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Food for Thought

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Seaweed ecosystems may not mitigate CO_2 emissions

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Global seaweed carbon sequestration estimates are currently taken as the fraction of the net primary production (*NPP*) exported to the deep ocean. However, this perspective does not account for CO_2 from the consumption of external subsidies. Here, we clarify: (i) the role of export relative to seaweed net ecosystem production (*NEP*) for a closed system and one more likely open to subsidies; (ii) the importance of subsidies by compiling published estimates of *NEP* from seaweed-dominated ecosystems; and (iii) discuss their impact on the global seaweed net carbon balance and other sequestration constraints as a mitigation service. Examples of seaweed *NEP* ($n = 18$) were sparse and variable. Nevertheless, the average *NEP* (-4.0 mmol C m^{-2} d^{-1} SE ± 12.2) suggested that seaweed ecosystems are a C source, becoming increasingly heterotrophic as their export is consumed. Critically, mitigation of greenhouse gas emissions was mixed relative to their replacement or baseline states, and where CO_2 is supplied independently of organic metabolism and atmospheric exchange, we caution a sole reliance on *NEP* or *NPP*. This will ensure a more accurate seaweed mitigation assessment, one that does exceed their capacity and is effective within a compliance and carbon trading scheme.

Keywords: carbon mitigation, golden carbon, net ecosystem production, seaweed aquaculture, subsidies.

Introduction

Anthropogenic greenhouse gas emissions (*GHG*) are largely responsible for global warming (Cook *et al.*, 2013). Concerns about warming have led to a call to reduce reliance on the burning of fossils fuels, but also to mitigate emissions using natural solutions. That is to say, solutions that focus on restoring and protecting existing natural carbon sinks that would otherwise be lost through climate change and other anthropogenic pressures (UNFCCC, 2015). The most visible of these vulnerable natural sinks are terrestrial forests. Nevertheless, there has been an increasing focus on the advantages and ability of blue carbon ecosystems to sequester *GHGs*, that is, saltmarsh, mangroves, and seagrass wetlands (Nellemann *et al.*, 2009; McLeod *et al.*, 2011; Lovelock and Duarte, 2019). These systems are not only highly productive, and unlike terrestrial forests, they do not readily combust and will continue to sequester carbon down a relatively rapidly accreting sediment column (McLeod *et al.*, 2011) that can respond, and in part determined, by sea-level rise (Lovelock and Reef, 2020). Furthermore, their ability to trap organic imports has resulted in a relatively high carbon sink density, estimated to contribute to half of the total carbon stored in the world's oceans, despite covering only $< 2\%$ of its area (Duarte, *et al.*, 2005).

Along with coastal wetlands, seaweeds are also increasingly being lost across the majority of global ecoregions (Krumhansl *et al.*, 2016). Similar to wetlands, losses are a combination of causes related to climate change, pollution, and harvesting, but also the result of overgrazing from the loss of top predators (Krumhansl *et al.*, 2016). However, unlike coastal wetlands, they do not support an ability to sequester carbon within their canopy footprint; they tend to occur in more exposed rocky areas where there is little local sediment accumulation. Nevertheless, a significant fraction of their net primary production (*NPP*; ∼43% *NPP*) is exported and subsequently sequestered directly to the deep ocean (∼11% *NPP*) as dislodged seaweed tissue and dissolved organic carbon (Smith, 1981; Gallagher, 2014; Krause-Jensen and Duarte, 2016; Krause-Jensen *et al.*, 2018; Filbee-Dexter and Wernberg, 2020; Bayley *et al.*, 2021). The remainder of that export is consumed within surface waters, and/or degraded within nearby coastal sediments (Hill *et al.*, 2015; de Bettignies *et al.*, 2020). Indeed, this fraction of exported *NPP* to the deep ocean is increasingly being touted as both a means to determine seaweed ecosystems sequestration rates, a value that appears to describe mitigation of anthropogenic CO_2 emissions through restoration and the preservation of vulnerable systems (Krause-Jensen *et al.*, 2018).

