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Major role of marine vegetation on the oceanic carbon cycle

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Abstract. The carbon burial in vegetated sediments, ignored in past assessments of carbon burial in the ocean, was evaluated using a bottom-up approach derived from upscaling a compilation of published individual estimates of carbon burial in vegetated habitats (seagrass meadows, salt marshes and mangrove forests) to the global level and a top-down approach derived from considerations of global sediment balance and a compilation of the organic carbon content of vegeatated sediments. Up-scaling of individual burial estimates values yielded a total carbon burial in vegetated habitats of 111 Tmol C y^{-1}. The total burial in unvegetated sediments was estimated to be 126 Tg C y^{-1}, resulting in a bottom-up estimate of total burial in the ocean of about 244 Tg C y^{-1}, two-fold higher than estimates of oceanic carbon burial that presently enter global carbon budgets. The organic carbon concentrations in vegetated marine sediments exceeds by 2 to 10-fold those in shelf/deltaic sediments. Top-down recalculation of ocean sediment budgets to account for these, previously neglected, organic-rich sediments, yields a top-down carbon burial estimate of 216 Tg C y^{-1}, with vegetated coastal habitats contributing about 50%. Even though vegetated carbon burial contributes about half of the total carbon burial in the ocean, burial represents a small fraction of the net production of these ecosystems, estimated at about 3388 Tg C y^{-1}, suggesting that bulk of the benthic net ecosystem production must support excess respiration in other compartments, such as unvegetated sediments and the coastal pelagic compartment. The total excess organic carbon available to be exported to the ocean is estimated at between 1126 to 3534 Tg C y^{-1}, the bulk of which must be respired in the open ocean. Widespread loss of vegetated coastal habitats must have reduced carbon burial in the ocean by about 30 Tg Cy^{-1}, identifying the destruction of these ecosystems as an important loss of CO_2 sink capacity in the biosphere.

1 Introduction

Oceanic carbon fluxes are believed to be dominated by microorganismal activity, as bacteria and microalgae are the dominant source of primary production and respiration in the ocean (e.g. Duarte and Cebrián, 1996; del Giorgio and Duarte, 2002). Marine ecosystems also include macrophyte-dominated communities, hereafter referred to as marine vegetation, in the coastal domain, including macroalgae, dominant in rocky shore, estuarine environments and coral reefs, and angiosperms, which are dominant in intertidal systems (mangroves in tropical regions and salt marshes in temperate ones) and seagrasses growing in sandy, and occasionally rocky sediments along the world's coasts (e.g. Alongi, 1998). Although vegetated habitats are acknowledged to be of major importance to sustain marine biodiversity (e.g. Duarte, 2001; Alongi, 2002), they are neglected from present accounts of the global ocean carbon cycle. The neglect of marine vegetation is possibly a consequence of the limited extent of marine vegetation, which cover only <2% of the ocean surface (Duarte and Cebrián, 1996). Moreover, the area covered by marine vegetation is rapidly declining, as the area covered by seagrass meadows, mangrove forests and salt marshes has declined significantly over the past decades (Valiela et al., 2001; Duarte, 2002; Alongi, 2002; Green and Short, 2003; Brevik and Homburg, 2004; Duarte et al., 2005b).

However, previous analyses of the carbon cycling in ecosystems dominated by marine vegetation suggest that these may be important, as their global respiration is about 7 to 8 Pg C y^{-1} (Middelburg et al., 2004) and, yet, they may account for an important fraction of carbon storage in the ocean

Table 1. Estimates of organic carbon burial rates in vegetated areas, derived from the geometric mean of a compilation of published reports of organic carbon burial and their relative contribution to burial in the coastal ocean and the global ocean. The estimates derived are compared to those derived from community mass balances (M.B.), estimated by correcting the estimates in Duarte and Cebrián (1996) for the revised area covered by the different communities used here.

