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CARBON AND CARBONATE METABOLISM IN COASTAL AQUATIC ECOSYSTEMS

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ABSTRACT

The coastal zone is where land, ocean, and atmosphere interact. It exhibits a wide diversity of geomorphological types and ecosystems, each one displaying great variability in terms of physical and biogeochemical forcings. Despite its relatively modest surface area, the coastal zone plays a considerable role in the biogeochemical cycles because it receives massive inputs of terrestrial organic matter and nutrients, is among the most geochemically and biologically active areas of the biosphere, and exchanges large amounts of matter and energy with the open ocean. Coastal ecosystems have therefore attracted much attention recently and are the focus of several current national and international research programs (e.g. LOICZ, ELOISE). The primary production, respiration, calcification, carbon burial and exchange with adjacent systems, including the atmosphere, are reviewed for the major coastal ecosystems (estuaries, macrophyte communities, mangroves, coral reefs, and the remaining continental shelf). All ecosystems

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examined, except estuaries, are net autotrophic. The contribution of the coastal zone to the global carbon cycle both during pristine times and at present is difficult to assess due to the limited metabolic data available as well as because of major uncertainties concerning the magnitude of processes such as respiration, exchanges at the open ocean boundary, and air-sea fluxes of biogases.

INTRODUCTION

The world coastline, which extends over about 350,000 km, displays a wide diversity of geomorphological types and ecosystems. The coastal ocean—where land, ocean and atmosphere interact—is shallow (<200 m), covering approximately 7% (26×10^6 km^2) of the surface of the global ocean. Despite its relatively modest surface area, the coastal zone plays a considerable role in the biogeochemical cycles because it (*a*) receives massive inputs of terrestrial organic matter and nutrient through run-off and groundwater discharge; (*b*) exchanges large amounts of matter and energy with the open ocean; and (*c*) constitutes one of the most geochemically and biologically active areas of the biosphere. For example, it accounts for 14–30% of the oceanic primary production, 80% of organic matter burial, 90% of sedimentary mineralization, 75–90% of the oceanic sink of suspended river load, and ca. 50% of the deposition of calcium carbonate (87, 109). Additionally, it represents 90% of the world fish catch (107). Its overall economic value has been recently estimated as 43% of the value of the world's ecosystem services and natural capital (29). The coastal ocean is also the area of greatest human impact on the marine environment since approximately 37% of the human population currently live within 100 km of the coastline (27). The anthropogenic pressure on it is increasing steadily.

Despite its potential importance, the coastal ocean has been relatively neglected until recently, probably because of its intrinsic complexity. It is the focus of several national and international on-going research programs. The Land-Ocean Interactions in the Coastal Zone (LOICZ) program was established as part of the IGBP Global Change Programme in 1993, and the European Union has launched a coastal core project (European Land-Ocean Interaction Studies, ELOISE; Ref. 22).

Several reviews on the biogeochemistry of the coastal ocean have recently been published (e.g. 87, 132, 146, 157).[1] The aim of the present paper is to review the available information using an ecosystem approach, with special emphasis on primary production, respiration, calcification, carbon burial and

[1] A recent and exhaustive book on coastal ecosystem processes (5a) has been published too late for discussion in this chapter. Readers are strongly advised to refer to this authoritative book for additional information.

exchange with adjacent systems, including the atmosphere. Whereas the metabolism of the open ocean is by far dominated by phytoplankton primary production, the coastal ocean exhibits a great diversity of primary producers, often inhabiting the same area, which makes it difficult to subdivide this region into subdomains. We first provide some definitions of metabolic terms and, after a brief review of land inputs in the coastal zone, discuss separately, and somewhat arbitrarily, estuaries, macrophyte communities, mangroves, coral reefs, and the remaining continental shelves. Finally, the contribution of costal ecosystems to the marine carbon cycle is reviewed.

DEFINITIONS

The contribution of any biological system (e.g. organism, community, or ecosystem) to the global carbon cycle relies on (*a*) the balance between organic carbon production and consumption, and (*b*) the balance between calcium carbonate precipitation and dissolution. A simple model allows prediction of the potential air-sea CO_2 flux driven by these processes (52). A system is net autotrophic (in terms of organic carbon) when production is higher than consumption and is, conversely, net heterotrophic when consumption exceeds production. Note that autotrophy does not necessarily imply an air-to-sea CO_2 flux because the direction of this flux is driven by the sign of the CO_2 pressure gradient across the air-sea interface. For example, upwellings are net autotrophic but are a source of CO_2 to the atmosphere due to the high pCO_2 of upwelled water (higher than 360 μatm, the present average atmospheric pCO_2).

It is difficult to apply these production concepts to data compiled from the literature. First, there is some confusion about which type of production is reported. Net primary production (P_n) is the balance between gross primary production (P_g) and respiration of the autotrophic components of the system (R_a). Excess production (E) or net ecosystem production (NEP) is the difference between P_g and ecosystem respiration (R), which includes both the autotrophic and heterotrophic components. Therefore $E\ (= NEP)$ is of interest for assessing the contribution of an ecosystem to net global processes. Another source of confusion is that it is not clear which type of production is measured by the ^{14}C technique (110). Last, metabolic data obtained on isolated photosynthetic organisms (P_n) are sometimes used instead of, or grouped with, ecosystem metabolic rate (NEP), which leads to overestimating NEP as the respiration rate of the heterotrophic components of the ecosystem is not taken into account.

Units of moles per m^2 and per year are used throughout this chapter. Some metabolic data expressed on a daily basis have been multiplied by 365 in order to get yearly rates; this, of course, neglects seasonal changes in the processes. The following abbreviations are used: $N =$ sample size; $p =$ probability;

Mmol = 10^6 moles; Gmol = 10^9 moles; Tmol = 10^{12} moles; Pmol = 10^{15} moles. Average data are reported as mean $\pm$ standard error of the mean (SE).

LAND INPUTS

River input constitutes the main flux of material from the continents to the ocean and can considerably influence the carbon metabolism of the coastal zone. Furthermore, both the riverine fluxes of nutrients and organic carbon have been significantly affected by human activities and have probably modified the autotrophic vs heterotrophic conditions in estuaries and locally on continental shelves.

Pristine and anthropogenic fluxes of dissolved and particulate carbon (C), nitrogen (N), and phosphorus (P) have been thoroughly investigated by Meybeck (92, 93). The global riverine flux of carbon is approximately 77 Tmol y^{-1}, among which are found 32 Tmol y^{-1} of dissolved inorganic carbon (DIC, 41%), 14 Tmol y^{-1} of particulate inorganic carbon (PIC, 18%), 17 Tmol y^{-1} of dissolved organic carbon (DOC, 22%), and 14 Tmol y^{-1} of particulate organic carbon (POC, 19%). The additional river fluxes of C due to human activity are estimated to be around 8 Tmol y^{-1} (DOC and POC; 93).

The natural flux of dissolved inorganic nitrogen is mainly due to nitrate (225 Gmol N y^{-1}), with a small contribution of ammonia (40 Gmol N y^{-1}). There is a significant contribution of dissolved and particulate organic nitrogen, estimated to be 700 and 2400 Gmol y^{-1}, respectively (93). Natural river fluxes of phosphorus are around 12 Gmol y^{-1} for the inorganic fraction, with a similar, but less well known, flux of dissolved organic phosphorus (93). The particulate flux of phosphorus is also poorly known, but is considerably higher than the dissolved flux—probably of the order of 600 Gmol y^{-1} (93). Meybeck's figures must be considered as minimal estimates because of the lack of data from rivers in developing nations, including the high standing islands in Oceania, which may have greater inputs than suggested by Meybeck (JD Milliman, personal communication).

