, C.L., Paine, E. Raven, J.A., Tamsitt, V. 2022. Ramifications of ocean afforestation for offshore biosecurity. *Nat. Ecol. Evol.* <https://doi.org/10.1038/s41559-022-01722-1>



Branch, G. & Griffiths, C. 1988. The Benguela ecosystem. Part v. The coastal zone. *Oceanogr. Mar. Biol. Ann. Rev.* 26:395-486.

Brylinsky, M. 1977. Release of dissolved organic matter by some marine macrophytes. *Mar. Biol.* 39:213-20.

Bué, M., Smale, D. A., Natanni, G., Marshall, H., Moore, P. J. & Beger, M. 2020. Multiple-scale interactions structure macroinvertebrate assemblages associated with kelp understory algae. *Divers. Distrib.* 26:1551-65.

Buschmann, A.H., Moreno1, C., Váasquez, J.A., & Hernández-González MC. 2006. Reproduction strategies of *Macrocystis pyrifera* (Phaeophyta) in Southern Chile: The importance of population dynamics. *J. Appl. Phycol.* 18:575–82.

Buschmann, A. H., Hernandez-Gonzalez, M. d. C. & Varela, D. 2008. Seaweed future cultivation in Chile: perspectives and challenges. *Int. J. Environ. Pollut.* 33:432-5.

C2ES - Centre for Climate and Energy Solutions <https://www.c2es.org/content/main-greenhouse-gases/>. Accessed 28<sup>th</sup> February 2022.

Carlson, C. A., Ducklow, H. W. & Michaels, A. F. 1994. Annual flux of dissolved organic carbon from the euphotic zone in the northwestern Sargasso Sea. *Nature* 371:405-8.

Carlson, C. A., Giovannoni, S. J., Hansell, D. A., Goldberg, S. J., Parsons, R., Otero, M. P., Vergin, K. & Wheeler, B. R. 2002. Effect of nutrient amendments on bacterioplankton production, community structure, and DOC utilization in the northwestern Sargasso Sea. *Aquat. Microb. Ecol.* 30:19-36.

Cartraud, A. E., Lavery, P. S., Rae, C. M. & Hyndes, G. A. 2021. Pathways to spatial subsidies by kelp in seagrass meadows. *Estuar. Coasts* 44:468-80.

Chung, I. K., Beardall, J., Mehta, S., Sahoo, D. & Stojkovic, S. 2011. Using marine macroalgae for carbon sequestration: a critical appraisal. *J. Appl. Phycol.* 23:877-86.

Chung, I. K., Oak, J. H., Lee, J. A., Shin, J. A., Kim, J. G. & Park, K. S. 2013. Installing kelp forests/seaweed beds for mitigation and adaptation against global warming: Korean Project Overview. *ICES J. Mar. Sci.* 70:1038-44.

Chung, I. K., Sondak, C. F. A. & Beardall, J. 2017. The future of seaweed aquaculture in a rapidly changing world. *Eu. J. Phycol.* 52:495-505.

Churkina, G., Organschi, A., Reyer, C. P., Ruff, A., Vinke, K., Liu, Z., Reck, B. K., Graedel, T. & Schellnhuber, H. J. 2020. Buildings as a global carbon sink. *Nat. Sustain.* 3:269-76.

Collins, N., Mediboyina, M.K., Cerca, M., Vance, C. & Murphy F. 2022. Economic and environmental sustainability analysis of seaweed farming: Monetizing carbon offsets of a brown algae cultivation system in Ireland. *Bioresour. Technol.* 346:126637

Delille, B., Delille, D, Fiala, M, Prevost, C. & Fankignoulle, M. 2000. Seasonal changes of pCO<sub>2</sub> over a sub-antarctic *Macrocystis* bed. *Polar Biol.* 23:706-16.

Duarte, C. M. 2017. Reviews and syntheses: Hidden forests, the role of vegetated coastal habitats in the ocean carbon budget. *Biogeosciences* 14:301-10.

Duarte, C. M., Losada, I. J., Hendriks, I. E., Mazarrasa, I. & Marbà, N. 2013. The role of coastal plant communities for climate change mitigation and adaptation. *Nat. Clim. Chang.* 3:961-68.

Duarte, C. M., Wu, J., Xiao, X., Bruhn, A. & Krause-Jensen, D. 2017. Can seaweed farming play a role in climate change mitigation and adaptation? *Front. Mar. Sci* 4:100.

Duarte C. M., Bruhn, A. & Krause-Jensen, D. 2021. A seaweed aquaculture imperative to meet global sustainability targets. *Nat. Sustain.* doi.org/10.1038/s41893-021-00773-9.

Duggins, D. O., Simenstad, C. A. & Estes, J. A. 1989. Magnification of secondary production by kelp detritus in coastal marine ecosystems. *Science* 245:170-3.

Dynarski, K. A., Bossio, D. A. & Scow, K. M. 2020. Dynamic stability of soil carbon: Reassessing the “permanence” of soil carbon sequestration. *Front. Environ. Sci.* 8:218.

Edson, J. B., Degrandpre, M. D., Frew, N. & McGillis, W. R. 2008. Investigations of air-sea gas exchange in the CoOP coastal air-sea chemical exchange project. *Oceanography* 21:34-45.

Elliott Smith, E. A. & Fox, M. D. 2021. Characterizing energy flow in kelp forest food webs: a geochemical review and call for additional research. *Ecography* 44:1-16.

Fan, W., Zhang, Z., Yao, Z., Xiao, C., Zhang, Y., Zhang, Y., Liu, J., Di, Y., Chen, Y. & Pan, Y. 2020a. A sea trial of enhancing carbon removal from Chinese coastal waters by stimulating seaweed cultivation through artificial upwelling. *App. Ocean Res.* 101:102260.

FAO, ITPS. 2015. *Status of the World's Soil Resource– (SWSR) - Main Report*. 1–648 (Food and Agriculture Organization of the United Nations and Intergovernmental Technical Panel on Soils).

Fan, W, Xiao, C., Li, P., Zhang, Z, Lin, T., Pan, Y., Di, Y. & Chen Y. 2020. Intelligent control system of an ecological engineering project for carbon sequestration in coastal mariculture environments in China. *Sustainability* 12:5227.

Filbee-Dexter, K., Pedersen, M. F., Fredriksen, S., Norderhaug, K. M., Rinde, E., Kristiansen, T., Albretsen, J. & Wernberg, T. 2020. Carbon export is facilitated by sea urchins transforming kelp detritus. *Oecologia* 192:213-25.

Filbee-Dexter, K. & Wernberg, T. 2020. Substantial blue carbon in overlooked Australian kelp forests. *Sci. Rep.* 10:12341.

