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Author for correspondence:
Marianne Holmer
e-mail: holmer@biology.sdu.dk

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Global change biology

Variation of carbon contents in eelgrass (*Zostera marina*) sediments implied from depth profiles

Theodor Kindeberg[1], Emilia Röhr[1,2], Per-Olav Moksnes[3], Christoffer Boström[2] and Marianne Holmer[1]

[1]Department of Biology, University of Southern Denmark, Odense, Denmark
[2]Environmental and Marine Biology, Åbo Akademi University, Åbo, Finland
[3]Department of Marine Sciences, University of Gothenburg, Gothenburg, Sweden

TK, 0000-0001-8151-8423; MH, 0000-0002-6095-5488

Seagrass meadows are able to store significant amounts of organic carbon in their underlying sediment, but global estimates are uncertain partly owing to spatio-temporal heterogeneity between and within areas and species. In order to provide robust estimates, there is a need to better understand the fate of, and mechanisms behind, organic carbon storage. In this observational study, we analyse a suite of biotic and abiotic parameters in sediment cores from 47 different eelgrass (*Zostera marina*) beds spanning the distributional range of the Northern Hemisphere. Depth profiles of particulate organic carbon (POC) revealed three patterns of vertical distribution where POC either increased, decreased or showed no pattern with sediment depth. These categories exhibited distinct profiles of $\delta^{13}C$ and C : N ratios, where high POC profiles had a proportionally larger storage of eelgrass-derived material whereas low POC profiles were dominated by phytoplanktonic and macroalgal material. However, high POC did not always translate into high carbon density. Nevertheless, this large-scale dataset provides evidence that the variability in organic matter source in response to natural and anthropogenic environmental changes affects the potential role of eelgrass beds as POC sinks, particularly where eelgrass decline is observed.

1. Introduction

Global estimates of carbon storage capacity in seagrass systems are associated with uncertainty, and there is an ongoing debate regarding the best way forward in assessing seagrass blue carbon [1]. In addition to a lack of accurate distribution estimates, there is also insufficient understanding of the variability among regions and within species [2,3].

There is considerable heterogeneity between seagrass systems, and vertical sediment depth profiles of particulate organic carbon (POC) vary in both shape and magnitude [3–5]. If sediment accumulation and below-ground production is constant, a pattern of decreasing POC with sediment depth implies that remineralization processes in the upper layers of the sediment are dominant, and this is typically the observed pattern in the top (0–25 cm) layers in seagrass sediments [1,3,6]. If sediment accumulation has increased recently, e.g. owing to eutrophication events, elevated POC pools in the surface sediments may also be observed. An increasing pattern of POC with depth may indicate that below-ground production contributes to the carbon content, or that environmental changes, such as changing light conditions in the water column, have occurred that depressed carbon inputs and/or released carbon to the water column in recent times, diminishing the pools of POC in the upper layers. Examples could be reduced seagrass cover or reduced seagrass productivity as a result of lower light availability [7], reduced sedimentation or erosion due to altered physical factors, such as installing protection barriers along beaches [8], or decreased eutrophication and thus a decreased input of sestonic particles [9,10].

Describing the variation in sediment depth profiles is critical for estimating the sediment carbon stock in seagrass meadows, particularly if the concentration of carbon and sediment density are extrapolated from shallow cores, as has been previously done [6]. There is a lack of studies that assess this variation for the distributional range of single species. Here we compile a global dataset of POC in eelgrass (*Zostera marina* L.) sediments that have been sampled with identical methods to describe the variation in sediment profiles.

