Missing the forest for the trees: A reappraisal of global seaweed carbon sequestration

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Abstract

Currently, global seaweed carbon sequestration estimates are taken as the fraction of the net primary production (*NPP*) exported to the deep ocean. The implication is that export is equivalent to net ecosystem production (*NEP*), and sequestration is the fraction of export that survives remineralisation. However, this perspective does not account for CO_2 production fuelled by the consumption of coastal and terrigenous subsidies. Here we clarify: i) the role of export relative to seaweed *NEP* for systems closed and open to subsidies; and ii) the importance of subsidies by compiling published estimates of *NEP* from seaweed-dominated ecosystems; and iii) discuss their impact on the global seaweed carbon balance and other sequestration constraints as a mitigation service. Literature values of seaweed *NEP* were sparse (n = 18) and highly variable. Nevertheless, the average *NEP* (-9.2mmol C m^{-2} day^{-1} SE ± 11.6) suggested that seaweed ecosystems are more likely to be a global source of CO_2. Moreover, the seaweeds' global carbon balance became overwhelmingly heterotrophic (-40.6mmol C m^{-2} day^{-1}) after accounting for the consumption of exported material. Critically, however, mitigation of greenhouse gas emissions must be assessed relative to their replacements ecosystems or states. We found replacement ecosystems such as shellfish reefs and turfs were notably more heterotrophic than seaweed systems, whilst urchin barrens were only marginally less than their seaweed counterparts; a ranking that appeared to be sustained after their amount of exported production had been remineralised. However, in circumstances where CO_2 is supplied independently of organic metabolism and atmospheric exchange (e.g. upwelling and calcification), we caution the sole reliance on *NEP* or *NPP* in mitigation assessments. Nevertheless, a complete metabolic carbon balance relative to replacement states will ensure a more accurate mitigation assessment, one that does not exceed the capacity of these ecosystems.

Keywords*:* carbon mitigation; net ecosystem production; subsidies; golden carbon; seaweed aquaculture

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 reduced reliance on the burning of fossils fuels, but also to restore and protect existing natural carbon sinks (UNFCCC, 2015). The most visible of these natural sinks are terrestrial forests, nevertheless, there has been an increasing focus on the advantages and ability of coastal

canopy systems to sequester *GHGs*, such as highly productive saltmarsh, mangroves, and seagrass habitats, which are collectively known as blue carbon ecosystems (Lovelock & Duarte, 2019; McLeod et al., 2011; Nellemann et al., 2009), Unlike forests, they do not readily combust and will continue to rapidly sequester carbon to constantly accreting sediments in response to sea-level rise (Lovelock & 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 (C. M. Duarte, Middelburg, & Caraco, 2005).

Seaweeds, on the other hand, tend to occur on rocky reefs in more exposed locations with little or no local sediments. Here, extensive amounts of seaweed breakage and excretion products are more typically exported to other coastal and oceanic environments rather than being sequestered locally (Carlos M. Duarte & Cebrián, 1996; Krause-Jensen & Duarte, 2016). Nevertheless, seaweed-dominated ecosystems are increasingly being considered to be an important part of a global carbon mitigation strategy (Filbee-Dexter & Wernberg, 2020; Hill et al., 2015; Krause-Jensen & Duarte, 2016; Krause-Jensen et al., 2018). This is largely because of their considerable global extent, combined with a high rate of net primary production (*NPP*) and potentially high rates of carbon export (~ 43% *NPP*), of which a significant fraction can be sequestered to the deep ocean (~11% *NPP*) (Carlos M. Duarte & Cebrián, 1996; J. B. Gallagher, 2014; Krause-Jensen & Duarte, 2016; S. V. Smith, 1981).

We contend, however, that the fraction of seaweed primary production exported to the deep ocean is an incomplete metric of both sequestration and mitigation. In this context, sequestration is the rate at which CO_2 is taken from the atmosphere and stored over climatic scales (e.g. >100 years), whilst mitigation is a measure of the impact on *GHS* emissions should that ecosystem be lost to anthropogenic pressures and replaced by an alternate ecosystem state. Neglecting for the moment the contribution of microalgal assemblages to a seaweed ecosystem *NPP*, the current seaweed sequestration construct implicitly ignores the consumption of imported organic subsidies. Such imports will inevitably result in additional CO_2 emissions from the stimulation of non-calcareous and calcareous faunas' respective organic metabolism and calcareous metabolism (Bach et al., 2021; Gattuso, Payri, Pichon, Delesalle, & Frankignoulle, 1997). Indeed, organic subsidies have led to the majority of freshwater systems and some degraded blue carbon ecosystems as sites of carbon emissions (Carlos M. Duarte & Prairie, 2005). Furthermore, mitigation services ultimately require some estimate of the carbon balance relative to either a previous state or a future replacement ecosystem. In other words, mitigation services should not be assessed relative to a ground state, but relative to the carbon balance of what would otherwise have been or likely to fill that biological space (J. B. Gallagher, 2017; Prairie et al., 2018; Siikamäki, Sanchirico, Jardine, McLaughlin, & Morris, 2013; P. Smith, Powlson, Smith, Falloon, & Coleman, 2000). For example, a degraded kelp forest may progress to an alternative state of an urchin barren or turf-dominated assemblage (Edwards et al., 2020; Strain, Thomson, Micheli, Mancuso, & Airoldi, 2014), whilst the loss of *Fucus vesiculosus* assemblages be replaced self organising mussel reefs (Petraitis, Methratta, Rhile, Vidargas, & Dudgeon, 2009). Conversely, anthropogenic pressures have replaced non-foliose coral reefs with turf

meadows (Dudgeon, Aronson, Bruno, & Precht, 2010) and pelagic phytoplanktonic systems with floating *Sargassum* seaweed mats (Bach et al., 2021).