Flannery, T. 2017. *Sunlight and Seaweed: An Argument For How To Feed, Power and Clean Up The World*. Text Publishing, Melbourne, Australia, 192 pp.

Floeter, S. R., Behrens, M., Ferreira, C., Paddock, M. & Horn, M. 2005. Geographical gradients of marine herbivorous fishes: patterns and processes. *Mar. Biol.* 147:1435-47.

Frigstad, H., Gundersen, H., Andersen, G.S., Borgersen, G., Kvile, K.O., Krause-Jensen, D., Boström, C., Bekkby, T., D'Auriac, M.A., Ruus, A., Thormar, J., Asdal, K. & Hancke, K. 2021. *Blue Carbon – climate adaptation, CO<sub>2</sub> uptake and sequestration of carbon in Nordic blue forests*. Nordic Council of Ministries, doi.org/10.6027/temanord2020-541

Froehlich, H. E., Afflerbach, J. C., Frazier, M. & Halpern, B. S. 2019. Blue growth potential to mitigate climate change through seaweed offsetting. *Curr Biol* 29:3087-93 e3.

Gameau, D. 2017. *2040*. Madman Entertainment, Australia, 92 minutes.  
<https://www.madman.com.au/catalogue/view/41979/2040>

Gameau, D. 2019b. *2040: A Handbook for the Regeneration based on the documentary 2040*. Pan Macmillan Australia PTY Limited, Sydney, Australia. 302 pp.

Gao, K. & McKinley, K. R. 1994. Use of macroalgae for marine biomass production and CO<sub>2</sub> remediation: a review. *J. App. Phycol.* 6:45-60.

Gallagher J.B., Shelamoff, V. & Layton, C. 2022. Seaweed ecosystems may not mitigate CO<sub>2</sub> emissions *ICES J. Mar. Sci.* fsac011

GESAMP 2019. High level review of a wide range of proposed marine geoengineering techniques. Boyd P.W. and Vivian, C.M.G. (eds). IMO/FAO/UNESCO-IOC/UNIDO/WMO/IAEA/UN/UN Environment/UNDP/ISA Joint Group of Experts on the Scientific Aspects of Marine Environmental Protection. Rep. Stud. GESAMP No. 98, 144 pp.

Graham, M.H., Vasquez, J.A. & Buschmann A.H. 2007. Global ecology of the giant kelp *Macrocystis*: from ecotypes to ecosystems. *Oceanogr. Mar. Biol.* 45:398-88.

Han, T., Shi, R., Qi Z., Huang, H. & Gong, X. 2021. Impacts of large-scale aquaculture activities on the seawater carbonate system and air-sea CO<sub>2</sub> flux in a subtropical mariculture bay, southern China. *Aquac. Environ. Interact.* 13:199–210.

Hansell, D. A. 2013. Recalcitrant dissolved organic carbon fractions. *Annu. Rev. Mar Sci.* 5:421-45.

Harris, N.L., Gibbs, D.A., Baccini, A., Birdsey, R.A., de Bruin, S., Farina, M., Fatoyinbo, L., Hansen, M.C., Herold, M., Houghton, R.A., Potapov, P.V., Suarez, D.R., Roman-Cuesta, R.M., Saatchi, S.S., Slay, C.M., Turubanova, S.A. & Tyukavina, A. 2021 Global maps of twenty-first century forest carbon fluxes. *Nat. Clim. Chan.* 11:234-240.

Hepburn, C. D. & Hurd, C. L. 2005. Conditional mutualism between the giant kelp *Macrocystis pyrifera* and colonial epifauna. *Mar. Ecol. Prog. Ser.* 302:37-48.

Hill, R., Bellgrove, A., Macreadie, P. I., Petrou, K., Beardall, J., Steven, A. & Ralph, P. J. 2015. Can macroalgae contribute to blue carbon? An Australian perspective. *Limnol. Oceanogr.* 60:1689-706.

Hoover, C.M., Birdsey, R.A., Heath, L.S & Stout, S.L. 2000. How to estimate carbon sequestration on small forest tracts. *J. For.* 98:13–19.

Hossain, M. S., Sharifuzzaman, S. M., Nobil, M. N., Chowdhury, M. S. N., Sarker, S., Alamgir, M., Uddin, S. A., Chowdhury, S. R., Rahman, M. M., Rahman, M. S., Sobhan, F. & Chowdhury, S. 2021. Seaweeds farming for sustainable development goals and blue economy in Bangladesh. *Mar. Policy* 128:104469

Howard, J., Sutton-Grier, A., Herr, D., Kleypas, J., Landis, E., McLeod, E., Pidgeon, E. & Simpson, S. 2017. Clarifying the role of coastal and marine systems in climate mitigation. *Front. Ecol. Environ.* 15:42-50.

Hu, C., Wang, M., Lapointe, B. E., Brewton, R. A. & Hernandez, F. J. 2021. On the Atlantic pelagic 'argassum's role in carbon fixation and sequestration. *Sci. Total Environ.* 781:146801

Hughes, A. D., Black, K. D., Campbell, I., Davidson, K., Kelly, M. S. & Stanley, M. S. 2012. Does seaweed offer a solution for bioenergy with biological carbon capture and storage? *Greenh. Gases* 2:402-07.

Hurd, C. L., Harrison, P. J., Bischof, K. & Lobban, C. S. 2014. *Seaweed Ecology and Physiology*. Cambridge University Press, Cambridge, UK, 551 pp.

Hwang, E.K. & Park, C. S. 2020. Seaweed cultivation and utilization of Korea. *Algae* 35: 107-21.

Hyndes, G. A., Nagelkerken, I., McLeod, R. J., Connolly, R. M., Lavery, P. S. & Vanderklift, M. A. 2014. Mechanisms and ecological role of carbon transfer within coastal seascapes. *Biol.* 89:232-54.

Ikawa, H. & Oechel, W.C. 2015. Temporal variations in air-sea CO<sub>2</sub> exchange near large kelp beds near San Diego, California. *J. Geophys. Res. Oceans* 120:50–63.

IPCC. 2021. Summary for Policymakers. In MassonDelmotte, V., Zhai, P., Pirani, A., Connors, S.L., Péan, C., Berger, S., Caud, N., Chen, Y., Goldfarb, L., Gomis, M.I., Huang, M., Leitzell, K., Lonnoy, E., Matthews, J.B.R., Maycock, T.K., Waterfield, T., Yelekçi, O., Yu, T. & Zhou, B. [Eds.] *Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, 40 pp.

Jansson, C., Faiola, C., Wingler, A., Zhu, X. G., Kravchenko, A., de Graaf, M. A., Ogden, A.J., Handakmbura, P.P., Werner, C., & Beckles, D.M. 2021. Crops for carbon farming. *Front. Plant Sci.* 12:doi.org/10.3389/fpls.2021.636709.