River fluxes of N and P have been strongly affected by anthropogenic activities, leading to eutrophication in heavily disturbed areas. According to Meybeck (93), the anthropogenic riverine flux of total dissolved nitrogen and phosphorus are about 500 and 30 Gmol y^{-1}, respectively. Wollast (156) estimated the river flux of particulate nitrogen of anthropogenic origin at 500 Gmol y^{-1}. The origins of the increased nutrient fluxes are numerous and, for nitrogen, include washout of fertilizer and intensive livestock operations. Discharge of untreated or partially treated industrial and domestic waste water is responsible for the high fluxes of nutrients and organic carbon observed in heavily populated areas. The magnitude of fluxes of dissolved carbon, nitrogen, and phosphorus of anthropogenic and natural origins are similar (93). The

increased riverine inputs of these elements due to anthropogenic activities have profoundly affected estuaries and the adjacent coastal zones (see next section). In the case of large rivers, the dissolved components are directly transferred to the coastal zone, whereas some of the particulate fraction accumulates in the delta. When river water passes across estuarine systems, large changes in the fluxes and speciation of the constituents typically occur.

ESTUARIES

Estuaries are difficult to define (see 69), and there is no consensus on their global surface area. We use a tentative estimate of 1.4×10^6 km^2, derived from areas where the salinity is lower than 34 (159). From a biogeochemical point of view, an estuary can be defined as a semi-enclosed zone where river water mixes with sea water. It should be noted, however, that in the case of large rivers, the flow is sufficiently great that water mixing mostly occurs on the continental shelf rather than in an embayment, and that the material carried by rivers is directly delivered to the shelf. The ecology and geochemistry of estuarine ecosystems, including salt marshes, have been the subject of recent reviews (39, 58, 68, 154).

Estuaries are pathways for the transfer of dissolved and particulate material from the continent to the marine system through rivers. They exhibit a wide range of diversity in terms of geomorphology, geochemistry of the drainage basin, river flow, and tidal influence. These affect physical attributes such as vertical stratification, longitudinal gradients, and residence time of fresh water. Estuaries are extremely dynamic systems usually characterized by strong physico-chemical gradients, enhanced biological activity, and intense sedimentation and resuspension (69). Profound changes are observed in the speciation of organic and inorganic compounds in response to these factors, particularly in macrotidal estuaries, where the tidal regime leads to an increased residence time of fresh water in the estuarine mixing zone and to the generation of a turbidity maximum.

One of the major changes due to human activity is the increased respiration of detrital organic carbon that usually occurs in the upper part of the estuaries, often in the turbidity maximum, and can lead to anoxic conditions that affect the behavior of other elements in the water (154). The turbidity maximum in macrotidal estuaries or deltas of large rivers is also an area of intense shoaling. Due to the flocculation of colloidal material transported by rivers when the salinity increases and to the presence of large quantities of particulate organic carbon, the sediments deposited are organically rich muds characterized by intense anaerobic processes. A large fraction of the particulate load transported by rivers can accumulate in these areas and never reach the continental shelf.

The balance between autotrophy and heterotrophy has been modified by human activity, but in a way still difficult to identify because of antagonistic responses (19, 58, 67, 94, 125, 132). The increased nutrient load leads to eutrophication, enhances net ecosystem production, and shifts the system toward increased autotrophy (e.g. 66, 85). On the other hand, respiration of the organic carbon leads to increased heterotrophy. Additionally, light may become limiting for primary production in the upper part of estuaries (e.g. 63); respiration is then the dominant metabolic process, and an oxygen-depleted zone may occur, stimulating various anaerobic processes. In such areas, the partial pressure of CO_2 in surface water may reach several thousand μatm, inducing very large fluxes of CO_2 to the atmosphere (45).

As a result of light limitation and nutrient availability (28), the maximum primary production in many estuaries occurs at intermediate salinities (125). *NEP* values in the literature display a wide range of variation (+2 to −23 mol C m^{-2} y^{-1}), which may be partly due to different methods used (58). The average value indicates that estuaries are net heterotrophic with a *NEP* significantly lower than 0 (-6 ± 2 mol C m^{-2} y^{-1}; $N = 21$, t-test, $p = 0.001$) and an average P_g/R ratio of 0.8 ± 0.1 (Table 1). Heterotrophy is more pronounced in the salinity range 0 to 30, at least in macrotidal (Figure 1*A*), where large CO_2 supersaturation is always observed (66; M Frankignoulle, unpublished observations) as a result of organic matter respiration. In the Scheldt estuary (North Sea), approximately 60% of the respiratory CO_2 is released to the atmosphere (45), 26% is transferred to the sediment (94, 101), and only 14% remains in the water column. Global P_g of estuaries is estimated to be approximately 31 Tmol C y^{-1}. The *NEP* is −8 Tmol C y^{-1}, a value that is in good agreement with a previous estimate (132) of −7 Tmol C y^{-1}. The benthic contribution to

Table 1 Surface area and metabolic data for the coastal zone (this paper) and open ocean (157)[a]

System	Surface area (10^6 km^2)	P_g (mol C m^{-2} y^{-1})	P_g (Tmol C y^{-1})	*NEP* (Tmol C y^{-1})	P_g/R
Coastal ecosystems					
Estuaries	1.4	22	31	−8	0.8 ± 0.05
Macrophyte-dominated	2.0	87	174	37	1.1 ± 0.1
Coral reefs	0.6	144	86	6	1.3 ± 0.2
Salt-marshes	0.4	185	74	7	1.2 ± 0.1
Mangroves	0.2	232	46	18	1.4 ± 0.4
Remaining shelf	21.4	18	377	171	1.4 ± 0.3
Sum	26		789	231	
Open ocean and slope	334	10	3396		

[a]The sources of the surface area are given in the text. The areal gross primary production and *NEP* are the average values of data collected from the literature (see legend of Figure 1). P_g and *NEP* of macrophyte-dominated ecosystems were adjusted empirically by a factor $\times 0.5$ to take into account the bias in the data base (see text). The P_g/R ratio was estimated using a geometric regression technique (see Figure 1).