We contend, however, that the seaweed *NPP* paradigm, which quantifies sequestration as the fraction of seaweed *NPP* exported to the deep ocean, is an incomplete metric of sequestration and by extension mitigation of atmospheric *GHGs*. The seaweed *NPP* paradigm implicitly ignores the consumption of imported organic subsidies. Indeed, organic subsidies contribute to many wetland systems and some degraded blue carbon ecosystems being rendered net sources of carbon emissions (Duarte and Prairie, 2005). Such imports inevitably result in additional CO_2 emissions from the stimulation of organic and calcareous metabolism by the seaweed community (Gattuso *et al.*, 1997; Bach *et al.*, 2021). Whilst mitigation is a measure of the impact on *GHG* emissions, should the ecosystem not just be lost but replaced by a sink or source as determined by degraded or an alternative ecosystem state. In other words, mitigation services should not be assessed relative to net carbon neutrality but instead, relative to the carbon balance of what would otherwise fill that biological space (Siikamäki *et al.*, 2013; Gallagher, 2017; Prairie *et al.*, 2018; Smith *et al.*, 2000). For example, a degraded kelp forest may progress to an alternative state of an urchin barren

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or turf-dominated assemblage (Strain *et al.*, 2014; Edwards *et al.*, 2020), and *Fucus vesiculosus* assemblages may be replaced by a mussel dominated reef system (Petraitis *et al.*, 2009). Any interventions from a carbon sequestration standpoint will then be dependent on their relative sequestration or emission strengths. This, then, should be the framework for a price on vulnerable natural carbon sinks; a service nevertheless constrained any losses of other ecosystem services such as biodiversity (Villa and Bernal, 2018).

Here, we aim to first explore and explain the role of organic subsidies in influencing seaweed ecosystem sequestration relative to the current *NPP* sequestration paradigm. We attempt this by disentangling the components of the ecosystem and its exported net carbon balance: first, for a hypothetical macroalgal system closed to inputs of organic subsidies (Case i), and second, relative to a more usual macro–microalgal ecosystem open to subsidies (Case ii). We then assess the importance of subsidies to both the ecosystem's local and net global carbon balance by compiling published net ecosystem production (*NEP*) estimates before applying export consumption and deposition parameters. These parameters are based on the global *NPP* paradigm model, a compilation average of 30 *NPP* examples across the globe, also previously applied at both continental and (Filbee-Dextor and Wernberg, 2020) oceanic regional scales (Bayley *et al.*, 2021). Finally, and where available, the expected differences between anthropogenically driven replacements' local and net global carbon balances are cited to assess where seaweed ecosystem mitigation services lie, whilst considering how measurements are constrained by the production of CO_2 during faunal and floral calcification, and the occurrence of any local upwelling and downwelling processes.

Material and methods

To explore the role of subsidies on seaweed ecosystems, we first partitioned the components of their carbon balance for the ecosystem and its exported material for one system closed and one open to those imported subsidies [Equations (1) and (3)]. To gauge the importance of subsidies, published estimates of *NEP* rates were collected from the *Web of Science* database (accessed March 2021) using the following search terms: macroalga∗ OR benth∗, "primary producti∗", AND ecosystem or community. This search initially identified 2313 papers, which were subsequently divided and screened by the authors for inclusion based on title and abstract. Only papers that reported, or allowed for, estimates of daily (24 h) *NEP* of seaweed-dominated communities were used. Results from papers reporting fluxes as oxygen was converted to carbon using a molar photosynthetic and respiratory quotients = 1. It should be noted, that these conversions likely represent a conservatively high estimate as no consideration is given to the potential production of CO_2 from calcification (Gattuso *et al.*, 1997; Bach *et al.*, 2021). When necessary, the data required to recalculate annual *NEP* from their components were digitally extracted from figures using Graph Grabber™ v2.0.1. We included studies that measured day- and night-time production/respiration for >1 h, from which we calculated daily estimates using a stated 12:12 day–night ratio (Miller *et al.*, 2009). For one article that reported for 12 h of daylight only (Miller *et al.*, 2011), we corrected for community respiration rates extrapolated over the night, and at one site, the average *NEP* between various canopy types was weighted using relative biomass (Supplementary material S1, Part 1). Studies that estimated production rates for whole communities based on the summed production rates of individual species were only included if they accounted for both shading by canopy species and respiration of the faunal community (e.g. Miller *et al.*, 2011). Finally, the references contained within the included studies were checked for additional appropriate studies. Data from two papers that measured the *NEP* of *F. vesiculosus* communities from the same sites but different methods of annual integration were pooled and averaged to minimize any overwhelming influence of this system on the overall mean value across the small pool of included studies ($n = 18$). Whilst the pool was relatively small, it resembled a similar sample scale across a range of climatic regions as used in the *NPP* paradigm ($n = 30$; Krause-Jensen and Duarte, 2016).

