Received: 11 April 2023 | Accepted: 16 July 2023
DOI: 10.1111/jpy.13381

RESEARCH ARTICLE

Seaweed biogeochemistry: Global assessment of C:N and C:P ratios and implications for ocean afforestation

Emily J. Sheppard[1] | **Catriona L. Hurd**[1] | **Damon D. Britton**[1] | **Daniel C. Reed**[2] | **Lennart T. Bach**[1]

[1]Institute for Marine and Antarctic Studies, University of Tasmania, Hobart, Tasmania, Australia

[2]Marine Science Institute, University of California Santa Barbara, Santa Barbara, California, USA

Correspondence
Emily J. Sheppard, Institute for Marine and Antarctic Studies, University of Tasmania, Hobart, Tasmania 7001, Australia.
Email: emily.sheppard@utas.edu.au

Funding information
ARC Discovery Project, Grant/Award Number: DP200101467; ARC Future Fellowship, Grant/Award Number: FT200100846; Tasmanian government Department of Natural Resources and Environment, Grant/Award Number: AIRF 2020/47; US National Science Foundation

Editor: M. Roleda

Abstract

Algal carbon-to-nitrogen (C:N) and carbon-to-phosphorus (C:P) ratios are fundamental for understanding many oceanic biogeochemical processes, such as nutrient flux and climate regulation. We synthesized literature data (444 species, >400 locations) and collected original samples from Tasmania, Australia (51 species, 10 locations) to update the global ratios of seaweed carbon-to-nitrogen (C:N) and carbon-to-phosphorus (C:P). The updated global mean molar ratio for seaweed C:N is 20 (ranging from 6 to 123) and for C:P is 801 (ranging from 76 to 4102). The C:N and C:P ratios were significantly influenced by seawater inorganic nutrient concentrations and seasonality. Additionally, C:N ratios varied by phyla. Brown seaweeds (Ochrophyta, Phaeophyceae) had the highest mean C:N of 27.5 (range: 7.6–122.5), followed by green seaweeds (Chlorophyta) of 17.8 (6.2–54.3) and red seaweeds (Rhodophyta) of 14.8 (5.6–77.6). We used the updated C:N and C:P values to compare seaweed tissue stoichiometry with the most recently reported values for plankton community stoichiometry. Our results show that seaweeds have on average 2.8 and 4.0 times higher C:N and C:P than phytoplankton, indicating seaweeds can assimilate more carbon in their biomass for a given amount of nutrient resource. The stoichiometric comparison presented herein is central to the discourse on ocean afforestation (the deliberate replacement of phytoplankton with seaweeds to enhance the ocean biological carbon sink) by contributing to the understanding of the impact of nutrient reallocation from phytoplankton to seaweeds under large-scale seaweed cultivation.

KEYWORDS
C:N ratio, C:P ratio, carbon cycling, carbon dioxide removal, carbon sequestration, kelp, seaweed, stoichiometry

INTRODUCTION

Carbon-to-nitrogen (C:N) and carbon-to-phosphorus (C:P) ratios in algal tissues are important metrics for determining biogeochemical processes in the ocean (Sarmiento & Gruber, 2006). Both nitrogen and phosphorus are essential macronutrients that can limit algal productivity. At a cellular level, C:N and C:P ratios reveal the amount of nitrogen and phosphorus assimilated by algae per mole of carbon fixed via photosynthesis.

Abbreviations: BCP, biological carbon pump; C:Fe, carbon to iron ratio; C:N, carbon-to-nitrogen ratio; C:P, carbon-to-phosphorous ratio; CDR, carbon dioxide removal; CO_2, carbon dioxide; DIN, dissolved inorganic nitrogen; N:P, nitrogen to phosphorous ratio.

Algal C:N and C:P ratios can help explain the flow of carbon between the atmosphere, surface ocean, and deep sea, and because carbon reservoirs of the Earth system are linked, changes to carbon reservoirs in the atmosphere and ocean inevitably influence terrestrial carbon reservoirs (Keller et al., 2018). A seminal study found that the average (molar mean) C:N and C:P stoichiometry of phytoplankton communities in the North Atlantic was relatively constant at 6.6 and 106, respectively (Redfield, 1934). In 1983, Atkinson and Smith sampled 59 seaweed species at nine globally distributed locations and found that the molar mean for these "benthic plants" (p. 569) was considerably higher (C:N 18.4 and C:P 623.8) than the global average for phytoplankton (Atkinson & Smith, 1983). However, their study had a relatively small sample size (59 of the 15,000+ species of seaweed globally; Huisman, 2019). Likewise, a compilation by Duarte (1992) done 9 years later reported a similarly high C:N (16.3) and C:P (800.0) based on 46 seaweed species, and Lapointe et al. (1992) reported an even higher C:N and C:P of 25 and 803 respectively (35 species).

Although there are many publications that have included seaweed C:N and C:P data since Atkinson and Smith (1983), Duarte (1992), and Lapointe et al. (1992), there has been, to the best of our knowledge, no further attempts to synthesize the data. In contrast, there have been several more recent global syntheses of phytoplankton C:N:P ratios that have illustrated the driving factors behind variability in C:N:P globally (Geider & La Roche, 2002; Lomas et al., 2021; Martiny, Pham, et al., 2013; Martiny, Vrugt, et al., 2013). Our study sought to update our knowledge of seaweed C:N and C:P ratios by data-mining the currently available literature. We have significantly enriched the database by adding new data from Tasmanian seaweed species, many of which have never had their carbon-to-nutrient stoichiometry reported before. Furthermore, we added a 20-y time series on C:N stoichiometry of ecologically important kelp (Order Laminarales) from California (*Macrocystis pyrifera*) to discuss the seasonality of stoichiometry. The N:P ratios were collected from the literature and are provided in the dataset for further use; however, the focus of this paper was on C:N and C:P only due to their relevance in the context of Ocean Afforestation, or growing seaweeds in the ocean to sequester atmospheric CO_2 (Bach et al., 2021; Wu et al., 2023). Our first goal with this research was to update and improve widely applied global and taxon-specific seaweed C:N and C:P ratios to elucidate broad-scale stoichiometric patterns.

Seaweed tissue C:N and C:P ratios are highly variable and influenced by several factors, including inorganic seawater nutrient concentrations (Reef et al., 2012), temperature (Lowman et al., 2021), season (Lapointe et al., 2021), and water motion (Visch et al., 2020). Thus, in addition to collecting stoichiometric ratios for the global database, we also gathered data on the environmental conditions and seasons the seaweeds were collected in. We used this data to investigate the effect of seasonality (which best captured these co-varying environmental drivers) and inorganic seawater nutrient concentrations (DIN, dissolved inorganic nitrogen, and PO_4^{3-}). We hypothesized that C:N and C:P ratios would reduce with increasing nutrient availability to a point of maximum tissue nutrient uptake. Given that seawater nutrients vary seasonally, we hypothesized that C:N and C:P ratios would be lowest in seasons with highest nutrient availability (e.g., winter and spring in temperate regions).