Component		Area 10^{12} m^2	g C m^{-2} y^{-1}	Tg y^{-1}	N	Tg y^{-1} M.B.	Notes
Vegetated habitats							
	Mangroves	0.2	139.0	23.6	27	17.0	1
	Salt Marsh	0.4	151.0	60.4	96	70.0	2
	Seagrass	0.3	83.0	27.4	5	44.0	3
Total vegetated habitats				111.4		131.0	
Depositional areas							
	Estuaries	1.8	45.0	81.0	24		4
	Shelf	26.6	17.0	45.2	15		5
Total coastal burial				237.6			
	% vegetated habitats			46.9			
Deep sea burial				6.0			6
Total oceanic burial				243.6			
	% vegetated habitats			45.7			

Notes: 1. Area covered from Valiela et al. (2001), organic burial data from Chmura et al. (2003); 2. Area covered from Woodwell et al. (1973), organic burial data from Chmura et al. (2003); 3. Area covered calculated from original extent of seagrass and reported fraction relative long-term decline rates (Green and Short, 2003; Duarte et al., 2005b), organic burial data from Gacia et al., 2002; Romero et al., 1994; Mateo et al., 1997, 2005, and Barron et al., 2004; 4. Area covered from Costanza et al. (1997), organic burial data from Heip et al. (1995) and Widdows et al. (2004); 5. Area covered from Costanza et al. (1997) assuming that depositional areas cover 10% of the shelf area, organic burial data from Middelburg et al. (1997a); 6. Berner (1982).
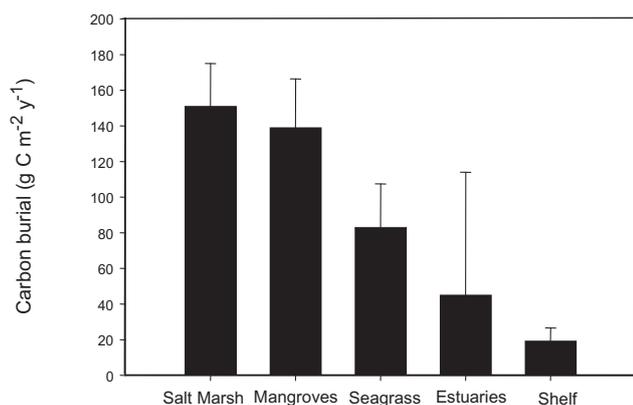
(Duarte and Cebrián, 1996; Jennerjahn and Ittekkot, 2002; Chmura et al., 2003). Further, analyses of the carbon budgets of marine vegetated benthic communities suggest that they export significant amounts of organic carbon to adjacent ecosystems and also store vast amounts of organic carbon in the sediments (Duarte and Cebrián, 1996; Jennerjahn and Ittekkot, 2002; Chmura et al., 2003; Brevik and Homburg, 2004). Moreover, their high burial rates can be sustained over millennia (Mateo et al., 1997; Brevik and Homburg, 2004). Marine vegetation turns over very slowly (Smith, 1981), as it is often dominated by long-lived organisms such as mangroves (decades, Tomlinson, 1994) and seagrasses (years to decades, Hemminga and Duarte, 2000), so that despite contributing only 10% of the primary production of the ocean (Smith, 1981; Duarte and Cebrián, 1996), marine vegetation holds a significant fraction of the autotrophic biomass therein (Smith, 1981). The view that the reduced extent of marine vegetation relative to the size of the ocean renders them irrelevant to global cycles can be, therefore, challenged (Smith, 1981).

Here we assess the role of marine vegetation in carbon fluxes in the coastal ocean and the consequences of the widespread destruction of these habitats for the marine organic carbon cycle. We first estimate carbon burial in vegetated habitats following two approaches, a bottom-up approach derived from upscaling individual estimates of car-

bon burial in vegetated habitats to the global level, and a top-down approach derived from considerations of the global sediment balance (Berner, 1982). We then construct a carbon budget for the coastal ocean, including carbon burial, respiration (from Middelburg et al., 2005), and gross primary production (from Duarte and Cebrián, 1996), and examine, using mass balance considerations, the possible organic export from vegetated habitats to the open ocean and the impact of destruction of marginal coastal habitats where marine vegetation dominates on the carbon budget of the global ocean.