Jayathilake, D.R. & Costello, M.J. 2020 A modelled global distribution of the kelp biome. *Biol. Conserv.* 252:10815.

Jiang, Z., Fang, J., Mao, Y., Han, T. & Wang, G. 2013. Influence of seaweed aquaculture on marine inorganic carbon dynamics and sea-air CO<sub>2</sub> flux. *J. World Aquac. Soc.* 44:133-40.

Johnston, C. S., Jones, R. G. & Hunt, R. D. 1977. A seasonal carbon budget for a laminarian population in a Scottish sea-loch. *Helgoländ. Wiss. Meer.* 30:527-45.

Jones, D. C., Ito, T., Takano, Y. & Hsu, W. C. 2014. Spatial and seasonal variability of the air-sea equilibration timescale of carbon dioxide. *Global Biogeochem. Cy.* 28:1163-78.

Karl, D. M. & Letelier, R. M. 2008. Nitrogen fixation-enhanced carbon sequestration in low nitrate, low chlorophyll seascapes. *Mar. Ecol. Prog. Ser.* 364:257-68.

Kelly, J. 2020. Australian Seaweed Industry Blueprint - A Blueprint For Growth. AgriFutures Australia, Wagga Wagga, NSW, Australia, 44 pp.

Khailov, K. M. & Burlakova, Z. P. 1969. Release of dissolved organic matter by marine seaweeds and distribution of their total organic production to inshore communities. *Limnol. Oceanogr.* 14:521-27.

Kim, J., Stekoll, M. & Yarish, C. 2019. Opportunities, challenges and future directions of open-water seaweed aquaculture in the United States. *Phycologia* 58:446-61.

Klemas, V. 2012. Remote sensing of coastal plumes and ocean fronts: overview and case study. *J. Coast. Res.* 28:1-7.

Klemas, V. 2013. Airborne remote sensing of coastal features and processes: An overview. *J. Coast. Res.* 29:239-55.

Köchy, M., Hiederer, R., & Freibauer., A. 2015. Global distribution of soil organic carbon – Part 1: Masses and frequency distributions of SOC stocks for the tropics, permafrost regions, wetlands, and the world. *Soil* 1:351-65.

Krause-Jensen, D. & Duarte, C. M. 2016. Substantial role of macroalgae in marine carbon sequestration. *Nat. Geosci.* 9:737-42.

Krause-Jensen, D., Lavery, P., Serrano, O., Marba, N., Masque, P. & Duarte, C. M. 2018. Sequestration of macroalgal carbon: The elephant in the Blue Carbon room. *Biol. Lett.* 14:20180236.

Lin, T., Fan, W., Xiao, C., Yao, Z., Zhang, Z., Zhao, R., Pan, Y. & Chen, Y. 2019. Energy management and operational planning of an ecological engineering for carbon sequestration in coastal mariculture environments in China. *Sustainability* 11:3162.

Liu, S., Jiang, Z., Wu, Y., Deng, Y., Chen, Q., Zhao, C., Cui, L. & Huang, X. 2019. Macroalgal bloom decay decreases the sediment organic carbon sequestration potential in tropical seagrass meadows of the South China Sea. *Mar. Pollut. Bull.* 138:598-603.

Liu, S., Trevathan-Tackett, S. M., Ewers Lewis, C. J., Huang, X. & Macreadie, P. I. 2020. Macroalgal blooms trigger the breakdown of seagrass blue carbon. *Environ. Sci. Technol.* 54:14750-60.

Luisetti, T., Ferrini, S., Grilli, G., Jickells, T.D., Kennedy, H., Kröger, S., Lorenzoni, I., Milligan, B., van der Molen, J., Parker, R., Pryce, T., Turner, R.K. & Tyllianakis, E. 2020. Climate action requires new accounting guidance and governance frameworks to manage carbon in shelf seas. *Nat. Commun.* 11:1–10.

Macreadie, P. I., Anton, A., Raven, J. A., Beaumont, N., Connolly, R. M., Friess, D. A., Kelleway, J. J., Kennedy, H., Kuwae, T., Lavery, P. S., Lovelock, C. E., Smale, D. A., Apostolaki, E. T., Atwood, T. B., Baldock, J., Bianchi, T. S., Chmura, G. L., Eyre, B. D., Fourqurean, J. W., Hall-Spencer, J. M., Huxham, M., Hendriks, I. E., Krause-Jensen, D., Laffoley, D., Luisetti, T., Marba, N., Masque, P., McGlathery, K. J., Megonigal, J. P., Murdiyarso, D., Russell, B. D., Santos, R., Serrano, O., Silliman, B. R., Watanabe, K. & Duarte, C. M. 2019. The future of blue carbon science. *Nat. Commun.* 10:3998.



McLeod, E., Chmura, G.L., Bouillon, S., Salm, R., Björk, M., Duarte, C.M., Lovelock, C.E., Schlesinger, W.H. & Silliman, B.R. 2011. A blueprint for blue carbon: Toward an improved understanding of the role of vegetated coastal habitats in sequestering CO<sub>2</sub>. *Front. Ecol. Environ.* 9:552–60.

Mann, K. H. 1973. Seaweeds: Their productivity and strategy for growth: The role of large marine algae in coastal productivity is far more important than has been suspected. *Science* 182:975-81.

Mappin, B., Ward, A., Hughes, L., Watson, J.E. M., Cosier, P. & Possingham, H.P. 2021 The costs and benefits of restoring a continent's terrestrial ecosystems. *J. Appl. Ecol.* doi: 10.1111/135-2664.14008

Maruyama, S., Tsubaki, K., Taira, K. & Sakai, S. 2004. Artificial upwelling of deep seawater using the perpetual salt fountain for cultivation of ocean desert. *J. Ocean.* 60:563-68.

Melara, A. J., Singh, U. & Colosi, L. M. 2020. Is aquatic bioenergy with carbon capture and storage a sustainable negative emission technology? Insights from a spatially explicit environmental life-cycle assessment. *Energy Conver. Manag.* 224:113300.

Mellbrand, K., Lavery, P. S., Hyndes, G. & Hambäck, P. A. 2011. Linking land and sea: Different pathways for marine subsidies. *Ecosystems* 14:732-44.

Moore, C. M., Mills, M. M., Arrigo, K. R., Berman-Frank, I., Bopp, L., Boyd, P. W., Galbraith, E. D., Geider, R. J., Guieu, C., Jaccard, S. L., Jickells, T. D., La Roche, J., Lenton, T. M., Mahowald, N. M., Marañón, E., Marinov, I., Moore, J. K., Nakatsuka, T., Oschlies, A., Saito, M. A., Thingstad, T. F., Tsuda, A. & Ulloa, O. 2013. Processes and patterns of oceanic nutrient limitation. *Nat. Geosci.* 6:701-10.

