

The fate of marine autotrophic production

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Abstract

The fate of photosynthetic carbon in marine ecosystems dominated by different types of primary producers was examined by compiling published reports on herbivory, autotrophic respiration, decomposition, carbon storage, and export rates as fractions of net primary production (NPP) in ecosystems dominated by different types of autotrophs (i.e. oceanic and coastal phytoplankton, microphytobenthos, coral reef algae, macroalgae, seagrasses, marsh plants, and mangroves). A large fraction (>40%) of the NPP of marine ecosystems is decomposed within the system, except for microphytobenthos (decomposition, ~25% of NPP). Herbivory tends to be highest for microalgae (planktonic and benthic, >40% of NPP) and macroalgae (33.6±4.9% of NPP) and is somewhat less for higher plants. Microphytobenthos export on average a much higher proportion of their NPP than do other microalgal communities, whereas marine macrophytes, except marsh plants, export a substantial proportion (24.3–43.5% on average) of their NPP. The fraction of NPP stored in sediments is 4-fold greater for higher plants (~10–17% of NPP) than for algae (0.4–6% of NPP). On average, ~90% of the phytoplankton NPP is used to support local heterotrophic metabolism (i.e. grazed or decomposed). This fraction is even higher in oceanic communities. Mangrove forests, and to a lesser extent seagrass meadows and macroalgal beds, produce organic carbon well in excess of the ecosystem requirements, with excess photosynthetic carbon (i.e. export rate plus storage) in these ecosystems representing ~40% of NPP. Extrapolation of these results to the global ocean identifies marine angiosperms, which only contribute 4% of total ocean NPP, as major contributors of the NPP stored (30% of total ocean carbon storage) and subsequently buried in marine sediments. Consideration of burial of NPP from marine angiosperms should lead to estimates of total burial of marine NPP that exceed current estimates by 15–50%.

Photosynthesis by marine organisms produces 30–60 Pg (1 Pg = 10¹⁵g) of organic carbon annually (e.g. Martin et al. 1987; Charpy-Robaud and Sournia 1990; Smith and Hollibaugh 1993), which represents ~40% of the total primary production of the earth (Schlesinger 1991; Melillo et al. 1993). This photosynthetic carbon is produced by autotrophic organisms ranging from cyanobacteria to trees (i.e. mangroves). Autotrophic carbon production of the open ocean, which represents the bulk (90%; Smith and Hollibaugh 1993) of oceanic primary production, is contributed by unicellular autotrophs, with a small contribution being made by floating macrophytes. In contrast, photosynthesis by marine macrophytes (macroalgae, seagrasses, marsh plants, and mangroves) is responsible for a significant fraction (at least 35–50%; Ryther 1963; Platt and Subba Rao 1975; Nixon et al. 1986) of the carbon production of the coastal ocean, where they represent ~75% of the autotrophic biomass (Smith 1981). In addition to these primary producers, photosynthetic organisms associated with corals (e.g. coral reef algae) support a sizable production (0.7 Pg C yr⁻¹; Crossland et al. 1991), which is locally important.

Estimates of primary production alone do not provide

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appropriate understanding of the ecological role of the plants or their function in the marine carbon cycle. A more elaborate evaluation of the role of marine plants in primary production requires examination of the fate of the carbon they produce. Communities dominated by photosynthetic organisms that either export or bury significant amounts of their primary production are likely to be autotrophic, since that fraction of primary production is unavailable for local heterotrophic use. In contrast, communities dominated by photosynthetic organisms that channel most of their production through herbivores or as detritus for local microbial use require only small inputs of allochthonous carbon to be heterotrophic.