2 Burial

We searched the published literature for estimates of carbon burial in vegetated habitats to derive estimates of average carbon burial of these communities. Because of the skewed nature of the resulting data sets, the geometric mean was used to characterise the central tendency of carbon burial in these communities (Table 1). Whereas the coverage of estimates of organic carbon burial is reasonable (N>25) for both mangroves and salt marshes, that for other communities is small, as only 5 estimates were available for seagrass meadows (Table 1). The data compiled identified mangroves and salt marshes as important sites for carbon burial, at rates twice as high as those for seagrass meadows (Fig. 1, Table 1). Up-scaling of individual burial estimates to the global
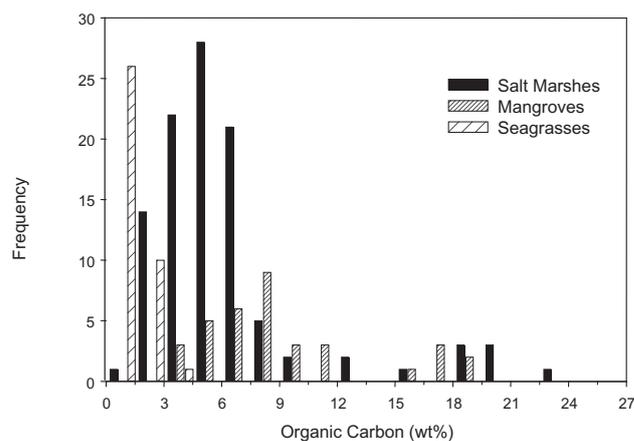
Fig. 1. Average (±SE) carbon burial rates in different coastal ecosystems. Data sources in Table 1.

Fig. 2. Frequency distribution of organic carbon content in salt marsh, mangrove and seagrass sediments. Data sources in Table 2.

scale yields a total carbon burial in vegetated habitats of 111 Tmol C y^{-1} (Table 1). This estimate is remarkably close to the estimate of carbon storage rates in vegetated habitats of 131 Tmol C y^{-1} derived in the past by up-scaling carbon budgets for marine vegetation communities compiled (Table 1, Duarte and Cebrián, 1996), therefore providing confidence on the robustness of these estimates.

The agreement between bottom-up approaches based on direct burial estimates with those derived from carbon budgets for the vegetation implies that a significant, although variable, proportion of the carbon buried should be of autochthonous origin, which is consistent with published evidence suggesting a significant contribution of autochthonous organic carbon in salt marsh (Ember et al., 1997; Middelburg et al., 1997b) mangrove (Jennerjahn and Ittekkot, 2002; Bouillon et al., 2004; Kennedy et al., 2004) and seagrass (Gacia et al., 2002; Kennedy et al., 2004; Holmer et al., 2004) sediments. Present estimates of the carbon burial in the ocean, as components of the global carbon budget (126–160 Tg y^{-1}, Berner, 1982; Hedges and Keil, 1995; IPPC, 2001), ignore vegetated coastal habitats and must, therefore, be revised upwards.

The estimate of burial in the ocean that enters present global carbon budgets is, however, derived from top-down considerations of the total sediment budget of the ocean (Berner, 1982) and cannot, therefore, be readily compared to the bottom-up estimates used above. Hence, we also estimated the contribution of unvegetated sediments in estuaries and shelf and deltaic environments. The data set on direct estimates of burial in estuarine (Heip et al., 1995; Widdows et al., 2004) and shelf sediments (Middelburg et al., 1997a) encompassed a total of 39 observations, with geometric average rates in these environments about one third of those for vegetated habitats (Fig. 1, Table 1). Up-scaling burial in these environments to the global scale is, however, not trivial as the estimates of burial in these dynamic environments are biased towards depositional basins (Middelburg et al., 1997a).