2. Material and methods

Samples were collected within the Zostera Experimental Network (ZEN) in 13 different countries across the Northern Hemisphere, totalling 141 cores in 47 sites [11] (see electronic supplementary material, table S1 for coordinates of all sites and figure S1 caption for location names). At each site, 25 cm cores ($n = 3$) were collected within the eelgrass bed. Samples were analysed for organic carbon content (POC), organic nitrogen content (ON), stable isotopic composition (δ^{13}C, δ^{15}N), and sediment (dry bulk density, porosity, water content) and environmental (water depth, salinity, temperature) variables. Profiles were categorized by depth-averaged POC content (less than 2% and greater than or equal to 2%) and pooled by profile pattern based on linear regression analyses of the change in POC as a function of sediment depth (electronic supplementary material, table S1). In addition, POC, ON, δ^{13}C and δ^{15}N were assessed for eelgrass leaves and roots and other plant species present, including macroalgae and macrophytes, whereas literature values were used for phytoplankton [2]. To quantitatively assess the contribution of different sources to POC, a stable isotope mixing model of δ^{13}C and δ^{15}N was applied using the software IsoSource 1.3.1 [12]. Increments and tolerance level were set to 1% and 1, respectively, and sources are reported as the mean ($\pm$s.e.) and range of their contribution. For detailed information on sampling procedure and analyses, refer to [2].

3. Results

By examining the 47 depth profiles, three recurring patterns of POC distribution as a function of depth emerged: (*a*) decreasing POC with sediment depth ($n = 16$); (*b*) mixed or no apparent vertical pattern ($n = 24$); (*c*) increasing POC with sediment depth ($n = 7$) (figure 1; electronic supplementary material, table S1). Profiles categorized as low POC (less than 2% POC, $n = 37$) more commonly displayed decreasing (38%) or mixed (57%) patterns (electronic supplementary material, table S1 and figure S1). Out of the 10 profiles categorized as high POC (greater than or equal to 2% POC), increasing patterns were most common (50%) (electronic supplementary material, table S1 and figure S1). Depth profiles of δ^{13}C and C : N ratio exhibited variable vertical zonation and were not always related to the pattern of POC profiles (figure 1).

However, in sites where POC was high (2.18 ± 0.24–$8.65 \pm 0.40\%$) and increased with depth, profiles of δ^{13}C typically approached the signal for eelgrass-derived detritus (electronic supplementary material, figure S1). The opposite was generally true for low POC profiles and POC profiles that decreased with sediment depth (electronic supplementary material, figure S1). Here, δ^{13}C became more depleted with depth, suggesting a relatively more important planktonic contribution to POC with depth. The same pattern was observed for C : N ratios, which often decreased with sediment depth at these sites, although this parameter was more heterogeneous (figure 1).

For all areas examined, the average (mean $\pm$ s.e., $n = 1007$) sediment POC, δ^{13}C and C : N ratio were $1.27 \pm 0.06\%$, -16.7 ± 0.2‰ and 13.06 ± 1.35, respectively (figure 2). However, many sites with higher POC values (greater than or equal to 2%) approached a δ^{13}C similar to the average values of eelgrass leaves, roots and rhizomes (-9.5 ± 0.1, -10.1 ± 0.1 and -12.0 ± 0.2‰, respectively) (figure 2*a*). Contrarily, samples with δ^{13}C resembling phytoplankton and macroalgae (-20.1 ± 0.5 and -21.0 ± 0.2‰, respectively) never exhibited high POC values (figure 2*a*). C : N ratios followed two distinctly different patterns where they increased (towards that of leaves and roots) with increasing POC or remained constant at a low value with increasing POC, suggesting a greater influence of macroalgae and phytoplankton-derived material in the latter (figure 2*b*). These features were reaffirmed when examining the relationship between δ^{13}C and C : N ratios. While most data exhibited a δ^{13}C and C : N ratio of macroalgal and phytoplanktonic sources, there was a distinct relationship between δ^{13}C and C : N ratio reflecting eelgrass detritus for some sites (figure 2*c*). Furthermore, the stable isotope mixing model of δ^{13}C and δ^{15}N suggested that although macroalgae and phytoplankton combined were the dominating sources for the whole dataset (28 ± 2 and $29 \pm 3\%$, respectively), eelgrass-derived material was dominating in areas of high POC ($65 \pm 5\%$) (electronic supplementary material, table S2). However, given the limitations of using a five-source mixing model with two variables, these results should be interpreted with caution.