It should also be noted that the methods used to determine the seaweed ecosystems' *NEP* differed across the data set varied. They included: (i) photorespirometry confined within multiple transparent benthic chambers (~1 m^2) deployed over the canopy bottom with attempts to recreate the turbulence experienced outside the chambers; (ii) eddy covariance, a means to measure the *in situ* vertical flux of oxygen over a large footprint (~10–100 m^2) immediately above canopy; (iii) a modified Eulerian approach that uses either change in oxygen or dissolved inorganic carbon concentrations above the canopy seascape and adjacent water column after accounting for local atmospheric exchange rates; and (iv) a bottom up annual integration of carbon balance measurements from micro–macroalgal assemblage and its ecosystem consumers. Each methodology will have its own set of biases, as discussed for benthic chambers and eddy covariance (Berg *et al.*, 2022). However, the differences generated by scale and turbulence are unlikely to be not so great, including comparisons with Eulerian methods, to confound the variability between sites and species (Tokoro *et al.*, 2014).

Partitioning the carbon balance

The components of the ecosystems' local net carbon balance (i.e. *NEP*) are assumed to represent a steady state over an annual cycle. In this way, seasonality is normalized, although the small number of studies conducted in the growing season likely represent overestimates of annual *NEP*, whilst studies not conducted during the growing season could underestimate annual *NPP*. This is the same level of analysis implicitly used in the global seaweed *NPP* paradigm as a compilation of examples using different methods, at different times, and across different regions (Krause-Jensen and Duarte, 2016). Furthermore, it was similarly assumed that any consumption by herbivores, detritivores, or microflora is directed to remineralization and not an increase in their net biomass or excretion rates. For illustrative purposes, seaweed export is represented as its litter being composed of both the more visible particulate and the less certain fate of its dissolved organic components (Gallagher, 2015; Krause-Jensen and Duarte, 2016). The role of dissolved inorganic carbon is acknowledged, but not included because of the uncertainty of its production rate and the fate of its export (Santos *et al.*, 2021).

Case i: the NPP paradigm, a seaweed assemblage closed to imports

This hypothetical system is one where there is no import of organic subsidies for a macroalgal system that dominates primary production. In other words, productivity and respi-

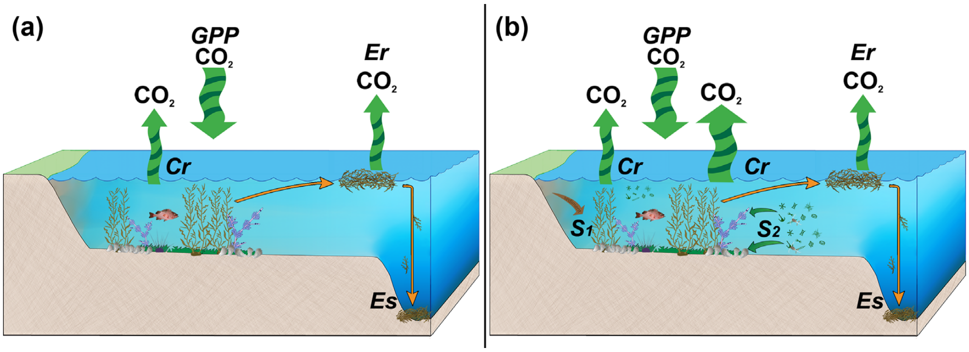

Figure 1. Representation of the components of the net global carbon balance for seaweed ecosystems (a) a hypothetical seaweed assemblage closed to the import of organic carbon subsidies, and (b) a more representative seaweed–phytoplanktonic ecosystem open to the import of subsidies. Where, *Cr* is community respiration partitioned between the algae and the faunal detritivore and herbivore assemblage, *GPP* is gross primary productivity of the primary producer assemblage, *E* is the organic carbon exported from the system, *Er* is the amount of exported organic carbon consumed then remineralized, *Es* is the remaining carbon sequestered in the deep ocean, *S1* represents the supply of any terrigenous organic subsidies, and *S2* the organic subsidies supplied from coastal waters, all consumed by the faunal assemblage. Symbols were imported from The Integration and Application Network (IAN; https://ian.umces.edu/media-library/) into Adobe Illustrator™ CS6 as standardized representatives of processes and biological components.

