Seaweed forests are carbon sinks that may help mitigate CO_2 emissions: a comment on Gallagher et al. (2022)

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Recently, Gallagher *et al.* (2022) suggested that seaweed ecosystems are net heterotrophic carbon sources due to CO_2 released from the consumption of external subsidies. Here we outline several flaws in their argument, which we believe confuse research on the blue carbon potential of seaweed ecosystems, and unjustifiably generate doubt around initiatives to protect and restore seaweed forests. Gallagher *et al.*'s evidence relies on 18 studies with highly variable measures of net ecosystem production, which do not statistically support their conclusion that most seaweed ecosystems are heterotrophic. This dataset is also inappropriate as it is incomplete and misrepresents seaweed ecosystems globally, particularly seaweed forests, which contribute disproportionately to global seaweed productivity. We maintain that the climate change mitigation value of an ecosystem depends on the net difference in CO_2 uptake between the original ecosystem and its replacement ecosystem. We provide evidence that most seaweed ecosystems, which drawdown the largest carbon flux of any vegetated coastal habitat, are indeed net autotrophic ecosystems. We recognize that substantial uncertainties remain concerning the magnitude of CO_2 drawdown by seaweed ecosystems and recommend that carbon fluxes around seaweed ecosystems should be considered more broadly and taken into account in estimates of their CO_2 mitigation potential.

Keywords: blue carbon, carbon dioxide removal, net ecosystem productivity, respiration, seaweed, seaweed forest.

Main text

The paper—*seaweed ecosystems may not mitigate CO_2 emissions* (Gallagher *et al.*, 2022)—claims that seaweed ecosystems could be carbon sources rather than carbon sinks because "respiration subsidies" (from inputs of allochthonous organic carbon) create negative net ecosystem production (NEP). This implies that seaweed ecosystems produce more CO_2 than they drawdown, and thus may not mitigate CO_2 emissions. Gallagher *et al.* (2022) draw this inference from a compiled dataset that shows that, on average, seaweed ecosystems are net heterotrophic. Here, we discuss four flaws in the study presented by Gallagher *et al.* (2022) which we believe confuse research on the CO_2 mitigation potential of seaweed ecosystems, and unjustifiably seed doubt around motivations and initiatives to protect and restore seaweed forests to deliver climate benefits.

(1) The dataset assembled by Gallagher *et al.* (2022) conflates vastly different seaweed ecosystems, many of which play a minor role in global seaweed carbon cycling. The average NEP they present is, therefore, not representative of seaweed ecosystems in general or seaweed forests (e.g. kelp forests) in particular, which dominate both global seaweed productivity and the current scientific discussion on the CO_2 mitigation po-

tential of seaweed ecosystems. Indeed, a regrouping of Gallagher *et al.*'s data into seaweed forests and other seaweed ecosystems suggests that seaweed forests may in fact be net autotrophic.

(2) Gallagher *et al.* (2022) present a limited data compilation that shows large variability in both NEP measures from individual studies as well as in the overall mean NEP. This negates the statistical basis of the argument.

(3) Gallagher *et al.*'s dataset repurposes studies that are not appropriate for measuring carbon sequestration in coastal ecosystems. This biases their data compilation towards heterotrophy.

(4) Gallagher *et al.* (2022) misrepresent the CO_2 mitigation potential of an ecosystem. It is not, as they claim, whether the ecosystem is autotrophic or heterotrophic *per se*. Rather, it is the effect of losses or gains of the ecosystem on net CO_2 emissions, including long-term carbon storage beyond the ecosystem, that determines the mitigation potential.

Below, we discuss each of these four elements. We highlight additional evidence that most seaweed forests are indeed net autotrophic, and we explore how to best incorporate community respiration components into seaweed carbon sequestration estimates. We also reinforce that Gallagher *et al.*'s assess-

ment of the climate change mitigation potential of seaweed ecosystems does not fully consider changes in CO_2 emissions when replacing seaweed forests with other ecosystems, which is critical to assessing the role of seaweed ecosystems in mitigating CO_2 emissions.