We therefore, following assessments of the extent of shelf depositional basins (de Haas et al., 2002), assumed that these basins represent only 10% of the shelf area (Table 1). The corresponding geometric estimates of burial in unvegetated estuarine and shelf sediments amounts, when scaled to this area, to 81 and 45 Tg C y^{-1}, respectively (Table 1). The total burial in unvegetated sediments (126 Tg C y^{-1}) is very similar to Berner's 130 Tg C y^{-1} estimate for deltaic-shelf sediments and somewhat below the Hedges and Keil (1995) revised estimate of burial in the coastal ocean (160 Tg C y^{-1}). The resulting bottom-up estimate of total burial in the ocean adds to 244 Tg C y^{-1} (Table 1), which is two-fold higher than estimates of oceanic carbon burial that presently enter global carbon budgets and implies, therefore, that the ocean is, because of the major – but previously neglected – contribution of vegetated habitats, a greater carbon sink than hitherto acknowledged. These calculations indicate that vegetated marine habitats, which only cover <2% of the ocean surface, contribute close to half of the carbon burial in the coastal and global, ocean at present (Table 1).

The significance and consequences of the major deviation between the Berner (1982) estimates and that derived using a bottom-up approach here for our understanding of the global carbon cycle implies that the basis for this difference must be identified. The Berner (1982) calculation is based on a global sediment input of 18 000 Tg y^{-1} to the ocean, assuming that 700 Tg is deposited in deep ocean basins and that all of the remaining materials are deposited in the coastal ocean, i.e. in deltaic-shelf environments. Based on an organic carbon content of 0.75%, he derived a coastal organic carbon burial of 130 Tg C y^{-1}. Whereas the total sediment input to the ocean is a reasonably well-constrained figure (20 000 Tg y^{-1}, Milliman and Syvitski, 1992; Hay, 1998), top-down estimates of organic carbon burial depend on where the sedimentation occurs because carbon contents differ (Berner, 1982; Hedges and Keil, 1995). Berner (1982) used an organic

Table 2. The average percent organic carbon (Corg, %) of vegetated and unvegetated sediments in the coastal ocean and the estimate of the organic carbon burial resulting from burial of the sediment load of 20 000 Tg y^{-1} (Milliman and Syvitski, 1992; Hay, 1998) entering the coastal ocean in these habitats.

	Burial Tg C y^{-1}	Corg (%)	Tg sediment	% sediment	% C-burial	Notes
Vegetated habitats						
Mangroves	23.6	8.5	278	1.4	10.9	1
Salt Marsh	60.4	5.4	1119	5.6	27.9	2
Seagrass	27.4	0.7	3914	19.6	12.7	3
Total vegetated habitats	111.4		5310	26.6	51.5	
Depositional areas	98.9	0.75	13 190	65.9	45.7	4
Total coastal burial	210.3		18 500	92.5	97.2	
Deep sea burial	6.0	0.4	1500	7.5	2.8	5
Total oceanic burial	216.3		20 000			

Notes: 1. Organic carbon contents from Chmura et al. (2003); 2. Organic carbon contents from Chmura et al. (2003); 3. Organic carbon contents estimated based on Gacia et al. (2002), Holmer et al. (2004), Kennedy et al. (2004), Duarte et al. (2005a) and unpublished data. 4. Organic carbon content of 0.75% is assumed and sediment burial is calculated by difference; 5. Organic carbon content is assumed (e.g. see Berner, 1982).