The relationship between POC and sediment parameters appeared to be divided in two, where high POC was primarily found in sediments with low dry bulk density (less than 0.6 g cm^{-3}; electronic supplementary material, figure S2*a*), and high water content (greater than 60%; electronic supplementary material, figure S2*b*). This was reflected in the sediment carbon density, where one group of locations in Denmark and France showed increasing density with increasing POC, and a location in Sweden (LN) showed low carbon density independent of the POC content (electronic supplementary material, figure S2*c*). For low POC sites, there was a significant linear relationship between POC and carbon density ($R^2 = 0.48$; $p \ll 0.001$).

4. Discussion

The extensive dataset presented here highlights the heterogeneity among eelgrass POC profiles, where markedly different patterns of vertical POC zonation emerge, indicating large variability in carbon pools. In areas where POC decreased with depth (34% of the cores examined) similar to depth profiles in seagrass sediments in general [3,6], the shape of the vertical profile can be explained by high turnover and remineralization that successively decreases with depth as the organic matter is decomposed, provided that POC input is constant [13]. The profile may also develop, if the POC input has been increasing over the years, which may be the case in eutrophic areas. A rapid decline with depth that then stabilizes, as observed in some sites (e.g. LI, QU, MX, BC), implies that the depth where remineralization can be neglected owing to