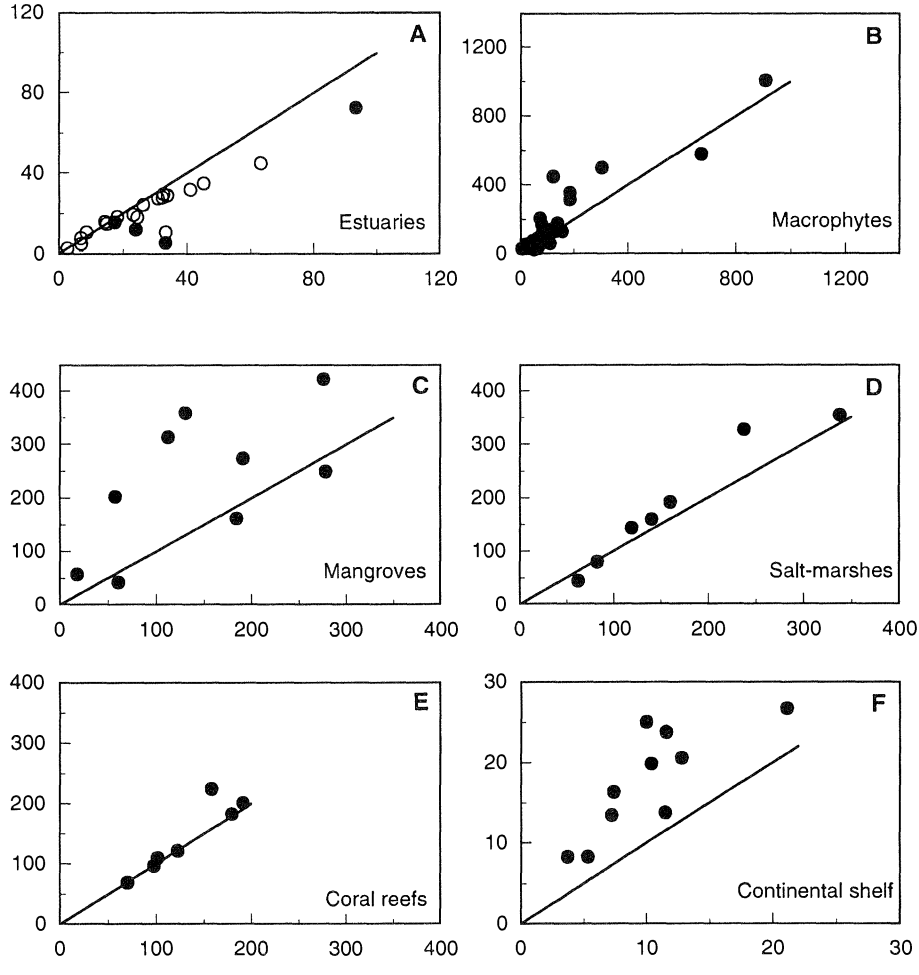

Figure 1 P_g vs R (both in mol C m^{-2} $year^{-1}$) in selected coastal ecosystems. *A*. Estuaries with macrotidal estuaries shown in dark symbols ($Y = 1.0 + 0.76X$; $r = 0.92$; $N = 21$). *B*. Macrophyte-dominated ecosystems ($Y = 19.7 + 1.13X$; $r = 0.85$; $N = 35$). *C*. Mangroves ($Y = 32.2 + 1.37X$; $r = 0.42$; $N = 9$). *D*. Salt-marshes ($Y = -11.7 + 1.22X$; $r = 0.94$; $N = 8$). *E*. Coral reefs ($Y = -24.6 + 1.28X$; $r = 0.85$; $N = 7$). F. Continental shelf ($Y = 3.9 + 1.36X$; $r = 0.648$; $N = 10$). The line shown is the 1:1 relationship; the regression equations were obtained using a geometric regression technique (114); r, correlation coefficient (all significantly different from 0 except for mangroves); N, sample size. The full data sets used, including the list of references, are available at the Annual Reviews web site (http://www.annurev.org/sup/material.htm) as well as at ftp://ccrv.obs-vlfr.fr/pub/gattuso/ares.xls.

total respiration is in the range of 25–50% (58). The ratio of benthic to planktonic respiration depends on the depth of the water, but planktonic respiration is higher than benthic respiration even in a shallow (ca. 3 m) estuary such as Tomales Bay, California (43).

Coastal eutrophication resulting from river inputs most often affects a relatively limited area in the immediate vicinity of the river mouth. The anoxic conditions in the water and/or in the sediments, associated with long residence times of the fresh water in estuaries, are extremely favorable for denitrification. A large part of the nitrate load is lost during the estuarine journey and never reaches the coastal zone. The importance of both the burial of nutrients in estuarine sediments and the denitrification process depends on the tidal prism and the depth of the estuary, two factors that affect the residence time of river water in the system (102).

Finally, carbon dioxide is not the only biogas produced in estuaries. The elevated nutrient loading enhances nitrous oxide (N_2O) production via denitrification of nitrate in the oxygen-depleted zones and nitrification of ammonia in more aerated waters (e.g. 136, 154). The photoproduction of carbon monoxide (CO) in surface water is probably stimulated by terrestrially derived dissolved organic matter. Anoxic sediments in the region of the turbidity maximum enhance hydrogen sulfide (H_2S) and methane (CH_4) production, with subsequent emission to the atmosphere. Eutrophic conditions are also very favorable for the production of gases of importance in climate regulation such as dimethyl sulfide (DMS) and carbonyl sulfide (COS). Despite their potential importance in biogas emission, very little is known about the coupling of estuaries to the atmosphere. On a global scale, estuaries may act as a significant source of these gases, and the magnitude of this source deserves further investigation.

MACROPHYTE-BASED ECOSYSTEMS

Macrophytes (seagrasses and macroalgae) do not constitute ecosystems by themselves and can be found in any shallow coastal or estuarine ecosystem. They cover approximately 2×10^6 km^2 worldwide (149), while the surface area available for micro- and macrophytobenthos has been estimated to be 6.8×10^6 km^2 (25). The areal biomass of macrophytes is about 400 times higher than that of phytoplankton, and their turnover time is much larger (ca. 1 year vs a few days). These attributes make them play a potentially significant role in the global carbon cycle (128). The macrophyte contribution to metabolism is highly variable among ecosystems, depending on their relative surface cover. For example, macrophytes account for less than 1% of net primary production in turbid and nutrient-rich estuaries, and more than 50% in non-turbid ones (58). Metabolism generally exhibits a strong seasonality in macrophyte-dominated

ecosystems. The balance of organic carbon varies widely depending on factors such as the dominant species, interspecific competition, climatic conditions (temperature and light), nutrient availability, herbivore pressure, and anthropogenic disturbance (1, 41, 42a, 42b, 58, 73, 88, 89, 103). Data are available on net primary production of several species of macrophytes (see 25), but there is comparatively little information on P_g and R at the community or ecosystem level. Epiphytes, despite their comparatively low biomass, can significantly contribute (up to 20%) to macrophyte production (e.g. 25, 58).

Studies on tropical seagrass beds have suggested that their carbon cycle is balanced: low export is balanced by allochtonous inputs of organic carbon, and most biomass is either stored or remineralized within the system (41, 42a). Some seagrass communities are nutrient limited (1), whereas others are not (42b), demonstrating the variability of nutrients status depending on species and sediment types. Our compilation of data (Figure 1*B*) suggests that macrophyte-dominated ecosystems are net autotrophic with a *NEP* of 37 ± 13 mol C m^{-2} y^{-1} ($N = 35$), a value that is significantly different from 0 ($p = 0.008$). An earlier estimate was 42 mol C m^{-2} $year^{-1}$ (128). The average P_g/R ratio is 1.1 ± 0.1 (Table 1).

The fate of P_n depends on the macrophyte ecosystem considered. P_n can be grazed by herbivores, exported outside the system, buried within the sediment, or enter the detrital pathway. Duarte & Cebrián (37) have compiled data from the literature on these pathways for several marine primary producers, including macroalgae, and seagrasses. Their major conclusions are that (*a*) decomposition within the system is an important process for each macrophyte system (>40% of P_n); (*b*) herbivore pressure is significant for macroalgae only (>30%); (*c*) export is significant (24–43%); and (*d*) storage within the sediment is negligible for macroalgal communities, but not for seagrass (>15%). These trends are quite variable from species to species; for example, 80% of the production of four Mediterranean seagrasses are consumed by detritivores (23).