ration contributions from its microalgal assemblage are considered negligible (Figure 1a). Here, the ecosystems' *NEP* as a carbon balance (*NEPc*, Equation (1)) is determined between the seaweed assemblage gross primary production (*GPP*) and respiration shared across the macroalgae (*Pr*), and its consumption, largely by herbivores (*Hr*) and detritivores (*Dr*; Duarte and Cebrián, 1996). The remaining production is by inference of a steady state is exported (*E*) to adjacent coastal and oceanic waters. As such, the export term then provides an estimate of the seaweed ecosystems' potential to sequester carbon and its equivalence with its *NEPc* [Equation (1)]. However, that sequestration potential will be reduced as it is consumed and remineralized (*Er*; Krause-Jensen and Duarte, 2016). What remains of the export (*Es*) has been shown to find its way to the deep ocean (Figure 1a), to become a proxy for the seaweeds' net ecosystem sequestration service (*NES*, Equation (2)). Or expressed more conveniently as the fraction of the seaweeds' *NPP* that reaches deeper waters (**–*θNPP***, Equation (2)). This, then, is the implicit rationale behind prominent current estimates (Krause-Jensen and Duarte, 2016).

$$\boldsymbol{NEPc} = GPP - Cr = GPP - Pr - Hr - Dr = \boldsymbol{E}. \quad (1)$$

$$NES = NEPc - Er = Es = -\boldsymbol{\theta NPP}. \quad (2)$$

Case ii: a seaweed ecosystem open to imports

In reality, though, these seaweed-dominated systems are open to organic imports (Foley and Koch, 2010; Miller and Page, 2012; Zuercher and Galloway, 2019) and support an interactive phytoplanktonic assemblage that shares the ecosystems' *NPP* (Borum and Sand-Jensen, 1996; Miller *et al.*, 2011; Figure 1b). As these imports are consumed by the faunal community, they subsidize the release of CO_2 (*Sr*) by further stimulating their organic and calcareous metabolism, thereby lowering the *NEP* (*NEPo*; Equation (3)). As for Case i, *Er* can be approximated as the amount of carbon exported from the seaweed assemblage. The relative contribution from phytoplankton export does not appear to be significant (see Supplementary material S1, Part 2).

$$NES = NEPc - Sr - Er = NEPo - Er. \quad (3)$$

It can be appreciated from Equation (3) that the additional respiration from the consumption of subsidies (*Sr*) is likely to be substantial when annual *NEPo* is either in balance or indeed, heterotrophic (i.e. –*NEPo*). Moreover, the greater the influence of *Sr* on the ecosystems' carbon balance, the greater the over-estimation of an *NES* based solely on the fraction of the seaweeds *NPP* (– *θNPP*) exported to the deep ocean (Case i).

Results

Studies with year-round sampling often showed strong seasonal effects with lower *NEP* values in the cooler/shorter day length seasons and higher *NEP* values in the warmer/longer day length seasons (i.e. increased growth; Cheshire *et al.*, 1996; Falter, *et al.*, 2001; Miller *et al.*, 2011; Attard *et al.*, 2014; Attard *et al.*, 2019a, b; Sullaway and Edwards, 2020; Marx *et al.*, 2021). Over annual cycles, however, *NEP* rates between the warmer and tropical–subtropical ecosystems, also characterized by higher light intensities, appeared to support similar sample means but a smaller sample variance (Figure 2; *t*-test unequal variance $p(\text{same mean}) = 0.23$); *F*-test $p(\text{same variance}) = 0.002$). Overall, the examples, which largely included average annual estimates, varied substantially around a heterotrophic mean (Figure 2) of −4.0 mmol C m^{-2} d^{-1} (SE ± 12.2). The standout exceptions were the *Fucus spp* wracks (*Fucus serratus* and *F. vesiculosus*) supporting highly autotrophic annual *NEP* rates, and the extreme heterotrophy of a turf dominated assemblage (Miller *et al.*, 2009; Table 1).