Here we aim to first explore the role of organic subsidies in influencing seaweed ecosystem sequestration. We attempt this by disentangling the components of the ecosystems' carbon balance when either closed or open to subsidies and relative to the fate of their exported production (Case i and Case ii respectively). Second, we assess the importance of subsidies to the carbon balance by compiling published net ecosystem production (*NEP*) estimates, and where available, the expected differences between anthropogenically driven replacements. Third, we assess the impact of these estimates on their global carbon balance by including the current parameters for fractions of exported material that are likely to have been remineralised.

Materials and Methods

To explore the role of subsidies on seaweed ecosystems, we first partitioned the components of their global carbon balance for one system closed and one open to those imports (Eq. 1 and 3). To gauge their importance, estimates of published *NEP* rates were collected from the *Web of Science* database (accessed March 2021) using the following search terms: (macroalga* OR benth*) AND "primary producti*" AND (ecosystem OR community). The search initially identified 2,313 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 hr) net ecosystem production (*NEP*) of seaweed-dominated communities were used for this review. Results from papers reporting fluxes as oxygen was converted to carbon using a molar photosynthetic and respiratory quotients = 1. When values were not stated but were available, 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-time and night-time production/respiration for >1 hr from which we calculated daily estimates using a stated 12:12 day:night ratio (R. J. Miller, Reed, & Brzezinski, 2009). For one article that reported for 12 hours of daylight only (Robert J. Miller, Reed, & Brzezinski, 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. (Robert J. Miller et al., 2011). A pool of common papers was also blindly assessed by all authors to ensure the consistency of selected papers and extracted results. Finally, the references contained within the included studies were checked for additional appropriate studies. From the search, we identified three additional studies that measured *NEP* for *F. vesiculosus* communities at the same study sites in the Baltic Sea (K. M. Attard et al., 2019; Karl M. Attard et al., 2019; Rodil, Attard, Norkko, Glud, & Norkko, 2019). The data from two papers from the same sites and depth range were pooled and averaged to minimise any overwhelming leverage as a trimmed mean from these papers on the small final pool of included papers (n = 18) (Table 1, Fig. 2).

Partitioning the carbon balance

The components of the ecosystems' carbon balance are assumed to represent a steady state over an annual cycle. This is the same level of analysis implicitly used in the seaweed sequestration construct of Krause-Jensen and Duarte (2016) for their *NPP*. In this way, algal standing biomass and production rate remain constant, and consumption by herbivores, detritivores, or microflora is directed to remineralisation, and not an increase in their 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 (J.B. Gallagher, 2015; Krause-Jensen & 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).

A seaweed assemblage closed to imports: Case i

This system is one where there is no import of organic subsidies and interactions with the coastal phytoplankton community (Fig. 1a). Here, the ecosystems' carbon balance (*NEPc*, Eq. 1) is determined between the seaweed assemblage gross primary production (*GPP*) and respiration shared across the alga (*Pr*), and its consumption largely by herbivores (*Hr*) and detritivores (*Dr*). The remaining production is then able to be exported (*E*) to adjacent coastal and oceanic waters and provides an estimate of the seaweed ecosystems' potential to sequester carbon and its equivalence with its *NEPc* (Eq. 1). However, that sequestration potential will be reduced as it is consumed and remineralised (*Er*) (Krause-Jensen & Duarte, 2016), with only the remaining export (*Es*) sequestered to the deep ocean (Fig. 1a). This residual fraction (*Es*) then becomes a proxy for the seaweeds' global carbon balance as its net ecosystem service (*NES*, Eq. 2), expressed more conveniently as the fraction of the seaweeds' *NPP* that reaches deeper waters (– $\boldsymbol{\theta NPP}$, Eq. 2). This then is the implicit rationale behind prominent current estimates (Krause-Jensen & Duarte, 2016).

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

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

A seaweed ecosystem open to imports: Case ii

In reality, though, these seaweed-dominated systems are open to organic imports (Foley & Koch, 2010; Robert J. Miller & Page, 2012; Zuercher & Galloway, 2019) and support an interactive phytoplanktonic assemblage that shares the ecosystems' *NPP* (Borum & Sand-Jensen, 1996; Robert J. Miller et al., 2011), and (Fig. 1b). As these imports are consumed by the faunal community, they subsidise the release of CO_2 (*Sr*) by further stimulating their organic and calcareous metabolism, and thereby lower the net ecosystem production (*NEPo*) (Eq. 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, Part 2).

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

It can be appreciated from Eq. 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).