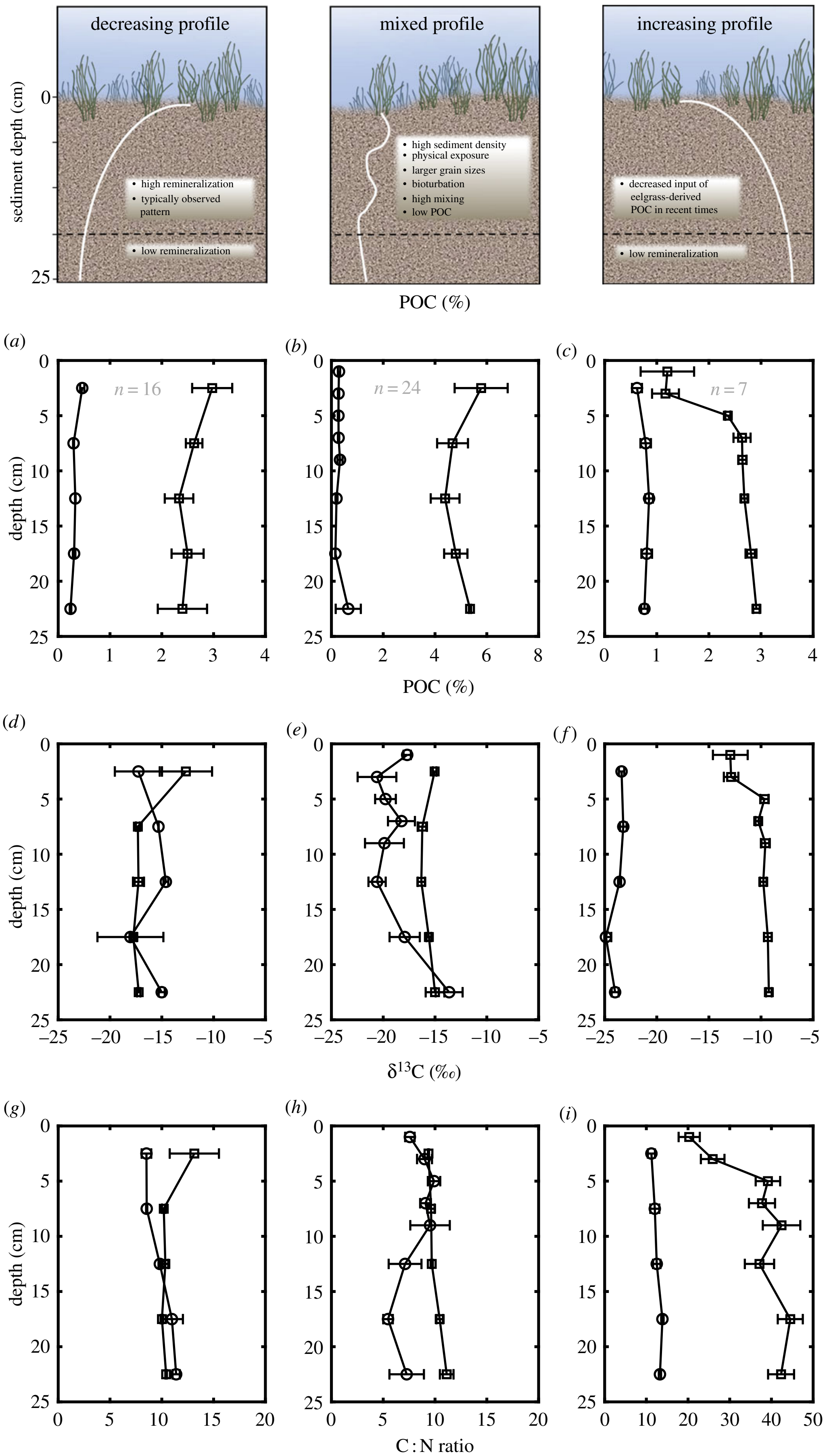

Figure 1. Conceptual figure of POC profile patterns and depth profiles of POC (*a*–*c*), $\delta^{13}C$ (*d*–*f*), and C : N ratio (*g*–*i*). Squares indicate profile with mean POC greater than or equal to 2% ($n = 9$) and circles indicate profile with mean POC less than 2% ($n = 38$). Error bars show ± s.e. ($n = 3$) and dashed horizontal line in the conceptual figure indicates where profile stabilizes. Note that *x*-axes are variable and that profiles are examples of sites with the most distinctive patterns and do not reflect the bulk of the sampled profiles (electronic supplementary material, figure S1). Seagrass symbol courtesy of the Integration and Application Network (IAN), University of Maryland (ian.umces.edu/symbols).

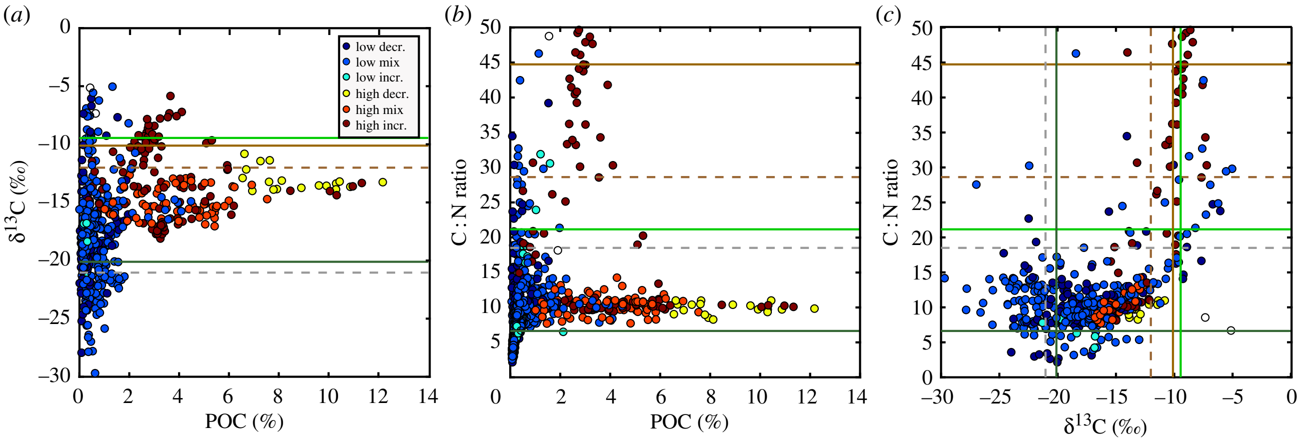

Figure 2. Correlation between sediment POC and δ^{13}C (*a*), POC and C : N ratio (*b*) and δ^{13}C and C : N ratio (*c*). Lines indicate mean value of eelgrass leaves (light green), eelgrass roots (brown), eelgrass rhizomes (brown, dashed), phytoplankton (dark green) and macroalgae (grey, dashed). No C : N ratio was obtained for phytoplankton, and the Redfield ratio of 6.6 was used.

low rates is surpassed and the POC stored below that threshold can be considered buried [1]. This highlights the importance of sampling deeper cores, beyond the remineralization depth, when assessing carbon pools.