For example, coastal marine ecosystems are known to have some of the highest areal rates of primary carbon production for marine systems (Boynton et al. 1982; Nixon et al. 1986), yet analyses of net ecosystem metabolism based on carbon and nutrient stoichiometry indicate that many such systems are sources rather than sinks of inorganic carbon (Smith and Mackenzie 1987; Smith and Hollibaugh 1993). A significant fraction of phytoplankton production is channeled to herbivores (55% on average; Cebrián and Duarte 1994) and is therefore more directly accessible to higher trophic levels than is the carbon production of, for example, mangroves, which is mostly channeled to decomposers (Lugo et al. 1988; Lee 1990). Most organic carbon produced by oceanic phytoplankton is used within the upper ocean, and only a minor fraction accumulates in deep water or is buried in the sediments (<1%; Lein 1984; Henrichs and Reeburgh 1987), thereby entering a long-term sink in the carbon cycle. In contrast, long-lived seagrasses may bury relatively large amounts

of the carbon they produce, such as the Mediterranean seagrass *Posidonia oceanica* (L.) Delile, which buries 20–200 g C m⁻²yr⁻¹ in sediments (Romero et al. 1994).

The fraction of marine photosynthetic carbon flowing through different paths, such as the herbivore and detrital paths, has been reported to be independent of primary production (Cebrián and Duarte 1994, 1995). This finding illustrates the need for knowledge of both the fate and amount of photosynthetic carbon production in order to fully understand the functioning of different types of marine ecosystems. Although our knowledge of the magnitude of marine primary carbon production by different photosynthetic organisms is well established, our knowledge of the fate of this production is less clear.

Here, we examine the fate of photosynthetic carbon in different types of marine ecosystems and discuss the implications of these differences. We do so based on a compilation of published reports on net primary production (NPP, g C m⁻²yr⁻¹) as well as the fate of NPP as described by the carbon mass balance equation

$$\text{NPP} = D + H + E + S, \quad (1)$$

where D is the carbon decomposed, H is the carbon consumed by herbivores, E is the carbon exported out of the system, and S is the potential carbon storage in the ecosystems.

Methods

We searched the literature for reports of the components of Eq. 1. We expressed each component as a percentage of NPP to represent the relative importance of each process as a component of the flow of photosynthetic carbon. The data set comprised 154 reports on NPP and subsequent photosynthetic carbon flow in marine ecosystems that are dominated by different types of primary producers, including phytoplankton (oceanic and coastal), microphytobenthos, coral reef algae, macroalgae, seagrass meadows, marsh plants, and mangroves. The data set is available from the authors upon request.

NPP was not always reported as such. We calculated NPP from gross primary production (GPP) data for ~19% of marsh plants and 60% of phytoplankton according to the equation

$$\text{NPP} = \text{GPP}(1 - R_a),$$

where R_a represents the average fraction of GPP respired by the plants themselves. Estimates of the average proportion of GPP respired by the autotrophs were also derived from a survey of the literature, which yielded 35.4 ± 2.3% for phytoplankton, 26.4 ± 2.9% for microphytobenthos, 14.1 ± 3.4% for coral reef algae, 50.8 ± 6.3% for macroalgae, 57.1 ± 5.7% for seagrasses, 69.4 ± 7.3% for marsh plants, and 52.1 ± 9.4% for mangroves.

Herbivory represents the consumption of living plant material. The production decomposed annually represents use of detrital carbon (dissolved and particulated) by decomposers. Direct estimates of this rate represented only 10% (for macroalgae) to 50% (for mangroves) of the

values in the data set, depending on the type of ecosystem examined. Additionally, some studies of microalgae, coral reef algae, and seagrasses reported community respiration rates. These estimates included the production consumed by the autotrophs themselves, that decomposed by heterotrophs, and that ingested by herbivores contained within the respiration chamber (microzooplankton in plankton, microfauna and meiofauna in benthic chambers). D was obtained from respiration rates by using the average values for these autotrophic organisms (see above) and subtracting autotrophic respiration. Additionally, herbivore consumption within the chambers was also subtracted from estimates of community respiration of microalgae-dominated communities by assuming this consumption to be on average ~50% of the total herbivory on communities of these primary producers (phytoplankton—e.g. Laws et al. 1988; Frost 1991; Strom and Welschmeyer 1991; microphytobenthos—Admiraal et al. 1983; McLachlan and Bate 1984; Carpenter 1986).