Conflating vastly different seaweed ecosystems obscures evidence that seaweed forests are autotrophic

Gallagher *et al.*'s dataset does not reflect known patterns of relative seaweed abundance and associated carbon fluxes, nor does it capture natural variation adequately. The global extent and carbon fluxes of seaweed ecosystems are overwhelmingly dominated by seaweed forests (Mann, 1973; Wernberg *et al.*, 2019), which contribute disproportionately to ecosystem net primary productivity (Newell *et al.*, 1982; Tait and Schiel, 2013). The dominant role of seaweed forests for total global seaweed productivity is also emphasized by recent global assessments (Duarte *et al.*, 2022; Pessarrodona *et al.*, 2022), which were not available at the time Gallagher *et al.* (2022) published their paper. Globally, seaweed forests (primarily composed of species belonging to the orders Laminariales and Fucales; *sensu* Fraser, 2012; Wernberg and Filbee-Dexter, 2019) drawdown >70% of the carbon assimilated by all seaweeds, making them by far the most productive vegetated ecosystem in the coastal ocean (Duarte *et al.*, 2022). Yet, over half of the NEP measures used by Gallagher *et al.* (2022) are from ecosystems that are fundamentally different from seaweed forests and, in some cases, represent the replacement ecosystems when seaweed forests are lost (e.g. Peleg *et al.*, 2020). These include sea urchin barrens, turf reefs, red algal reefs, and intertidal seaweed turfs (Gattuso *et al.*, 1997; Bensoussan and Gattuso, 2007; Miller *et al.*, 2009; Gruber *et al.*, 2017; Rovelli *et al.*, 2019), all of which are effectively missing a productive canopy component. Gallagher *et al.*'s dataset also includes a synthetic community installed in an artificial "ocean" in the Arizona desert (Falter *et al.*, 2001). Whilst calcifying algae are only estimated to draw ∼5% of the carbon assimilated by seaweeds globally (Duarte *et al.*, 2022), >20% of the studies in Gallagher *et al.*'s dataset contain estimates from this group (Bensoussan and Gattuso, 2007; Attard *et al.*, 2014; Roth *et al.*, 2019; Rovelli *et al.*, 2019). The inappropriate representation of global seaweed ecosystems in Gallagher *et al.*'s compilation ($n = 18$) obscures the dominant feature (i.e. seaweed forests) of global seaweed carbon cycling and sequestration. The suggestion that seaweed ecosystems as a whole are net heterotrophic counters long-established knowledge, based on the fate of their net primary production, community metabolism, and export fluxes (Smith, 1981; Duarte and Cebrián, 1996; Gattuso *et al.*, 1998). Indeed, when the studies complied by Gallagher *et al.* (2022) are divided into seaweed forests versus replacement ecosystems, it supports the notion that seaweed forests are net autotrophic (Table 1).

The NEP calculations are based on uncertain, incomplete, and biased data

Gallagher *et al.*'s dataset ($n = 18$ total) does not hold much value as a global estimate of the NEP of seaweed ecosystems as the search criteria or data selection decisions taken by the authors seems to have failed to capture much of the literature on macroalgal carbon metabolism. For instance, a re-

cent compilation of primary production studies in seaweed ecosystems reports that >100 studies used benthic chambers (Pessarrodona *et al.*, 2022), many of which used similar methods as the ones used by Gallagher *et al.* (2020) to estimate NEP (*in situ* incubations measuring oxygen or carbon fluxes on reefs). Importantly, Gallagher *et al.* (2020) appear to have missed numerous studies reporting large positive NEP (i.e. autotrophic) in several seaweed ecosystems. For example, NEP in *Sargassum* forests in Japan ranged from 302 to 1378 mmol C m^{-2} d^{-1} depending on the season (Watanabe *et al.*, 2020), whilst *Macrocystis* forests are reported have NEP values of up to 1250 mmol C m^{-2} d^{-1} in the Southern Ocean (Delille *et al.*, 2000, 2009). Dominant seaweed communities in the Mediterranean are reported to be net autotrophic (NEP = 17.8 ± 0.5 mmol C m^{-2} d^{-1}), whilst their replacement ecosystems (e.g. algal turfs and invasive algae) are net heterotrophic (Peleg *et al.*, 2020). Kelp forests in the northwest Pacific are also net carbon sinks (positive NEP), drawing down an average of 59 mmol C m^{-2} d^{-1} (range 20–180 mmol C m^{-2} d^{-1} [Ikawa and Oechel, 2015]). Other evidence that seaweed forests are net autotrophic comes from carbon budgets for these ecosystems such as those reported in the global review by Duarte *et al.* (2005) (362 mmol C m^{-2} d^{-1}, mean across all seaweed species) and Duarte and Agusti (1998), which are consistent with observations of persistent pCO$_2$ sub-saturation in seaweed ecosystems (Delille *et al.*, 2000; Krause-Jensen *et al.*, 2016).