Msuya, F.E., Bolton, J., Narrain, K., Nyonje, B., Cottier-Cook, E.J. 2022 Seaweed farming in Africa: current status and future potential. *J. Appl. Phycol.* doi.org/10.1002/s10811-o21-0276-w.

Muraoka, D. 2004. Seaweed resources as a source of carbon fixation. *Bull. Fish. Res. Agency Japan* 1:59-64.

N'Yeurt, A. d. R., Chynoweth, D. P., Capron, M. E., Stewart, J. R. & Hasan, M. A. 2012. Negative carbon via ocean afforestation. *Process Saf. Environ. Prot.* 90:467-74.

Orr, J. C. & Sarmiento, J. L. 1992. Potential of marine macroalgae as a sink for CO<sub>2</sub>: Constraints from a 3-D general circulation model of the global ocean. *Water Air Soil Pollut.* 64:405-21.

Ortega, A., Geraldi, N. R., Alam, I., Kamau, A. A., Acinas, S. G., Logares, R., Gasol, J. M., Massana, R., Krause-Jensen, D. & Duarte, C. M. 2019. Important contribution of macroalgae to oceanic carbon sequestration. *Nat. Geosci.* 12:748-54.

Ortega, A., Geraldi, N. R. & Duarte, C. M. 2020. Environmental DNA identifies marine macrophyte contributions to Blue Carbon sediments. *Limnol. Oceanogr.* 65:3139-49.

Oschlies, A. Pahlow, M., Yool, A. & Matear, R.J. 2010. Climate engineering by artificial ocean upwelling: Channelling the sorcerer's apprentice. *Geophys. Res. Lett.* 37:4

Paine, E. R., Schmid, M., Boyd, P. W., Diaz-Pulido, G. & Hurd, C. L. 2021. Rate and fate of dissolved organic carbon release by seaweeds: A missing link in the coastal ocean carbon cycle. *J. Phycol.* 57:1375-91.

Pan, Y., Birdsey, R. A., Phillips, O. L. & Jackson, R. B. 2013. The structure, distribution, and biomass of the world's forests. *Ann. Rev. Ecol. Evol.* 44:593-622.

Pedersen, M. F., Filbee-Dexter, K., Frisk, N. L., Sárossy, Z. & Wernberg, T. 2021. Carbon sequestration potential increased by incomplete anaerobic decomposition of kelp detritus. *Mar. Ecol. Prog. Ser.* 660:53-67.

Pedersen, M. F., Filbee-Dexter, K., Norderhaug, K. M., Fredriksen, S., Frisk, N. L., Fagerli, C. W. & Wernberg, T. 2020. Detrital carbon production and export in high latitude kelp forests. *Oecologia* 192:227-39.

Pessarrodona, A., Filbee-Dexter, K., Krumhansl, K. A., Moore, P. J. & Wernberg, T. 2021. A global dataset of seaweed net primary productivity. Cold Spring Harbor Laboratory. doi.org/10.1101/2021.07.12.452112.

Pilli, R., Anfodillo, T. & Carrer, M. 2006. Towards a functional and simplified allometry for estimating forest biomass. *For. Ecol. Manage.* 237:583-93.

Poore, A.G.B., Campbell, A.H., Coleman, R.A., Edgar, G.J., Veijo, J., Reynolds, P.L., Sotka, E.E., Stachowicz, J.J., Taylor, R.B., Vanderklift, M.A. & Duffy, J.E. 2012. Global patterns in the impact of marine herbivores on benthic primary producers. *Ecol. Lett.* 15:912–22.

Poorter, H., Niklas, K. J., Reich, P. B., Oleksyn, J., Poot, P. & Mommer, L. 2012. Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. *New Phytol.* 193:30-50.

Queirós, A. M., Stephens, N., Widdicombe, S., Tait, K., McCoy, S. J., Ingels, J., Rühl, S., Airs, R., Beesley, A., Carnovale, G., Cazenave, P., Dashfield, S., Hua, E., Jones, M., Lindeque, P., McNeill, C. L., Nunes, J., Parry, H., Pascoe, C., Widdicombe, C., Smyth, T., Atkinson, A., Krause-Jensen, D. & Somerfield, P. J. 2019. Connected macroalgal-sediment systems: blue carbon and food webs in the deep coastal ocean. *Ecol. Monogr.* 89:e01366.

Raven, J. 2018. Blue carbon: past, present and future, with emphasis on macroalgae. *Biol. Lett.* 14:20180236.

Raven, J. A. 2017. The possible roles of algae in restricting the increase in atmospheric CO<sub>2</sub> and global temperature. *Eu. J. Phycol.* 52:506-22.

Raven, J. A. & Hurd, C. L. 2012. Ecophysiology of photosynthesis in macroalgae. *Photosynth. Res.* 113:105-25.

Redmond, S., Green, L., Yarish, C., Kim, J. & Neefus, C. 2014. New England Seaweed Culture Handbook. *Seaweed Cultivation*. Paper 1. [http://digitalcommons.uconn.edu/seagrant\\_weedcult/1](http://digitalcommons.uconn.edu/seagrant_weedcult/1). 92 pp.

Reef, R., Atwood, T.B., Samper-Villarreal, J., Adame, M.F., Sampayo, E.M. & Lovelock, C.E. 2017. Using eDNA to determine the source of organic carbon in seagrass meadows. *Limnol. Oceanogr.* 62:1254-65

Ritschard, R. L. 1992. Marine algae as a CO<sub>2</sub> sink. *Water Air Soil Pollut.* 64:289-303.

Santos, I. R., Burdige, D. J., Jennerjahn, T. C., Bouillon, S., Cabral, A., Serrano, O., Wernberg, T., Filbee-Dexter, K., Guimond, J. A. & Tamborski, J. J. 2021. The renaissance of Odum's outwelling hypoxia in 'Blue Carbon' science. *Estuar. Coast. Shelf Sci.* 255:10761.

Scharlemann, J. P., Tanner, E. V., Hiederer, R. & Kapos, V. 2014. Global soil carbon: understanding and managing the largest terrestrial carbon pool. *Carbon Management* 5:81-91.

Schiel, D. R. & Foster, M. S. 2015. *The biology and ecology of giant kelp forests*. University of California Press, Oakland, CA, 395 pp.

Shen, Y. & Benner, R. 2018. Mixing it up in the ocean carbon cycle and the removal of refractory dissolved organic carbon. *Sci. Rep.* 8:2542.

Sieburth, J. M. 1969. Studies on algal substances in the sea. III. The production of extracellular organic matter by littoral marine algae. *J. Exp. Mar. Biol. Ecol.* 3:290-309.