Seaweed ecosystems' global carbon balance

Along with *NEP*, an account must also be made of the amount of exported seaweed production that is consumed and subsequently remineralized during export to the deep ocean. This is implicit in the *NPP* paradigm calculation as the fraction of *NPP* exported that remains after consumption. It can be taken as the difference between estimates of the average fraction of *NPP* exported (43%) and the remains to the deep ocean (11%) as previously used across global, continental, and oceanic island scales (Krause-Jensen and Duarte, 2016; Filbee-Dextor and Wernberg, 2020; Bailey *et al.*, 2021; Equa-

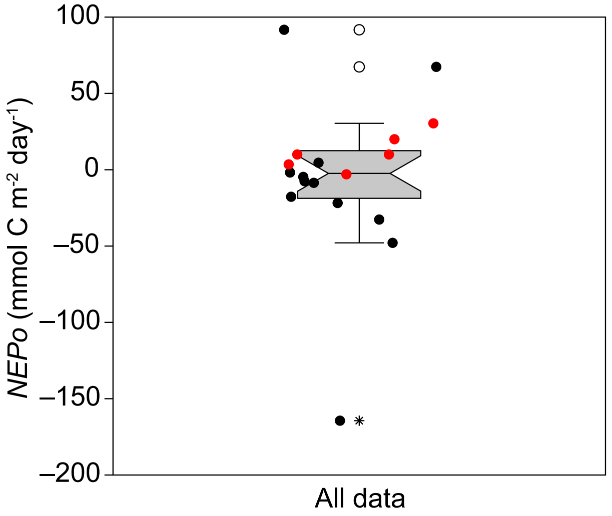

Figure 2. Box and whisker plot for seaweed ecosystem net ecosystem production *NEPo* extracted from the literature for polar to tropical communities (● temperate to polar systems; ● subtropical to tropical systems). The box plot and statistics were produced in PAST™. The central static is the median within the box limits set at 25 and 75% quartiles of 18 data points (interpolation method), with one data point representing the average of two values for *F. vesiculosus* of the Baltic Sea (Table 1). The notches visualizes the 95% confidence interval for the median and the whiskers are drawn from the top of the box up to the largest data point less than 1.5 times the box height from the box limits (the "upper inner fence"), and similarly below the box (the lower inner fence). Values further than three times the box height from the box outside the "inner fences" and outer fences" are outliers, shown as circles (O) and stars (✱), respectively.

tion (4)).

$$Er = E - Es = 0.43NPP - 0.11NPP. \quad (4)$$

By substituting Equation (4) into Equation (3), the *NES* for seaweed ecosystems open to the import of subsidies then becomes the difference between the measured *NEPo* and 32% of the seaweeds *NPP* [Equation (5)].

$$NES = NEPo - 0.32NPP. \quad (5)$$

We can then substitute our mean *NEPo* value (−4.0 mmol C m^{-2} d^{-1}) and the mean *NPP* for seaweed systems around the globe (n = 30; Krause-Jensen and Duarte, 2016), to estimate the net ecosystem service (*NES*; Equation (6)).

$$NES = -4.0 - (0.32 \times 98.17)$$
$$= -35.4 \text{ mmol C m}^{-2}\text{ d}^{-1}. \quad (6)$$

To clarify, such a calculation is only intended to illustrate pertinent concepts and relies on whether the *NPP* sample mean ($n = 30$) lies close or within the same part of the population distribution as our *NEPo* trimmed compilation ($n = 18$). Like the *NPP* paradigm, it does not necessarily provide an accurate estimate of global seaweed sequestration. There are also regional bathymetric, climatic time-scales, and species effects to be addressed as the science progresses. Nevertheless, like the *NPP* paradigm, the extent of the net global balance identifies an important global carbon vector. In this case, the large differences between the two conceptual models provide a more considered insight on the likely extent of additional consumption of exported material on the seaweeds' global net carbon balance, be it large or small relative to the global sample average *NEPo*.