carbon content of 0.75% that is representative of the shelf and deltaic sediments, where the deposition was supposed to occur. Hedges and Keil (1995) argued that two-third of the river particulate accumulated in deltaic sediment with an organic content of 0.7% and one-third in shelf and upper slope sediment with 1.5% organic carbon and revised the burial estimate upward to 160 Tg C y^{-1}. These studies ignore the carbon-rich deposits of marine vegetated systems. Indeed, a compilation of organic carbon concentrations in vegetated marine sediments indicates that these are particularly high for mangroves and salt marshes, holding, 2 to 10-fold greater concentrations than shelf and deltaic sediment do (Fig. 2, Table 2). Consequently, the top-down estimate of burial in the ocean can be corrected, using a similar approach to that of Berner (1982). By combining the bottom-up estimates for carbon burial in vegetated sediments and deep-sea sediments with estimates of their organic carbon content, we can derive sediment accumulation in these habitats. The difference between particle delivery to the ocean and the sum of vegetated and deep-sea sedimentation can then be attributed to unvegetated coastal deposition. These calculations indicate that 26% of the sediment acumulate in vegetated systems and only about 8% in the deep-sea, the remaining 65% accumulates in estuaries, deltaic, shelf and upper slope environments. Following Berner (1982) we combined a conservative organic carbon content of 0.75% for unvegetated coastal sediments with a sediment accumulation rate of about 13 000 Tg and derived an unvegetated coastal burial rate of 99 Tg C y^{-1}, somewhat lower than the sum of estuarine and shelf carbon burial reported in Table 1 (126 Tg C y^{-1}). The total top-down carbon burial estimate obtained was then 210 Tg C y^{-1} (Table 2), reasonably close to that of 244 Tg C y^{-1} (Table 1) derived from the bottom-up approach described above, with vegetated coastal habitats contributing about 50% in both approaches (Tables 1, 2). Hence, the conclusion that organic carbon burial in the ocean exceeds the estimate of burial in the ocean that enters present global carbon budgets almost by a factor two is, as supported both by bottom-up and top-down approaches, a robust one.

A further top-down constraint on the possible C burial in shallow-water coastal ecosystems is the fact that a very high burial rate sustained over a long time span may raise the sea floor above the mean sea level. To assess whether this may constrain the estimates presented here we calculated the accretion rate implicit in our burial estimates by combining the C burial rate (Table 1) with the organic C content of the sediments (Table 2), assuming a bulk sediment density of 1 g cm^{-3}. The estimated accretion rates ranged between 1.6 mm yr^{-1} for mangrove forests to a maximum of about 12 mm yr^{-1} for seagrass meadows. These numbers are consistent with published estimates of sediment accretion rates across these habitats, with reported accretion rates for mangrove forests up to 8 mm yr^{-1} (Woodroffe, 1992) and seagrass accretion rates ranging from 0.2 to 40 mm yr^{-1} (Mateo et al., 1997; Walker and Wolkerling, 1998; Gacia et al., 2002). High sediment accretion in seagrass meadows does not pose a problem a priori, as these grow deeper than mangroves and salt marshes, and high sediment accretion in salt marsh and mangrove areas is partially compensated by subsidence (e.g. Callaway et al., 1996; Patrick and Delaune, 1990; Woodroffe, 1992).

The estimates of C burial in vegetated coastal habitats derived here should be considered, however, conservative, as deposition is only considered in angiosperm-dominated habitats. Whereas macroalgae often grow in rocky shores, where substantial sedimentation rates are unlikely, many of them can also thrive in sandy and muddy bottom where C may be buried. However, the possibility of C burial in macroalgal

Table 3. The metabolic balance of the benthic coastal communities, as represented by the respiration rates (R, average and global values from Middelburg et al., 2005), gross primary production (GPP), computed using average values from net primary production and autotrophic respiration estimates in Duarte and Cebrián (1996) and GPP estimates in Gattuso et al. (1998) for coral reefs, upscaled to the global coastal ocean using the surface areas covered by the communities reported in Table 1, and Duarte and Cebrián (1996) for macroalgae and microphytobenthos; and the net ecosystem production (NEP=GPP–R) for these ecosystems.