A large number of profiles (51%) exhibited vertical variability from which no distinctive pattern could be inferred (mixed profile, figure 1*b*). These were generally low in POC (88% less than 2% POC) and typically exhibited high within-site variability. Studies show that plant variables such as high shoot density or high below-ground biomass do not translate into high carbon content [2]. Instead, sites with low POC were generally characterized by coarser grain sizes with high sediment density, located on exposed sites (e.g. SF, LÅ, NY), suggesting that advective forces dominate over diffusive [2,4]. Consequently, these sediments may exhibit a deeper mixing depth and/or high POC remineralization [1]. However, the small-scale variability can also be due to redox oscillations owing to factors such as bioturbation [14] and radial oxygen loss from eelgrass roots [15]. Carbon pools are low in these mixed sediments which are unlikely to represent significant blue carbon systems, despite high eelgrass productivity. This emphasizes the significant role of sediment mixing, remineralization and local hydrodynamics, processes that are often overlooked in the blue carbon literature [1].

Notably, five of the 10 sites that were characterized as high POC exhibited an increase in POC across the top 25 cm (figure 1*c*), which contrasts with general observations of seagrass sediment profiles showing decreasing POC with depth [3,6]. The fact that δ^{13}C profiles in the high POC sediments often followed the same increasing pattern suggests that the input of autochthonous organic matter has decreased over time, possibly owing to reduced eelgrass cover and a shift towards increased input of macroalgae and phytoplankton with faster remineralization rates [16,17]. In fact, these sites were from areas (Denmark and Sweden) where eelgrass has diminished [18]. This is an important finding as seagrasses are in decline globally and eutrophication is a ubiquitous issue which can have negative impacts on the carbon pools in seagrass beds [19].

In conclusion, this study provides important insight into the variability of POC vertical zonation in different eelgrass environments. Furthermore, we stress the importance of considering the shape of the carbon profile when extrapolating profiles from 25 to 100 cm depth, a practice common in the blue carbon literature [3,6]. Only if the core extends the mixing depth and the POC profile has stabilized can an adequate extrapolation be done. Understanding the mechanisms behind organic carbon vertical variability is imperative to assess carbon content in seagrass sediments and this study provides, we believe, a first, species-specific insight into this matter.

Data accessibility. Data are available as electronic supplementary material.

Authors' contributions. M.H. and T.K. conceived and designed the study. T.K. carried out data analysis and drafted the manuscript. E.R. and C.B. carried out data analysis and revised the manuscript. P.-O.M. collected data and revised the manuscript. All authors gave final approval for publication.

Competing interests. We declare no competing interests.

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References

1. Johannessen SC, Macdonald RW. 2016 Geoengineering with seagrasses: is credit due where credit is given? *Environ. Res. Lett.* **11**, 113001. (doi:10.1088/1748-9326/11/11/113001)

2. Röhr ME *et al.* 2018 Blue carbon storage capacity of temperate eelgrass (*Zostera marina*) meadows. *Glob. Biogeochem. Cycles* **32**, 1457–1475. (doi:10.1029/2018GB005941)

3. Lavery PS, Mateo MA, Serrano O, Rozaimi M. 2013 Variability in the carbon storage of seagrass habitats and its implications for global estimates of blue carbon ecosystem

service. *PLoS ONE* **8**, 12. (doi:10.1371/journal.pone.0073748)