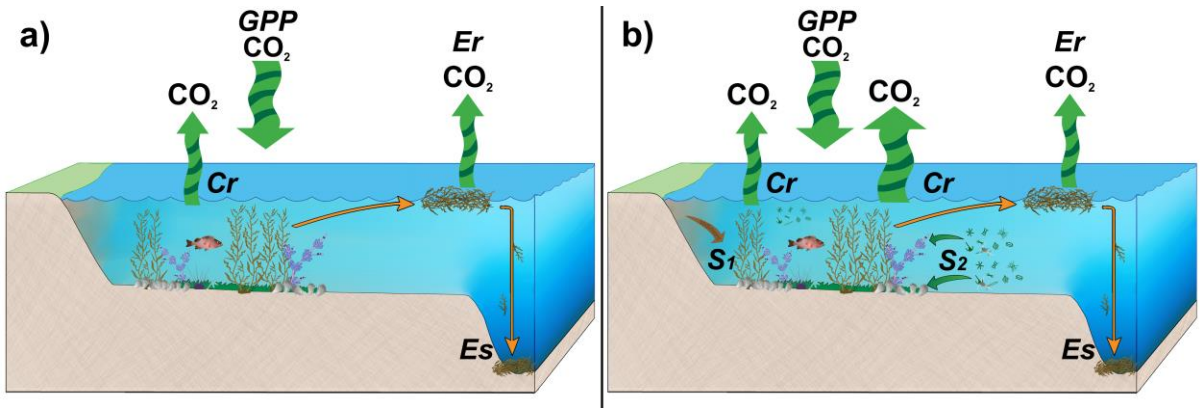

Fig. 1 Representation of the components of the carbon balance for seaweed ecosystems a) a seaweed assemblage closed to the import of organic carbon subsidies, and b) a seaweed–phytoplanktonic ecosystem open to the import of subsidies. Where *Cr* is community respiration partitioned between the algae 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 remineralised, *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.

Results

Studies with year-round sampling often showed strong seasonal effects with lower *NEP* values in the cooler/shorter daylength seasons and higher *NEP* values in the warmer/longer daylength seasons (Attard, Glud, McGinnis, & Rysgaard, 2014; K. M. Attard et al., 2019; Karl M. Attard et al., 2019; Cheshire, Westphalen, Wenden, Scriven, & Rowland, 1996; Falter, Atkinson, & Langdon, 2001; Robert J. Miller et al., 2011; Sullaway & Edwards, 2020). Indeed, longer day lengths over the full year appear to be consistent with tropical–subtropical ecosystems supporting *NEP* rates greater than their more heterotrophic temperate–polar counterparts (p(same median) < 0.04 Mann-Whitney U) (Fig. 2). Overall, the examples, largely from average annual estimates, varied substantially around a heterotrophic mean (Fig. 2) of -9.2mmol C m^{-2} day^{-1} (SE ± 11.6). The stand-out exceptions were *F. vesiculosus* supporting highly autotrophic annual *NEP* rates and extreme heterotrophy demonstrated by some turf assemblages (R. J. Miller et al., 2009) (Fig. 2, Table 1).

Table 1 Net ecosystem productivity (NEPo) of seaweed assemblages from the published literature; AEC = aquatic eddy covariance

Community description	Location	Method	Average *NEP* (mmol C m^{-2} day^{-1})	Sampling including multiple seasons	Reference
Temperate and polar					
Crustose algae/urchins, Fjord	Greenland	AEC	-4.7	Yes	Attard et al. (2014)
Fucus vesiculosus	Baltic sea, Finland	AEC	68.5	Yes	K. M. Attard et al. (2019)
Fucus vesiculosus	Baltic sea, Finland	AEC	66.2	Yes	Karl M. Attard et al. (2019)
Brown alga (Phaeophyceae) dominated community	Southern Australia	Chamber	4.6	Yes	Cheshire et al. (1996)
Eualaria fistulosa	Alaska, USA	Chamber	-7.5	No	Edwards et al. (2020)
Turf algae	California, USA	Chamber	-164.4	No	R. J. Miller et al. (2009)
Foliose algae	California, USA	Chamber	-32.64	No	R. J. Miller et al. (2009)
Macrocystis pyrifera & understory	California, USA	Chamber and growth rates	-8.57	Yes	Robert J. Miller et al. (2011)
Macrocystis pyrifera understory species	California, USA	Chamber	-47.9	Yes	Robert J. Miller et al. (2011)
Laminaria pallida and *Ecklonia maxima*	South Africa	Community carbon balance	-17.7	Yes	Newell and Field (1983)
Fucus vesiculosus	Baltic sea, Finland	AEC	11.2	No	Rodil et al. (2019)
Mixed macroalgae (15-20m)	West Antarctic Peninsula	AEC	-21.8	No	Rovelli, Attard, Cárdenas, and Glud (2019)
Sargassum horneri	California, USA	Chamber	-1.8	Yes	Sullaway and Edwards (2020)
Tropical and subtropical					
Sargassum sp, (0.4-3.4m)	Tropical reef, Australia	Open water sampling, other	10	Yes	Gruber, Lowe, and Falter (2017)
Corallina elongata, coral reef	Northwest Mediterranean	Open water sampling, other	20	No	Bensoussan and Gattuso (2007)
Mixed macrophyte/coral reef mesocosm	Arizona, USA	Open water sampling, other	-3	Yes	Falter et al. (2001)
Mixed macrophyte/coral reef, fringing degraded reef	French Polynesia	Open water sampling, other	10	No	(Gattuso et al., 1997)
Mixed macrophyte/coral reef	Central Red sea	Chamber	30.4	No	Roth et al. (2019)