Component	Area 10^{12} m^2	R g C m^{-2} y^{-1}	Global R Tg y^{-1}	GPP g C m^{-2} y^{-1}	Global GPP Tg y^{-1}	NEP g C m^{-2} y^{-1}	Global NEP Tg y^{-1}
Vegetated habitats							
Mangroves	0.2	1866	373	2087	417	221	44
Salt Marsh	0.4	2010	804	3595	1438	1585	634
Seagrass	0.3	692	228	1903	628	1211	400
Macroalgae	1.4	2116	2962	3702	5183	1587	2221
Coral Reefs	0.6	1572	943	1720	1032	148	89
Total vegetated habitats			5310		8698		3388
Unvegetated sediments	23.9	83	1992	67.9	1622	−15	−370
Global benthic coastal ocean			7302		10 320		3018
% vegetated habitats			73		84.3		

beds has not been studied and, therefore, cannot be included in this assessment.

# 3 Metabolism of vegetated habitats and the organic carbon budget of the ocean

Estimates of respiration (R) in vegetated habitats have been recently compiled using a dual top-down and bottom-up approach as done here (Middelburg et al., 2005). The resulting estimate of R in vegetated habitats was 5310 Tg C y^{-1}, with a particularly high contribution by macroalgae (Table 3). The important contribution of macrophytes to the respiration in benthic vegetated habitats (Middelburg et al., 2005) is in contrast with respiration in other oceanic habitats, which is dominated by bacteria (del Giorgio and Williams, 2005). The gross primary production (GPP) rates of vegetated habitats are quite high (Duarte and Cebrián, 1996) yielding, when scaled to the global extent of these communities, a GPP of 8698 Tg C y^{-1}. These estimates yield a positive metabolic balance (NCP=GPP–R>0) for vegetated habitats estimated at about 3388 Tg C y^{-1} (Table 3), where macroalgae, seagrass beds and salt marshes are the dominant contributors to excess production. These values need to be increased by the GPP and R of benthic unvegetated and estuarine systems, which are estimated to be net heterotrophic at the global scale (Table 3), to yield a NCP for benthic coastal communities of 3018 Tg C y^{-1} (Table 3).

The excess production of the benthic compartment has two possible fates, to be stored in sediments contributing to burial therein or to be exported for use in the pelagic compartment. As the total organic carbon burial rate in the coastal ocean is about 9% of the calculated NCP figure, it follows that the bulk (>91%, as some of the buried material is of terrestrial origin), of the benthic net ecosystem production (NEP) must either be exported to the open ocean or support respiration in the pelagic compartment. The pelagic compartment of coastal ecosystems is often heterotrophic (Smith and Hollibaugh, 1983; Duarte et al., 2004; Lucea et al., 2005), and a NEP range for the pelagic coastal ocean of −2304 Tg C y^{-1} to 104 Tg C y^{-1} has been proposed (Robinson and Williams, 2005). The excess benthic NEP that must be exported to support respiration in the global ocean can be calculated as,

$$\text{Export} = \text{Benthic NEP} + \text{Terrestrial inputs} - \text{Burial} \quad (1)$$
$$+\text{Pelagic coastal NEP}$$

which provided a terrestrial input of organic carbon of 650 Tg C y^{-1} (Duarte and Cebrián, 1996), yields an organic carbon export from the coastal to the open ocean ranging between 769 to 3177 Tg C y^{-1}, with this range depending on the uncertainty about the pelagic coastal NEP (Fig. 3). The estimated coastal export of 1126 to 3534 Tg C y^{-1} is then available to be used – or buried – in the open ocean. As burial in the open ocean is estimated at a much lower figure of 6 Tg C y^{-1} (Table 1), it follows that essentially all of the organic carbon received from the coastal ocean must be respired in the open ocean. This export, which is of the same order as the inputs necessary to balance the calculated net heterotrophy of the open ocean (Duarte and Agustí, 1998), would contribute, as proposed in the past (Duarte et al., 1999), to drive the open ocean to a net heterotrophic status (Duarte and Agustí, 1998; del Giorgio and Duarte, 2002). Most past estimates of the organic export from the coastal to the open ocean are below the figure above (Liu et al., 2002; Ducklow and McCallister, 2005), likely because these estimates neglected, again, the contribution of vegetated habitats. Indeed, more encompassing accounts (del Giorgio and Duarte, 2002) cover the range of export estimates derived above.
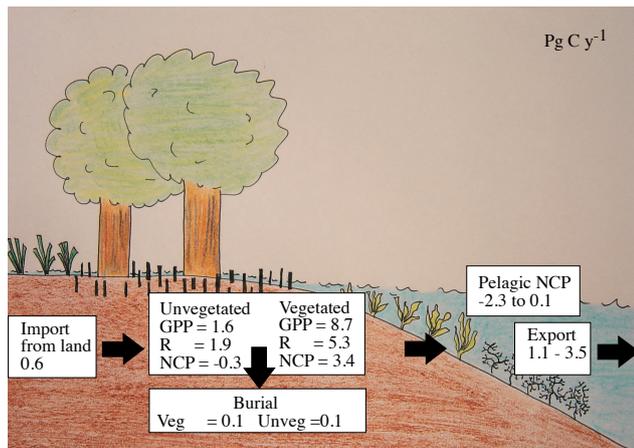
Fig. 3. Summary of the organic carbon budget (units Gt C y^{-1}) of the global coastal ocean. NCP=Net community production. GPP=Gross Primary Production. R=Respiration.