Discussion

Seaweed carbon balances

It appears that on the whole, seaweed ecosystems are substantially impacted by the consumption of organic subsidies to the extent that on average they appear to be heterotrophic (−4.0 mmol C m^{-2} d^{-1}) at local scales. Furthermore, their average global carbon balance becomes increasingly a carbon source to the water column by accounting for remineralization of their exported production (*cal* −35.4 mmol C m^{-2} d^{-1}, Equation (6)), and not a global sink (*cal.* +10.80 mmol C m^{-2} d^{-1}, Krause-Jensen and Duarte, 2016). Indeed, our estimate suggests that the average seaweed *NEPo* would need to exceed 31.41 mmol C m^{-2} d^{-1} (i.e. the sum of 0.32 and 98.17, Equation (6)) just to maintain a global carbon balance. For many seaweeds supporting a *NEPo* sufficient to overcome the amount of export remineralized appear not to be likely (Table 1). However, this does not exclude other seaweeds such as the temperate subtidal and intertidal *Fucus spp* Wracks (*F.vesiculosus* and *F. serratus*, respectively) and tropical–subtropical examples that appear to support more autotrophic regimes even during the winter period (Figure 2 and Table 1). Whether this is because of a relatively large *NPP* or smaller import and consumption of subsidies relative to other sites and genera around the globe is not clear.

The current research on seaweeds remains mostly restricted to natural coastal benthic systems. Nevertheless, the *NPP* paradigm has also been applied to natural floating *Sargassum spp* (Bach *et al.*, 2021), collectively termed golden carbon (Gouvêa *et al.*, 2020), and floating rope seaweed aquaculture (Chung *et al.*, 2011; Duarte *et al.*, 2017). However, as far as we are aware, testing the *NPP* paradigm across seaweed aquaculture and relative to sites without seaweed has been restricted to a single study from the Yellow Sea, China (Jiang *et al.*, 2013). The study calculated the atmospheric CO_2 flux from annual changes in their water columns' $p\text{CO}_2$ (34.85 ± 17.46 mmol C m^{-2} d^{-1}). While the value was significantly greater than sites adjacent to the seaweed arrays (24.17 ± 14.14 mmol C m^{-2} d^{-1}), the difference was reduced towards carbon neutrality when compared to the reported baseline values for the area (32.71 ± 17.23 mmol C m^{-2} d^{-1}). Nevertheless, their overall mitigation services are likely to be significant given that export as in harvesting, is conceivably greater than for natural systems (Chung *et al.*, 2011). Information on natural floating *Sargassum spp* ecosystems; however, is confined to community respiration (*Cr*) of herbivores (*Hr*), detritivores (*Dr*), and the algal assemblage (*Pr*) and their *GPP* components [Equation (1)] determined from two separate studies of *Sargassum natans* from the oceanic and neritic waters south of Bermuda and the NW Atlantic shelf, respectively (Smith *et al.*, 1973; Lapointe, 1995). Together, the *Cr* for neritic and oceanic regions appeared to be more than 3–5 times larger than their *GPP* respectively (Supplementary material S1, Part 3), suggesting that subsidies also play a major role in constraining the *NEPo* of those ecosystems.

Mitigation services

Critically, estimates of a seaweed systems' global carbon balance [Equation (6)] in isolation, while valuable, require comparisons of global balances of their actual or potential alternative replacement states (Smith *et al.*, 2000; Siikamäki *et al.*, 2013; Gallagher, 2017). However, *NEPo* measurements for kelp replacements such as barrens and turfs-dominated sys-

Table 1. Net ecosystem productivity (*NEPo*) of seaweed assemblages from the published literature: AEC = aquatic eddy covariance, where PI = photosynthesis light response and seasonal as the average of different deployments refers to different methods used to calculate annual values for the Baltic *F. vesiculosus* ecosystem. Others refer to concentrations of respiratory gases corrected for atmospheric and/or advective exchange. Note that the thermal condition of the waters does not always coincide with the latitudinal definition of tropics to polar regions, but reflects the origin of the water supplied from large-scale geostrophic currents.