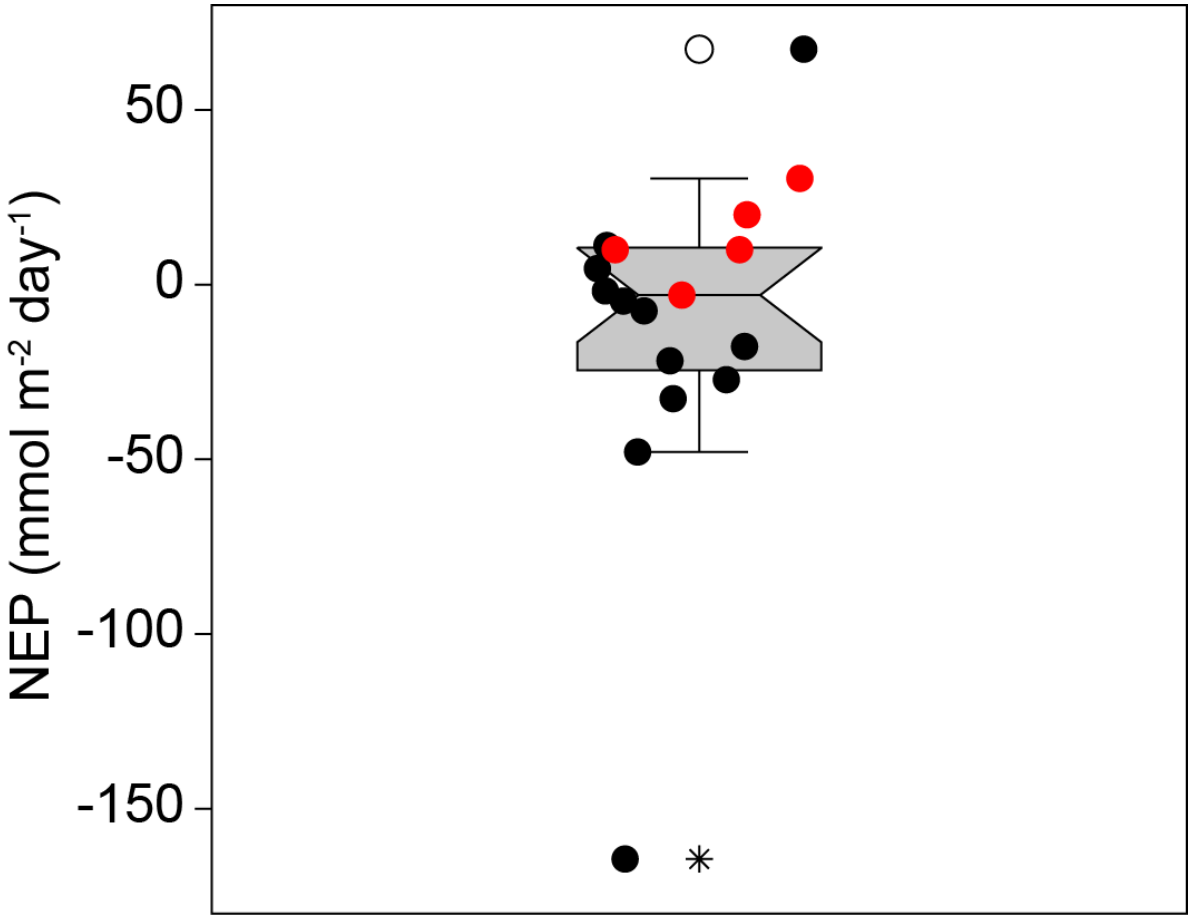

Fig. 2 Box and whisker plot for seaweed ecosystem net ecosystem production (*NEPo*) extracted from the literature for polar to tropical communities. Outliers are represented by the symbols (✱) and (○**)**. The top outlier is the average across two *F. vesiculosus* studies from in the same area and depths of the Baltic Sea, with the central static representing the median of the distribution.

Seaweed ecosystems' global carbon balance

Along with net ecosystem production, an account must also be made of the amount exported seaweed production that is remineralised. This is implicit in the calculation of Krause and Duarte (2016) for the amount sequestered and can be taken as the difference between their estimates of the average fraction of *NPP* exported (43%) and the remains to the deep ocean (11%) (Eq. 4).

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

By substituting Eq. 4 into Eq. 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* (Eq. 5).

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

We can then substitute our trimmed mean *NEPo* value (-9.6 mmol C m^{-2} day^{-1}) and the mean *NPP* for seaweed systems around the globe (Krause-Jensen and Duarte (2016), to estimate the net ecosystem service (*NES*) (Eq. 6).

$$NES = -9.2 - (0.32 \text{ x } 98.17) = -41.6 \text{mmol C m}^{-2} \text{ day}^{-1} \qquad (6)$$

To clarify, such a calculation is only intended to illustrate pertinent concepts, rather than provide a robust estimate of seaweed sequestration 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 = 17).

Discussion

The following section discusses the results of the coastal seaweed ecosystems' local and global carbon balances and relative to the limited information available for floating seaweeds and aquaculture. Constraints of these new carbon balance estimates as carbon mitigation services relative to replacements are highlighted with some examples, along with other considerations that constrain the use of the carbon balance as a metric for CO_2 atmospheric exchange.