Silverstone, H., Sheetz, M., Pedneault, S. & Rudewicz, F. 2012. *Forensic Accounting and Fraud Investigation for Non-Experts 3rd edition*. John Wiley & Sons Inc, Hoboken, NJ, USA, 336 pp.

Singh, A., Sharma, R., Pant, D. & Malaviya, P. 2021. Engineered algal biochar for contaminant remediation and electrochemical applications. *Sci. Total Environ.* 774:145676.

Skadberg, K. 2008. *Patterns and Drivers of Nearshore Coastal Air-Sea Carbon Dioxide Exchange*. University of California, Davis and San Diego State University, San Diego, CA, USA, 93 pp.

Smale, D.E., Burrows, M.T., Moore, P., O'Connor, N. & Hawkins, S.J. 2013 Threats and knowledge gaps for ecosystem services provided by kelp forests: A northeast Atlantic perspective. *Ecol. Evol.* 3:4016-38.

Smale, D. A., Moore, P. J., Queirós, A. M., Higgs, N. D. & Burrows, M. T. 2018. Appreciating interconnectivity between habitats is key to blue carbon management. *Front. Ecol. Environ.* 16:71-73.

Sondak, C. F. A., Ang, P. O., Beardall, J., Bellgrove, A., Boo, S. M., Gerung, G. S., Hepburn, C. D., Hong, D. D., Hu, Z., Kawai, H., Largo, D., Lee, J. A., Lim, P. E., Mayakun, J., Nelson, W. A., Oak, J. H., Phang, S.-M., Sahoo, D., Peerapornpis, Y., Yang, Y. & Chung, I. K. 2017. Carbon dioxide mitigation potential of seaweed aquaculture beds (SABs). *J. Appl. Phycol.* 29:2363-73.

Suárez-Jiménez, R., Hepburn, C. D., Hyndes, G. A., McLeod, R. J., Taylor, R. B. & Hurd, C. L. 2017. The invasive kelp *Undaria pinnatifida* hosts an epifaunal assemblage similar to native seaweeds with comparable morphologies. *Mar. Ecol. Prog. Ser.* 582:45-55.

Taylor, R. B. & Cole, R. G. 1994. Mobile epifauna on subtidal brown seaweeds in northeastern New Zealand. *Mar. Ecol. Prog. Ser.* 115:271-82.

Thomas, J.B.E., Sodr  Ribeiro, M., Potting, J., Cervin, G., Nylund, G.M., Olsson, J., Albers, E., Undeland, I., Pavia, H., Gr ndahl, F. 2021. A comparative environmental life cycle assessment of hatchery, cultivation and preservation of the kelp *Saccharina latissimi*. *ICES J. Mar. Sci.* 78:451-67.

Tian, Y., Kang, X., Li, Y., Li, W., Zhang, A., Yu, J. and Li, Y. 2013. Identifying rhodamine dye plume sources in near-shore oceanic environments by integration of chemical and visual sensors. *Sensors* 13:3776-98.

Trevathan-Tackett, S. M., Kelleway, J., Macreadie, P. I., Beardall, J., Ralph, P. & Bellgrove, A. 2015. Comparison of marine macrophytes for their contributions to blue carbon sequestration. *Ecology* 96:3043-57.

United Nations Global Compact. 2021. Seaweed as a nature-based climate solution. Vision Statement. United Nations Global Compact, 685 Third Avenue New York, NY 10017, USA  
United States Environmental Protection Agency,  
<https://www.epa.gov/ghgemissions/understanding-global-warming-potentials>, accessed 17 Feb 2022.

Utto, A, Heiskanen, A.S., Lignesll, R., Autio, R. & Rajunime, R. 1997. Summer dynamics of the coastal planktonic food web in the northern Baltic Sea. *Mar. Ecol. Prog. Ser.* 151:27-41.

van der Velde, I. R., van der Werf, G. R., Houweling, S., Maasakkers, J. D., Borsdorff, T., Landgraf, J., Tol, P., van Kempen, T. A., van Hees, R. & Hoogeveen, R. 2021. Vast CO<sub>2</sub> release from Australian fires in 2019–2020 constrained by satellite. *Nature* 597:366-9.

Visser, R. & Obi O.F. 2020 Automation and robotics in forest harvesting applications: identifying near-term opportunities. *Croat. J. Forest Engineer.* 42:13-24.

Volk, T. & Hoffert, M. I. 1985. Ocean carbon pumps: Analysis of relative strengths and efficiencies in ocean-driven atmospheric CO<sub>2</sub> changes. In Sundquist, E.T. & Broecker, W.S. [Eds.] *The carbon cycle and atmospheric CO<sub>2</sub>: natural variations Archean to present*. American Geophysical Union, Washington DC, USA, 32:99-110.

Wang, M., Hu, C., Barnes, B. B., Mitchum, G., Lapointe, B. & Montoya, J. P. 2019. The great Atlantic *Sargassum* belt. *Science* 365:83-87.

Wanninkhof, R., Asher, W. E., Ho, D. T., Sweeney, C. & McGillis, W. R. 2009. Advances in Quantifying Air-Sea Gas Exchange and Environmental Forcing. *Ann. Rev. Mar. Sci.* 1:213-44.

Waring, B., Neumann, M., Prentice, I. C., Adams, M., Smith, P. & Siegert, M. 2020. Forests and Decarbonization – Roles of Natural and Planted Forests. *Front. For. Glob. Chang.* 3:58.

Watanabe, K., Yoshida, G., Hori, M., Umezawa, Y., Moki, H. & Kuwae, T. 2020. Macroalgal metabolism and lateral carbon flows can create significant carbon sinks. *Biogeosci.* 17:2425–40.

Wernberg, T. & Filbee-Dexter, K. 2019. Missing the marine forest for the trees. *Mar. Ecol. Prog. Ser.* 612:209-15.

Wu, J., Zhang, H., Pan, Y., Krause-Jensen, D., He, Z., Fan, W., Xiao, X., Chung, I., Marbà, N., Serrano, O., Rivkin, R. B., Zheng, Y., Gu, J., Zhang, X., Zhang, Z., Zhao, P., Qiu, W., Chen, G. & Duarte, C. M. 2020. Opportunities for blue carbon strategies in China. *Ocean Coast. Manag.* 194:105241.

Xie, X., Volkman, J. K., Qin, J., Borjigin, T., Bian, L. & Zhen, L. 2014. Petrology and hydrocarbon potential of microalgal and macroalgal dominated oil shales from the Eocene Huadian Formation, NE China. *Int. J. Coal Geol.* 124:36-47.

Zaborska, A., Włodarska-Kowalczyk, M., Legeżyńska, J., Jankowska, E., Winogradow, A. & Deja, K. 2018. Sedimentary organic matter sources, benthic consumption and burial in west Spitsbergen fjords – Signs of maturing of Arctic fjordic systems? *J. Mar. Syst.* 180:112–23.