Finally, this study applied updated information of seaweed C:N:P ratios to a novel lens on Ocean Afforestation, an atmospheric CO_2 removal strategy discussed by many researchers (Bach et al., 2021; Boyd et al., 2022; Chung et al., 2013; Duarte et al., 2017; Froehlich et al., 2019; Gallagher et al., 2022; Hurd et al., 2022; Krause-Jensen et al., 2018; Krause-Jensen & Duarte, 2016; Ritschard, 1992; Ross et al., 2022) and widely discussed in public discourse (Climate Foundation, n.d.; Bate & Rowland, 2021; Gameau, 2019; The Intrepid Foundation, 2019). Although several studies have focused on the high growth rates and primary production of seaweeds as a beneficial parameter for Ocean Afforestation (de Ramon N'Yeurt et al., 2012; Krause-Jensen et al., 2018; Pessarrodona et al., 2022), this study broadens discussions to argue that carbon assimilation in biomass per available amount of limiting nutrient resource is perhaps a more crucial parameter to consider in the discussion of constraints on the enhancement of the biological carbon pump (BCP) through Ocean Afforestation (Bach et al., 2021; Ross et al., 2022; Wu et al., 2023). This argument is based on the constraint that there is a finite amount of nutrient resource available to the surface ocean to support primary production and that primary producers utilize all of this resource in many parts of the ocean where Ocean Afforestation is being considered (DeVries et al., 2012; Sarmiento & Gruber, 2006). Within this concept, the amount of carbon fixation by primary producers is constrained by the amount of limiting nutrient resource (Orr & Sarmiento, 1992). However, carbon fixation can increase if a prevailing primary producer (e.g., phytoplankton) is replaced by a new one (e.g., seaweed) that depletes the same nutrient reservoir but assimilates more carbon while using the same available amount of nutrients. This potential increase in carbon assimilation relative to the phytoplankton-dominated baseline system has a profound influence on the "additionality" of carbon sequestration achievable with Ocean Afforestation (Bach et al., 2021), with additionality being a crucial parameter to assess whether a CO_2 removal strategy has been successful (Gustavsson et al., 2000).

To further the debate on the potential of Ocean Afforestation, we discuss if Ocean Afforestation could make the BCP more efficient by causing additional CO_2 sequestration via their presumed stoichiometric advantage in C:N and C:P stoichiometry relative to phytoplankton based on our updated global database.

METHODS

Literature synthesis of seaweed C:N:P ratios

The Web of Science was searched in June 2021 with the following terms to find articles containing C:N:P data: TOPIC: ("macro algae" OR macroalgae OR macro-algae OR "macro Algal" OR macroalgal OR macro-algal OR kelp OR seaweed OR "marine plants" OR "marine plant" OR "aquatic plants" OR "aquatic plant" OR macrophyte) AND TOPIC: (stoichiometry OR "C:N" or "C/N" OR "C–N" OR "C:N:P" OR "C/N/P" OR "C–N–P" OR "N:P" OR "N/P" OR "C:P" OR "C/P" OR "carbon-to-nitrogen" OR "carbon-to-nitrogen" OR "carbon/nitrogen" OR "carbon-to-phosphorus" OR "carbon-to-phosphorus" OR "carbon/phosphorus" OR "nitrogen to phosphorus" OR "nitrogen-to-phosphorus" OR "nitrogen/phosphorus").

We only included peer-reviewed studies that reported seaweed C:N or C:P data from salt marsh, brackish, and marine habitats in laboratory, mesocosm, and field studies. Studies on seagrass and mangroves were excluded, as well as those on seaweed in freshwater environments. Only studies that were accessible through University of Tasmania's library subscription or open access articles were used in the analysis, which excluded around 10% of the retrieved literature. The following data was gathered from literature articles where available: reference, site name, latitude and longitude, phylum and species, juvenile or adult, type of experiment, seawater parameters (temperature; nutrients NH_3, NH_4^+, NO_2^-, NO_3^-, DIN, SRP, and PO_4^{3-}; dissolved oxygen; pH; collection depth, date, and season; light intensity; photoperiod; transport conditions; drying method; grinding method; %C, %N, %P; C:N, N:P, and C:P; and number of replicates). We calculated dissolved inorganic nitrogen (DIN) from studies that reported both NO_3^- and NH_4^+. Concentrations of NH_3 and NO_2^- were also included in our DIN calculations when they were reported. WebPlotDigitizer (version 4.5) was used to extract values reported only in graphical form (Rohatgi, 2021). AlgaeBase was used to determine the current taxonomic status of seaweeds (Guiry & Guiry, 2023).

Data organization

All C:N:P ratios reported in g:g were converted to mol:mol, and all data are reported in molar ratios. When studies did not report a unit, authors were emailed requesting the unit used. If the unit could not be determined, the study was excluded from analysis. Through the process of emailing authors, some responded with additional studies on seaweed C:N or C:P, and/or raw data from their studies, which were included in our dataset. There was a large species bias present in the global C:N:P dataset for seaweeds, in which some species were represented by many samples and others with only one sample. To deal with this bias in the analyses, the global dataset was sorted into a single row per species, reporting the average (mean) and *SD* for each species. We also sorted the Atkinson and Smith (1983) seaweed data in this way for comparison to the global dataset. These re-arranged datasets were used in creation of Figures 3 and 4 and the accompanying text of mean, ranges, and *SD* (including in the abstract). When seaweeds were not identified to species level, unidentified species of the same genus were grouped. Seawater nutrients were reported in varying units in the literature, which were all converted to µM. For representation of the spatially resolved data (Figure 1), mean C:N and mean C:P ratios were taken when samples were at identical latitudes and longitudes (to an accuracy of 0.05 degrees).

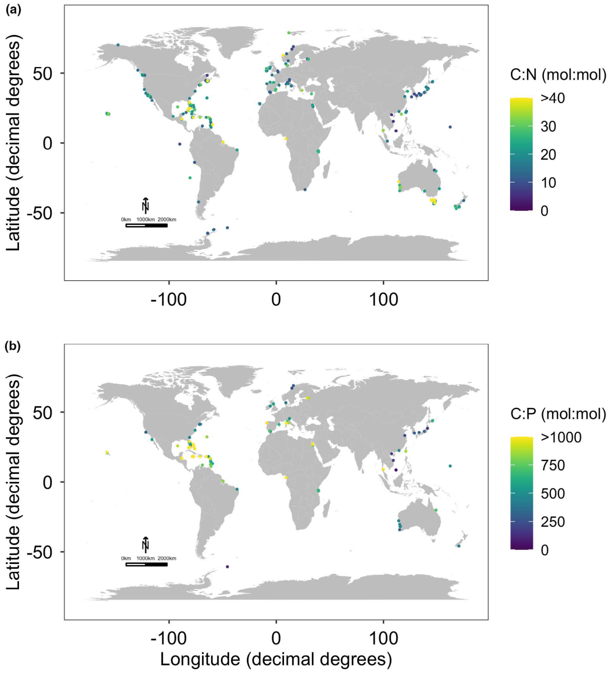

FIGURE 1 Map of seaweed C:N and C:P samples from the global dataset (a) Mean seaweed C:N (mol:mol) (b) Mean seaweed C:P (mol:mol).

Phytoplankton data

Phytoplankton C:N:P ratios were used to compare seaweed and phytoplankton stoichiometry to help assess if Ocean Afforestation could lead to additional carbon sequestration relative to the plankton ecosystem they would replace. The phytoplankton dataset from the most recent large-scale synthesis by Martiny et al. (2014) was downloaded from Dryad at https://datadryad.org/stash/dataset/doi:10.5061/dryad.d702p. Negative values were removed, and the dataset was filtered to include only samples collected at depths shallower than 50 m for relevance to the depth where most seaweeds grow. The phytoplankton data is based on natural seawater samples and thus not only includes phytoplankton but also some detrital particles and small zooplankton that are typically collected on filters (e.g., ciliates or flagellates). Thus, in the following when we compared seaweed stoichiometry with what we have called "phytoplankton stoichiometry," strictly speaking we were comparing individual specimen data with more comprehensive ecosystem data (e.g., including all organisms in a pelagic community that were collected on filters). We justify this comparison in section the Discussion section under The relevance of seaweed C:N and C:P stoichiometry for Ocean Afforestation.