For the few studies captured by Gallagher *et al.* (2022) the actual NEP is inadequately reported. For example, Gallagher *et al.* (2022) report a biased NEP estimate of −47.9 and −8.57 mmol C m^{-2} d^{-1} (i.e. net heterotrophic) from Miller *et al.* (2011), as the former includes only a fraction of the total ecosystem net production, and does not incorporate the significant phytoplankton production measured within the seaweed habitat. Gallagher *et al.*'s decision to include this study (with only part of the NPP) contradicts their argument that whole ecosystem metabolism must be considered in estimates of carbon sequestration, and challenges their assertion that the contribution of phytoplankton production is negligible in all seaweed ecosystems, countering other current evidence (Kavanaugh *et al.*, 2009; Pfister *et al.*, 2019). Gallagher *et al.* (2022) also incorrectly assume that daytime community respiration is the same as nighttime, even though nighttime respiration tends to be lower (Barrón and Duarte, 2009; Miller *et al.*, 2011).

Additionally, a third of Gallagher *et al.*'s compiled studies do not consider seasonal variation, and of those seasonal studies, twice as many were conducted in winter compared to summer, including the lowest and third lowest NEP measures from benthic chamber studies on turf seaweeds (−164 mmol C m^{-2} d^{-1}) and foliose algae (−32.6 mmol C m^{-2} d^{-1}) (Miller *et al.*, 2009). This is problematic and has likely biased the estimates towards low values, as NEP can be >200 times lower in winter compared to spring and summer (Attard *et al.*, 2019a), when intense macroalgal growth generally occurs (Delille *et al.*, 2000; Rodgers and Shears, 2016; Wernberg *et al.*, 2019; Pedersen *et al.*, 2020).

Most importantly, the interpretations and conclusions of Gallagher *et al.* (2022) are not supported by their own dataset. The authors conclude that "*the [negative] average NEP suggests that seaweed ecosystems are a C source.*" Yet, statistical analysis of their dataset shows that the mean of their studies is not significantly different from 0 (two-sided *t*-test, $p > 0.95$),

Table 1. Average net ecosystem production (NEP) for seaweed forests and replacement ecosystems selected from the dataset compiled by Gallagher *et al.* (2022).

Dataset	NEP (mmol C m^{-2}d^{-1})		N	Source
	Average	SE		
Gallagher's estimate	− 4.02	12.21	18	Table 1 in Gallagher et al. (2022)
Seaweed forest ecosystems	17.26	14.14	8	Attard *et al.*, 2019a, b, Bordeyne et al. 2020; Cheshire et al. 1996; Gruber *et al.*, 2017; Sullaway and Edwards, 2020 (fucoids), Miller *et al.*, 2011; Edwards *et al.*, 2020, Newell and Field, 1983(kelp)
Replacement ecosystems	− 55.19	37.83	4	Attard *et al.*, 2014 and Edwards *et al.*, 2020 (barrens), Miller *et al.*, 2009 (turf), Miller *et al.*, 2011 (understory)
Other seaweed ecosystems	0.92	8.42	7	Miller *et al.* 2009; Rovelli *et al.*, 2019, Marx et al. 2021(other foliose macroalgae), Bensoussan and Gattuso, 2007 (crustose macroalgae and coral), Gattuso *et al.*, 1997; Falter *et al.*, 2001; Roth *et al.*, 2019 (other foliose macroalgae and coral)

Seaweed forests include laminarian and fucalean kelp species. Replacement ecosystems include turf reefs, sea urchin barrens, and understory communities where canopy kelps were removed. Edwards *et al.*, (2020) are listed in two categories because they report NEP for kelp forests and barrens.

with the standard error being three times larger than the mean. This high variability also exists at the level of the individual studies, with several studies reporting standard errors 1–2 times greater than the mean (Edwards *et al.*, 2020; Sullaway and Edwards, 2020). Gallagher *et al.* (2022) ignore this variability, and yet their dataset cannot reject the null hypothesis that seaweed ecosystems in their dataset are in metabolic balance (i.e. neither net carbon sources nor sinks).