Buried material within the sediment is estimated to be four times more abundant in higher plant than in algal communities. Marine angiosperm communities, which account for 4% of the oceanic net primary production, could store up to 30% of the total oceanic buried carbon (37). Moreover, seagrasses contain more carbon than N and P compared to pelagic communities: Their C:N:P ratios range from 204:4:1 to 3550:61:1 (126), with an average of 474:24:1 (36).

Posidonia oceanica is characterized by a large difference between above-ground (leaves) and below-ground (*matte* = roots and rhizomes) parts: the turnover of leaves is about 1 y compared to *matte* turnover on the order of a century (121). The latter behaves as a sink for biogenic material (120, 121), which has been estimated at 26% of the produced carbon (90). Large differences have, however, been observed from site to site, suggesting that accretion rate is

controlled by local factors (91). Light also controls the transfer of C from shoots to roots in the eelgrass *Zostera marina*, underlining the importance of light in light-limited areas (162).

The global gross primary production and *NEP* of macrophyte-dominated ecosystems estimated from our compilation of the literature are 348 and 74 Tmol C y^{-1}. These figures are likely overestimates because (*a*) more data are available for the more productive tropical than for the less productive temperate ecosystems, and (*b*) more data were obtained in very shallow areas than in deeper, light-limited areas. An empirical adjusting factor of 0.5 can be tentatively and arbitrarily used to account for these biases; the resulting estimate for P_g and *NEP* are 174 and 37 Tmol C y^{-1}, respectively (Table). Previous estimates of *NEP* range from at least 83 (128, 140) to 254 Tmol C y^{-1} (25, 33). Macrophyte-dominated ecosystems appear to be net C sinks but Smith's (128) conclusion of 1981 that their quantitative significance in the global carbon budget was poorly known still stands today.

There is major concern about the survival of seagrasses worldwide due to anthropogenic disturbances. While large, presumably natural, changes in seagrass distribution have occurred (113), human activity severely disturbs seagrass communities in several ways. The eutrophication of coastal areas results in a higher pelagic activity, with subsequent light limitation to benthic communities that induces a decrease in primary production (14), or even seagrass mortality (103). In Chesapeake Bay, it has been suggested that the long-term survival of *Zostera marina* depends on water turbidity rather than on changes in the nutrient concentration or salinity (98). Brown tides, induced by coastal eutrophication, are major causes of seagrass decline (104, 141). However, primary production depends more on temperature than on light availability in some seagrasses species such as *Thalassia testudinum* and *Cymodocea nodosa* (80, 88). A strong correlation has been observed between the standing stock of *Zostera marina* in a Netherlands estuary and the concentration of dissolved silicon that may decrease due to coastal eutrophication (59). Large tidal ranges combined with stresses are responsible for the decline of *Z. marina* in Long Island Sound (73). Worldwide, the mortality of seagrasses is higher than growth rate (89).

MANGROVES

Mangroves are intertidal forests growing above mean sea level, distributed on sheltered shores of the tropics and subtropics (31°N to 39°S); they cover 0.18×10^6 km^2 (138). Mangrove ecosystem function has been the subject of several reviews (3, 4, 56, 86, 115, 144). The major primary producers are mangrove trees, but seedlings, macroalgae, periphyton, and phytoplankton also contribute. The respective contribution of these producers to total mangrove

primary production varies with their relative surface cover, delivery of nutrients, and turbidity.

Net assimilation of leaves and above-ground P_n of mangrove trees have been estimated using indirect (allometric) methods, but P_n of whole trees is poorly known because there are no reliable estimates of the respiration rate of the stem and roots (including the above-ground portion known as prop roots) due to the unknown contribution to gas exchange by non-photosynthetic components (26).

Community metabolism of mangrove trees displays considerable variation at both the local and regional scales, primarily as a response to environmental forcings (tide, climate, and seawater composition); forest type is of secondary importance (16). The net primary production of mangrove trees derived from indirect measurements ranges from 12 to 142 mol C m^{-2} y^{-1}(mean = 58 ± 7; N = 22). The only measurement of root production is an indirect estimate of about 9 mol C m^{-2} y^{-1}, i.e. ca. 10% of the above-ground P_n of that site (77). Twilley et al (144) compiled data on wood production and provided a global estimate of 13.3 Tmol C y^{-1}.

Most leaf production enters the detrital pathway as litter fall (119). Leaves and, to a lesser extent, twigs, branches, and bark are shed as litter throughout the year. Reproductive parts are shed seasonally. Litterfall, which is negatively correlated with latitude, ranges from 5 to 70 mol C m^{-2} y^{-1} (mean = 32; Ref. 124).

Submerged primary production is often limited by high turbidity and changes in salinity. Water column metabolism is largely heterotrophic (e.g. 57, 106, 116). Despite its generally low quantitative importance, phytoplankton production may play an important role in sustaining secondary production because of the poor nutritional quality of mangrove detrital material (117). Macrophytes are generally absent from mangrove ecosystems, but seagrass beds can thrive in areas adjacent to mangrove stands and significantly contribute to total primary production of lagoons (31). Prop root periphyton can be relatively important when shading is moderate (P_n = 12–34 mol C m^{-2} y^{-1}). Benthic microalgal production is generally very low or undetectable (e.g. 5) because of: (*a*) light limitation resulting from shading by the mangrove canopy (76), (*b*) inhibition by sedimentary organic compounds such as tannins (see 3), and (*c*) nutrient limitation (76). P_g of benthic microalgae ranges from 0 to 26 mol C m^{-2} y^{-1}(mean = 6 ± 2; N = 28).

Sediment respiration is different in submerged and emergent conditions, and data obtained with the widely used O_2 technique are doubtful because anaerobic processes are of major importance in mangrove sediments (3). There is, however, little doubt that the sediment is largely net heterotrophic (average P_g/R = 0.6; P_n = −3 ± 1.5 mol C m^{-2} y^{-2}; N = 31).

The major source of C for benthic heterotrophs is litter fall, followed by deposited phytoplankton and benthic micro- and macrophytes. The retention

and processing of litter within the mangrove system is much greater than initially thought due to consumption and hiding by crabs (116). Mangrove leaf litter supports a very high benthic bacterial productivity (2, 15, 100, 139). It is now recognized, despite methodological uncertainties (2), that carbon flow through microbial pathways probably accounts for a large proportion of total C flow in mangrove ecosystems. Densities of micro-, meio-, and macrofauna are generally very low and are not correlated with bacterial production (3). The so-called 'carbon sink hypothesis' (3, 4) satisfactorily addresses this discrepancy by suggesting that only a small proportion of the large bacterial biomass is consumed in the sediment and that the remaining bacterial carbon is recycled very efficiently though natural mortality and carbon turnover within the sedimentary microbial food web. There are very few estimates of total community metabolism of mangrove systems (Figure 1*C*). Most systems investigated are net autotrophs as shown by a *NEP* significantly different from 0 (89 ± 28 mol C m^{-2} y^{-1}; $N = 12$; $p = 0.008$), despite large variation of the P_g/R ratio (1.4 ± 0.4; $N = 9$; Table 1).

