

Substantial role of macroalgae in marine carbon sequestration

Dorte Krause-Jensen^{1,2*} and Carlos M. Duarte³

Vegetated coastal habitats have been identified as important carbon sinks. In contrast to angiosperm-based habitats such as seagrass meadows, salt marshes and mangroves, marine macroalgae have largely been excluded from discussions of marine carbon sinks. Macroalgae are the dominant primary producers in the coastal zone, but they typically do not grow in habitats that are considered to accumulate large stocks of organic carbon. However, the presence of macroalgal carbon in the deep sea and sediments, where it is effectively sequestered from the atmosphere, has been reported. A synthesis of these data suggests that macroalgae could represent an important source of the carbon sequestered in marine sediments and the deep ocean. We propose two main modes for the transport of macroalgae to the deep ocean and sediments: macroalgal material drifting through submarine canyons, and the sinking of negatively buoyant macroalgal detritus. A rough estimate suggests that macroalgae could sequester about 173 TgC yr⁻¹ (with a range of 61–268 TgC yr⁻¹) globally. About 90% of this sequestration occurs through export to the deep sea, and the rest through burial in coastal sediments. This estimate exceeds that for carbon sequestered in angiosperm-based coastal habitats.

The realization that vegetated coastal habitats support globally relevant rates of organic carbon burial that rank among the highest in the biosphere¹ led to the development of strategies to mitigate climate change through the conservation and restoration of seagrass, mangrove and saltmarsh habitats, termed blue carbon strategies^{2–5}. Macroalgae, the most productive marine macrophytes on a global scale^{6,7}, have been excluded from such blue carbon assessments as most macroalgae grow on rocks, where burial is precluded^{2,4,8}. However, some macroalgae grow on sandy sediments⁹, with burial averaging 0.4% of net primary production⁷. More importantly, macroalgae export about 43% of their production⁷ both as particulate organic carbon (POC)^{10,11} and dissolved organic carbon (DOC)^{8,12–14}. Some of this carbon may reach depositional areas and be sequestered in sediments, or reach the deep sea, where the carbon is locked away from exchange with the atmosphere. Macroalgae can thereby act as carbon donors to sink reservoirs located elsewhere^{6,8} and it has recently been argued that they should be included in blue carbon assessments^{8,15–17}. However, the evidence required to estimate their contribution has been published under a range of research fields. For instance, macroalgal export has been studied because of its consequences for the dispersal of species and genes^{18,19}, the relocation of rocks across the seafloor²⁰, connectivity among habitats and the stimulation of secondary production in adjacent and distant habitats^{10,11}, including the supply of food to deep-sea fauna²¹ and carbonate to the deep sea²².

Sequestration of macroalgal carbon in marine sediments

Macroalgae may have contributed to carbon sequestration for over 2.1 billion years, based on the oldest dating of a multicellular organism, *Grypania spiralis*, which is suggested to be a macroalga²³. They have certainly done so through the past 500 million years, as macroalgae have been reported to be the source of a number of oil deposits^{24,25}. One of the prerequisites

for macroalgae to contribute to CO₂ sequestration, that is, for their carbon be sequestered over centennial timescales, is thereby amply fulfilled.

Reports of the presence of macroalgal carbon in marine sediments are relatively few, but suggest that macroalgal carbon may be widespread, extending from shallow to deep-sea sediments and from polar to tropical regions, as well as across a broad range of depths into the sediment, from surface and subsurface layers down to deeper than a hundred metres into the sediment (Fig. 1, Supplementary Table 1). Macroalgal carbon is typically identified in depositional environments^{10,11,26}, including anoxic basins, submarine canyons, sedimentation areas within complex rocky shores and the deep sea (Fig. 1, Supplementary Table 1). Macroalgal-specific markers such as stable carbon isotopes coupled with lipids, sterols and carotenoids have been used to trace the contribution of macroalgae to sediments^{9,27} and food webs²⁶. The preservation potential of macroalgal carbon in sediments depends on the lability of the organic carbon, which varies between species¹⁷.

Export of macroalgal carbon to the deep sea

Multiple reports, including the presence of fresh *Sargassum* in the guts of abyssal isopods²¹, confirm the prevalent presence of macroalgal drift on the deep seafloor down to 6,475 m (Fig. 1, Supplementary Table 1). These reports are dominated by observations of brown algae, with abundant reports of *Sargassum* from subtropical latitudes, kelps in the temperate zone and kelps and Desmarestiales in the polar regions (Fig. 1, Supplementary Table 1). Macroalgal drift also appears to be particularly abundant on the discharge area of submarine canyons (Supplementary Table 1). Such canyons are widespread across all oceans (660 major canyons have so far been documented²⁸) and are important conduits that focus the export of materials, including macroalgal carbon (Fig. 2), from the continental shelf to the deep sea²⁹. For instance, more

¹Department of Bioscience, Aarhus University, Vejlsvøvej 25, DK-8600 Silkeborg, Denmark. ²Arctic Research Centre, Department of Bioscience, Aarhus University, Ny Munkegade 114, bldg. 1540, 8000 Århus C, Denmark. ³King Abdullah University of Science and Technology (KAUST), Red Sea Research Center, Thuwal 23955-6900, Saudi Arabia.*e-mail: djk@bios.au.dk