Seaweed carbon balances

It appears that on the whole, seaweed ecosystems are impacted by the consumption of organic subsidies to the extent that on average they appear to be heterotrophic (-9.2mmol C m^{-2} day^{-1}). Furthermore, their average global carbon balance becomes increasingly a carbon source to the water column by accounting for remineralisation of their exported production (-40.6mmol C m^{-2} day^{-1}, Eq. 6), and not a global sink (*cal.* +10.80mmol C m^{-2} day^{-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} day^{-1} (i.e. the sum of 0.32 and 98.17, Eq. 6) just to maintain a global carbon balance. For many kelps supporting a *NEPo* sufficient to overcome the amount of export remineralised appear not to be likely (Table 1). However, this does not exclude other seaweeds such as the temperate *F. vesiculosus* and tropical–subtropical examples that appear to support more autotrophic regimes (Fig. 2, Table 1). Whether this is because of a relatively large *NPP* or smaller import and consumption of subsidies is not clear. Although, the light intensity and daylight hours may well distinguish the case for the tropics and subtropical systems.

The current research on seaweeds remains mostly restricted to coastal benthic systems. As far as we are aware, measurements of sequestration from seaweed aquaculture are restricted to a single study from the Yellow Sea, China (Jiang, Fang, Mao, Han, & Wang, 2013), which calculated the atmospheric CO_2 flux from annual changes in pCO_2 within the water columns (34.85 ± 17.46 mmol C m^{-2} day^{-1}). That value was significantly greater than sites adjacent to the seaweed arrays (24.17 ± 14.14mmol C m^{-2}/day^{-1}) but reduced towards carbon neutrality when compared to the reported baseline values for the area (32.71 ± 17.23 mmol C m^{-2} day^{-1}). Nevertheless, their overall mitigation services are likely to be significant given that export, like

harvesting, is conceivably greater than natural systems (Chung, Beardall, Mehta, Sahoo, & Stojkovic, 2011),. Information on floating *Sargassum spp.* ecosystems, however, is confined to *Cr* and *GPP* components determined from two separate studies of *Sargassum natans* from the oceanic and neritic waters south of Bermuda and the NW Atlantic shelf respectively (Lapointe, 1995; K. L. Smith, Burns, & Carpenter, 1973). Together, the *Cr* for neritic and oceanic regions appeared to be more than 3 to 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 (Eq. 6) in isolation, while valuable, requires comparisons of global balances of their actual or potential alternative replacement states (J. B. Gallagher, 2017; Siikamäki et al., 2013; P. Smith et al., 2000). However, *NEPo* measurements for kelp replacements such as barrens and turfs-dominated systems are limited, and the results mixed. Turf ecosystems can support a *NEPo* carbon balance of around -164.4mmol C m^{-2} day^{-1} (Table 1 (R. J. Miller et al., 2009)). This is significantly more heterotrophic than the previous mixed *M. pyrifera* assemblage (-8.57mmol C m^{-2} day^{-1}) from the same region (Table 1 (Robert J. 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 -4.76mmol C m^{-2} day^{-1} (SE ± 1.35) (Attard et al., 2014) to -3.75mmol C m^{-2} day^{-1} (SE ± 10.56) (Edwards et al., 2020). These are only marginally less heterotrophic than the kelp forest counterparts (-7.5mmol C m^{-2} day^{-1} SE ± 7.7) from similar environments (Edwards et al., 2020). For the highly autotrophic *F. vesiculosus* ecosystems, their potential to sequester carbon (66.2 and 68.4mmol C m^{-2} day^{-1} Table 1) may be amplified when considering the *NEPo* carbon balance of the mussel reef replacement the same area (-39.5mmol C m^{-2} day^{-1}) (Karl M. Attard et al., 2019). Furthermore, any in their global carbon balances (i.e. *NES*, Eq. 5) is unlikely to be great, as net primary production within and between coastal seaweed and phytoplanktonic ecosystems appear to converge (Borum & Sand-Jensen, 1996) along with the fraction of the export remineralised (Supplementary material S1, Part 2).

Other limitations: Inorganic carbon supply and outwelling

We have primarily focussed on the organic carbon balance over a more recent consideration of dissolved inorganic carbon exported, describe as outwelling (Santos et al., 2021). There is, however, an aspect of this outwelling as a long-term carbon storage service 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, more associated with a barren, can significantly increase the dissolution of calcium carbonate and conceivably increase the amount of bicarbonate outwelling (Eyre, Andersson, & Cyronak, 2014). In contrast, within a canopy system photosynthesis can significantly reduce acidification and turbulence (Morris, Graham, Kelvin, Ghisalberti, &

Swearer, 2019; Murie & Bourdeau, 2020). We now have a possible situation in which the replacement state *NES* may move closer or exceed its canopy counterpart.