Estimates of D derived from plankton community respiration rates and corrected for microherbivory and autotrophic respiration underestimate the total decomposition of phytoplankton NPP because such estimates do not consider decomposition of the sinking photosynthetic carbon. Decomposition of the sinking photosynthetic carbon was assumed to be ~17% of NPP (Martin et al. 1987) to estimate the total proportion of phytoplankton NPP decomposed. The remaining estimates of the annual production decomposed were derived from the annual production of detritus (P_d), excluding that exported from the system (i.e. $P_d = \text{NPP} - H - E$), by using average decomposition rates (k , d⁻¹) for the different type of marine phototrophs (microalgae, 0.0526 ± 0.0049; macroalgae, 0.0144 ± 0.0042; seagrasses, 0.0107 ± 0.002; marsh plants, 0.0381 ± 0.006; mangroves, 0.0082 ± 0.0035; Enríquez et al. 1993) and the equation

$$D = P_d[1 - \exp(-k \times 365)].$$

The detritus that is not decomposed within a year accumulates on the sediment surface and represents the stored carbon (S). Hence, our estimates of S represent the excess carbon that accumulates annually in the system and do not represent carbon burial, which is referred to long-term carbon storage. Carbon stored in the sediments at the annual time scale is subject to remineralization through diagenetic processes, which involve losses of ~70% and 97% of the carbon entering coastal and deep ocean sediments (Berner 1982; Lein 1984; Henrichs and Reeburgh 1987). Similarly, the carbon accumulated as dissolved organic carbon (DOC) in deep oceanic waters, which is >200-fold that contained within living marine organisms (Slegenthaler and Sarmiento 1993), may also be oxidized by biotic and abiotic processes (i.e. photooxidation; Mopper et al. 1991) when deep waters are upwelled into the upper ocean. The inputs of DOC to the ocean must be balanced by these losses if the total DOC pool is to remain approximately constant, so this pool does not represent long-term storage of carbon (Mopper et al. 1991).