Zhang, Y.Y., Zhang, J.H., Liang, Y.T., Li, H.M., Li, G., Chen, X., Zhao, P., Jiang, Z.J., Zou, D.H., Liu, X.Y. & Liu, J.H. 2017. Carbon sequestration processes and mechanisms in coastal mariculture environments in China. *Sci. China Earth Sci.* 60:2097–107.

Zimmerman, R.C. & Robertson, D.L. 1985. Effects of El Niño on local hydrography and growth of the giant kelp, *Macrocystis pyrifera*, at Santa Catalina Island, California. *Limnol. Oceanogr.* 30:1298-302

Table 1. Glossary of terms used in this manuscript, in the context of carbon dioxide removal and carbon sequestration by seaweeds.

---

Autotrophic respiration ( $A_R$ ) – respiration undertaken by autotrophs, including seaweeds and phytoplankton

Carbon cycle – the movement of inorganic and organic carbon through living and non-living systems

Carbon Dioxide Removal (CDR) – A process that removes  $CO_2$  from the atmosphere and results in sequestration

Carbon dioxide influx – the net movement of  $CO_2$  from the atmosphere into the surface ocean

Carbon fixation – the conversion of  $CO_2$  to organic matter

Carbon dioxide outgassing – the net movement of  $CO_2$  from the surface ocean into the atmosphere

Carbon sequestration – the secure storage of carbon-containing molecules for  $> 100$  years outside the atmosphere

Carbon sink – a system that absorbs more  $CO_2$  than it releases

Seaweed standing stock/biomass – the dry mass of seaweed per unit area of seabed ( $kg\ m^{-2}$ )

Carbon storage – living or inert store of carbon on various time scales

Carbon standing stock – the mass of carbon in living seaweed tissue per unit area of seabed ( $kg\ C\ m^{-2}$ )

Gross photosynthesis – the total rate of carbon fixation by a system

Heterotrophic respiration ( $H_R$ ) – respiration undertaken by heterotrophs including marine invertebrates, fish, bacteria

Net Primary Production (NPP) – The difference between the rates of gross primary production and respiration in a system.

Photosynthesis – the metabolic process whereby light energy is harvested to power biological carbon fixation

Respiration – metabolic processes whereby organic molecules are oxidised, resulting in the release of  $CO_2$

Steady state – constant annually-averaged biomass over  $>100$  years, in the context of living seaweed beds being considered as ‘sequestered carbon’



Table 2. An illustrative checklist of the type of parameters that must be measured in order to undertake Forensic Carbon Accounting-Seaweeds (FCA-S) for carbon dioxide removal and carbon sequestration by natural seaweed beds, coastal and open ocean seaweed aquaculture. Baseline measurements need to be made on temporal and spatial scales relevant to each system being studied (e.g., monthly, seasonally) in order to constrain the carbon sequestration potential of the natural system. Undertaking FCA-S must factor in additional fabrication (e.g. underwater structures to raft seaweeds) and energy costs, and requires a multi-disciplinary team. Some key references are included and see the text for additional resources.

Components required to undertake Forensic Carbon Accounting	Parameter(s) that require measurement	Scientific Discipline	Reference(s)
NPP of natural seaweed beds/aquaculture systems			
	Gross photosynthesis and respiration of individual seaweeds or a community	Algal physiology, benthic ecology	Pessarrodona et al. (2021)
	Carbon content of seaweed biomass within a bed	Benthic ecology	Filbee-Dexter and Wernberg (2020)
Measuring CO <sub>2</sub> influx and out-gassing			
	Background measurements of the seawater carbonate	Chemical oceanography	Dickson et al. (2007)

	system. Any two of DIC, pH, CO <sub>2</sub> , alkalinity, CO <sub>3</sub> <sup>2-</sup> plus temperature and salinity		
	Background measurements of air-sea CO <sub>2</sub> equilibrium to explore its main site-specific drivers	Physical and chemical oceanography	Skadberg (2008), Wanninkof et al. (2009), Jones et al. (2014)
	Verification of CO <sub>2</sub> re-equilibration of the CO <sub>2</sub> deficit generated by seaweed NPP	Physical and chemical oceanography, biogeochemistry, modelling	Bach et al. (2021)
Dispersion and transport of seawater from seaweed bed	Advection and dilution	Physical oceanography, modelling, remote sensing	Tian et al. (2013), Klemas (2012, 2013)
Inorganic and organic carbon loss terms for a seaweed bed or aquaculture system			
	Heterotrophic respiration (the rate of release of CO <sub>2</sub> from sessile and mobile micro- and macro-invertebrates	Benthic ecology	Gallagher et al. (2022)

	Quantifying alkalinity loss and gain through calcification feedbacks	Chemical and biological oceanography	Bach et al. (2021) DeLille et al (2000)
	Grazing by micro- and macro-herbivores	Benthic ecology	Poore et al. (2012)
	POC and DOC production rates of the seaweeds	Benthic ecology, physiology	Queirós et al. (2019), Smith and Fox (2021), Paine et al. (2021)
Export of seaweed carbon to other systems			
	Detection and quantification of DOC in pelagic near and offshore systems including the deep ocean	Biological oceanography	Legendre et al. (2015), Paine et al. (2021)
	Detection and quantification of seaweed POC in pelagic systems including the deep ocean	Biological oceanography, paleo-oceanography, molecular biology	Queirós et al. (2019), Pedersen et al. (2021) Ortega et al. (2019)
	Detection and quantification of seaweed POC in other coastal sediments e.g. seagrass beds, soft	Benthic ecology	Krause-Jensen et al. (2018), Cartraud et al. (2021), Geraldi et al.

	sediments, beaches		(2019)
Earth system analyses			
	Carbon budget of the existing phytoplankton-based system, including seawater carbonate system and atmosphere/ocean CO <sub>2</sub> equilibria (above).	Biological oceanography	Orr and Sarmiento (1992), Bach et al. (2021)
	Earth system analysis of carbon fluxes related to the purposeful introduction of a new species to a functioning ecosystem	Oceanography and modelling	Bach et al. (2021)
	Determine if there is an altered nitrogen balance in global ocean as nitrogen will affect NPP	Oceanography and modelling	Orr and Sarmiento (1992), Bach et al. (2021)
Life cycle analyses of carbon during processing			
	Carbon gains/losses of aquaculture system including fabrication, ongoing costs (e.g. transport), seaweed processing	Environmental engineering	Melera et al. (2020), Thomas et al. (2021)

Figure 1. Carbon cycling in a typical terrestrial forest.  $\text{CO}_2$  is assimilated in leaves via photosynthesis, expressed as gross primary production (GPP). Assimilated carbon is then either respired by the plant (autotrophic respiration:  $R_A$ ) or incorporated into plant leaves, roots and stems. Leaves typically have a short lifespan with leaf carbon entering the litter layer. Fine roots have a very short lifespan and also secrete organic molecules, with the sum of root exudates and dead roots termed rhizodeposition. Rhizodeposited roots and aboveground plant litter are then incorporated into the soil, first as undecomposed plant residues but then as soil organic matter (SOM) as the residue is decomposed through chemical, physical and biological processes. SOM is then converted into the soil carbon pools, with the carbon becoming increasingly resistant to decomposition as it becomes more processed. Decomposition of plant residues including coarse woody debris, SOM and soil carbon is associated with heterotrophic respiration and together with root respiration is termed soil respiration. Long-term carbon storage results from the long residence times of standing wood and major roots, coarse woody debris and the slow and recalcitrant soil carbon pools.