The *NEPo* carbon balance is a measure of its 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 & Oechel, 2015; Thorhaug et al., 2020), and faunal (Gattuso et al., 1997) and algal calcification, notably the extensive production from seaweed *Halimeda spp* (Borowitzka & 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, the job of providing mitigation assessments is not finished. Assessments will likely require additional resources to measure atmospheric exchange between the seaweed ecosystem and its replacement, from the same area. Together with a *NEPo* and the fate of local export will there be sufficient information and predictive capability 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; 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 (Johannessen & Macdonald, 2016; Repetto, 2013). Carbon credits may become more expensive for polluters to compensate their emission above their cap and increases 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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Declarations

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Conflict of interest/competing interests

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

Availability of data and material

All data is contained found with the text of Table 1 with details of any recalculations to obtain the data and additional supporting analysis in Supplementary Information (S1)

Authors' contributions

Authors contributed to the study conception [John Barry Gallagher] and [Victor Shelamof] with contributions to insights on alternative states [Cayne Layton]. Authors contributed to the collection and processing of the data [John Barry Gallagher], [Victor Shelamof] and [Cayne Layton], and data synthesis [John Barry Gallagher]. The first draft of the manuscript was written by [John Barry Gallagher] and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript

References

Attard, K. M., Glud, R. N., McGinnis, D. F., & Rysgaard, S. (2014). Seasonal rates of benthic primary production in a Greenland fjord measured by aquatic eddy correlation. *Limnology and Oceanography, 59*(5), 1555-1569. doi:10.4319/lo.2014.59.5.1555

Attard, K. M., Rodil, I. F., Berg, P., Norkko, J., Norkko, A., & Glud, R. N. (2019). Seasonal metabolism and carbon export potential of a key coastal habitat: The perennial canopy-forming macroalga Fucus vesiculosus. *Limnology and Oceanography, 64*(1), 149-164. doi:10.1002/lno.11026

Attard, K. M., Rodil, I. F., Glud, R. N., Berg, P., Norkko, J., & Norkko, A. (2019). Seasonal ecosystem metabolism across shallow benthic habitats measured by aquatic eddy covariance. *Limnology and Oceanography Letters, 4*(3), 79-86. doi:10.1002/lol2.10107

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*(1), 2556. doi:10.1038/s41467-021-22837-2

Borowitzka, M. A., & Larkum, A. W. D. (1976). Calcification in the Green Alga Halimeda III. The sources of inorganic carbon for photosynthesis and calcification and a model of the mechanism of calcification. *Journal of Experimental Botany, 27*(5), 879-893. doi:10.1093/jxb/27.5.879

Borum, J., & Sand-Jensen, K. (1996). Is total primary production in shallow coastal marine waters stimulated by nitrogen loading? *Oikos, 76*(2), 406-410. doi:http://www.jstor.org/stable/3546213

Bensoussan, N., & Gattuso, J. (2007). Community primary production and calcification in a NW Mediterranean ecosystem dominated by calcareous macroalgae. Marine Ecology Progress Series, 334, 37-45. doi:10.3354/meps334037

Cheshire, A. C., Westphalen, G., Wenden, A., Scriven, L. J., & Rowland, B. C. (1996). Photosynthesis and respiration of phaeophycean-dominated macroalgal communities in summer and winter. *Aquatic Botany, 55*(3), 159-170. doi:10.1016/S0304-3770(96)01071-6

Chung, I. K., Beardall, J., Mehta, S., Sahoo, D., & Stojkovic, S. (2011). Using marine macroalgae for carbon sequestration: a critical appraisal. *Journal of Applied Phycology, 23*(5), 877-886. doi:10.1007/s10811-010-9604-9

Cook, J., Nuccitelli, D., Green, S. A., Richardson, M., Winkler, B., Painting, R., . . . Skuce, A. (2013). Quantifying the consensus on anthropogenic global warming in the scientific literature. *Environmental Research Letters, 8*(2), 024024. doi:10.1088/1748-9326/8/2/024024

Duarte, C. M., & Cebrián, J. (1996). The fate of marine autotrophic production. *Limnology and Oceanography, 41*(8), 1758-1766. doi:10.4319/lo.1996.41.8.1758

Duarte, C. M., Middelburg, J. J., & Caraco, N. (2005). Major role of marine vegetation on the oceanic carbon cycle. *Biogeosciences, 2*(1), 1-8. doi:10.5194/bg-2-1-2005

Duarte, C. M., & Prairie, Y. T. (2005). Prevalence of Heterotrophy and Atmospheric CO2 Emissions from Aquatic Ecosystems. *Ecosystems, 8*(7), 862-870. doi:10.1007/s10021-005-0177-4

Dudgeon, S. R., Aronson, R. B., Bruno, J. F., & Precht, W. F. (2010). Phase shifts and stable states on coral reefs. *Marine Ecology Progress Series, 413*, 201-216. doi:10.3354/meps08751

Edwards, M., Konar, B., Kim, J.-H., Gabara, S., Sullaway, G., McHugh, T., . . . Small, S. (2020). Marine deforestation leads to widespread loss of ecosystem function. *PloS one, 15*(3), e0226173. doi:10.1371/journal.pone.0226173

Eyre, B. D., Andersson, A. J., & Cyronak, T. (2014). Benthic coral reef calcium carbonate dissolution in an acidifying ocean. *Nature Climate Change, 4*, 969. doi:10.1038/nclimate2380

Falter, J. L., Atkinson, M. J., & Langdon, C. (2001). Production-respiration relationships at different timescales within the Biosphere 2 coral reef biome. *Limnology and Oceanography, 46*(7), 1653-1660. doi:10.4319/lo.2001.46.7.1653

Filbee-Dexter, K., & Wernberg, T. (2020). Substantial blue carbon in overlooked Australian kelp forests. *Scientific Reports, 10*(1), 12341. doi:10.1038/s41598-020-69258-7

Foley, M., & Koch, P. (2010). Correlation between allochthonous subsidy input and isotopic variability in the giant kelp Macrocystis pyrifera in central California, USA. *Marine Ecology Progress Series, 409*, 41-50. doi:10.3354/meps08600

Gallagher, J. B. (2014). *Explicit and implicit assumptions within the blue carbon conceptual model: A critique.* Paper presented at the International Conference on Marine Science and Aquaculture (2014): Ecosystem perspectives in sustainable development Kota Kinabalu, Sabah, Malaysia.