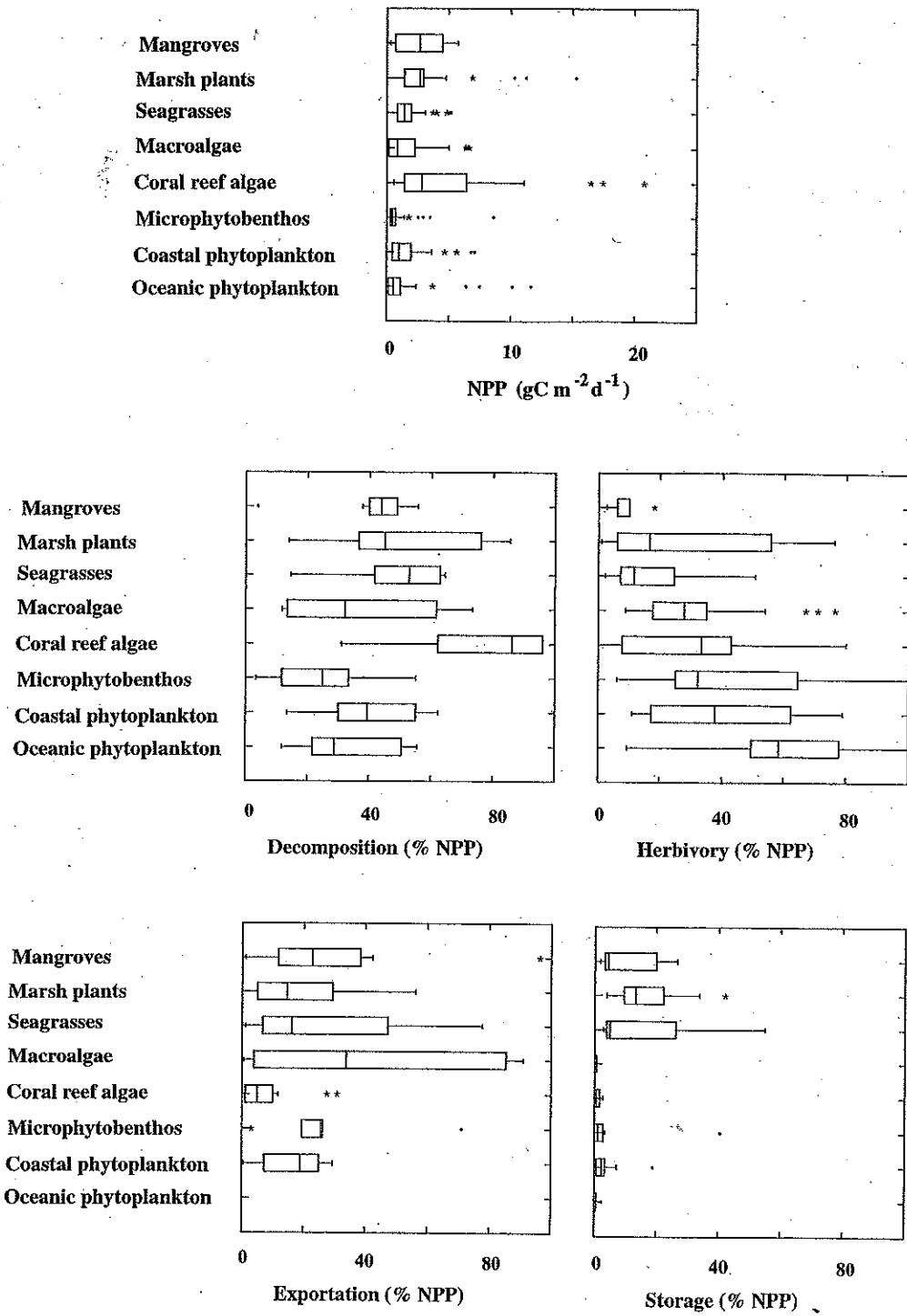


Fig. 1. Distribution of NPP by different marine autotrophs and the fraction of NPP that is decomposed, consumed by herbivores, exported, and stored in the sediments. Boxes encompass 25% and 75% quartiles, the central line represents the median, and bars encompass 95% of the values. Asterisks and filled circles indicate observations outside the 95% limits. Horizontal export of oceanic phytoplankton was assumed to be negligible.

Export of photosynthetic carbon represents the horizontal transport of carbon away from the ecosystem. Hence, our estimates of exported carbon production (E) do not include sedimentation of photosynthetic carbon

away from the photic zone in the ocean, which, at the annual scale, is either decomposed, accumulated in deep water, or is buried in the sediments. Whereas loss of phytoplanktonic production by horizontal advection in

the open ocean can generally be neglected, coastal ecosystems, where horizontal transport often exceeds vertical transport, may export substantial photosynthetic carbon (Wollast 1991; Prego 1993). However, estimation of exported production depends on the definition of physical boundaries for the systems studied. Because the definition of these boundaries requires substantial knowledge about the systems, we uncritically accepted the boundaries established by the authors of the estimates.

Results

Marine primary production ranged widely both within and among ecosystems in the data set, with microphytobenthos and phytoplankton communities supporting relatively low NPPs (Fig. 1). Most (~75%) of the NPP of coral reef algae was decomposed within the system. This path comprised ~40–50% of the NPP of other marine plants, except for microphytobenthos, for which only ~25% of NPP is decomposed within the system (Figs. 1, 2). Herbivory tended to be highest for microalgae (planktonic and benthic, >40% of NPP) and macroalgae ($33.1 \pm 4.9\%$ of NPP) and was somewhat smaller for higher plants, except for marsh plants, which may experience substantial herbivory. Microphytobenthos exported on average a much larger proportion of their NPP than did other microalgal communities, whereas marine macrophytes (except marsh plants) exported a substantial (24.3–43.5%) proportion of their NPP (Figs. 1, 2). The fraction of NPP stored in the sediments (S) is 4-fold greater for higher plants (~10–17% of NPP) than for algae (0.4–6% of GPP), although S can be relatively high in some microphytobenthic communities.