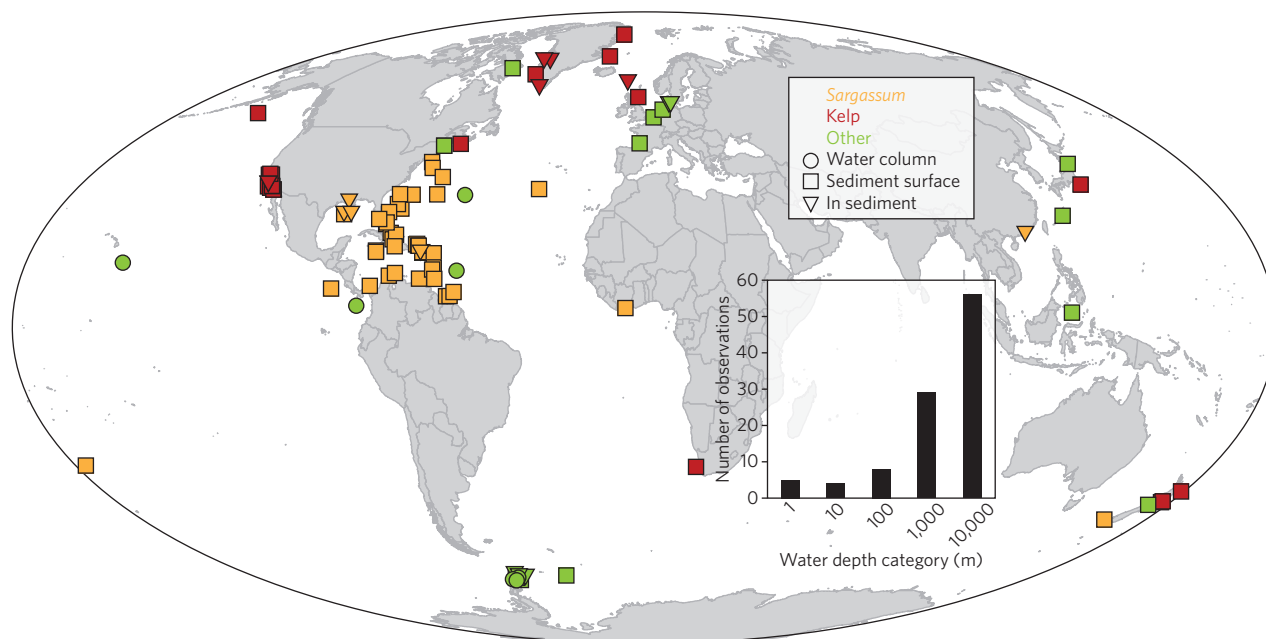


Figure 1 | Map of the locations where macroalgal carbon storage has been reported. The types of macroalgae are indicated for observations from sediment traps that are in the water column, on the sediment surface and buried in sediments. Inset, the frequency distribution of the water depths of macroalgal observations, with the majority representing the deep sea (<1,000 m). All references of observations are available in Supplementary Table 1.

than 130,000 t of kelp is exported yearly through the canyon adjacent to the Monterey Peninsula³⁰. In addition to observations of macroalgae on deep-sea sediments, sinking algal fragments have often been collected in open ocean pelagic sediment traps at depths of up to 1900 m (Fig. 1, Supplementary Table 1). This suggests two modes of transport: bed-load transport of drift material and sinking fluxes of negatively buoyant macroalgal detritus³¹ (Fig. 2).

Through shedding of old fronds, kelps support a continuous flux of export material. The substantial drag of large kelps leads to detachment from the substrate during high-energy events as well as removal by moderate swells^{10,32}. The gas vesicles characteristic of many brown algae (pneumatocysts, Fig. 2) favour the formation and long-distance drift of floating aggregates of macroalgae^{18,19}. This ability to drift, in combination with their relative unpalatability due to phenols and refractory carbon compounds such as fucoidan¹⁷, explain their prevalent role as carbon source in deep sediments (Figs 1 and 2, Supplementary Table 1). Detached macroalgal tissue is transported offshore by currents, which support long-range export (Fig. 2). For instance, a 588 km² patch of detached brown algae, *Colpomenia* sp., organized into windrows by wind-driven Langmuir circulation, was reported off the Great Bahamas Bank³³. Drifting rafts of giant kelp may occur at very high densities, with 39,000 to 348,000 rafts identified in the Southern California Bight alone, exporting the kelp more than 300 km offshore³⁴. Drifting surface mats of *Sargassum* are also abundant^{22,35,36}.