Gallagher, J. B. (2015). The implications of global climate change and aquaculture on blue carbon sequestration and storage within submerged aquatic ecosystems. In S. Mustafa & R. Shapawi (Eds.), *Aquaculture Ecosystems* (pp. 243-280). Oxford: Wiley Blackwell.

Gallagher, J. B. (2017). Taking stock of mangrove and seagrass blue carbon ecosystems: A perspective for future carbon trading. *Borneo Journal of Marine Science and Aquaculture, 1*(1), 71-74.

Gattuso, J.-P., Payri, C. E., Pichon, M., Delesalle, B., & Frankignoulle, M. (1997). Primary production, calcification, and air-sea co2 fluxes of a macroalgal-dominated coral reef community (Moorea, French Polynesia). *Journal of Phycology, 33*(5), 729-738. doi:10.1111/j.0022-3646.1997.00729.x

Gruber, R. K., Lowe, R. J., & Falter, J. L. (2017). Metabolism of a tide-dominated reef platform subject to extreme diel temperature and oxygen variations. *Limnology and Oceanography, 62*(4), 1701-1717. doi.org/10.1002/lno.10527

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. *Limnology and Oceanography, 60*(5), 1689-1706. doi.org/10.1002/lno.10128

Ikawa, H., & Oechel, W. C. (2015). Temporal variations in air-sea CO2exchange near large kelp beds near San Diego, California. *Journal of Geophysical Research: Oceans, 120*(1), 50-63. doi:10.1002/2014jc010229

Jiang, Z., Fang, J., Mao, Y., Han, T., & Wang, G. (2013). Influence of Seaweed Aquaculture on Marine Inorganic Carbon Dynamics and Sea-air CO2 Flux. *Journal of the World Aquaculture Society, 44*(1), 133-140. doi:10.1111/jwas.12000

Johannessen, S. C., & Macdonald, R. W. (2016). Geoengineering with seagrasses: is credit due where credit is given? *Environmental Research Letters, 11*(11), 113001. doi:10.1088/1748-9326/11/11/113001

Krause-Jensen, D., & Duarte, C. M. (2016). Substantial role of macroalgae in marine carbon sequestration. *Nature Geoscience, 9*(10), 737-742. doi:10.1038/ngeo2790

Krause-Jensen, D., Lavery, P., Serrano, O., Marbà, N., Masque, P., & Duarte, C. M. (2018). Sequestration of macroalgal carbon: the elephant in the Blue Carbon room. *Biology Letters, 14*(6), 20180236. doi:10.1098/rsbl.2018.0236

Lapointe, B. E. (1995). A comparison of nutrient-limited productivity in Sargassum natans from neritic vs. oceanic waters of the western North Atlantic Ocean. *Limnology and Oceanography, 40*(3), 625-633. doi:10.4319/lo.1995.40.3.0625

Lovelock, C. E., & Duarte, C. M. (2019). Dimensions of Blue Carbon and emerging perspectives. *Biology Letters, 15*(3), 20180781. doi:10.1098/rsbl.2018.0781

Lovelock, C. E., & Reef, R. (2020). Variable Impacts of Climate Change on Blue Carbon. *One Earth, 3*(2), 195-211. doi:10.1016/j.oneear.2020.07.010

McLeod, E., Chmura, G. L., Bouillon, S., Salm, R., Björk, M., Duarte, C. M., . . . Silliman, B. R. (2011). A blueprint for blue carbon: toward an improved understanding of the role of vegetated coastal habitats in sequestering CO 2. *Frontiers in Ecology and the Environment, 9*(10), 552-560. doi:10.1890/110004

Miller, R. J., & Page, H. M. (2012). Kelp as a trophic resource for marine suspension feeders: a review of isotope-based evidence. *Marine Biology, 159*(7), 1391-1402. doi:10.1007/s00227-012-1929-2

Miller, R. J., Reed, D. C., & Brzezinski, M. A. (2009). Community structure and productivity of subtidal turf and foliose algal assemblages. *Marine Ecology Progress Series, 388*, 1-11. doi:10.3354/meps08131

Miller, R. J., Reed, D. C., & Brzezinski, M. A. (2011). Partitioning of primary production among giant kelp (Macrocystis pyrifera), understory macroalgae, and phytoplankton on a temperate reef. *Limnology and Oceanography, 56*(1), 119-132. doi:10.4319/lo.2011.56.1.0119

Morris, R. L., Graham, T. D. J., Kelvin, J., Ghisalberti, M., & Swearer, S. E. (2019). Kelp beds as coastal protection: wave attenuation of Ecklonia radiata in a shallow coastal bay. *Annals of Botany*. doi:10.1093/aob/mcz127

Murie, K. A., & Bourdeau, P. E. (2020). Fragmented kelp forest canopies retain their ability to alter local seawater chemistry. *Scientific reports, 10*(1), 11939. doi:10.1038/s41598-020-68841-2

Nellemann, C., Corcoran, E., M., D. C., Valdrés, L., Young, C. D., Fonseca, L., & G, G. (2009). *Blue Carbon: The Role of Healthy Oceans in Binding Carbon*. (ISBN: 978-82-7701-060-1). GRID-Arenda; United Nations Environment Programme.