Community description	Location	Method	Average *NEPo* (mmol C m^{-2} d^{-1})	Sampling including multiple seasons	Reference
Temperate and polar waters					
Crustose algae/urchins, Fjord	Greenland	AEC	– 4.7	Yes	Attard *et al.* (2014)
F. vesiculosus	Baltic Sea, Finland	AEC (PI curves)	68.5	Yes	Attard *et al.* (2019a, b)
F. vesiculosus		AEC (Seasonal)	66.2	Yes	
Fucus serratus (intertidal)	Brittany, France	AEC	91.7	Yes	Bordeyne *et al.* (2020)
Brown alga (Phaeophyceae) dominated community	Southern Australia	Chamber	4.6	Yes	Cheshire *et al.* (1996)
Eualaria fistulosa	Alaska, USA	Chamber	– 7.5	Polar summer	Edwards *et al.* (2020)
Turf algae	California, USA	Chamber	– 164.4	Subtropics winter	Miller *et al.* (2009)
Foliose algae	California, USA	Chamber	– 32.64	Subtropics winter	Miller *et al.* (2009)
Macrocystis pyrifera and understory	California, USA	Chamber and growth rates	– 8.57	Yes	Miller *et al.* (2011)
Macrocystis pyrifera understory species	California, USA	Chamber	– 47.9	Yes	Miller *et al.* (2011)
Laminaria pallida and *Ecklonia maxima*	South Africa	Community carbon balance	– 17.7	Yes	Newell and Field (1983)
Mixed macroalgae (15–20 m)	West Antarctic Peninsula	AEC	– 21.8	Polar summer	Rovelli *et al.* (2019)
Sargassum horneri	California, USA	Chamber	– 1.8	Yes	Sullaway and Edwards (2020)
Tropical and subtropical waters					
Sargassum sp, (0.4–3.4 m)	Tropical reef, Australia	Open water sampling, other	10	Yes	Gruber *et al.* (2017)
Corallina elongata and coral reef	Northwest Mediterranean	Open water sampling, other	20	Late winter	Bensoussan and Gattuso (2007)
Mixed macrophyte coral biome: ocean, fore-reef, reef-flat, and shallow lagoon	Arizona, USA	Open water sampling, other	–3	Yes	Falter *et al.* (2001)
Mixed macrophyte/coral reef and fringing degraded reef	French Polynesia	Open water sampling, other	10	Winter	Gattuso *et al.* (1997)
Mixed macrophyte/coral reef	Central Red sea	Chamber	30.4	Unknown season	Roth *et al.* (2019)
Halimeda incrassata	Western Mediterranean	Chamber	3.5	Yes	Marx *et al.* (2021)

tems are limited, and the results mixed. Turf ecosystems can support a *NEPo* carbon balance of around −164.4 mmol C m^{-2} d^{-1} (Table 1; Miller *et al.*, 2009). This is significantly more heterotrophic than the previous mixed *Macrocystis pyrifera* assemblage (−8.57 mmol C m^{-2} d^{-1}) from the same region (Table 1; Miller *et al.*, 2011). In contrast, urchin barrens across many sites within a polar region appear to be moderately heterotrophic. On average, their *NEPo* range from −4.76 mmol C m^{-2} d^{-1} (SE ± 1.35; Attard *et al.*, 2014) to −3.75 mmol C m^{-2} d^{-1} (SE ± 10.56; Edwards *et al.*, 2020). These are only marginally less heterotrophic than the kelp forest counterparts (−7.5 mmol C m^{-2} d^{-1} SE ± 7.7) from similar environments (Edwards *et al.*, 2020). The reasons behind this variability between more or less heterotrophic than its parent canopy system are not clear. It may just be a function of the variability in the system's natural balance between producers and consumers of its autotrophic and allochthonous subsidies. More recently, the role of kelp detritus supplied to sandy non-vegetated sediments has suggested another role of allochthonous subsidies to *NEP*. The kelp detritus supplied to sandy systems retain a sustained ability to photosynthesize over the time it degrades within the sediments (Frontier *et al.*, 2021). For the highly autotrophic *Fucus spp wrack* ecosystems (Table 1), their potential to sequester carbon may be amplified when considering the *NEPo* carbon balance of the mussel reef replacement in the same area as the *F. vesiculosus* ecosystem (−39.5 mmol C m^{-2} d^{-1}; Attard *et al.*, 2019a). Furthermore, further differences in their global net carbon balances (i.e. *NES*, Equation (5)) are unlikely to be great. The *NPP* within and between coastal seaweed and phytoplanktonic ecosystems appear to converge (Borum and Sand-Jensen, 1996) along with the amount of the export remineralized (Supplementary material S1, Part 2).