On average, ~80–90% of the NPP of phytoplankton is used to support local heterotrophic metabolism (i.e. grazed or decomposed), and this fraction is even higher in oceanic communities. The fraction of NPP used within coral reef ecosystems and marsh ecosystems is also very high (>80% of NPP). Mangrove forests and, to a lesser extent, seagrass meadows, microphytobenthos, and macroalgal beds produce organic carbon well in excess of the ecosystem requirements, with excess photosynthetic carbon (i.e. $E + S$) in these ecosystems representing ~40% of NPP (Fig. 2). Statistical analysis of the average carbon budgets derived revealed significant (ANOVA on log-transformed values, $P < 0.001$) differences among ecosystem types in the fraction of NPP that is decomposed, eaten by herbivores, exported, and stored in the sediments.

Discussion

The relative importance of different carbon pathways among marine ecosystems (Fig. 2) reflects both the intrinsic properties of the producers and the physical nature of the environments. Differences in the fraction of the photosynthetic production consumed by herbivores may be related to the general decline in growth rate (Cebrián and Duarte 1994) and palatability and nutrient (N and

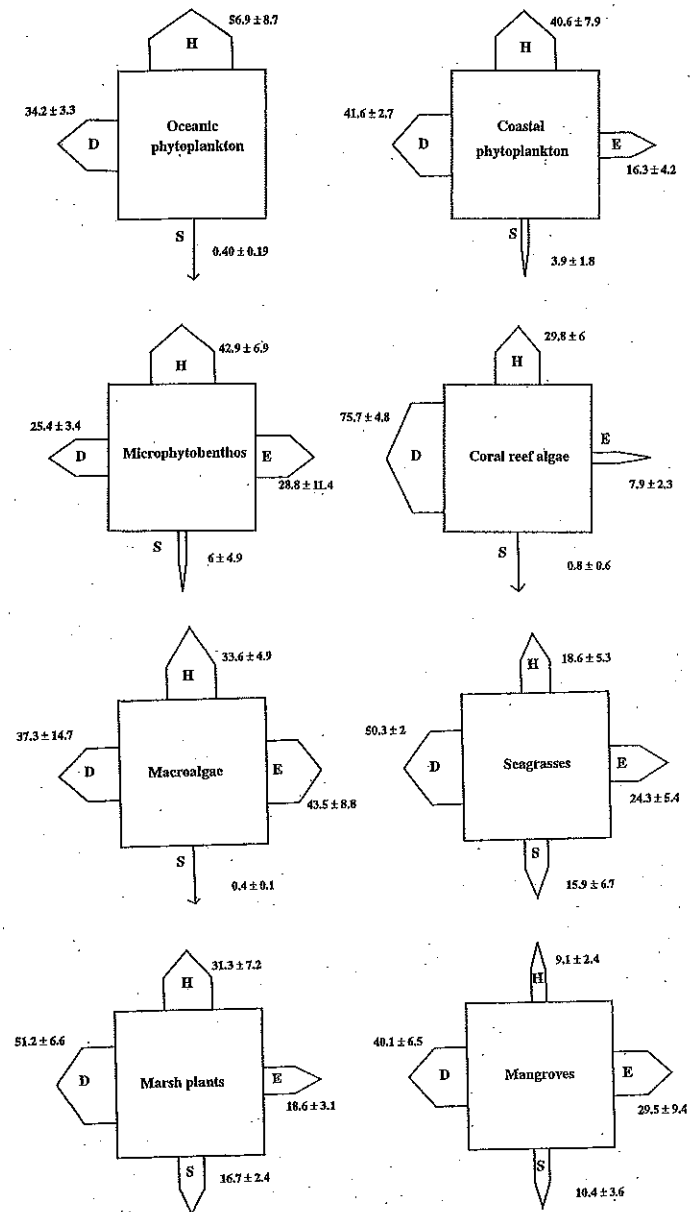


Fig. 2. Average carbon budgets for the different marine autotrophs. The budgets are derived from the average (\pm SE) percentage of net primary production decomposed within the system (D), consumed by herbivores (H), exported (E), and stored in the sediments (S). The widths of the arrows denoting these fluxes are proportional to the fraction of net primary production they represent, with the sides of the boxes representing 100% of NPP. Because these estimates were derived by averaging independent estimates, the budgets shown need not add up to 100%.