A number of mechanisms have been identified for the delivery of drifting macroalgae to marine sediments. Wind-induced Langmuir circulation can entrain floating macroalgal fragments at depth, where pressure can collapse their gas vesicles, rendering the macroalgae negatively buoyant and removing them from the neuston (Fig. 2). For instance, the gas vesicles of *Sargassum* have been found to collapse in 5 h under a pressure of only 30 dbar, although those of the Sargasso Sea *Sargassum* seem to be more resistant³⁷. Another delivery mechanism is the ballasting of floating macroalgae by the stones dislodged by excessive drag forces (Fig. 2) — a phenomenon of global geological relevance that

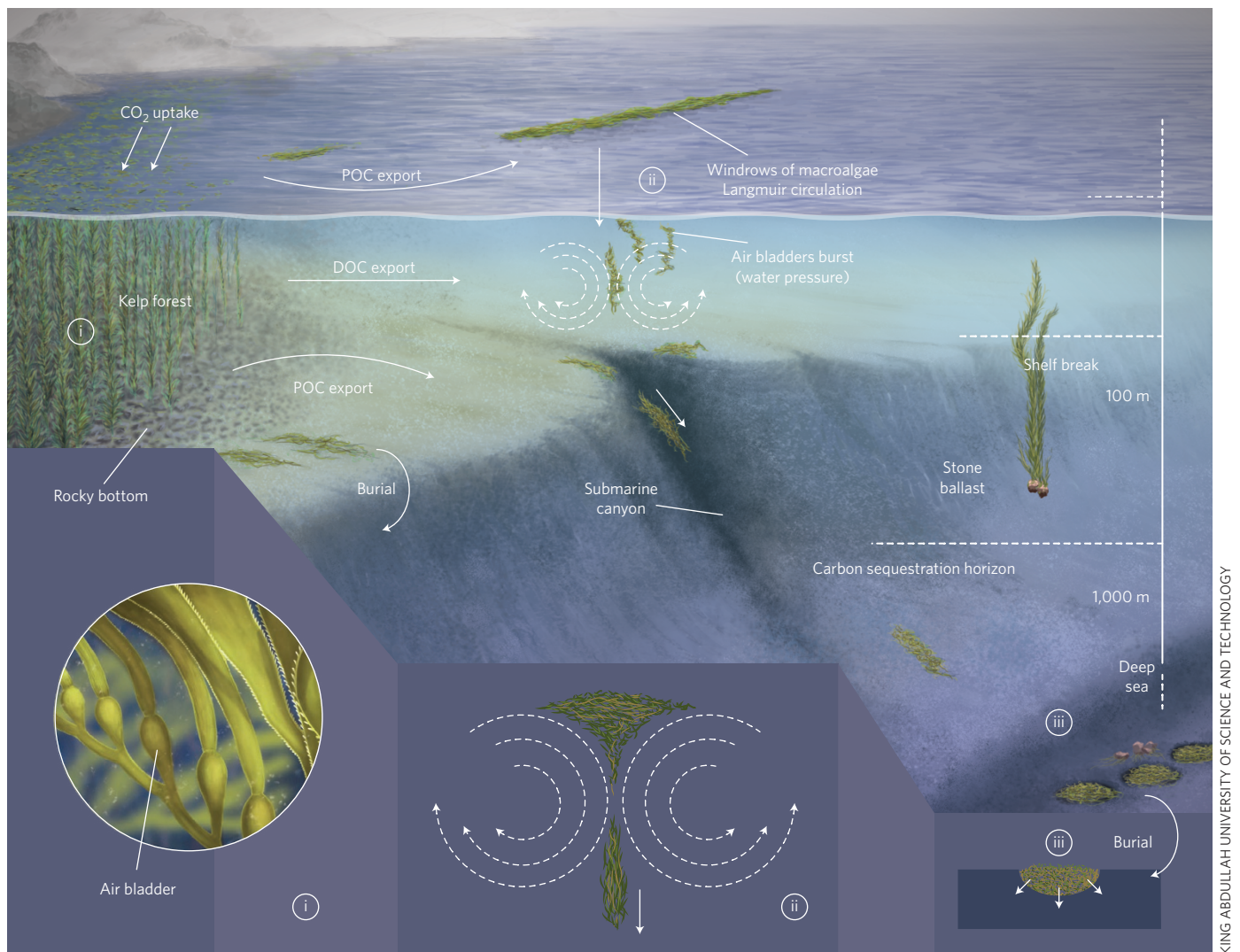
results in deep-sea soft sediment plains being paved with stones²⁰. The growth of calcifiers on macroalgal surfaces can also add to their density and contribute to their subsequent sinking²².

The offshore export of macroalgal fragments from the coastal zone fuels a potentially large flux of macroalgal carbon to the deep sea: there are reports of 16.5 gC m⁻² d⁻¹ of giant kelp being exported through the Carmel Canyon, California³⁸, and of 0.4 gC m⁻² yr⁻¹ of *Sargassum* reaching 3,600 m depth in the Northwest Atlantic³⁵. These fluxes can also be highly episodic, such as the estimated input in excess of 7 × 10¹⁰ gC potentially reaching the seafloor at 1800 m depth off the Bahaman shelf³³ during a storm.