Tasmanian seaweed and seawater nutrient collection

Seaweeds were collected in March 2021 in Tasmania at Rocky Cape (−40.860639°, 145.513111°), Temma Harbour (−41.231444°, 144.688889°), nungu/West Point (−40.945556°, 144.613917°), East Beach (−41.061167°, 146.803000°), Waterhouse Beach (−40.837778°, 147.643722°), Beerbarrel Beach (−41.282361°, 148.359083°), Waubs Bay (−41.871028°, 148.303333°), Spring Beach (−42.564556°, 147.899750°), Coal Point (−43.335287°, 147.324707°) and Taroona (−42.954889°, 147.345556°). Maximum collection depth was 6 m in an approximately 50-m^2 area, and samples were collected via snorkeling from shore, except at Taroona and Coal Point where max depth was 15 m and seaweeds were collected via SCUBA.

From each site, samples of individual seaweeds were taken from the most visually dominant species of the phyla Chlorophyta, Ochrophyta, or Rhodophyta. Mature thalli in the average size range present at the site were chosen, as well as some juvenile individuals. Clean and healthy individuals not covered in epiphytes were prioritized, although this was not always possible given the proliferation of epiphytes in late summer, especially at more wave-sheltered sites. Individual seaweeds were pulled or cut from the holdfast, taking care to preserve the whole sample where possible. Smaller subsamples from large individuals such as *Durvillaea* spp. and *Macrocystis pyrifera* were taken. Intertidal seaweeds were sampled when submersed whenever possible; however, *Ulva* spp. were sampled while emersed at Beerbarrel Beach and Waubs Bay due to the low tide. Samples were wrapped in a damp paper towel, placed in ziplock bags, and transported in an insulated container loaded with ice packs to the laboratory. All samples were processed within 24 h of collection, except for Rocky Cape samples (within 48 h). In the laboratory, samples were identified as juvenile or adult and to the species level, when possible, before being cut into smaller pieces incorporating an average of the different parts of morphology present (stipe, blade, holdfast, pneumatocysts). Around 95% of visible epiphytes were removed, and samples were weighed, then dried in the oven at 60°C. Once dried, samples were stored in ziplock bags inside a sealed container with silica gel.

All dried seaweed samples were ground to a homogenous powder using a ball mill or mortar and pestle, then weighed in tin cups. Calcified seaweeds were fumigated with 32% HCL to remove inorganic carbon. A known weight of dry and homogeneous sample was placed into a silver cup to which 40 mL of MILLI-Q® water was added before undergoing fumigation in a desiccator for 24 h. The samples were then oven-dried at 60°C for 12 h, and the silver cups were folded and immediately analyzed. The fumigation and analysis for total tissue nitrogen and carbon were determined by the Central Science Laboratory, University of Tasmania, using a Thermo Finnigan EA 1112 Series Flash Elemental Analyzer.

Seawater nutrient samples were collected in cleaned and pre-rinsed (with seawater in situ) 500-mL Nalgene® polycarbonate bottles while snorkeling at a depth of approximately 2 m. Care was taken not to contaminate the sample, by swimming fast while sampling and holding the bottle in front of the swimmer. Samples were immediately filtered (pore size of 0.22 μM) with syringe filters and stored as triplicates in new PE tubes (pre-rinsed with seawater sample). Tubes were kept on ice and then frozen as soon as possible (between 1 and 6 h after collection) to preserve nutrients. Concentrations of nitrate, ammonium, and phosphate were determined using a QuickChem® 8000 Automated Ion Analyzer (LaChat Instruments) at the Institute of Marine and Antarctic Studies (IMAS). Salinity was measured at the site shoreline with a Hach 600® salinometer, except in the case of the northwest sites, where samples were taken and immediately filtered, then stored in the refrigerator for 1 week until measurements of salinity were taken. Temperature was sampled at each site using the Hach 600® salinometer.

Macrocystis pyrifera collection and analysis from California

Tissue samples were obtained from mature blades of *Macrocystis pyrifera* collected at three kelp forests each month from 2002 to 2021 (Santa Barbara Coastal

LTER et al., 2021). Blades were collected from 10 to 15 different individuals at approximately 2 m from the growing tip of a frond reaching the surface and transported to the laboratory in dark insulated containers. In the laboratory, a 5-cm^2 diameter disk was excised from the central portion of each blade cleaned of epiphytes, rinsed in a 10% HCl solution, and shaken to remove excess water. The disks were dried for 2–5 d at 60°C and ground to a powder using a mortar and pestle. The powdered samples from all 15 blades were combined to form a composite sample for each site on each sampling date. The percent carbon and nitrogen of each composite sample was measured using an elemental analyzer (Carlo-Erba Flash EA 1112 series, Thermo-Finnigan Italia). Two replicate samples were analyzed for each composite sample.

Data analysis

All statistical analysis was conducted in R (R CoreTeam, 2022). To compare our global C:N and C:P values with that of Atkinson and Smith (1983) and phytoplankton (Martiny et al., 2014), we conducted Welch's *t*-tests. Our raw data did not meet the assumptions of the model (homoscedacity and normality of residuals), and as such, a log-transform was required for both C:N and C:P data to undertake the tests. Phytoplankton C:N and C:P have been plotted on a secondary axis at a different scale to seaweed C:N and C:P in Figure 3c,d, due to the greater quantity of data for phytoplankton than seaweed (e.g., >30,000 vs. 415 data points, respectively, for C:N). If plotted on the same scale, the seaweed data would have been dwarfed by the phytoplankton data; thus, this secondary axis allows visual comparison of phytoplankton versus seaweed C:N and C:P distribution. To compare C:N and C:P ratios across seasons, data was sorted into temperate and tropical regions and analyzed separately. Only "field" data was used for this analysis. Comparisons between seasons (temperate = 4 levels: summer, autumn, winter and spring; tropical = 2 levels: wet and dry) were made using Generalized Linear Mixed Models (GLMM) using the lmer function in the package lmerTest (Kuznetsova et al., 2017). For all seasonal models, species and latitude were included as random factors in the model. For both temperate and tropical datasets, Boxcox transformations were used (Box & Cox, 1964): C:N was transformed by $Y^{-0.3}$, and for the temperate C:P dataset, C:P was transformed by $Y^{0.55}$, followed by the use of residual versus fitted plots and normal Q–Q plots to check that the models conformed to the assumptions of normality of residuals and homeoscedacity. To further cross-check for species bias on seasonality in C:N in our global dataset, we also included an analysis of a single species (*Macrocystis pyrifera*) variation in C:N per season over two decades.

To investigate the effect of DIN and PO_4^{3-} on C:N and C:P values respectively, we created dot plots with data for field and other studies (laboratory, mesocosm, cultivated) shown separately, given the presence of artificially high nutrient concentrations in the latter. These were presented on a $\log_{10}$ scale to enable viewing of the data (which was concentrated at lower nutrient levels) at a higher resolution. The 10 species with the highest C:N and C:P were based on species with the highest reported mean C:N and C:P in at least three independent studies. Calcifying seaweed species were excluded from this analysis, as our intent was to identify the most suitable species for Ocean Afforestation. As calcification releases CO_2, calcifying species would unlikely be suitable organisms for Ocean Afforestation (Bach et al., 2021).