4. Röhr ME, Boström C, Canal-Vergés P, Holmer M. 2016 Blue carbon stocks in Baltic Sea eelgrass (*Zostera marina*) meadows. *Biogeosciences* **13**, 6139–6153. (doi:10.5194/bg-13-6139-2016)
5. Dahl M, Deyanova D, Gütschow S, Asplund ME, Lyimo LD, Karamfilov V, Santos R, Björk M, Gullström M. 2016 Sediment properties as important predictors of carbon storage in *Zostera marina* meadows: a comparison of four European areas. *PLoS ONE* **11**, e0167493. (doi:10.1371/journal.pone.0167493)
6. Fourqurean JW *et al.* 2012 Seagrass ecosystems as a globally significant carbon stock. *Nat. Geosci.* **5**, 505–509. (doi:10.1038/ngeo1477)
7. Macreadie PI, Trevathan-Tackett SM, Skilbeck CG, Sanderman J, Curlevski N, Jacobsen G, Seymour JR. 2015 Losses and recovery of organic carbon from a seagrass ecosystem following disturbance. *Proc. R. Soc. B* **282**, 20151537. (doi:10.1098/rspb.2015.1537)
8. Cabaço S, Santos R, Duarte CM. 2008 The impact of sediment burial and erosion on seagrasses: a review. *Estuar. Coast. Shelf Sci.* **79**, 354–366. (doi:10.1016/j.ecss.2008.04.021)
9. Samper-Villarreal J, Mumby PJ, Saunders MI, Barry LA, Zawadzki A, Heijnis H, Morelli G, Lovelock CE. 2017 Vertical accretion and carbon burial rates in subtropical seagrass meadows increased following anthropogenic pressure from European colonisation. *Estuar. Coast. Shelf Sci.* **5**, 474. (doi:10.1016/j.ecss.2017.12.006)
10. Mazarrasa I, Marbà N, Garcia-Orellana J, Masqué P, Arias-Ortiz A, Duarte CM. 2017 Effect of environmental factors (wave exposure and depth) and anthropogenic pressure in the C sink capacity of *Posidonia oceanica* meadows. *Limnol. Oceanogr.* **62**, 1436–1450. (doi:10.1002/lno.10510)
11. Duffy JE *et al.* 2015 Biodiversity mediates top–down control in eelgrass ecosystems: a global comparative-experimental approach. *Ecol. Lett.* **18**, 696–705. (doi:10.1111/ele.12448)
12. Phillips DL, Gregg JW. 2003 Source partitioning using stable isotopes: coping with too many sources. *Oecologia* **136**, 261–269. (doi:10.1007/s00442-003-1218-3)
13. Arndt S, Jørgensen BB, LaRowe DE, Middelburg J, Pancost R, Regnier P. 2013 Quantifying the degradation of organic matter in marine sediments: a review and synthesis. *Earth Sci. Rev.* **123**, 53–86. (doi:10.1016/j.earscirev.2013.02.008)
14. Aller RC. 1994 Bioturbation and remineralization of sedimentary organic matter: effects of redox oscillation. *Chem. Geol.* **114**, 331–345. (doi:10.1016/0009-2541(94)90062-0)
15. Jensen SI, Kühl M, Glud RN, Jørgensen LB, Priemé A. 2005 Oxic microzones and radial oxygen loss from roots of *Zostera marina*. *Mar. Ecol. Prog. Ser.* **293**, 49–58. (doi:10.3354/meps293049)
16. Krause-Jensen D, Markager S, Dalsgaard T. 2012 Benthic and pelagic primary production in different nutrient regimes. *Estuar. Coasts* **35**, 527–545. (doi:10.1007/s12237-011-9443-1)
17. Jankowska E, Michel LN, Zaborska A, Wlodarska-Kowalczuk M. 2016 Sediment carbon sink in low-density temperate eelgrass meadows (Baltic Sea). *J. Geophys. Res. Biogeosci.* **121**, 2918–2934. (doi:10.1002/2016jg003424)
18. Boström C *et al.* 2014 Distribution, structure and function of Nordic eelgrass (*Zostera marina*) ecosystems: implications for coastal management and conservation. *Aquat. Conserv. Mar. Freshw. Ecosyst.* **24**, 410–434. (doi:10.1002/aqc.2424)
19. Macreadie PI, Allen K, Kelaher BP, Ralph PJ, Skilbeck CG. 2012 Paleoreconstruction of estuarine sediments reveal human-induced weakening of coastal carbon sinks. *Glob. Change Biol.* **18**, 891–901. (doi:10.1111/j.1365-2486.2011.02582.x)