Global carbon sequestration by macroalgae

Macroalgae are the dominant primary producers in the coastal zone^{1,6} with a global net primary production (NPP) of 1,521 TgC yr⁻¹ (range: 1,020–1,960 TgC yr⁻¹; Fig. 3) over an estimated area of 3.5 million km² (range: 2.8–4.3 million km²; see Tables 1 and 2). There are few studies that document the fate of NPP and export to the deep sea, but they do help to provide a first-order estimate of the contribution of macroalgae to carbon sequestration from burial in coastal sediments and export to the deep sea (defined as >1,000 m depth), where the carbon is precluded from exchanging with the atmosphere over extended timescales even after being remineralized (Fig. 3). We combine existing information on the fate of macroalgal carbon (Table 1) and propagate uncertainties through the calculations using a Monte Carlo approach (see Methods, Tables 1 and 2) to derive this crude estimate of the contribution of macroalgae to carbon sequestration.

On average, about 0.4% of macroalgal NPP is buried directly in the habitat⁷ for macroalgae that grow on soft sediments (a mean of 6.2 TgC yr⁻¹, Fig. 3). An estimated 43% of macroalgal NPP is exported, supporting a global flux of about 679 TgC yr⁻¹ (Fig. 3). We estimated the fraction exported as DOC by combining the mean area-specific estimate of macroalgal DOC release (101 gC m⁻² yr⁻¹)¹² with the estimated global macroalgal area (Tables 1 and 2), yielding 355 TgC yr⁻¹ or 52% of the total



KING ABDULLAH UNIVERSITY OF SCIENCE AND TECHNOLOGY

Figure 2 | Conceptual diagram of the pathways for export and sequestration of macroalgal carbon. Air bladders are common among brown algal taxa and facilitate their long-range transport (i). Langmuir circulation forms windrows of macroalgae (ii) and can force the algae to depths where water pressure makes the air bladders burst and the algae then sink. Macroalgal carbon can be sequestered either via burial in the habitat or by transport to the deep sea where it is sequestered whether buried or not (iii).

export (Fig. 3). The remaining export (48%, 323 TgC yr^{-1}) is in particulate form (Fig. 3, Tables 1 and 2).

We estimate that 33% of the DOC flux (117 TgC yr^{-1}) is exported below the mixed layer, representing an upper boundary for the amount of macroalgal DOC reaching the deep sea (Fig. 3). This value is supported both by the finding that the net oceanic primary production (approximately 50 PgC yr^{-1}), of which about 13% (that is, 6.5 PgC yr^{-1}) is released as DOC, results in a downward DOC export of 2 PgC yr^{-1} (approximately 30%) below the mixed layer (details in Table 1) and the large inputs of DOC from ocean margins to the ocean interior³⁹. We assume that the same fraction of macroalgal DOC is exported below the mixed layer and potentially reaches the deep sea (Table 1).

Regarding the fate of macroalgal POC export, three independent studies suggest that about 11% (35 TgC yr^{-1}) reaches the deep sea. One study reports that around 10% of drift *Sargassum* reaches the deep seafloor as particulate material³⁵, a second reports that approximately 3% of NPP³¹ (that is, equivalent to around 10% of the POC export) reaches the deep seafloor as phytodetritus and a third work finds that around 13% of drift kelp is exported through canyons (an average of two surveys before hurricane⁴⁰)

(Fig. 3, Table 1). The remaining 89% of the export POC flux is assumed to stay in the coastal ocean. Of this fraction, an estimated 4.6% (14 TgC yr^{-1}) is buried in shelf sediments⁴¹ (Fig. 3, Tables 1 and 2) and we assume that the rest (95.4%) is mineralized.

Together these findings yield a first-order estimate of the contribution of macroalgae to carbon sequestration of about 173 TgC yr^{-1} (range: $61\text{--}268 \text{ TgC yr}^{-1}$), of which about 88% is sequestered in the deep sea (Fig. 3). This estimate exceeds that for carbon buried in angiosperm-based coastal habitats ($111\text{--}131 \text{ TgC yr}^{-1}$)¹ and provides evidence of the importance of macroalgae in biological CO_2 sequestration. However, the range around this estimate varies by an order of magnitude, highlighting the need for targeted efforts to address the main sources of this uncertainty, which include the area covered by macroalgae, the amount of macroalgal-derived carbon that is sequestered in sediments and the fate of macroalgal-derived DOC exported from the mixed layer.

An assessment of the potential changes in the global rates of CO_2 sequestration of macroalgae requires a global evaluation of the trends and drivers of this sequestration, which, unlike those of seagrasses, mangroves and salt-marshes⁴, has not yet been

Table 1 | Details of the data used in the uncertainty propagation analysis.

Variable	Minimum	Maximum	Mean	Standard deviation
Global macroalgae area (million km ²)	1.4*	5.7 [†]	3.54 [‡]	1.06 [‡]
NPP (gC m ⁻² yr ⁻¹)	91 [§]	750	420 [‡]	165 [‡]
Global NPP (TgC yr ⁻¹)	-	-	1521 [¶]	732 [¶]
Percentage of NPP buried in algal beds	-	-	0.4 [#]	0.54 [#]
Percentage of NPP exported from algal beds	-	-	43.5 [#]	48 [#]
DOC exported from algal beds (gC m ⁻² yr ⁻¹)	-	-	101 [*]	55 [*]
Percentage of DOC exported below the mixed layer	-	-	30 ^{**}	9 ^{**}
POC exported from algal beds (TgC yr ⁻¹)	-	-	323 ^{††}	907 ^{††}
Percentage of POC exported to the deep sea	-	-	11 ^{‡‡}	1.7 ^{‡‡}
POC export retained in the shelf environment (TgC yr ⁻¹)	-	-	288 ^{§§}	808 ^{§§}
POC buried in shelf sediments (gC m ⁻² yr ⁻¹)	-	-	4.65	2.47