RESULTS

Results of literature synthesis

Samples were collected in predominantly coastal oceanic regions from polar to equatorial regions, with a greater number of locations for C:N than for C:P (Figure 1). The literature synthesis, combined with Tasmanian data collected from this study and supplementary data from researchers resulted in 199 studies that were used for the analyses and 4986 samples of seaweed C:N, N:P, or C:P. Of these samples, 2970 were from phylum Ochrophyta, 1097 from Rhodophyta, and 919 from Chlorophyta (Figure 2a). The most frequently reported ratio was C:N (4,599 samples), followed by N:P (1,397 samples), and C:P (987 samples; Figure 2b). Most studies collected seaweed from the field (3490 samples), although some data came from laboratory studies (615 samples), mesocosms (470 samples), aquaculture (132 samples), and blooms (75 samples; Figure 2c). For field studies, samples were taken more often in summer (850 samples) than in autumn (754 samples), spring (644 samples), or winter (574 samples). Some data were also presented from annual collections (152 samples) as well as in the dry season (96 samples) or wet season (47 samples) in equatorial regions (Figure 2d). Our synthesis revealed inconsistencies in how C:N:P data was reported among authors. Ten percent reported in g:g, 40% in mol:mol, and 50% without specifying a unit.

Updated global C:N and C:P ratios for seaweed

Overall the global mean C:N (mol:mol) for seaweeds was 20.2 ± 14.5 *SD* (range 5.6–122.5), which is higher than the Atkinson and Smith (1983) mean of 18.4 ± 11.1 *SD* (range 6.0–77.7; Figure 3a). Global seaweed C:P

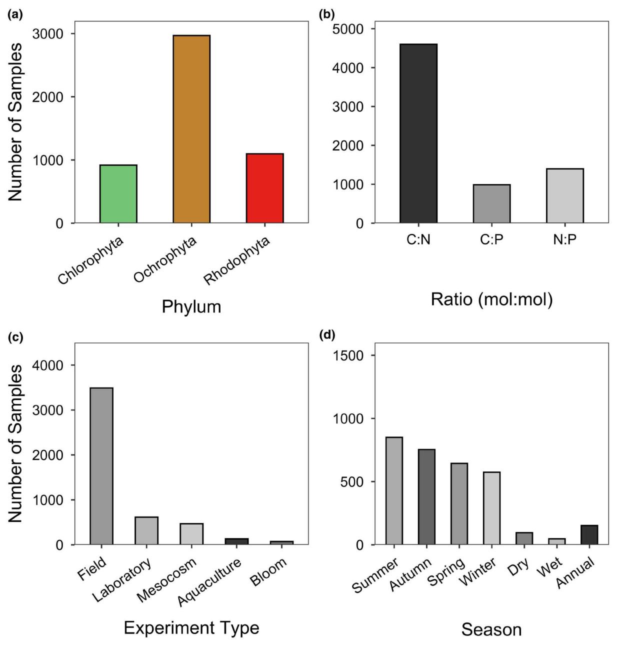

FIGURE 2 Distribution of data extracted from the literature. a. Number of samples of C:N, C:P, and N:P by phylum. b. Number of samples of C:N, C:P, and N:P by ratio. c. Number of samples of C:N, C:P, and N:P by experiment type. d. Number of field samples of C:N, C:P, and N:P by season.

(mol:mol) had a mean of 800.9 ± 648.1 *SD* (range 76.3–4102.3) compared to Atkinson and Smith's (1983) mean of 623.8 ± 411.1 *SD* (range 137.0–1927.0; Figure 3b). The differences between our updated data set and the Atkinson and Smith dataset were not statistically significant for either C:N or C:P ($p = 0.427$ and 0.060, respectively; Welch's *t*-test, log-transformed data). Mean C:N was significantly higher for seaweeds (20.2) compared to phytoplankton communities (7.1 ± 4.5 *SD*, range 0.5–324.0; Figure 3c), and mean C:P was also significantly higher in seaweeds (800.9) compared to phytoplankton (200.1 ± 333.9 *SD*, range 5.3–8570.7; Figure 3d; $p = < 0.001$ for both C:N and C:P; Welch's *t*-test, log-transformed data).

Taxonomic influences on seaweed C:N and C:P

Mean C:N varied by phylum (Figure 4). Ochrophyta had the highest C:N (mean = 27.5 ± 18.6 *SD*, range 7.6–122.5), followed by Chlorophyta (mean = 17.8 ± 9.5 *SD*, range 6.2–54.3) and Rhodophyta (mean = 14.8 ± 8.4 *SD*, range 5.6–77.6; Figure 4a). For C:P, the highest mean ratios were found in Chlorophyta (mean = 848.8 ± 619.9 *SD*, range 186.0–3031.0), followed by Rhodophyta (mean = 789.3 ± 783.4 *SD*, range 76.3–4102.3) and Ochrophyta (mean = 773.3 ± 525.5 *SD*, range 109.5–2457.2; Figure 4b). The 10 species with the highest C:N were all from the phylum Ochrophyta (Figure 5a).

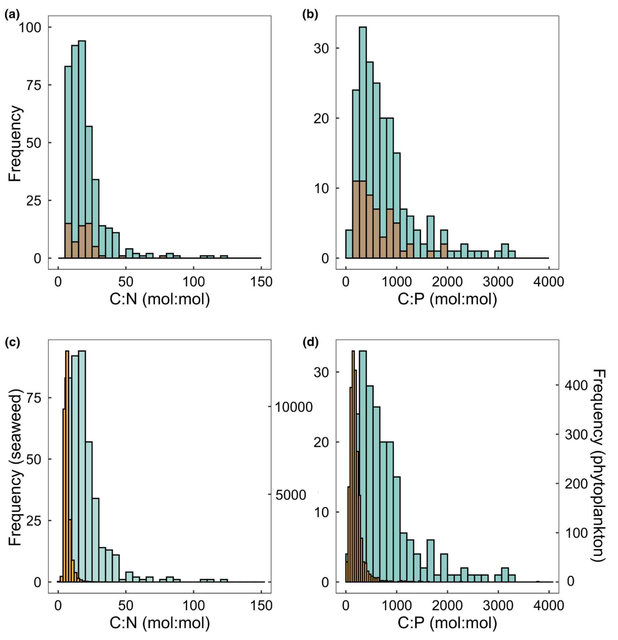

FIGURE 3 Histograms of our global dataset for seaweed C:N and C:P overlaid with comparisons to other datasets. Our dataset and Atkinson and Smith (1983) data are re-arranged to an average (mean) C:N / C:P per species (see Methods). Phytoplankton data are taken from Martiny et al. (2014). (a) Comparison of our global C:N data (turquoise) to Atkinson and Smith C:N data (brown). (b) Comparison of our global C:P data (blue) to Atkinson and Smith C:P data (brown). (c) Comparison of our global C:N data (turquoise) to phytoplankton communities C:N (brown). (d) Comparison of our global C:P data (turquoise) to phytoplankton communities C:P (brown).

Durvillaea spp. had the highest mean C:N at 43.6 ± 13.8 *SD* (range 21.6–75.5). However, there was large variability in the range of C:N values reported, with some individual samples of *Phyllospora comosa*, *Sargassum* spp., and *Ecklonia radiata* having higher C:N than any sample of *Durvillaea* spp. Seaweeds from all three major phyla were represented in the top 10 C:P (Figure 5b), and *Laurencia intricata* (phylum Rhodophyta) had the highest mean C:P at 3072.1 ± 3, 342.3 *SD* (range 144.7–12,205).