NEP as calculated by Gallagher *et al.* (2022) cannot resolve seaweed carbon mitigation potential

NEP represents the total amount of organic carbon in an ecosystem available for storage, export as organic carbon, or nonbiological oxidation (Lovett *et al.*, 2006). Accurately quantifying NEP in order to infer available organic carbon at the relevant spatial scales remains an important challenge in marine ecosystems (Attard *et al.*, 2019b), as these are open systems characterized by highly dynamic fluxes of production and respiration from benthic and pelagic sources (Jahnke, 2010; Bauer *et al.*, 2013; Smale *et al.*, 2018; Santos *et al.*, 2021). Over half of Gallagher *et al.*'s NEP estimates come from benthic chamber studies, which yield an unrealistic account of the carbon available for export or storage [note that Bordeyne *et al.* (2020) are incorrectly reported to have used the Aquatic Eddy Covariance method (AEC)]. This is because benthic chambers enclose only a small volume (typically <1 m^3) of a benthic community for a short time period (typically <24 h), which allows *in situ* measurements of the metabolism of confined and selected species, but is unlikely to capture the broader exchange of organic matter across the entire ecosystem (Champenois *et al.*, 2007; Olivé *et al.*, 2016). Chamber studies may underestimate ecosystem photosynthesis and overestimate respiration (Rodgers and Shears, 2016; White *et al.*, 2021) and are therefore largely inappropriate to make inferences on global carbon balances and sequestration budgets—which indeed was not the aim of any of the chamber studies compiled. Crucially, studies that provide estimates of NEP over larger spatial scales (10 s of m^2, e.g. AEC and open water measurements capturing organic and inorganic processes) in Gallagher *et al.*'s Table 1 yield positive NEP, again suggesting that most seaweed ecosystems are CO_2 sinks. The few studies using AEC available show that seaweed forests are highly autotrophic (Attard *et al.*, 2019a, 2019b), whereas ecosystems not dominated by large seaweeds (e.g. sea urchin barrens and sandy sediments with sparse seaweeds) are slightly heterotrophic (Attard *et al.*, 2014), which further supports evidence of net uptake of carbon by the former. Continuous measurements of air-sea CO_2 flux for seven years near a kelp forest using the AEC method revealed the kelp forest to be a major CO_2 sink, with the strength of the flux being strongly related to the extent and productivity of the ecosystem (Ikawa and Oechel, 2015).

Climate change mitigation depends on the net change in greenhouse gases, carbon sequestration, and CO_2 emissions

As pointed out by Gallagher *et al.* (2022), the climate change mitigation value of an ecosystem ultimately depends on the difference in CO_2 uptake capacity between the original ecosystem and its replacement ecosystem (Lovelock and Duarte, 2019). Gallagher *et al.* (2022) assert that the change in carbon mitigation following the loss of seaweed forests is "mixed", citing evidence that algal turfs are more heterotrophic than seaweed forests, whereas sea urchin barrens are not (Edwards *et al.*, 2020). The fact that the replacement of seaweed forests by turfs would imply a reduction in NEP and a substantial loss of CO_2 mitigation capacity is not a minor point, as this is indeed what is happening to large areas of seaweed forests impacted by climate change globally (Krumhansl *et al.*, 2016; Filbee-Dexter and Wernberg, 2018; Pessarrodona *et al.*, 2021). Indeed, a study not included by Gallagher *et al.* (2022) shows how shallow reefs turn from net carbon sinks to net carbon sources when seaweed forests are lost (Peleg *et al.*, 2020). As far as sea urchin barrens are concerned, Gallagher *et al.* (2022) do not mention that their cited study actually appeared to exclude sea urchins, resulting in unnaturally elevated productivity inside the benthic chambers due to the lack of urchin respiration and concurrent growth of benthic microalgal mats (Edwards *et al.*, 2020), which might have made them unnaturally autotrophic. Hence, contrary to Gallagher *et al.*'s suggestion, it seems that the loss of seaweed forests would lead to a net reduction in CO_2 uptake capacity even if the seaweed forests were slightly heterotrophic. It

follows, therefore, that avoiding losses of seaweed forests and restoring degraded habitats could represent a nature-based solution to reduce net CO_2 emissions.