4 Destruction of marine vegetated habitats and oceanic carbon burial

The preceding analysis portrays vegetated marine habitats as critical sites for carbon burial, production and respiration as well as to subsidise the metabolism of the open ocean. Mangrove and seagrass habitats are, however, experiencing widespread destruction due to multiple causes, involving logging, land reclamation and deforestation for mangroves (Valiela et al., 2001; Alongi, 2002), eutrophication, siltation and coastline alteration for seagrasses (cf. Duarte, 2002; Short and Green, 2003; Duarte et al., 2005b) and coastal erosion, filling, dyking, and conversion to aquaculture ponds for salt marshes (Adam, 2002; Brevik and Homburg, 2004). The rates of habitat destruction for these communities are mounting, with about 35% to 50% of the world mangrove area destroyed, mostly since World War II (Valiela et al., 2001; Alongi, 2002), and an estimated loss of 18% of the documented seagrass area over the last two decades (Green and Short, 2003), which is likely to be an underestimate due to poor coverage for some areas. These losses render seagrass meadows and mangrove forests as some of the world's most threatened habitats, with multi-decadal average annual rates of decline of 2% y^{-1} for mangroves (Valiela et al., 1998) and >1% y^{-1} for seagrasses, (Duarte, 2002; Short and Green, 2003; Duarte et al., 2005b).

Whereas the calculations of the important role of these habitats in carbon burial in the ocean were based on the estimated extant area they cover (Table 1), the great rates of decline these habitat experience suggests that their role in carbon burial in the ocean should have been far larger than that calculated at present. An estimate of the historical carbon burial in the coastal zone can be calculated, using the two approaches derived above. The bottom-up calculation (Table 1), assumes rates similar to those presently observed

extended to an undisturbed area covered by mangroves and seagrass of 0.25 10^{12} m^2 and 0.5–0.6 10^{12} m^2 (Duarte and Cebrián, 1996; Green and Short, 2003), respectively. These calculations derived a carbon burial in vegetated carbon burials previous to anthropogenic disturbance of 140 Tg Cy^{-1}, or 25% higher than the present estimate. This estimate represents an underestimate, as it does not consider losses of salt-marshes (e.g. Adam, 2002; Brevik and Homburg, 2004), for which no global estimate is currently available. The top-down rationale provided above suggests that this loss would correspond to the difference in carbon content of the sediment being buried (Berner, 1982). A difference of 1% C corresponds to a loss in organic carbon burial capacity due to loss of vegetated habitat of about 30 to 50 Tg C y^{-1}, or 13 to 25% of the present burial in the global ocean. Although these losses are sizeable, they cannot be resolved through budgetary exercises such as those used here, which involve uncertainties about the global burial figures in excess of the 25% estimate.