Figure 2. Conceptual figure of processes influencing atmosphere-ocean exchange of  $\text{CO}_2$  in the coastal-offshore nexus. Nearshore waters are tidally-stirred with uniform properties (i.e., a single layer) in contrast offshore waters are dominated by wind-mixing and often have a multiple layers demarcated by density gradients (stratification). A combination of physical (e.g., bubble injection), chemical (e.g., slicks/surfactants which retard exchange) and biological (detailed in Fig. 3) processes drive atmosphere-ocean exchange, and their relative importance varies with locale and season (see main text for examples).

Figure 3. Carbon cycling in a typical temperate seaweed bed which consists of understory red, green and brown seaweeds, and over-story kelp. The seawater system is mixed from surface to the seabed via wind and tidal action (ellipse). When  $\text{CO}_2$  enters seawater, it reacts with water molecules to establish the seawater carbonate system (inset bottom right). Seaweeds take up dissolved carbon dioxide, or bicarbonate which is converted to  $\text{CO}_2$ , and then  $\text{CO}_2$  is assimilated within the seaweed cells (gross photosynthesis). Assimilated  $\text{CO}_2$  is incorporated into the seaweed thallus, and a proportion is respired back into the seawater ( $R_A$ ). A substantial number of invertebrates (abalone, snails, urchins) and fish are associated with seaweed beds and seaweed blades are often heavily colonised by mobile and sessile invertebrates, such as hydrozoans,

bryozoans, amphipods and isopods (insert, bottom left). All the animals that grow within seaweeds beds respire ( $R_H$ ).  $R_A$  and  $R_H$  release  $CO_2$  back into seawater and this can be returned to the atmosphere or transported laterally to outgas in a different part of the ocean. Seaweeds lose substantial proportions of fixed carbon as POC and DOC. Within the seaweed bed (inset, bottom left), POC is consumed by filter feeders, macro-grazers such as sea urchins, snails and abalone, mobile micro-grazers (amphipods, urchins), and DOC provides carbon for bacteria and small zooplankton. POC and DOC are also exported laterally by currents to provide an energy subsidy to other coastal and offshore systems. Seaweed biomass that is ripped of the rock substratum during storms can be deposited on sandy beaches (dead seaweed) and can then enter the terrestrial carbon cycle.

Figure 4. Schematic illustrating independent effects of physical (A) and (B) biological factors on seawater  $CO_2$  deficit result from seaweed photosynthesis. In both figures, photosynthesis results in an influx of atmospheric  $CO_2$  into the surface ocean, and a reduction in  $CO_2$  concentration surrounding the seaweed. (A) Physical factors – If the water parcel containing the  $CO_2$  deficit resulting from seaweed photosynthesis remains or advects to a highly dynamic, wave-exposed system, then the time-scales for  $CO_2$  re-equilibration are short and the dissolved  $CO_2$  concentration will recover rapidly. If the water parcel is transported off shore, or to a low-dynamic coastal system, then  $CO_2$  influx will be slower, whereas subduction of the water parcel prevents re-equilibration until the water ventilates at the surface. (B) Biological factors - If the parcel of seawater advects laterally over a heterotrophic system e.g. a mussel or oyster bed,  $CO_2$  input from respiration will raise dissolved  $CO_2$  and so reduce the amount of  $CO_2$  taken up from the atmosphere during re-equilibration (black line). Conversely, if the water advects over a system in which autotrophy is greater than heterotrophy e.g. another kelp bed, then the potential for  $CO_2$  removal from the atmosphere increases. If autotrophy balances heterotrophy, then the potential for  $CO_2$  influx from the atmosphere remains the same.

Fig. S1. Media release by CarbonCredits.com on the development of seaweed farms for carbon credits/offsets. <https://carboncredits.com/blue-carbon-floating-farms-seaweed/>.

Accessed on 9<sup>th</sup> February 2022.

Fig. S2. Link to NGO Oceans 2050 Seaweed Project, which aims to validate seaweed carbon sequestration with a view to monetise seaweed carbon as carbon credits.

<https://www.oceans2050.com/seaweed>

Accessed on 9<sup>th</sup> February 2022.

Fig. S3. a) Stripe Climate program. An example of company investing in the development of oceanic kelp farms in order to build a portfolio for a carbon market.

<https://stripe.com/newsroom/news/spring-21-carbon-removal-purchases>

Accessed 7<sup>th</sup> February 2022. b) Stripe Climate program. Link to an open access (funded) research proposal from Running Tides to grow seaweeds in the open ocean and sink them, with a view to building a portfolio for a carbon market. Accessed 7<sup>th</sup> February 2022.

<https://github.com/stripe/carbon-removal-source-materials/blob/master/Project%20Applications/Spring2021/Running%20Tide%20-%20Stripe%20Spring21%20CDR%20Purchase%20Application.pdf>

Fig. S4. NGO – Running Tide. Web site illustrates methods and rationale of growing floating ‘micro-forests’ of kelp in the open ocean, then sinking them to the deep ocean to remove atmospheric CO<sub>2</sub>. Accessed 7<sup>th</sup> February 2022.

<https://www.runningtide.com/>

Fig. S5. NGO – Climate Foundation. Marine Permaculture and using seaweeds to slow down or stop climate change. Accessed 7<sup>th</sup> February 2022.

<https://www.climatefoundation.org/2040-make-a-change.html>

Fig. S6. NGO - Climate Council. Article reporting that covering 9% of the global ocean with kelp will provide sufficient biofuels to replace fossil fuels, and remove 53 billion tonnes of CO<sub>2</sub> from the atmosphere. Accessed 7<sup>th</sup> February 2022.