*From ref. 1, recalculated from the total macrophyte area in ref. 51 (which is based on ref. 52) by subtracting the 0.6 million km² that corresponds to seagrass beds¹ Ref. 53 combined estimates of underwater light penetration, global bathymetry and the light requirements of macroalgae to estimate the potential area available for macroalgae to be 5.7 million km².[†]The midpoint of the range (minimum–maximum) is assumed to be the mean; the range is assumed to span two standard deviations. [‡]Ref. 54 (based on literature data) provides an NPP value for macroalgae of 365 g DW m⁻² yr⁻¹ (DW, dryweight); given a 25% C content of DW for macroalgae²⁵ this corresponds to 91 gC m⁻² yr⁻¹. ^{||}Estimate from ref. 56 on the basis of a literature review. [¶]Propagated by combining [‡] and [§]. [#]From the mean and standard error reported in ref. 7, for *n* = 30, where *n* is the number of observations. ^{*}From the mean and standard deviation reported in ref. 12. This value is multiplied by the global area of macroalgae to estimate the total DOC export from macroalgae through the error propagation analysis. ^{**}This mean estimate is supported by the finding that the net oceanic primary production (around 50 PgC yr⁻¹), of which about 13%⁵⁷ (that is, 6.5 PgC yr⁻¹) is released as DOC, supplies a downward DOC export of 2 PgC yr⁻¹ (approximately 30%) below the mixed layer (fig. 6.1 in ref. 58). We assume that the same fraction of macroalgal DOC is exported below the mixed layer and potentially reaches the deep sea. Where no estimate of error is available, we assumed that the standard deviation must be at least 30% of the mean (that is, 9%). ^{††}Calculated as the total export – DOC export through the uncertainty analysis. ^{‡‡}The mean and standard error of three independent studies^{31,35,40}. ^{§§}Calculated as total POC export – POC exported to the deep sea through the uncertainty analysis. ^{|||}Calculated from two experiments reported in ref. 59.

Table 2 | Distribution of values originating from the uncertainty analysis.

Variable	Macroalgal area (million km ²)	Primary production (gC m ⁻² yr ⁻¹)	Global production (PgC yr ⁻¹)	Burial in algal bed (PgC yr ⁻¹)	Burial in algal bed (PgC yr ⁻¹)	DOC export (PgC yr ⁻¹)
Quantiles						
Maximum	7.31	998	4.778	0.0456	5.001	1.507
75%	4.28	535	1.960	0.0113	1.155	0.486
50%	3.51	430	1.419	0.0051	0.571	0.330
25%	2.80	322	1.020	0.0002	0.099	0.194
Minimum	0.52	-77	-0.295	-0.042	-2.685	-0.316
Sum. stats.						
Mean	3.54	430	1.521	0.0062	0.679	0.355
s.d.	1.06	157	0.732	0.0094	0.887	0.229
s.e.	0.03	5	0.023	0.0003	0.028	0.007
Variable	POC export (PgC yr ⁻¹)	DOC export below mixed (PgC yr ⁻¹)	POC deep sea (PgC yr ⁻¹)	POC export to shelf (PgC yr ⁻¹)	POC burial in shelf (PgC yr ⁻¹)	Total C sequestr. (PgC yr ⁻¹)
Quantiles						
Maximum	4.517	0.456	0.466	4.098	0.249	0.899
75%	0.787	0.194	0.085	0.705	0.031	0.268
50%	0.237	0.113	0.026	0.210	0.006	0.155
25%	-0.229	0.036	-0.025	-0.204	-0.007	0.061
Minimum	-3.631	-0.197	-0.392	-3.239	-0.217	-0.455
Sum stats.						
Mean	0.323	0.117	0.035	0.288	0.014	0.173
s.d.	0.907	0.115	0.100	0.808	0.044	0.172
s.e.	0.029	0.004	0.003	0.026	0.001	0.005

The different variables reflect the flux in macroalgal production (Fig. 3) from the uncertainty analysis (conducted using 1,000 simulations; *n* = 1000). The uncertainty in the area and NPP per unit area were combined to generate the uncertainty in the global NPP. See Table 1 for details of the uncertainty analysis. The uncertainty is represented in Fig. 3 as the 50% interquartile range (that is, 25% and 75% quartiles) of the propagated values. Sum. stats., summary statistics; s.d., standard deviation; s.e., standard error.

attempted. Climate change leads to the loss of kelp forests near their southern distribution limit^{42,43}, but may favour their poleward expansion into the Arctic^{44,45} and may change macroalgal NPP and detrital export in the future⁴⁶. Other global drivers of change⁴⁷, including eutrophication⁴⁸ and the growing macroalgal harvest and aquaculture industry^{49,50}, may also influence the

contribution of macroalgae to carbon sequestration by affecting the future area of macroalgal growth and production. Such changes in the sequestration of macroalgal carbon should be monitored and macroalgae should be considered both in carbon accounting reports and within blue carbon conservation and restoration strategies to mitigate climate change.