The net organic matter produced can be accumulated or exported to adjacent systems. The content of organic carbon in mangrove sediment varies widely depending on the type of forest and the geomorphology of the site (e.g. 0.21–18 wt%; Ref. 96a). The rate of sedimentation is 0.3–2.4 mm y^{-1}, and the average rate of C accumulation is 23 mol C m^{-2} y^{-1} (144). Burial leads to the accumulation of peat deposits containing up to 17 mmol C g $sed.^{-1}$ (145). The total carbon sequestered in mangrove peat is about 1.7 Tmol C y^{-1} (144). The quality and quantity of material exported from mangroves depend on forest type (riverine, fringe, or basin) and productivity, as well as on physical constraints (strength and frequency of tidal inundation, river flow, wind speed and direction) and biological forcings (e.g. consumption of litterfall by macrodetritivores). In open habitats subjected to tidal flushing (riverine mangroves), a large proportion of leaf litter is exported as debris to the adjacent systems (bays) where it is decomposed (ca. 30% in Pacific mangroves; Ref. 118). Inland habitats (basin forests) are comparatively less subject to tidal flushing, export is very low (e.g. <0.3%; Ref. 81), and decomposition primarily occurs within the mangrove. As a result, the material exported comprises little particulate matter but a greater proportion of dissolved organic compounds (e.g. 143). Consumption and hiding of detritus by macrodetritivores can greatly diminish (by up to 30%) the amount of litter available for export.

Physical forcing, and its effect on export, has been relatively well studied. Outwelling is favored by tidal flow, rates of which are higher during ebb tide than flood tide (152), but lateral trapping in forested tidal rivers (152) and high-salinity plugs (150) can limit export. Export of DOC can change seasonally

with tidal inundation and rainfall. DOC is clearly the dominant form of total exported C in two basin forests in Florida (ca. 70%; 3 and 4 mol C m^{-2} y^{-1}; Ref. 143). To our knowledge, the contribution of land-derived DOC and in situ production to total DOC export has not been estimated, but a small net import of DOC (<1% of P_n) was measured in a tidally dominated (i.e. without terrestrial runoff or groundwater input) creek at Hinchinbrook Island, Australia (18). It is therefore possible that a large proportion of DOC export may actually originate with freshwater inputs (116), although there is also evidence of export in a non-estuarine mangrove forest (99). Export of DOC via groundwater seepage has received very little attention, although it represents 20% of the TOC exported from a Florida forest (143). Mangroves generally act as exporters of organic C, although some forests are net importers due to a limited inundation regime (82). Global export has been estimated at 4.2 Tmol C y^{-1} (144). Exported C can have a significant influence on nearshore benthic processes (6), especially where hydrodynamic features inhibit the mixing of estuarine and offshore waters. Its influence appears to be limited offshore (5–15 km) due to its dispersion and its refractory nature (116).

No data are available for air-water CO_2 fluxes in mangrove areas, and there are only limited data on seawater pCO_2, which seems to remain higher than atmospheric pCO_2 during most of a diurnal cycle (at ca. 1114 μatm) in two mangrove areas in India (53). Efflux of methane from mangrove sediment appears to be very small (<0.1 mmol m^{-2} y^{-1}; Ref. 95), but significant fluxes have been measured when pore water salinity is <1 (9). Mangrove forests are net autotrophic, with a global *NEP* of 18 Tmol C y^{-1} (Table 1). Marshes, another angiosperm-based ecosystem, bear some similarity to mangrove forests, but are not fully discussed here. The surface area of these temperate ecosystems is twice that of mangroves (0.4 vs 0.2 $\times$ 10^6 km^2), but marshes make a smaller contribution to the global carbon cycle (*NEP* = 7 vs 18 Tmol C y^{-1}) because they are less net autotrophic (P_g/R ratio: 1.2 vs 1.4; Figure 1*D* and Table 1). *NEP* data based on burial rates can be greatly overestimated in some marsh communities because import and storage of allochthonous carbon is not always accounted for (96b).

Mangroves are carbon sinks but are being increasingly cleared by humans for activities such as wood production, farming, mining, peat extraction, and other forms of land exploitation (56). It is estimated that 50% of mangrove ecosystems have been transformed or destroyed by human activities (160). The loss of mangrove forest not only diminishes fixation of atmospheric CO_2 and C burial, but also results in the oxidation and release to the atmosphere of the organic C stored in sediments. Approximately 39.3 Mmol C are released per ha of mangrove swamp cleared and excavated, and 31.3 Mmol C are released per 1000 t of dry peat combusted (32).

CORAL REEFS

Coral reefs are carbonate structures located at or near sea level, dominated by scleractinian corals and algae, that display high rates of organic carbon metabolism and calcification. They are mostly distributed in the tropics, although they can also reach higher latitudes (32.5°N; 31.5°S), and they cover approximately 0.6×10^6 km^2 (71, 127). Information on various aspects of reef ecology and metabolism can be found in recent reviews (12, 38, 137).

Most community metabolism data were obtained on reef flat communities, which are technically suited for measurement because they are relatively shallow, protected from the swells and subject, in many cases, to a unidirectional flow, which allows the use of flow respirometry techniques. Consequently, despite the numerous community metabolism data available, the database is biased, and there is comparatively little information available for reef slopes, lagoons, and complete reef systems. The contribution of reef slopes to reef metabolism cannot be ignored in principle, since slopes are generally the most actively growing part of the system. However, they represent a small contribution to the surface area of reef systems (15% in the central Kaneohe Bay sector; Ref. 135), and it is likely that a relatively large proportion of their communities are light-limited.

Reef metabolism is dominated by benthic processes. Phytoplankton community production is very minor, often dominated by picoplankton, and ranges from 0.3 to 22 mol C m^{-2} y^{-1} in atoll lagoons (reviewed in 24). The highest values were in the few sites with elevated nutrient concentrations.

Coral/algal reef flats display a wide range of P_g (79–584 mol C m^{-2} y^{-1}), R (76–538 mol C m^{-2} y^{-1}), and G (5–126 mol $CaCO_3$ m^{-2} y^{-1}). This variability is owing to the absolute and relative surface area covered by the major communities (e.g. corals, macrophytes, and sediments) as well as to seasonal and environmental conditions (see 84). Modal rates of metabolic performances have nevertheless been proposed (e.g. 70, 129). Such standards can be applied only to reefs having similar structure and zonation, and have little predictive value (111). The average P_g/R ratio, estimated using a geometric regression technique, is $1.07 \pm 0.1 (N = 43)$, perhaps indicating a slight net autotrophy.

Algal-dominated reef communities generally display higher rates of organic C metabolism ($P_g = 30-1369$ and $R = 6-910$ mol C m^{-2} y^{-1}) and lower rates of net calcification ($G = -0.4$ to 40 mol $CaCO_3$ m^{-2} y^{-1}) than coral/algal reef flats. Sediments represent the largest physiographic zone of many reef ecosystems (e.g. 95% of the surface area of the SW Caledonian reef complex; J Clavier, personal communication) but have received comparatively less attention than coral/algal reef flats, probably because carbon and carbonate fluxes in reef sediments are of lower magnitude ($P_g = 8-82$ and $R = 1-73$ mol C m^{-2} y^{-1}; $G = -1$ to 12 mol $CaCO_3$ m^{-2} y^{-1}). Sedimentary

areas contribute 3–30% of the community excess production of a Pacific barrier reef flat (18).