Environmental influences on seaweed C:N and C:P

In the field, there appeared to be the highest variation of C:N ratios at 1–2 μM DIN, with C:N values ranging from 8 to 132 within this DIN range (Figure 6a). Less variation and generally reduced C:N values were seen at very low (<1 μM) DIN, as well as at DIN > 2 μM, with C:N reducing further at >10 μM DIN. For mesocosm, laboratory, and cultivated data, there appeared to be relatively high variation in C:N at all DIN levels, with no clear trend apparent (Figure 6b). Field samples of C:P versus PO_4^{3-} showed a somewhat similar pattern (albeit with a smaller sample size), with C:P variation (290–5538)

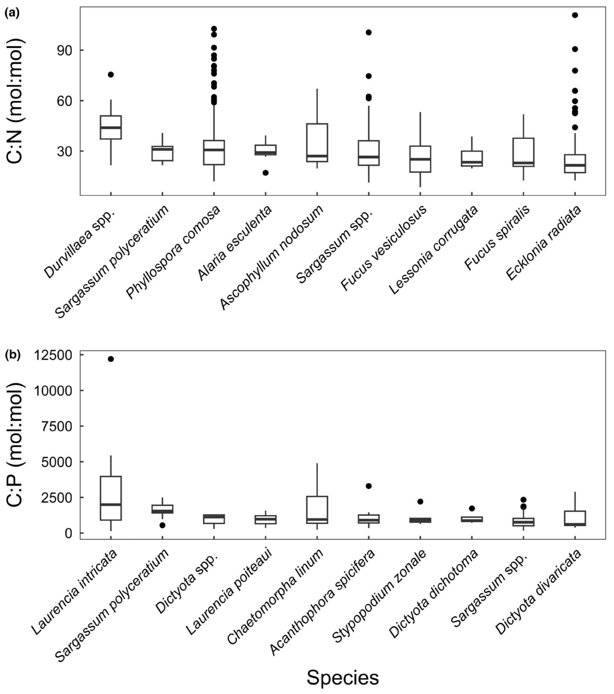

FIGURE 4 Seaweed C:N and C:P by phylum, using re-arranged dataset (see Methods). (a) C:N by phylum. (b) C:P by phylum.

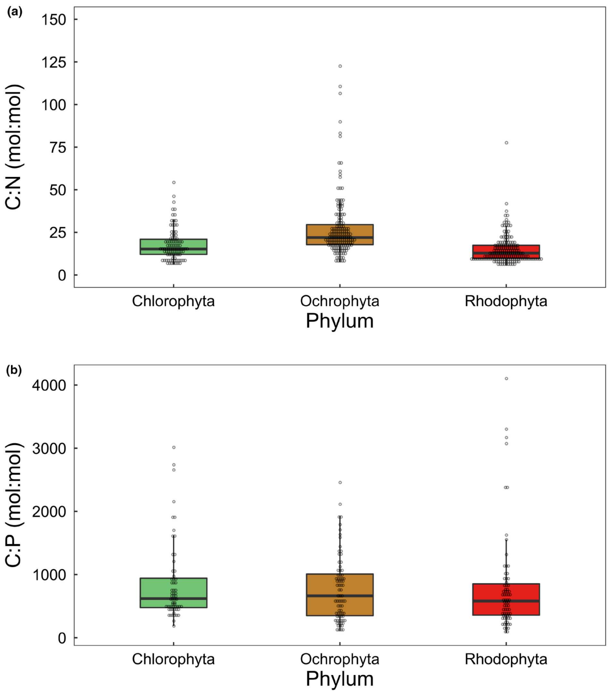

FIGURE 5 Top 10 seaweeds for C:N and C:P. (a) Seaweeds with the highest C:N from at least three independent studies. (b) Seaweeds with the highest C:P from at least three independent studies. Seaweeds are in descending order by median C:N or C:P.

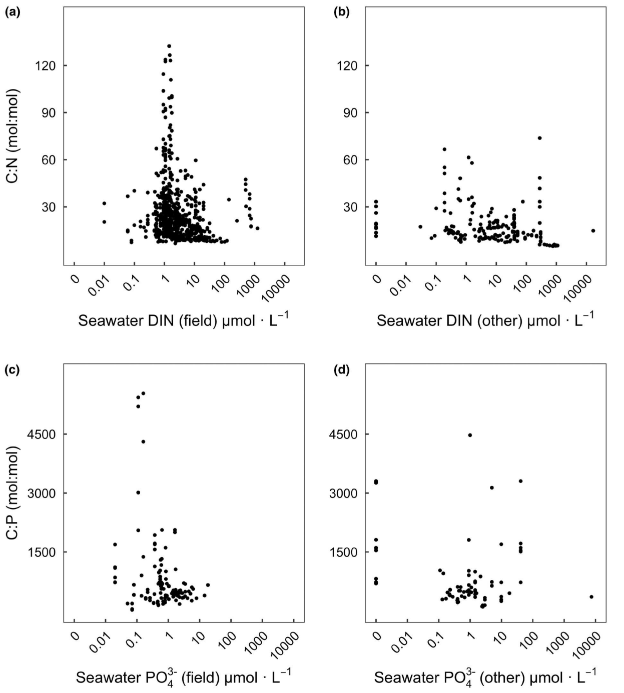

FIGURE 6 Influence of seawater nutrients on seaweed C:N and C:P. (a) Seawater DIN concentration influence on C:N taken from field studies only. (b) Seawater DIN concentration influence on C:N taken from laboratory, mesocosm, and cultivated studies only. (c) Seawater phosphate concentration influence on C:P taken from field studies only. (d) Seawater phosphate concentration influence on C:P taken from laboratory, mesocosm, and cultivated studies only.

peaking at 0.1–0.2 μM PO_4^{3-} and generally lower C:P values (<2000) below 0.1 μM PO_4^{3-} and above 0.2 μM PO_4^{3}, reducing further above 3 μM PO_4^{3-} (Figure 6c). The variation in mesocosm, laboratory, and cultivated data appeared to be more evenly spread throughout the range of PO_4^{3-} values (Figure 6d).

For temperate seaweeds, mean C:N was significantly different across all seasons (GLMM: $F_{(3/2371.7)} = 148.08$, $p < 0.001$). The C:N was highest in autumn (mean = 27.5 ± 18.3 *SD*, range 6.1–132.3), followed by summer (mean = 20.3 ± 9.7 *SD*, range 4.9–75.5), winter (mean = 18.4 ± 7.5 *SD*, range 5.8–49.1), and spring (mean = 15.7 ± 6.8 *SD*, range 4.7–59.6). For tropical seaweeds, there were no significant differences in C:N ratios between wet and dry seasons (GLMM: $F_{(1/104.19)} = 0.805$, $p = 0.37$; Figure 7a). Seasonality had an influence on mean C:P in temperate seaweeds when accounting for latitude and species as random variables (GLMM: $F_{(3/267.03)} = 3.396$, $p = 0.018$). Values in autumn (mean = 708.8 ± 441.6 *SD*, range 193.9–2061.9) were significantly greater than in spring (mean = 656.5 ± 486.3 *SD*, range 24.1–4158.2). Other seasons did not differ significantly from each other, nor did C:P differ significantly between the wet and dry seasons for tropical seaweeds (GLMM: $F_{(1/34.09)} = 0.9816$, $p = 0.33$; Figure 7b). Seasonality also followed the same trend for C:N of *Macrocystis pyrifera* over two decades (Figure 8): highest in autumn (mean = 24.6, *SD* = 8.6, range 10.3–54.0), followed by summer (mean = 20.6, *SD* = 8.4,