Newell, R., & Field, J. (1983). *The Contribution Of Bacteria And Detritus To Carbon And Nitrogen Flow In A Benthic Community*.

Petraitis, P. S., Methratta, E. T., Rhile, E. C., Vidargas, N. A., & Dudgeon, S. R. (2009). Experimental confirmation of multiple community states in a marine ecosystem. *Oecologia, 161*(1), 139-148. doi:10.1007/s00442-009-1350-9

Prairie, Y. T., Alm, J., Beaulieu, J., Barros, N., Battin, T., Cole, J., . . . Vachon, D. (2018). Greenhouse Gas Emissions from Freshwater Reservoirs: What Does the Atmosphere See? *Ecosystems, 21*(5), 1058-1071. doi:10.1007/s10021-017-0198-9

Repetto, R. (2013). Cap and Trade Contains Global Warming Better Than a Carbon Tax. *Challenge (05775132), 56*(5), 31-61. doi:10.2753/0577-5132560502

Rodil, I. F., Attard, K. M., Norkko, J., Glud, R. N., & Norkko, A. (2019). Towards a sampling design for characterizing habitat-specific benthic biodiversity related to oxygen flux dynamics using Aquatic Eddy Covariance. *Plos One, 14*(2), e0211673. doi:10.1371/journal.pone.0211673

Roth, F., Wild, C., Carvalho, S., Radecker, N., Voolstra, C. R., Kurten, B., . . . Jones, B. H. (2019). An in situ approach for measuring biogeochemical fluxes in structurally complex benthic communities. *Methods in Ecology and Evolution, 10*(5), 712-725. doi:10.1111/2041-210x.13151

Rovelli, L., Attard, K. M., Cárdenas, C. A., & Glud, R. N. (2019). Benthic primary production and respiration of shallow rocky habitats: a case study from South Bay (Doumer Island, Western Antarctic Peninsula). *Polar Biology, 42*(8), 1459-1474. doi:10.1007/s00300-019-02533-0

Santos, I. R., Burdige, D. J., Jennerjahn, T. C., Bouillon, S., Cabral, A., Serrano, O., . . . Tamborski, J. J. (2021). The renaissance of Odum's outwelling hypothesis in 'Blue Carbon' science. *Estuarine, Coastal and Shelf Science, 255*, 107361. doi:https://doi.org/10.1016/j.ecss.2021.107361

Siikamäki, J., Sanchirico, J. N., Jardine, S., McLaughlin, D., & Morris, D. (2013). Blue Carbon: Coastal Ecosystems, Their Carbon Storage, and Potential for Reducing Emissions. *Environment: Science and Policy for Sustainable Development, 55*(6), 14-29. doi:10.1080/00139157.2013.843981

Smith, K. L., Burns, K. A., & Carpenter, E. J. (1973). Respiration of the pelagic Sargassum community. *Deep Sea Research and Oceanographic Abstracts, 20*(2), 213-217. doi:10.1016/0011-7471(73)90052-1

Smith, P., Powlson, D. S., Smith, J. U., Falloon, P., & Coleman, K. (2000). Meeting Europe's climate change commitments: quantitative estimates of the potential for carbon mitigation by agriculture. *Global Change Biology, 6*(5), 525-539. doi:10.1046/j.1365-2486.2000.00331.x

Smith, S. V. (1981). Marine Macrophytes as a Global Carbon Sink. *Science, 211*(4484), 838-840. doi:10.1126/science.211.4484.838

Strain, E. M. A., Thomson, R. J., Micheli, F., Mancuso, F. P., & Airoldi, L. (2014). Identifying the interacting roles of stressors in driving the global loss of canopy-forming to mat-forming algae in marine ecosystems. *Global Change Biology, 20*(11), 3300-3312. doi:10.1111/gcb.12619

Sullaway, G. H., & Edwards, M. S. (2020). Impacts of the non-native alga Sargassum horneri on benthic community production in a California kelp forest. *Marine Ecology Progress Series, 637*, 45-57. doi:10.3354/meps13231

Thorhaug, A., Gallagher, J. B., Kiswara, W., Prathep, A., Huang, X., Yap, T.-K., . . . Berlyn, G. (2020). Coastal and estuarine blue carbon stocks in the greater Southeast Asia region: Seagrasses and mangroves per nation and sum of total. *Mar Pollut Bull, 160*, 111168. doi:10.1016/j.marpolbul.2020.111168

UNFCCC. (2015). Paris Agreement. Retrieved from http://unfccc.int/paris_agreement/items/9485.php

Zuercher, R., & Galloway, A. W. E. (2019). Coastal marine ecosystem connectivity: pelagic ocean to kelp forest subsidies. *Ecosphere, 10*(2), e02602. doi:10.1002/ecs2.2602