There are only nine data sets for complete reef systems, some of which do not provide both organic and inorganic carbon metabolism. P_g and R are well correlated (Figure 1*E*). The estimated P_g/R ratio (1.28 ± 0.2; Table 1) suggests a net autotrophy, although it is not statistically significant. It is, moreover, dominated by a single data set (75), which casts some doubt on that conclusion. Additionally, P_g and R are measured separately, and each has significant error terms, which are cumulative when calculating the P_g/R ratio or *NEP*. The approach of ecosystem stoichiometry (e.g. 130) enables estimation of *NEP* directly by upscaling changes in the concentration of dissolved inorganic phosphorus to *NEP* using the ecosystem C:N:P ratio. The overall average *NEP* obtained with both approaches is slightly higher than the previous estimate of Crossland et al (10 ± 7 vs 3 mol C m^{-2} y^{-1}; Ref. 30) but is not significantly different from 0 ($p = 0.21$, $N = 9$). It can therefore be concluded that the organic C metabolism of complete reef systems is essentially balanced. The average net calcification rate is 10 ± 3 mol $CaCO_3$ m^{-2} y^{-1} ($N = 7$).

Several sources of nutrients sustain reef primary production, but the contribution of each is largely site-dependent and generally poorly known. *NEP* of reef ecosystems is not significantly different from that of tropical oligotrophic oceans (30). It seems unlikely that reef productivity is sustained by the same nutrient source as the surrounding ocean (advective inputs from below) due to physical limitation, although active upwelling along the slope (e.g. 151) and internal tidal bores (83) can sometimes provide a significant nutrient supply. Smith (129) offered two alternative explanations. First, the C:N:P ratio of reef benthic plants (550:30:1; Ref. 7) is much higher than the typical Redfield ratio (106:16:1). Therefore, the production of organic carbon is much more efficient in reef systems per unit of nitrogen and phosphorus. Second, oceanic water impinging reefs is typically depleted in nitrogen relative to phosphorus. The well-established capacity of several reef organisms and physiographic zones to fix nitrogen enables reef communities to overcome nitrogen limitation. The convection resulting from upward geothermal heat flow drives circulation of nutrient-rich deep oceanic water within the reef matrix (endo-upwelling; Ref. 122). The magnitude of this nutrient source remains unknown, but it is probably relatively small (79) and not required to sustain excess primary production on reefs (142). Last, phytoplankton and planktonic microbial communities advected from the ocean are a significant source of nutrients; their retention rates are virtually identical to the net excess primary production of a Pacific reef (2.7 vs 3 mol C m^{-2} y^{-1}; Ref. 8).

The net organic and inorganic carbon production can be accumulated as biomass or reef structure, buried in sediments, or exported to adjacent ecosystems. The importance of these alternative fates is poorly known, but it is

somewhat different for organic and inorganic carbon. The rate of $CaCO_3$ accumulation is limited by sea level on reef flats (ca. 1 mm y^{-1}; see 135) but not in lagoons. A budgetary approach (135) suggests that 65% of total carbonate production of an hypothetical atoll is stored in the lagoon, 25% is exported, and about 10% is accumulated in the fore reef and reef flat areas. The rate of $CaCO_3$ export increases sharply as lagoon area decreases. In contrast, there is little accumulation of organic carbon in reef sediments (ca. 15% of E), which contains typically less than 0.7 weight % C (reviewed in 137), and in biomass (ca. 2% of E; 55). Approximately 10% of E is available for human harvest, a potential not realized at present, but most of the very little net excess organic carbon produced appears to be exported as particulate or dissolved organic carbon or in the form of migrating organisms (50–75% of E; 30, 135).

Air-sea CO_2 fluxes in reef ecosystems and communities can be investigated using either direct measurements or a budgeting approach based on community metabolism data (52). The few direct measurements indicate that the sites studied were sources of CO_2 to the atmosphere at the time of measurement (46, 51). The same conclusion was reached using indirect estimates (50, 52, 131, 148). Data on organic C burial in reef sediments support such conclusion on longer time scales (21). A few recent reports suggest, however, that some fringing reefs are sinks for atmospheric CO_2 (62, 74, 75, 161), and localized results have been extended to a global scale (64). Although the interpretation and generalization of some of these data were inappropriate (21, 48), most studies suggesting that reefs may be sinks of CO_2 were carried out on fringing reefs, which are more likely subject to anthropogenic stresses than are other reef systems. It is well established that such disturbances shift reef communities from a coral-dominated to an algal-dominated state (e.g. 35, 61). The resulting changes in community metabolism (increased primary production and/or decreased calcification) can turn the systems from a CO_2 source into a CO_2 sink (49).

The global production of reef carbonate (6 Tmol $CaCO_3$ y^{-1}) represents, respectively, 26% and 11% of the coastal and total marine $CaCO_3$ precipitation estimated by Milliman (97). Crossland et al (30) have estimated the global significance of reef metabolism to oceanic processes. Gross primary production is 86 Tmol C y^{-1}, a value higher than the previous estimate of 58 Tmol C y^{-1} (30) due to the recent addition of metabolic data collected in algal-dominated fringing reefs. The *NEP* is probably better constrained than P_g as there are more data because of the inclusion of some direct determinations. Our estimate of *NEP* is slightly higher than the previous estimates of Crossland et al (6 vs 1.7 Tmol C y^{-1}; Ref. 30) for reasons outlined above. As pointed out by Ware et al (148) and Smith (131), coral reefs have a minor role in the present global carbon cycle, and their release of CO_2 is 0.4–1.4% of the current rate of anthropogenic CO_2 production. According to the so-called coral reef hypothesis, reefs may

have played a significant role in the change of atmospheric pCO_2 that occurred during the last glacial-interglacial cycle (10, 20, 105).

CONTINENTAL SHELF

The continental shelf comprises the area between the continents and the open ocean. It is limited by the ocean margin, which corresponds to the abrupt bathymetric change that occurs between the shelf and the slope, at an average depth of 130 m. The world coastline is about 350,000 km long; the shelf has a mean width of 70 km. The total surface area of the coastal zone represents 26×10^6 km^2 or 7% of the total surface area of the ocean (360×10^6 km^2). Here we consider the main aspects of the carbon cycle occurring on the continental shelf, with the exception of the ecosystems discussed in the previous sections. Several recent reviews (87, 97, 132, 146, 157) provide detailed information on the carbon and carbonate cycling of continental shelves. There are distinct differences in physical, chemical, and biological properties of the neritic and oceanic provinces, leading to marked gradients that generate fluxes at the ocean margins. Because of the diversity of processes at the margins and the large variability of coastal systems, the exchanges of energy and of dissolved or particulate matter between the shelf and the open ocean remain poorly understood (87). The circulation and mixing of water are especially complicated by the steep bathymetric change introduced by the continental slope and rise (62). As a consequence, the exchange of organic matter and nutrients between the coastal zone and the open ocean is poorly known. Attempts are being made, in the framework of LOICZ, to establish mass balances of dissolved nutrients using a limited amount of field data for a variety of shelf environments (54). The difference between the input and output fluxes of phosphorus is scaled to carbon and is assumed to represent the *NEP* of the system considered. One of the critical data required in these calculations is the mixing rate of water masses at the open ocean boundary. It is estimated from the mass balance of salt, and usually assumes the system is at steady state, which may be a crude approximation on an annual basis. The development and improvement of models may soon provide a better evaluation of the role of the coastal zone on a global basis. We cite in this section the studies for which the fluxes of carbon linked to various elemental processes have been estimated for sufficiently long periods of time.