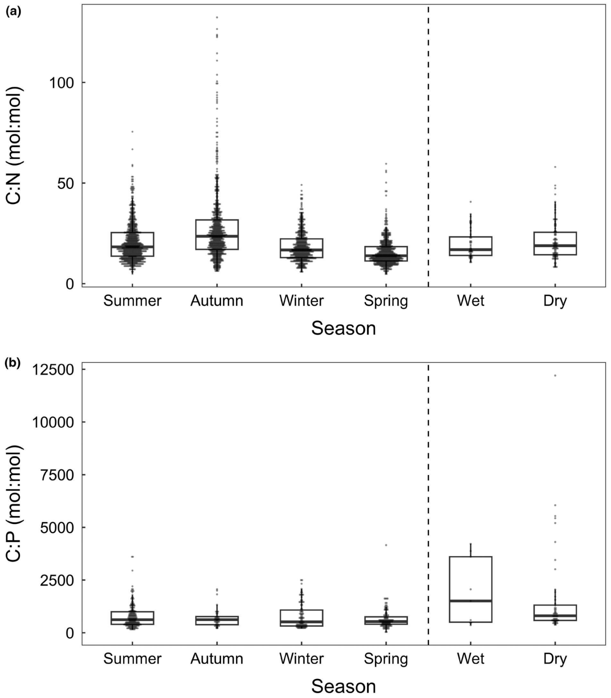

FIGURE 7 Seasonal differences in seaweed C:N and C:P taken from field studies only. Analyses for temperate (summer, autumn, winter, and spring) and tropical (wet and dry) seasons were conducted separately. (a) Seasonal differences in C:N: global dataset (b) Seasonal differences in C:P: global dataset.

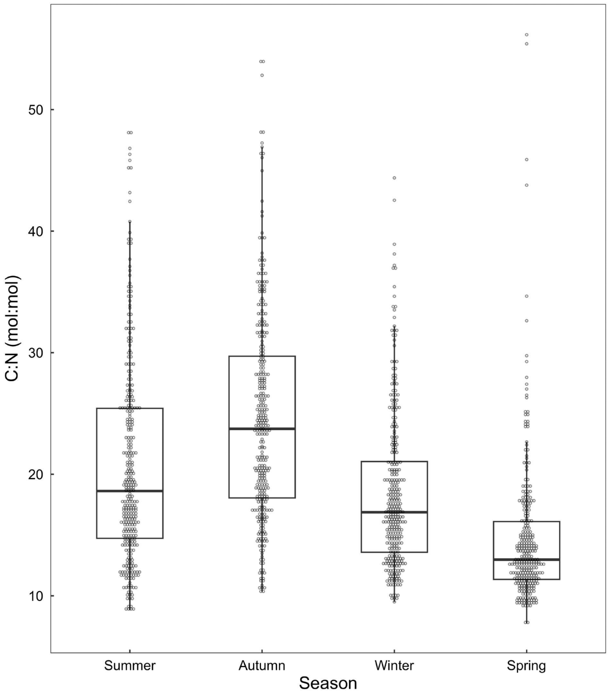

FIGURE 8 Seasonal variation in C:N per season across two decades in *Macrocystis pyrifera*.

range 8.8–48.1), winter (mean = 18.4, *SD* = 6.4, range 9.5–44.4) and spring (mean = 14.7, *SD* = 6.0, range 7.7–56.2). A Kruskal–Wallis test revealed all four seasons were statistically different from each other ($p = <0.002$).

DISCUSSION

This study has provided, to the best of our knowledge, the first global synthesis of seaweed C:N:P ratios and the environmental factors that influence them since Atkinson and Smith (1983), Duarte (1992), and Lapointe et al. (1992). We observed that C:N ratios varied by phyla and were highest in Ochrophyta seaweeds (discussed in the next subsection). Additionally, C:N and C:P ratios were influenced by seawater nutrients and seasonality (discussed in subsequently in the subsection Environmental influence on seaweed C:N and C:P). We found that on average, seaweeds have 2.8 and 4.0 times higher C:N and C:P, respectively, than phytoplankton. This finding contributes to discourse on Ocean Afforestation by offering an understanding the impact of nutrient reallocation from phytoplankton to seaweeds under large-scale seaweed cultivation for atmospheric CO_2 removal (discussed subsequently under The relevance of seaweed C:N and C:P stoichiometry for Ocean Afforestation).

Taxonomic influences on seaweed C:N

Seaweeds of the phylum Ochrophyta had higher C:N than the C:N for either Rhodophyta or Chlorophyta, which is consistent with observations made in previous studies (Fiset et al., 2019; Niell, 1976). Phylogenetic differences in pigment type and content, along with amount of structural material could help explain this trend in C:N. All seaweeds have chlorophyll *a*, but the accessory pigments of seaweeds differ among the three major phyla (Hurd et al., 2014). The accessory pigments found in Chlorophyta and Rhodophyta seaweeds (chlorophylls and phycobiliproteins, respectively) are rich in nitrogen and can act as nitrogen stores when nutrients are limiting (Harrison & Hurd, 2001; Paine et al., 2020). Thus, the higher contents of nitrogen in the pigments of Rhodophyta and Chlorophyta seaweeds may explain their higher tissue %N and corresponding average lower C:N ratios compared with Ochrophyta seaweeds. Also, the largest species of seaweed belong to the Ochrophyta (Scott, 2017), and therefore, they may need additional structural support in the form of carbon-rich cell wall polysaccharides and alginates to prevent wave-damage and breakage (Atkinson & Smith, 1983; Fiset et al., 2019). This likely contributes to the higher C:N ratio in Ochrophyta compared with other phyla. We found that in our global dataset, the differences in C:P between phyla were much smaller than for C:N, suggesting that taxonomic drivers are not an important influence on C:P ratios.

Environmental influence on seaweed C:N and C:P

Many studies have found that high C:N (C:P) ratios generally occur more frequently at low DIN (PO_4^{3-}) concentrations (Atkinson & Smith, 1983; Douglas et al., 2014; Fong et al., 1994; Gevaert et al., 2001; Lapointe et al., 2004; Lee & Kang, 2020; Menendez et al., 2002; Reef et al., 2012; Rico & Fernandez, 1996). The obvious explanation for the observed pattern is that lower DIN (or DIP) concentrations restrict the assimilation of these nutrients in seaweed biomass, which can be reflected in the occurrence of high C:N (C:P) ratios. This finding is somewhat consistent with our study, although we found that at very low (<1 μm DIN and <0.1 μm PO_4^{3-}) nutrient concentrations, higher C:N (C:P) ratios were less frequent. However, this could be due to a lack of samples at these very low nutrient levels. Lin et al. (2007) determined that there were species differences in response to seawater DIN increases and that additional factors such as thallus form and exposure to air (for intertidal seaweeds) may be important factors in influencing C:N.