[https://www.climatecouncil.org.au/seaweed-climate-change/?atb=DSA01b&gclid=CjwKCAjwndCKBhAkEiwAgSDKQXvBtJ09OxonICREOau3Jsw0dViIoCoEsUjqK6v0iH5qoqNnr74NwhoCVQEQA\\_vD\\_BwE](https://www.climatecouncil.org.au/seaweed-climate-change/?atb=DSA01b&gclid=CjwKCAjwndCKBhAkEiwAgSDKQXvBtJ09OxonICREOau3Jsw0dViIoCoEsUjqK6v0iH5qoqNnr74NwhoCVQEQA_vD_BwE)

Fig. S 7. Media report on start-up company Phycos (<https://www.phykos.co/>) that is developing technology for underwater seaweed farms for capturing atmospheric CO<sub>2</sub>. Accessed 7<sup>th</sup> February 2022.

<https://www.fastcompany.com/90680321/these-carbon-capturing-robotic-seaweed-farms-are-like-planting-forests-in-the-ocean>

Fig. S8. Media report - *New Scientist*: Seaweed to prevent catastrophic climate change via removal of atmospheric CO<sub>2</sub>. Accessed 7<sup>th</sup> February 2022.

<https://www.newscientist.com/article/mg24632821-100-kelp-is-coming-how-seaweed-could-prevent-catastrophic-climate-change/>

Fig. S9. Media: TV show 'Catalyst' (Australian Broadcasting Company) that discusses the benefits of seaweeds, including their use to remove atmospheric CO<sub>2</sub> and for marine permaculture.

<https://www.abc.net.au/catalyst/can-seaweed-save-the-world/11017106>

Fig. S10. Harvard University Blog: on how seaweeds draw-down atmospheric CO<sub>2</sub> via sinking to the deep ocean. Accessed 7<sup>th</sup> February 2022. <https://sitn.hms.harvard.edu/flash/2019/how-kelp-naturally-combats-global-climate-change/>

Fig. S11. Media report on the role of kelp in removing atmospheric CO<sub>2</sub>, and selective breeding for thermal tolerance as part of a restoration kelp projects. Accessed 7<sup>th</sup> February 2022.

<https://reasonstobecheerful.world/super-kelp-carbon-emissions-climate-change-oceans/>

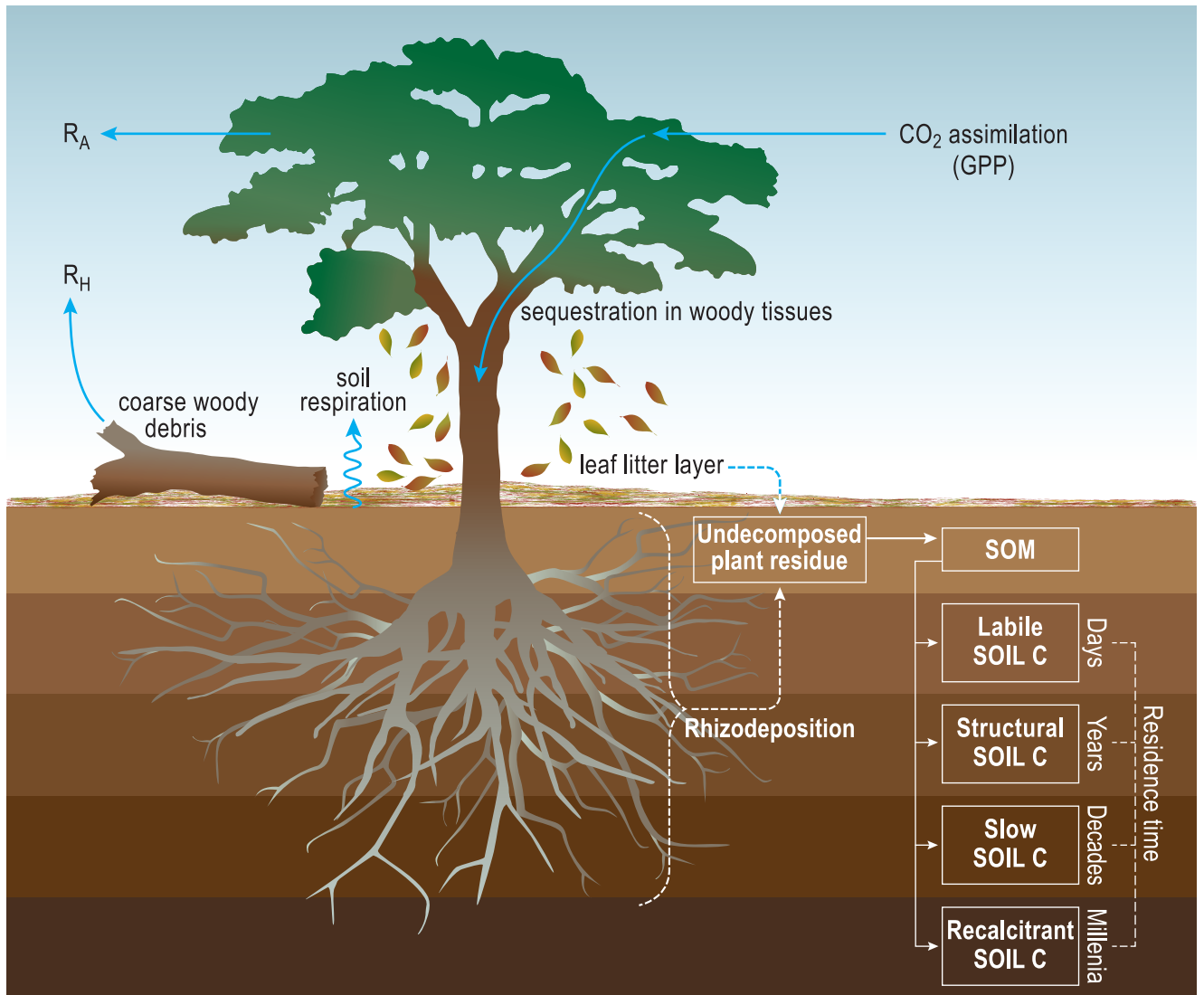
Fig. S12. Media report on the development of kelp farming for atmospheric CO<sub>2</sub> removal.

Accessed 7<sup>th</sup> February 2022. <https://www.npr.org/2021/03/01/970670565/run-the-oil-industry-in-reverse-fighting-climate-change-by-farming-kelp>

Fig. S13. Scottish Parliament Information Centre (SPICe) document. Kelp as part of the blue carbon portfolio, presented as million tonnes of CO<sub>2</sub> equivalent. Accessed 7<sup>th</sup> February 2022.

<https://spice-spotlight.scot/2021/03/24/out-of-the-blue-is-blue-carbon-the-next-frontier-for-climate-change-mitigation-in-scotland/>





**GPP** – Gross Primary Production

**$R_A$**  – Autotrophic respiration

**$R_H$**  – Heterotrophic respiration

**SOM** – Soil Organic Matter