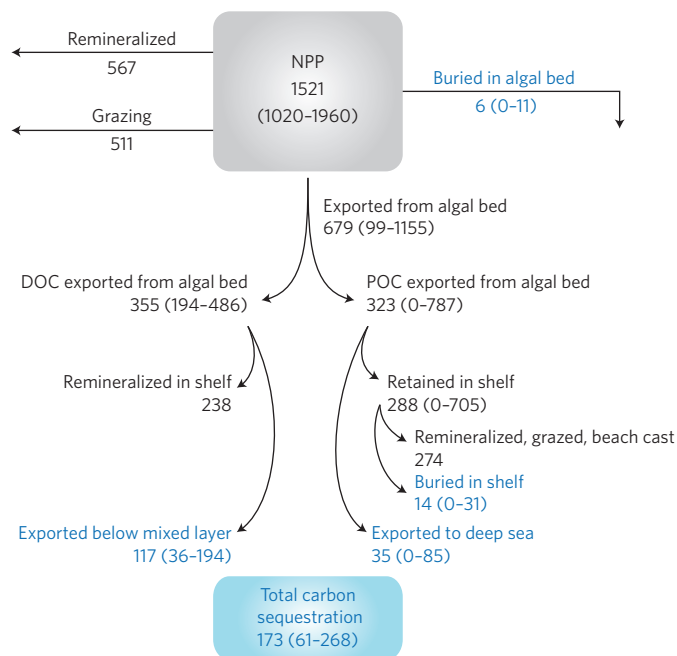


Figure 3 | Pathways for the sequestration of macroalgal carbon in the ocean. Each step of the carbon flow from global macroalgal net primary production (NPP) to carbon sequestration (in blue) is supported by the literature or inferred by a difference between a total and subcomponents supported by literature (Table 1). The means (with 25 to 75% quartile ranges in parentheses) shown are derived from a difference propagation analysis (Methods), except for those fluxes not conducive to carbon sequestration (all values are in TgC yr⁻¹). As the estimates have been derived independently, their total does not necessarily match to the mean global NPP estimate. Grazing (33.6% of the NPP) and remineralization (37.3% of the NPP) in the algal bed are adopted from a previous budget⁷.

Methods

Methods, including statements of data availability and any associated accession codes and references, are available in the [online version of this paper](#).

Received 9 February 2016; accepted 20 July 2016; published online 12 September 2016