Although the potential for seaweed forests—which dominate the global seaweed biome—to contribute to climate change mitigation is increasingly recognized (Hill *et al.*, 2015; Krause-Jensen *et al.*, 2018; Macreadie *et al.*, 2019), the amount of seaweed carbon that reaches carbon sinks is still poorly quantified and not spatially resolved (Hurd *et al.*, 2022). Gallagher *et al.*'s study does not contribute to resolving any of these outstanding uncertainties. Instead of also capturing long-term carbon storage beyond the habitat, Gallagher *et al.* (2022) only calculate the balance between respiration and production of seaweed ecosystems (including external subsidies) in the coastal zone—a region of high exchange where much of the consumed organic material is recycled back to CO_2 and dissolved nutrients that are immediately available for subsequent primary production (Passow and Carlson, 2012). The extent to which these external subsidies would get respired in the presence or absence of seaweed forests remains debatable, and Gallagher *et al.* (2022) do not convincingly articulate that these external subsidies would only be respired if the seaweed ecosystem is present. Even assuming seaweed forests facilitate the respiration of allochthonous carbon, what is more relevant are the pathways through which carbon produced in the coastal zone can become sequestered in the long term. There is evidence that these pathways are enhanced when seaweed forests are present, through export to and long-term burial in shelf sediments (Frigstad *et al.*, 2021) and transport to deep ocean regions with slow ventilation times (Ortega *et al.*, 2019; Baker *et al.*, 2022; Filbee-Dexter *et al.*, 2022).

Conclusion

Gallagher *et al.*'s suggestion that seaweed ecosystems are net heterotrophic carbon sources misrepresents NEP in seaweed ecosystems, is based on a limited and inappropriate data selection, and lacks statistical support. We provide evidence that most seaweed forests, which drawdown the largest carbon flux of any vegetated habitat in the coastal ocean, are indeed net autotrophic ecosystems (i.e. carbon sinks), and export substantial amounts of organic matter that may contribute to carbon sequestration. Therefore, actions to restore seaweed forests, improve their condition, and/or halt their decline may contribute to climate change mitigation through increased drawdown of CO_2, although quantifying their actual contribution to mitigation remains challenging. We recognize and recommend that carbon (and other greenhouse gases) fluxes around seaweed ecosystems should be considered more broadly and integrated into estimates of their climate change mitigation potential. This requires better resolving long-term carbon cycling by associated fauna, better understanding the fluxes of CO_2 between the atmosphere and seaweed forests, better understanding the exchange of carbon between seaweed ecosystems and their surrounding environments, and improving measures of productivity and NEP for existing and replacement ecosystem states such as turf reefs and sea urchin barrens. Substantial uncertainties also remain regarding the role of other biogeochemical processes, such as calcification and nutrient reallocation, as well as altered ocean albedo, fluxes of other climatically active gases, and inorganic fluxes in the magnitude of CO_2 drawdown by seaweed

ecosystems (Bach *et al.*, 2021, Santos *et al.*, 2021, Hurd *et al.*, 2022). These processes warrant full exploration in order to properly assess the carbon sequestration potential of seaweed forests and ecosystems, which rival, in area and productivity, the Amazonian forest (Duarte *et al.*, 2022). In this context, Gallagher *et al.*'s arguments do not inform the debate on the role of seaweeds in mitigating CO_2 emissions.

Data availability statement

All data supporting the findings of this article are available within the article.

Conflict of interest statement

The authors declare no conflict of interest.

Author contributions

All authors contributed to conceptualizing, drafting, and revising the response.

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