P) concentrations (Duarte 1992, 1995) from microalgae to higher plants, which have a need for nutrient-poor structural tissues (Enríquez et al. 1993). The thickness of the photosynthetic tissues may also explain the differences in grazing intensity; that is, microscopic algae can be ingested by a range of planktonic and benthic organisms, whereas the comparatively thick photosynthetic tis-

sues of higher plants and slow-growing macroalgae may diminish grazing intensity (Duarte 1995). Moreover, a significant fraction of the production of higher plants is placed as roots and rhizomes in the sediments (Lipkin 1979; Prentice and Fung 1990) and is therefore unavailable to most herbivores.

The differences among ecosystems in the fraction of NPP that is decomposed may be attributable to similar factors, because both tissue nutrient concentrations and the thickness and toughness of photosynthetic tissues influence decomposition rates (Melillo et al. 1982; Valiela et al. 1984; Enríquez et al. 1993). Hence, microalgal detritus and the carbon they excrete, with their higher nutrient concentrations (Duarte 1992), are more readily decomposed than are the tissues of higher plants (Enríquez et al. 1993). Additionally, the belowground production of marine macrophytes is nutrient-poor relative to that of photosynthetic tissues (Walker and McComb 1988; Short et al. 1993) and may be placed deep in the sediments, where anaerobic conditions may prevent efficient decomposition (Harrison 1989). Higher plants also allocate a sizable fraction of the carbon they produce to structural compounds that decompose slowly (Enríquez et al. 1993). As a result, carbon storage is 4-fold greater for higher plants than for algae, except for microphytobenthos, which may also accumulate substantial excess carbon.

Differences in export rates, on the other hand, reflect the physical conditions of the environments occupied by marine plants. For example, coastal plant communities often occupy areas that have substantial horizontal transport. Accordingly, detritus derived from these plants is likely to be advected out of the system (Nixon 1980; Lugo et al. 1988; Hemminga et al. 1991). Similarly, coastal phytoplankton is often exported out of the estuaries and coastal areas where it grows (Welsh et al. 1972; Malone and Chervin 1979).

These differences in the relative importance of different routes of photosynthetic carbon transfer have major implications at the ecosystem level. Ecosystems dominated by autotrophic organisms that channel most of their production to herbivores or decomposers should undergo efficient nutrient recycling, with most of their production representing, under near steady-state situations, recycled rather than new production. Similarly, these communities are likely to show a close balance between photosynthetic production and community respiration ($P:R$ ratio ~ 1), with new production being very small relative to NPP (Quiñones and Platt 1991). These communities are therefore likely to have a much smaller role as sinks for atmospheric carbon than is expected from their net primary production. These effects are particularly evident for coral reef algae, where the close coupling between primary producers and heterotrophs ensures efficient nutrient recycling and coupling between production and respiration (Crossland et al. 1991).

Although both herbivory and decomposition of photosynthetic carbon lead to regenerated carbon production and a tendency of $P:R$ ratios to approach 1, these effects

should be even greater when decomposition exceeds grazing. Ecosystems that channel most of their photosynthetic carbon to decomposers should be dominated by microbial rather than by metazoan food webs. Close coupling between photosynthetic production and microbial growth should increase the efficiency of recycling and reduce the probability of export of organic carbon and nutrients, as opposed to the greater probability of export associated with the motility of herbivores. Additionally, ecosystems dominated by autotrophs that channel most of the production to herbivores are more likely to support efficient production of harvestable marine protein (e.g. fisheries) than are those that channel their production to microbial decomposers (Legendre and Rassoulzadegan 1995). Whether production is channeled to decomposers or herbivores is modulated, at least for planktonic communities, by the differences in community structure associated with different levels of turbulence. High turbulence leads to diatom-dominated phytoplankton communities (Cushing 1989), which are efficiently and relatively quickly consumed by herbivores or sedimented out (cf. Legendre and Rassoulzadegan 1995). In contrast, low turbulence leads to autotrophic communities dominated by nano- and picoplankton (Cushing 1989), whose production is mostly transferred to decomposers within the microbial food web rather than to metazoan herbivores (Legendre and Rassoulzadegan 1995). Moreover, these small primary producers have negligible sedimentation rates, so that most of the carbon produced is used in the upper ocean, leading to the very low rates of carbon storage of these ecosystems (Fig. 2).