References

- Duarte, C. M., Middelburg, J. & Caraco, N. Major role of marine vegetation on the oceanic carbon cycle. *Biogeosciences* **2**, 1–8 (2005).
- Nellemann, C. *et al.* *Blue Carbon: a Rapid Response Assessment* (United Nations Environment Programme, 2009).
- McLeod, E. *et al.* A blueprint for blue carbon: toward an improved understanding of the role of vegetated coastal habitats in sequestering CO₂. *Front. Ecol. Environ.* **7**, 362–370 (2011).
- Duarte, C. M., Losada, I. J., Hendriks, I. E., Mazarrasa, I. & Marbà, N. The role of coastal plant communities for climate change mitigation and adaptation. *Nat. Clim. Change* **3**, 961–968 (2013).
- Blue Future: coastal wetlands can have a crucial role in the fight against climate change. *Nature* **529**, 255–256 (2016).
- Smith, S. V. Marine macrophytes as a global carbon sink. *Science* **211**, 838–840 (1981).
- Duarte, C. M. & Cebrián, J. The fate of marine autotrophic production. *Limnol. Oceanogr.* **41**, 1758–1766 (1996).
- Hill, R. *et al.* Can macroalgae contribute to blue carbon? an Australian perspective. *Limnol. Oceanogr.* **60**, 1689–1706 (2015).
- Hardison, A. K. *et al.* Microphytobenthos and benthic macroalgae determine sediment organic matter composition in shallow photic sediments. *Biogeosciences* **10**, 5571–5588 (2013).
- Krumhansl, K. A. & Scheibling, R. E. Production and fate of kelp detritus. *Mar. Ecol. Prog. Ser.* **67**, 281–302 (2012).
- Filbee-Dexter, K. & Scheibling, R. E. Detrital kelp subsidy supports high reproductive condition of deep-living sea urchins in a sedimentary basin. *Aquat. Biol.* **23**, 71–86 (2014).
- Barron, C., Apostolaki, E. T. & Duarte, C. M. Dissolved organic carbon fluxes by seagrass meadows and macroalgal beds. *Front. Mar. Sci.* **1**, 42 (2014).
- Barrón, C. & Duarte, C. M. Dissolved organic carbon pools and export from the coastal ocean. *Glob. Biogeochem. Cycles* **29**, 1725–1738 (2015).
- Reed, D. C. *et al.* Patterns and controls of reef-scale production of dissolved organic carbon by giant kelp *Macrocystis pyrifera*. *Limnol. Oceanogr.* **60**, 1996–2008 (2015).
- Sondak, C. F. & Chung, I. K. Potential blue carbon from coastal ecosystems in the Republic of Korea. *Ocean Sci. J.* **50**, 1–8 (2015).
- van der Heijden, L. H. & Kamenos, N. A. Reviews and syntheses: calculating the global contribution of coralline algae to carbon burial. *Biogeosciences* **12**, 6429–6441 (2015).
- Trevathan-Tackett, S. M. *et al.* Comparison of marine macrophytes for their contributions to blue carbon sequestration. *Ecology* **96**, 3043–3057 (2015).
- Fraser, C. I. in *Seaweed Phylogeography* (ed. Fraser C. I.) Ch. 5, 131–146 (Springer, 2016).
- Macaya, E. C., López, B., Tala, F., Tellier, F. & Thiel, M. in *Seaweed Phylogeography* (ed. Fraser C. I.) Ch. 4, 97–130 (Springer, 2016).
- Garden, C. J. & Smith, A. M. Voyages of seaweeds: the role of macroalgae in sediment transport. *Sediment. Geol.* **318**, 1–9 (2015).
- Wolff, T. The systematics and biology of bathyal and abyssal Isopoda Asellota. *Galathea Rep.* **6**, 1–320 (1962).
- Fabry, V. J. & Deuser, W. G. Aragonite and magnesian calcite fluxes to the deep Sargasso Sea. *Deep Sea Res.* **38**, 713–728 (1991).
- Han, T. & Runnegar, B. Megascopic eukaryotic algae from the 2.1-billion-year-old Negaunee Iron-Formation, Michigan. *Science* **257**, 232–235 (1992).
- Sun, Y., Mao, S., Wang, F., Peng, P. & Chai, P. Identification of the Kukersite-type source rocks in the Ordovician stratigraphy from the Tarim Basin, NW China. *Chinese Sci. Bull.* **58**, 4450–4458 (2013).
- Xie, X. *et al.* Petrology and hydrocarbon potential of microalgal and macroalgal dominated oil shales from the Eocene Huadian Formation, NE China. *Int. J. Coal Geol.* **124**, 36–47 (2014).
- Renaud, P. E., Lokken, T. S., Jørgensen, L. L., Berge, J. & Johnson, B. J. Macroalgal detritus and food-web subsidies along an Arctic fjord depth-gradient. *Front. Mar. Sci.* **2**, 31 (2015).
- Chikaraishi Y. in *Treatise on Geochemistry 5: Organic Geochemistry* (eds Birrer, B. *et al.*) Ch. 12.5, 95–123 (Elsevier, 2014).
- De Leo, F. C., Smith, C. R., Rowden, A. A., Bowden, D. A. & Clark, M. R. Submarine canyons: hotspots of benthic biomass and productivity in the deep sea. *Proc. R. Soc. B.* **277**, 2783–2792 (2010).
- Canals, M. *et al.* Flushing submarine canyons. *Nature* **444**, 354–357 (2006).
- Harrold, C. & Lisin, S. Radio-tracking rafts of giant kelp: local production and regional transport. *J. Exp. Mar. Biol. Ecol.* **130**, 237–251 (1989).
- Palanques, A. *et al.* Downward particle fluxes and sediment accumulation rates in the western Bransfield Strait: implications of lateral transport for carbon cycle studies in Antarctic marginal seas. *J. Mar. Res.* **60**, 347–365 (2002).
- de Bettignies, T. *et al.* Phenological decoupling of mortality from wave forcing in kelp beds. *Ecology* **96**, 850–861 (2015).
- Dierrsens, H. M., Zimmerman, R. C., Drake, L. A. & Burdige, D. J. Potential export of unattached benthic macroalgae to the deep sea trough wind-driven Langmuir circulation. *Geophys. Res. Lett.* **36**, L04602 (2009).
- Hobday, A. J. Abundance and dispersal of drifting kelp *Macrocystis pyrifera* rafts in the Southern California Bight. *Mar. Ecol. Prog. Ser.* **195**, 101–116 (2000).
- Rowe, G. T. & Staresinic, N. Sources of organic matter to the deep-sea benthos. *Ambio Special Report* **1**, 19–23 (1979).
- Kingsbury, J. M. Christopher Columbus as a botanist. *Arnoldia* **52**, 11–28 (1992).
- Johnson, D. L. & Richardson, P. L. On the wind-induced sinking of Sargassum. *J. Exp. Mar. Biol. Ecol.* **28**, 255–267 (1977).
- Harrold, C., Light, K. & Lisin, S. Organic enrichment of submarine canyon and continental shelf benthic communities by macroalgal drift imported from nearshore kelp forests. *Limnol. Oceanogr.* **43**, 669–678 (1998).
- Bauer, J. E. & Druffel, E. R. Ocean margins as a significant source of organic matter to the deep open ocean. *Nature* **92**, 482–485 (1998).
- Josselyn, M. N. *et al.* Composition, export and faunal utilization of drift vegetation in the Salt River submarine canyon. *Estuar. Coast. Shelf Sci.* **17**, 447–465 (1983).
- Hardison, A., Canuel, E. A., Anderson, I. C. & Veuger, B. Fate of macroalgae in benthic systems: carbon and nitrogen cycling within the microbial community. *Mar. Ecol. Prog. Ser.* **414**, 41–55 (2010).