When investigating the samples that accounted for the C:N “peak” (highest values and largest variation in C:N values in the field) between 1 and 2 μM DIN, we observed that all samples >60 C:N came from Ochrophyta seaweeds collected for this study. The high C:N ratios found in Ochrophyta seaweeds in Tasmanian waters (especially in autumn) is consistent with other studies (Paine, Brewer, et al., 2023; Wernberg et al., 2019). Paine, Brewer, et al. (2023) hypothesized this may be due to these seaweeds using up stored nitrogen when external supplies were low. These abnormally high C:N values seen in Tasmanian Ochrophyta species in autumn indicate they are highly nitrogen limited. (C:N >20 is thought to be an indication nitrogen limitation; Hurd et al., 2014). Although a comprehensive overview of DIN has not been undertaken around the Tasmania coastline, initial seawater nutrient samples show that Tasmanian waters have ubiquitously lower nutrients year-round compared with other temperate regions (Hurd et al., 2023). We undertook a similar analysis for the C:P peak in field studies at 0.1–0.2 μm PO_4^{3-} and observed that all samples >2000 C:P were from the study by Lapointe et al. (2004). These high C:P ratios were found at the sites with lower nutrients, while predominantly lower (<2000) C:P ratios were found at the nutrient-enriched study site (Lapointe et al., 2004), following the general trend as discussed above.

Given that the effect of seawater nitrogen (and phosphorous) on C:N and C:P ratios is confounded by other factors such as temperature and daylight, seasonality may be a more accurate predictor of C:N and C:P ratios as it accounts for these complex interactions (Endo et al., 2017). Such was the case for our global dataset that showed strong temperate seasonality in C:N and C:P with the highest values in autumn and the lowest in spring, which is in line with conclusions of several other studies (Douglas et al., 2014; Gomez et al., 1995; Lapointe et al., 2021; Rico & Fernandez, 1996). We also showed this seasonal C:N trend within a single species, *Macrocystis pyrifera*, which has shown strong seasonality over two decades, with highest values in autumn and lowest in spring. In our global synthesis, there was a sampling bias toward summer, which tended to have higher C:N ratios than winter or spring. Therefore, the global average C:N ratios may be lower than reported here. However, seasonal influence on tissue stoichiometry is not ubiquitous. If seawater nutrient availability is consistently high (as in eutrophic areas and in parts of the Southern Ocean; Henley et al., 2020), then seasonal trends may not be evident (Lourenco et al., 2006). Additionally, our study found no statistically significant change in C:N or C:P in tropical regions between wet and dry seasons. It is possible that the environmental factors influencing C:N and C:P ratios are not correlated to season in tropical areas as much as they are to season in temperate regions.

The relevance of seaweed C:N and C:P stoichiometry for ocean afforestation

Ocean Afforestation seeks to enhance the efficiency of the BCP to sequester more atmospheric CO_2 in the ocean than the natural BCP already does. The BCP efficiency is defined by how much of the available surface ocean nutrient pool can be utilized by biology before these nutrients are lost from the surface ocean (e.g., via downwelling; Ito & Follows, 2005). As such, the BCP efficiency could be increased (i.e., Ocean Afforestation could be successful) by implementing Ocean Afforestation in areas where currently not all of the surface ocean nutrient pool is being utilized (Marinov et al., 2006; Primeau et al., 2013), for example, far south in the Southern Ocean (Xie et al., 2022). A second way for Ocean Afforestation to increase BCP efficiency is by decreasing carbon flux attenuation relative to the plankton-dominated system with which seaweeds compete for limiting nutrients. A reduced flux attenuation would lead to a deeper injection of carbon and nutrients into the deep ocean, thereby slowing return flux of remineralized carbon and nutrients, and thus concentration, in the surface ocean over timescales of >100 y (Kwon et al., 2009; Taucher et al., 2014). Seaweeds are on average likely sinking faster than plankton-derived organic matter (Baker et al., 2017; Johnson & Richardson, 1977; Laurenceau-Cornec et al., 2020; Wernberg & Filbee-Dexter, 2018), and current evidence suggests rather limited remineralization during sinking (Bach et al., 2021; Baker et al., 2017; Ortega et al., 2019). Accordingly, current modeling on Ocean Afforestation has assumed that all carbon and nutrients fixed in seaweed biomass ends up on the seafloor (Wu et al., 2023), the most optimistic assumption for the BCP efficiency with regards to this mechanism.

The third possible mechanism for how Ocean Afforestation could increase BCP efficiency is by increasing the fixation of carbon with the available pool of limiting nutrients. This mechanism is the focus of the present paper and is relevant in the vast oligotrophic regions of the ocean where nearly all surface ocean nutrients are utilized (meaning that BCP efficiency is already very high; Devries et al., 2012; Sarmiento & Gruber, 2006). Here, the BCP efficiency increases if the afforested seaweeds utilize more carbon per unit of limiting nutrient than the phytoplankton did before seaweeds were introduced (Bach et al., 2021; Berger et al., 2023; Wu et al., 2023). Previous data collections on phytoplankton and seaweed C:N:P stoichiometry have generally suggested that seaweeds have higher C:N and C:P ratios than phytoplankton (Atkinson & Smith, 1983; Martiny et al., 2014). The following discussion uses our updated dataset on seaweed carbon-to-nutrient ratios to assess if and how much seaweed has a stoichiometric advantage relative to phytoplankton, to inform the debate on whether Ocean Afforestation could be effective. We assess the range of stoichiometric advantages and point toward species with the highest differences. Before continuing, we emphasize that stoichiometry is one important aspect in determining the potential of Ocean Afforestation to generate additional CO_2 removal but that many other processes play roles in determining the effect of the method on climate radiative forcing (Bach et al., 2021).

Our study compared the range of species-specific carbon-to-nutrient ratios of seaweeds with carbon-to-nutrient ratios from phytoplankton communities from filtered water samples (Martiny et al., 2014). These samples comprised not only phytoplankton, but all suspended organic particles (e.g., microzooplankton and detritus) that were sampled with a CTD rosette and ended up on a filter after filtering about 1 L of sea water. This raises the question of whether the comparison between seaweed species and plankton communities is meaningful, or whether phytoplankton-specific carbon-to-nutrient ratios (e.g., derived from monocultures as in Garcia et al., 2018) would need to be compared with seaweed data instead. We considered this question when designing our study and concluded that phytoplankton community data is needed for our comparison. This is because Ocean Afforestation aims to grow (mono-) cultures of benthic seaweeds in pelagic environments, and a single seaweed species (analogous to a crop) demands resources (e.g., nutrients) from a diverse, natural plankton community that drives the BCP collectively through food webs that ultimately lead to carbon export (Boyd et al., 2019). Within this framework, our comparison of seaweed species with plankton communities that included all sources of particulate C in the planktonic food web is meaningful.

Our literature synthesis found the mean global seaweed C:N ratio was 2.8 times higher than that estimated for phytoplankton communities, indicating that seaweeds have, on average, a considerably higher capacity to fix carbon per mole of limiting N than natural phytoplankton communities. This capacity is even higher when particular Ochrophyta species are considered (e.g., *Durvillaea* spp., *Sargassum polyceratium*, and *Phyllospora comosa*). The large range of C:N across species underscores the relevance of selecting potentially carbon-efficient species for Ocean Afforestation. However, the choice of species for Ocean Afforestation is constrained by the ability to culture them and the ability of the species to grow in often oligotrophic pelagic habitats to which they may not be adapted (DeAngelo et al., 2023). For example, for the 10 species with the highest C:N and C:P (Figure 5), except some species of *Sargassum*, cultivation techniques have not yet been developed or are in their infancy (Buschmann et al., 2017; Kelly, 2020).