Unfortunately, in only a few studies have P_g and the total (benthic and pelagic) respiration of coastal waters been investigated simultaneously. The average areal P_g is 18 ± 2 mol C m^{-2} y^{-1}, and the corresponding global gross primary production is 377 Tmol C y^{-1}.

The relative importance of recycled production, resulting from the regeneration of nutrients by the bacterial degradation of dead biomass, and of new

production sustained by nutrients from an external source, is different on the continental shelf and in the open ocean. New production represents between 5% and 15% of P_g in the oligotrophic central gyres of the open ocean (40), and its contribution is close to 50% on the shelves if the remineralization of the nutrients in the sediments is taken into account (72, 157). In the open ocean, new production is essentially due to upwelling and vertical mixing of deep, nutrient-rich water with surface water. The source and fluxes of nutrients required to sustain the high productivity of the coastal zone is still controversial. The origin of nutrients is much more complex than in the open ocean and involves fluxes at the margins of deep ocean water, in addition to riverine and atmospheric inputs. Furthermore, nutrients recycled in the sediments can be rapidly transferred to the overlying waters by diffusion.

Most attention has been devoted to the fluxes of nitrogen, which is often the limiting nutrient. The occurrence of two species, ammonium and nitrate, also enables one to distinguish between new and recycled production. The main source of nitrogen is the deep ocean reservoir, which is transferred to the shelf by upwelling and vertical mixing resulting from the shelf break (60, 147, 156). This flux represents about half the nitrogen required to sustain new production in the North Atlantic, the river input accounting for the other half (47). Atmospheric deposition (8%) and nitrogen fixation (1%) are negligible. On a global basis, Wollast (157) estimated that the contribution of the open ocean represents 80% of the nitrogen flux required to sustain new production of the continental shelf, an evaluation close to an earlier estimate (147). Riverine input of nitrogen, although heavily enhanced by anthropogenic activities, accounts for less than 15%, and atmospheric deposition and nitrogen fixation constitute about 5% of the total required N.

The behavior and fate of organic matter produced in the water column are also very different in the coastal zone and open ocean. First, the number of trophic levels decreases markedly with increasing primary production. As many as six trophic levels can be identified in oligotrophic waters; there are as few as three in upwelling areas (78). In addition, coastal phytoplankton is typically dominated by large cells, whereas micro- and picophytoplankton dominate in the open ocean (78). Fecal pellets produced by organisms grazing small phytoplankton in the open ocean are small and are not exported from the photic zone efficiently as a result of low settling velocities (108). Due to the large size of fecal pellets (157) and shallow depth of the coastal zone, a large fraction of primary production and detrital matter imported by the rivers may be deposited and stimulate biological activity in the sediments. Figure 1*E* compares total respiration (pelagic plus benthic) to gross primary production in various shelf areas. Approximately 30% of the production is respired in the water column, and an equivalent amount is mineralized in the sediments.

Total respiration is therefore 10 ± 2 mol C m^{-2} y^{-1} or 214 Tmol C y^{-1} for the global coastal zone, which would make the continental shelf net autotrophic with a P_g/R ratio of 1.4 ± 0.3 (Table 1) and a *NEP* of 171 Tmol C y^{-1} that must be exported (157). These observations are in good agreement with the high values of new production found for the coastal area (40, 72). Although coastal sediments accumulate about 90% of detrital organic carbon on a global basis, this represents only 3–4% of shelf production. The remaining 36% of total production must therefore be exported to the open ocean, re-exporting simultaneously particulate organic nutrients, which compensate for the transfer of dissolved nutrients from the ocean across the shelf (157). An alternative fate may exist for nitrogen if denitrification, which occurs mainly in shelf sediments, is significant. This hypothesis has been proposed for the North-Atlantic (102). Note that such denitrification must be balanced by an equivalent flux of nitrogen fixation in the open ocean to maintain a steady-state condition in the marine system. It must be emphasized that temperate shelf ecosystems can be net heterotrophic in winter and net autotrophic in summer, when high rates of photosynthesis occur (146).

Eutrophication resulting from the discharge of estuarine nutrient-rich water to the coastal sea can induce a wide range of ecological and societal consequences. For example, a correlation between primary production and the supply of inorganic nitrogen from the Mississippi River has been observed in the Gulf of Mexico (85). An increasingly large part of the Gulf becomes hypoxic or anoxic in summer, with considerable potential effect on catches in this leading US fishery area. In the southern Bight of the North Sea, which is under the influence of several macro-tidal and polluted estuaries (Rhine, Scheldt, and Thames), pCO_2 varies from 100 to 800 μatm depending on river flow, water temperature, and light availability (44).

SIGNIFICANCE OF COASTAL ECOSYSTEMS IN THE GLOBAL OCEANIC CARBON CYCLE

Metabolic data from coastal ecosystems are summarized in Table 1. The P_g/R ratios vary considerably but are, in most cases, not statistically different from 1. All coastal ecosystems are net autotrophs ($P_g/R > 1$; $NEP > 0$) except estuaries, which are net heterotrophs exhibiting a negative net ecosystem production (-8 Tmol C y^{-1}). These data can be integrated to provide an independent estimate of coastal metabolism for comparison with estimates obtained by other approaches, a method that has several limitations. The sites for which metabolic data are available are scarce for some ecosystems (e.g. $N = 7$ for coral reefs) and may not adequately represent the range of metabolic parameters. Average areal productions are not weighted averages, so large error can result when

they are scaled up to derive global production estimates (see the section on macrophyte-dominated ecosystems). Additionally, most *NEP* data are estimated as the difference between P_g and R, each of which has an associated error. If, for example, these errors are 25% and are independent, P_g and R must differ by more than 35% for the *NEP* to be statistically different from 0 (130). Nevertheless, our estimate of P_g (789 Tmol C y^{-1}; i.e. 23% of the global marine gross primary production (see Table 1), is of the same order of magnitude as the previous estimate of 500 Tmol C y^{-1} (132, 157). The latter estimate (e.g. 157) did not specifically take into account systems such as macrophyte-dominated ecosystems and mangroves, which might partly explain the difference.

Although there is a consensus on the magnitude of P_g, there are differences in the estimates of the global coastal *NEP*. The ecosystem approach provides an estimate of 231 Tmol C y^{-1}, a value in good agreement with that provided by Wollast (200 Tmol C y^{-1}; 157) but much higher than the −7 Tmol C y^{-1} proposed by Smith & Hollibaugh (132) or the 12 Tmol C y^{-1} given by Rabouille (112). Smith & Hollibaugh (132) used a linear relationship between *NEP* and P_g based on 22 nearshore and estuarine sites, as well as the average P_g of estuaries and the remaining continental shelves, to predict the *NEP* of both systems. They concluded that estuaries are net heterotrophic ($NEP = -7$ Tmol C y^{-1}), that the remaining coastal ocean has a balanced organic carbon metabolism ($NEP \approx 0$), and that the coastal ocean is thus net heterotrophic ($NEP = -7$ Tmol C y^{-1}). They therefore estimated R indirectly at 507 Tmol C y^{-1}. Most values of *NEP* used in the linear regression were obtained as the difference between separate estimates of P_g and R, a procedure that induces great uncertainty in *NEP*. Also, most data used to derive the predictive equation were from nearshore sites, the outer shelf areas being poorly represented. On the other hand, Wollast's estimate of R (and *NEP*) is based on the observed average remineralization rate of P_g (60%; 157) of 500 Tmol C y^{-1}, so R and *NEP* are respectively estimated to be 300 and 200 Tmol C y^{-1}. This approach is also limited by the average remineralization rate being calculated from a small data set ($N = 10$) exclusively based on temperate and boreal shelves of the northern hemisphere. The continental shelf proper (excluding specific ecosystems) is the major contributor to *NEP* of the coastal zone (75%) followed by macrophyte-dominated ecosystems (16%), mangroves (7%), marshes (3%), and coral reefs (2.6%). Respiratory processes are poorly known, not only on the continental shelves but also in the open ocean (34).