Other limitations: inorganic carbon supply and outwelling

We have primarily focused on the organic carbon balance over a more recent consideration of dissolved inorganic carbon exported as a long-term dissolved sequestration pool, described as outwelling (Santos *et al.*, 2021). There is, however, an aspect of this outwelling that has not yet been addressed. This is the impact of an acidifying ocean and turbulence between a vegetated and non-vegetated system on the dissolution of their edaphic calcareous sands and fauna. Turbulence together with ocean acidification can significantly increase the dissolution of calcium carbonate and conceivably increase the amount of bicarbonate outwelling (Eyre *et al.*, 2014). In contrast, photosynthesis within a seaweed canopy can significantly reduce acidification and turbulence (Morris *et al.*, 2019; Murie and Bourdeau, 2020). In other words, the canopy is reducing the outwelling sequestration pool relative to a non-vegetated alternative or baseline system. We now have a possible situation where the non-vegetated system is the preferred carbon sequestration sink. However, maintaining or transiting to such a system may not be justified if it is also accompanied by smaller biodiversity (Villa and Bernal, 2018) or arguably, the loss of other natural capital services.

The *NEPo* carbon balance is a measure of CO_2 flux to or from the atmosphere for enclosed and semi-enclosed systems (Prairie *et al.*, 2018). In open coastal waters, however, CO_2 can be supplied independently of atmospheric exchange and organic metabolism. Most notably, from geostrophic currents and upwelling (Ikawa and Oechel, 2015; Thorhaug *et al.*, 2020), as well as faunal (Gattuso *et al.*, 1997) and algal calcification, notably the extensive production from seaweed *Halimeda* spp. (Borowitzka and Larkum, 1976). These additional sources can conceivably not only not affect atmospheric exchange independent of the *NEPo*, but also invalidate *NEP* and *NPP* concepts as processes driven by CO_2 sequestered from the atmosphere. Under such conditions, assessments will likely require additional resources to measure atmospheric exchange between the seaweed ecosystem and its replacement, from the same area. A combined understanding of *NEPo* and the fate of local export appear to be the prerequisites necessary for a predictive capacity to fully assess a seaweed ecosystems' capacity to mitigate *GHG* emissions.

Future research and conclusions

Seaweed ecosystems may not be the significant sequesters of global carbon that they were previously thought. There are several data gaps and conceptual shortcomings that still need to be addressed, including (1) additional measurements of seaweed *NEPo* over annual cycles; (2) and comparison of these measurements relative to the local alternative or degraded state; (3) further understanding of organic subsidy supply and consumption; (4) estimates of atmospheric flux of CO_2 to disentangle any physical from the biological divers of atmospheric exchange; and (5) measurements of exported production and sequestration at local scales. Until then, robust assertions of carbon sequestration and mitigation by seaweeds appear premature and should be interpreted with prudence. It must also be noted that such overestimates when presented as important at global scales are not always benign. This is particularly the case when considering a carbon credit offset and trade scheme (Repetto, 2013; Johannessen and Macdonald, 2016). Carbon credits may become more expensive for polluters to compensate their emission above their cap and increase GHG emissions above the sequestration capacity of the ecosystem. Finally, and most importantly, irrespective of the role that seaweed-dominated ecosystems play in carbon mitigation of *GHGs*, they should remain highly valued for the vast array of critical ecosystem services they provide, including their incontrovertible support of coastal productivity and biodiversity.

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Supplementary material

The following supplementary material (Supplementary material S1, Parts 1, 2, and 3) is available at ICESJMS online version of the manuscript. Part 1 sets out the details of the *NEP* recalculated from the ecosystem's carbon balance components reported by Miller *et al.* (2011) for their different sites. Part 2 provides more details behind the assumption that the fraction of a seaweed ecosystem's export is largely the macrophyte and not its phytoplankton assemblage. Part 3 sets out the calculation and data used to calculate *NEP* for the *Sargassum spp*. occupying parts of the Sargasso Sea.

Data availability statement

No new data compiled in Table 1 were generated or analysed in support of this research. Details of any recalculations of published data components to obtain the appropriate concept are outlined in Supplementary material S1.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

Authors' contributions

Gallagher: conceptualization, methodology, formal analysis, investigation, and writing—original draft preparation and visualization. Shelamoff: conceptualization, methodology, investigation, and writing—reviewing and editing. Layton: methodology, investigation, and writing—reviewing and editing.

Conflict of interest

The authors have no conflicts of interest to declare.

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