When assessing the stoichiometric advantage of seaweeds relative to phytoplankton in the context of Ocean Afforestation it is also crucial to consider that plankton community C:N:P ratios, while lower on average, are also highly variable (Figure 3c,d). Plankton community C:N:P ratios have been shown to have a pronounced latitudinal gradient and to change with nutrient availability (Martiny et al., 2014). Furthermore, different plankton species can have inherently different C:N:P stoichiometries (Garcia et al., 2018), so predominance of certain species can leave an imprint on plankton community C:N:P stoichiometry. For example, the important cyanobacterium *Trichodesmium* sp. has been shown to have substantially higher C:P than other phytoplankton and to provide its own nitrogen via dinitrogen-fixation (Finkel et al., 2010) so that nitrogen is not a limiting resource. Thus, the stoichiometric advantage seaweeds have on average would decline when contrasted against a phytoplankton community dominated by, for example, *Trichodesmium* sp. However, the stoichiometric advantage would increase when contrasted against, for example, a community dominated by diatoms, which are known to have inherently lower C:N and C:P ratios (Quigg et al., 2003). These examples reveal one of the difficulties facing Ocean Afforestation when it comes to constraining the increase of the seaweed C:N:P ratio relative to the ecosystem they replace (plankton): One must not only constrain the C:N:P ratios of the “seaweed crop" used for Ocean Afforestation but also the C:N:P of the plankton ecosystem that is being replaced.

It is important to note that our study focused on C:N and C:P, not on C:Fe (carbon to iron) or other micronutrients, to assess stoichiometric advantages in carbon assimilation of seaweeds relative to phytoplankton. The focus on macronutrients was because seaweeds are (with few exceptions) benthic organisms that are highly exposed to benthic fluxes of trace metals such as iron. They are therefore not considered to be limited by iron or other trace metals. In the case of Ocean Afforestation, however, floating platforms with seaweed growing on them may be deployed in the open ocean (de Ramon N'Yeurt et al., 2012; DeAngelo et al., 2023; Wu et al., 2023). In such cases, iron and other trace metals can limit photosynthetic carbon fixation of phytoplankton (Moore et al., 2013), which are adapted to these limiting conditions. A recent study showed that *Macrocystis pyrifera*—a species that has been proposed for Ocean Afforestation—dies in <2 weeks when cultivated in open ocean seawater due to iron limitation (Paine, Boyd, et al., 2023). This finding suggests that iron would have to be provided artificially if ocean afforestation was implemented in iron-limited ocean regions (Paine, Boyd, et al., 2023). Thus, according to Liebig's Law of the Minimum (de Baar, 1994), the macronutrients nitrogen and phosphorus would ultimately limit seaweed growth in the open ocean if iron limitation (and potential limitation by other micronutrients) were to be alleviated artificially. Based on this rationale it is reasonable to compare C:N and C:P ratios of seaweeds and phytoplankton to assess the net gain of CO_2 sequestration through ocean afforestation.

Some authors have proposed fertilizing open ocean seaweed farms via artificially induced upwelling of deep, nutrient-rich water (Fan et al., 2020) or via diel depth cycling (Navarrete et al., 2021) to enhance seaweed growth rates and ultimately CO_2 removal. Our study revealed probabilities for high seaweed C:N (and to some extent high C:P) were increased under low DIN (DIP) concentrations across the diverse range of species included in the analysis (Figure 6). Furthermore, the seasonal plots provide evidence that seaweed C:N is lower in seasons where nutrient concentrations are higher (Figures 7 and 8). Similar observations have recently been made for pelagic *Sargassum* spp., for which increasing nutrient load coincided with reduced C:N (Lapointe et al., 2021). These results, counterintuitively, suggest that enhancing seaweed growth rates by nutrient fertilization could be detrimental for the CO_2 removal efficiency of Ocean Afforestation. Thus, from a nutrient-stoichiometric perspective, Ocean Afforestation would become most efficient when farming seaweeds in way that maximizes their C:N ratios upon harvest, not their growth rates.

CONCLUSIONS

This study updated global mean molar seaweed C:N and C:P ratios and the factors that influence them through a large-scale literature synthesis and original data collection. The inclusion of environmental factors in our synthesis can contribute to a broader discussion of driving forces behind C:N and C:P variability globally. We observed that effects of taxonomic and environmental factors on seaweed stoichiometry can be statistically significant and that their relative importance varies in nuanced ways. A further research questions includes how biogeographic region influences seaweed C:N:P, given that regional differences have been observed to significantly influence phytoplankton stoichiometry (Lomas et al., 2021; Martiny, Pham, et al., 2013). More research is also needed on the effects of light and wave exposure on seaweed C:N and C:P, as well as on understudied biotic factors such as thallus age and type. Our comparisons between the most updated C:N and C:P for seaweeds and phytoplankton contribute to a novel perspective about how to evaluate the carbon sequestration efficiency of Ocean Afforestation. We confirm that seaweeds have higher C:N and C:P than phytoplankton on average, but that substantial differences exist between seaweed species. Thus, Ocean Afforestation could be made more efficient when choosing a seaweed “crop” that establishes the highest difference in C:N (or C:P) relative to phytoplankton We also confirm that the C:N and C:P ratios for both phytoplankton and seaweed can vary substantially with environmental conditions, and the carbon assimilation advantage for seaweeds is potentially higher when growing them in low nutrient conditions.

AUTHOR CONTRIBUTIONS

Emily Jocelyn Sheppard: Data curation (lead); formal analysis (lead); investigation (lead); methodology (supporting); project administration (lead); writing – original draft (lead); writing – review and editing (lead). **Catriona L. Hurd:** Conceptualization (supporting); funding acquisition (supporting); investigation (supporting); methodology (supporting); supervision (supporting); writing – original draft (supporting); writing – review and editing (supporting). **Damon Britton:** Formal analysis (supporting); funding acquisition (supporting); methodology (supporting); writing – review and editing (supporting). **Reed Daniel:** Data curation (supporting); funding acquisition (supporting); investigation (supporting); methodology (supporting); writing – review and editing (supporting). **Lennart Bach:** Conceptualization (lead); data curation (supporting); formal analysis (supporting); funding acquisition (supporting); investigation (equal); methodology (equal); supervision (lead); writing – original draft (supporting); writing – review and editing (supporting).

ACKNOWLEDGEMENTS

We thank Ellie Paine, Allyson Nardelli, Kaeo Landon-Lane, Yenhang Wang, Mike Porteus, Simon Talbot, Graeme Ewing and Stuart Isles for help collecting seaweed for this study as well as Neville Barrett and Cayne Layton for help with seaweed identification. We also thank Thomas Rodemann and Wouter Visch for support on C:N and seawater nutrient analysis. This project was funded by an ARC Future Fellowship FT200100846 to Lennart Bach and ARC Discovery Project DP200101467 to Catriona Hurd. The US National Science Foundation supported the Santa Barbara Coastal Long Term Ecological Research program. Damon Britton was supported by a grant from the Tasmanian government Department of Natural Resources and Environment (AIRF 2020/47). DPIPWE provided a permit for seaweed collection. Open access publishing facilitated by University of Tasmania, as part of the Wiley - University of Tasmania agreement via the Council of Australian University Librarians.

DATA AVAILABILITY STATEMENT

The dataset created for this paper is accessible at https://doi.org/10.5281/zenodo.8185140

ORCID

Emily J. Sheppard https://orcid.org/0000-0001-5725-4464
Catriona L. Hurd https://orcid.org/0000-0001-9965-4917

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How to cite this article: Sheppard, E. J., Hurd, C. L., Britton, D. D., Reed, D. C., & Bach, L. T. (2023). Seaweed biogeochemistry: Global assessment of C:N and C:P ratios and implications for ocean afforestation. *Journal of Phycology*, *00*, 1–14. https://doi.org/10.1111/jpy.13381