42. Wernberg, T. *et al.* Seaweed communities in retreat from ocean warming. *Curr. Biol.* **21**, 1828–1832 (2011).
43. Smale, D. A., Burrows, M. T., Moore, P., O'Connor, N. & Hawkins, S. J. Threats and knowledge gaps for ecosystem services provided by kelp forests: a northeast Atlantic perspective. *Ecol. Evol.* **3**, 4016–4038 (2013).
44. Poloczanska, E. S. *et al.* Global imprint of climate change on marine life. *Nat. Clim. Change* **3**, 919–925 (2013).
45. Krause-Jensen, D. & Duarte, C. M. Expansion of vegetated coastal ecosystems in the future Arctic. *Front. Mar. Sci.* **1**, 77 (2014).
46. Krumhansl, K. A., Lauzon-Guay, J. S. & Scheibling, R. E. Modeling effects of climate change and phase shifts on detrital production of a kelp bed. *Ecology* **95**, 763–774 (2014).
47. Duarte, C. M. Global change and the future ocean: a grand challenge for marine sciences. *Front. Mar. Sci.* **1**, 63 (2014).
48. Smetacek, V. & Zingone, A. Green and golden seaweed tides on the rise. *Nature* **504**, 84–88 (2013).
49. Duarte, C. M. *et al.* Will the oceans help feed humanity? *BioScience* **59**, 967–976 (2009).
50. Olsen, Y. How can mariculture better help feed humanity? *Front. Mar. Sci.* **2**, 46 (2015).
51. Gattuso, J. P., Frankignoulle, M. & Wollast, R. Carbon and carbonate metabolism in coastal aquatic ecosystems. *Annu. Rev. Ecol. Syst.* **29**, 405–434 (1998).
52. Whittaker, R. H. & Likens, G. E. Carbon and the biota. *Brookhaven Symp. Biol.* **24**, 281–302 (1973).
53. Gattuso, J. P., Gentili, B., Duarte, C. M., Kleypas, J. A., Middelburg, J. J. & Antoine, D. Light availability in the coastal ocean: impact on the distribution of benthic photosynthetic organisms and their contribution to primary production. *Biogeosciences* **3**, 489–513 (2006).
54. Cebrian, J. & Duarte, C. M. The dependence of herbivory on growth rate in natural plant communities. *Funct. Ecol.* **4**, 518–525 (1994).
55. Duarte, C. M. Nutrient concentration of aquatic plants: patterns across species. *Limnol. Oceanogr.* **37**, 882–889 (1992).
56. Charpy-Roubaud, C. & Sournia, A. The comparative estimation of phytoplanktonic, microphytobenthic and macrophytobenthic primary production in the oceans. *Mar. Microb. Food Webs* **4**, 31–57 (1990).
57. Baines, S. B. & Pace, M. L. The production of dissolved organic matter by phytoplankton and its importance to bacteria: patterns across marine and freshwater systems. *Limnol. Oceanogr.* **36**, 1078–1090 (1991).
58. Ciais, P. *et al.* in *Climate Change 2013: The Physical Science Basis* (eds Stocker, T. F. *et al.*) Ch. 6, 465–570 (IPCC, Cambridge Univ. Press, 2013).
59. Hardison, A., Canuel, E. A., Anderson, I. C. & Veuger, B. Fate of macroalgae in benthic systems: carbon and nitrogen cycling within the microbial community. *Mar. Ecol. Prog. Ser.* **414**, 41–55 (2010).

Acknowledgements

The study was funded by the COCOA project under the BONUS programme, which is funded by the EU 7th Framework Programme, the Danish Research Council and KAUST. We thank I. Gromicho (KAUST) for the artwork in Fig. 2 and A. Kjeldgaard and T. Christensen for help with Fig. 1. The study is also a contribution to the Greenland Ecosystem Monitoring programme (www.G-E-M.dk) and the Arctic Science Partnership (www.asp-net.org).

Additional information

Supplementary information is available in the online version of the paper. Reprints and permissions information is available online at www.nature.com/reprints. Correspondence should be addressed to D.K.-J.

Competing financial interests

The authors declare no competing financial interests.

Methods

Estimates of the uncertainty in the global net primary production of macroalgae and its fate required the mean and range for the macroalgal carbon sequestered annually either in sediments or the deep sea to be calculated. An uncertainty propagation analysis was then undertaken using Monte Carlo simulations. For each component of the global net primary production of macroalgae and its fate, 1,000 randomly generated values were obtained by sampling randomly from a normal distribution with the corresponding mean and standard deviation (Table 1). Individual estimates were calculated by combining each of the 1,000 simulated values, thereby yielding 1,000

estimates for each step in the calculations that combined all of the uncertainties from the terms entering these calculations (Table 1). We then retrieved the mean from the 1,000 estimates of macroalgal production, which is generated by combining the uncertainties in the area covered globally and the NPP per unit area (Table 1) and carbon flux, and characterized the uncertainty by the central 50% interquartile range of the values (that is, the 25% to 75% quartiles of the values generated; Table 2).

Data availability. The data that support the findings of this study are available within the text and Supplementary Information.