The decline in coastal burial derived from the loss of vegetated habitats is compounded with the reduced delivery of terrestrial sediments to the ocean from increased sediment retention in reservoirs, which have been estimated to reduce global sediment delivery to the oceans by about 30% (Vörösmarty et al., 2003). Hence, the loss of benthic vegetated habitats have reduced C burial in vegetated habitats by about 25%, and the reduced sediment delivery to the ocean, formerly deposited along with organic carbon in the coastal ocean, has reduced oceanic C burial by a further 30% of the total C burial, suggesting a combined possible loss of carbon burial in the ocean of as much as 50% of the pre-disturbance rate.

5 Conclusions

The results presented confirm that vegetated coastal habitats, including seagrass meadows, mangrove forests and salt marshes are hot spots for carbon burial in the ocean. The significant of mangrove and salt marshes has been recently raised on the basis of bottom-up approaches (Jennerjahn and Ittekkot, 2002; Chmura et al., 2003), and an important role of vegetated habitats had been suggested on the basis of community carbon budgets (Duarte and Cebrián, 1996). Here we show that use of bottom-up scaling of direct burial estimates, community carbon budgets, and top-down examinations that consider, for the first time, the enhanced organic carbon concentration of vegetated coastal sediments converge to estimate organic carbon burial in the coastal ocean at 210–244 Tg C y^{-1}, almost twice as high as that presently considered in drawing the global carbon budget (IPCC, 2001). This discrepancy is due to the neglect in previous assessments of vegetated coastal habitats, which despite encompassing <2% of the ocean surface contribute close to half of the carbon burial in the coastal and global ocean at present. Hence, our

analysis identifies vegetated coastal habitats as important, but previously neglected, sites for CO_2 sequestration. However, even this upward revised estimate of organic carbon burial can not accommodate for the removal of anthropogenic carbon dioxide from the atmosphere (Berner, 1992).

Our assessment depicts, in agreement with previous assessments (e.g. Duarte and Cebrián, 1996; Gattuso et al., 1998), vegetated coastal habitats to be net autotrophic ecosystems. Despite the important size of organic carbon burial in these habitats, our results suggest that only 5% of our estimated 2661 Tg C y^{-1} excess production (NCP) of benthic coastal habitats meet a fate in burial. The bulk of the net production of vegetated coastal habitats, must be exported at a rate estimated at between 769 to 3177 Tg C y^{-1}, to partially support the high respiratory requirements of open ocean ecosystems (del Giorgio and Duarte, 2002; Arístegui et al., 2004), helping explain the tendency of unproductive oceanic ecosystems to be net heterotrophic (Duarte et al., 1998, 1999; del Giorgio et al., 2002). The uncertainty about the extent of vegetated coastal habitats is a main source of uncertainly about our estimates. This is particularly severe for submerged macrophytes, particularly seagrass meadows, where present estimates of area cover are derived from consideration of the habitat requirements of seagrass beds, rather than observations (Green and Short, 2003). Whereas the observational basis is much better for salt marshes and mangroves, which can be delineated from space, the rapid loss of these habitats also render estimates of global area covered highly unstable. Realisation of the important role of coastal vegetated habitats on the marine C cycle should provide the impetus needed to improve present estimates of the area these habitats cover and how this is changing.

The important role of vegetated coastal habitats in the ocean carbon budget is, however, eroded by the high losses experienced by these ecosystems, where between 1/3 and 1/2 of the original area covered of seagrass meadows and mangrove forests and a large, but unknown fraction of the global salt marsh cover have been lost by anthropogenic destruction of these habitat. More than 25% of the CO_2 sink capacity of these ecosystems has been lost, and their capacity to support the metabolism of open ocean ecosystems must have declined accordingly. Besides the large impact on biodiversity, these losses represent an important loss of CO_2 sink capacity. The important consequences of the destruction of marine vegetated habitats on the oceanic carbon budget adds to the dramatic consequences these losses have on local biodiversity (Adam, 2002; Alongi, 2002; Duarte, 2002) to conform an environmental crisis that requires immediate attention.

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