The coastal ocean contributes more than 40% of marine calcium carbonate production (23 vs 53 Tmol $CaCO_3$ y^{-1}; 97). The highest deposition occurs in coral reef habitats (9 Tmol y^{-1}, according to Ref. 97, and 6 Tmol y^{-1} according to our own estimate), followed by banks and embayments (4 Tmol y^{-1}), carbonate shelves (6 Tmol y^{-1}), and non-carbonate shelves (4 Tmol y^{-1}). However,

Milliman (97) has suggested that a significant fraction (4 Tmol y^{-1}) of the calcium carbonate produced on the shelf is exported and deposited on the continental slope and rise. This was confirmed by Sabine & Mackenzie (123), who observed abundant carbonate skeleton debris, characteristic of shallow water organisms, in traps deployed along the Hawaiian slope.

The delivery of carbon to the coastal ocean has been enhanced by human activities and is presently ca. 85 Tmol C y^{-1} (93). In the marine system, the riverine DIC is believed to be partitioned equally between deposition of carbonate minerals and CO_2 evasion to the atmosphere. The organic carbon delivered is either oxidized to CO_2, accumulated in coastal sediment, or exported to the deep open ocean. The importance of these various fates is poorly known and is one of the major source of uncertainty in the global carbon cycle. The extent of export from the ocean margin has recently been examined using radiocarbon (^{14}C) data and a mass balance approach by Bauer & Druffel (9a). Their results suggest that inputs of DOC and POC from ocean margins to the deep open ocean may be more than an order of magnitude greater than inputs of recently produced organic carbon derived from the surface ocean.

It is increasingly evident that the higher fertility of the coastal ocean compared to the open ocean and slope (20 vs 8 mol C m^{-2} y^{-1}; 11, 146, 157) is mainly due to the large fluxes of nutrients transferred from the deep ocean to the shelf by upwelling or vertical mixing. The recycled production is relatively low, and thus the new production related to the large nutrient input must be balanced by the export of an equivalent amount of these elements. Walsh (147) and Wollast (156) have suggested that a significant fraction of the primary production is exported to the open ocean and that the nutrients are re-exported as particulate organic matter. However, along the northwest Atlantic coast, only 5% of the primary production is exported from the shelf to the adjacent slope (13). Nixon et al (102) concluded that only phosphorus, presumably in dissolved form, is largely exported to the open ocean, but that most of the nitrogen, mainly imported from the open ocean, is lost by denitrification on the shelf. This implies a considerable rate of denitrification in the sediments, contrasting with a high lability and release of the phosphorus constituents from the bottom to the water column.

Until recently, models of the global carbon cycle did not incorporate the coastal ocean, but directly linked ocean and continents. The status of the coastal ocean in global models is still a matter of debate because the magnitude of the transfer of carbon between the coastal zone and the open ocean is poorly constrained. There is no doubt that, in pristine times, the total riverine input of organic carbon in the coastal zone was greater than organic carbon preserved in shelf sediments. The coastal ocean was net heterotrophic and a source of CO_2 to the atmosphere (7 Tmol C y^{-1}), assuming little or no transfer of C at

the margins (132, 158; Ver et al, submitted). If these transfers are assumed to be significant (112; C. Rabouille, personal communication), it was slightly autotrophic and a net sink of atmospheric CO_2 (20 Tmol C y^{-1}).

Anthropogenic disturbance has led to an increased delivery of inorganic nutrients, organic carbon, and suspended matter into the coastal ocean. The excess nutrients may locally enhance planktonic primary production and carbon sequestration. Even though the total load of riverine N and P has more than doubled with respect to pristine conditions (93), it has not significantly affected the productivity of the coastal zone on a global basis. This perturbation is, however, responsible for the eutrophication in zones adjacent to polluted estuaries, especially in semi-enclosed areas. The increased amount of organic carbon delivered to the coastal zone can be stored in the sediment and/or oxidized to CO_2. In the latter case, remineralization releases nutrients and promotes primary production. The present rate of sedimentation in the coastal zone is probably twice that of preindustrial times because of increased continental erosion resulting from deforestation and changes in agricultural practices. This should increase the rate of C burial in coastal sediments (155). The balance between increased primary production and increased respiration may shift the coastal zone toward a more heterotrophic or a more autotrophic state relative to initial conditions (158). According to Smith & Hollibaugh (132), the present coastal zone remains heterotrophic (but a sink for fossil fuel CO_2). The changes in air-sea CO_2 flux relative to pristine conditions depend on the response of both ocean carbonate chemistry and atmospheric CO_2 to anthropogenic perturbations. Increased carbonate precipitation and increased heterotrophy (or decreased autotrophy) result in a source of CO_2 smaller than the rise of atmospheric pCO_2 due to anthropogenic activities. The CO_2 sink potential of the coastal ocean is therefore diminished. A model that assumes a low rate of C transfer at the margin estimates that CO_2 flux has changed both in direction (from net evasion to net invasion) and magnitude (by 6.7 Tmol C y^{-1}) relative to the year 1700 (Ver et al, submitted). Finally, Rabouille (112) has suggested that the various human-induced modifications of the coastal carbon cycle have resulted in decreased autotrophy of the coastal ocean (20 to 11 Tmol C y^{-1}).

CONCLUSIONS

Kempe (67) asserted that whether coastal seas are net sinks or sources of CO_2 for the atmosphere cannot be determined. There are currently few carbon budgets available for coastal ecosystems. An important research initiative was recently launched by the LOICZ program to develop modeling guidelines (54), compile 150–200 carbon (and nitrogen) budgets for coastal ecosystems in key regions, and extend these budgets to a global scale using a functional coastal zone

classification system (109). Approximately 30 budgets are available (e.g. 133), and it is anticipated that the compilation will be completed in the near future (SV Smith, personal communication).

It is difficult to evaluate the autotrophic/heterotrophic character of the coastal zone on the basis of the balance between inputs and outputs because of the very limited knowledge of circulation and water exchange between the shelf and the open ocean. The net flux of material at this boundary is poorly constrained: it is the difference between two huge numbers, both of which are affected by large uncertainties. An additional difficulty lies with the extremely non-stationary conditions of the coastal zone. Hydrodynamically, river discharge exhibits strong seasonal and annual variations, and the shelf is periodically affected by storms that resuspend freshly deposited sediments, and favor export to the slope area and open ocean.

The available data suggest that riverine and atmospheric inputs of dissolved and particulate carbon represent a negligible fraction of the high primary production of the coastal zone on a global scale. New production on the shelf represents at least 50% of primary production and thus only 50% or less is respired and recycled (40, 72, 146, 155–157). Some of the production that is not recycled accumulates in the sediments, but most of the detrital organic matter—dissolved or particulate—must be exported to the slope and open ocean. Changes in riverine fluxes of organic matter and nutrients or suspended matter due to human activities are also small with respect to natural fluxes, and have probably affected the global carbon cycle only slightly.

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