Ecosystems that use most of the autochthonous production, such as those dominated by phytoplankton, coral reef algae, and marshes (herbivory + respiration $> 80\%$ of NPP), must therefore show a close balance between photosynthetic production and ecosystem respiration (Odum 1956). Hence, small ($< 20\%$ of NPP) allochthonous carbon inputs may drive these systems to a net heterotrophic status (Odum 1956). These inputs may be derived from neighboring ecosystems, such as benthic ecosystems and mangroves, which export a sizable fraction ($> 20\%$, Fig. 2) of their net primary production (cf. Lugo et al. 1988; Lee 1990; Hemminga et al. 1991, 1995), or from inputs from land. Ecosystems that export a substantial fraction of their production and those in which a substantial fraction of the production is buried in the sediments are likely to lose substantial nutrients along with the carbon. Sustained primary production in these ecosystems are therefore closely dependent on external nutrient inputs.

As a result, the production of ecosystems that either export or bury an important fraction of their primary production should have a tendency to be controlled by nutrient supply (i.e. bottom-up control), in contrast to the expected dominance of biotic control, such as microbial regeneration of nutrients or herbivore control, in ecosystems where primary production is mostly grazed or decomposed. The relationship between export and buried carbon and ecosystem nutrient losses varies based on

Table 1. Estimates of total NPP by different primary producers and the amount of this production that is consumed by herbivores, decomposed, or stored in sediments. Values in parentheses are percentage of total herbivory, decomposition, or storage in the ocean. Estimates of NPP and the area covered by different primary producers were derived from different sources, except for total NPP for mangroves and marsh plants, which were calculated from our data set. The missing export carbon (decomposed or stored in sediments) is $\sim 5.5 \text{ Pg C yr}^{-1}$ or $\sim 10\%$ of the total NPP (see text).

Primary producer	Area covered (10^6 km^2)	Total NPP (Pg C yr^{-1})	Herbivory (Pg C yr^{-1})	Decomposition	Storage
Oceanic phytoplankton	332*	43 ^s	24.4(88)	14.7(77.5)	0.17(26.5)
Coastal phytoplankton	27*	4.5 [†]	1.8(6.5)	1.8(9.8)	0.18(27.0)
Microphytobenthos	6.8 [‡]	0.34 [‡]	0.15(0.5)	0.09(0.4)	0.02(3.1)
Coral reef algae	0.6 [§]	0.6	0.18(0.6)	0.45(2.0)	0(0.7)
Macroalgae	6.8 [‡]	2.55 [‡]	0.86(3.1)	0.95(4.2)	0.01(1.6)
Seagrasses	0.6 [‡]	0.49 [#]	0.09(0.3)	0.25(1.1)	0.08(12.0)
Marsh plants	0.4 [¶]	0.44	0.14(0.5)	0.23(1.0)	0.07(11.3)
Mangroves	1.1**	1.1	0.10(0.3)	0.44(1.9)	0.11(17.6)
Total	—	53.0	27.8(52)	19.0(36)	0.65(1.2)

* Sverdrup et al. 1942. † Smith and Hollibaugh 1993. ‡ Charpy-Robaud and Sournia 1990. § Smith 1978. || Crossland et al. 1991. # de Vooy 1979. ¶ Woodwell et al. 1973. ** Lugo et al. 1988.

the C:N:P stoichiometry of the primary producers and the detritus they produce. Most of the organic matter exported and buried by higher marine plants (e.g. marsh plants, seagrasses, mangroves) corresponds to nutrient-poor detritus (e.g. Hemminga et al. 1991, 1995), so the nutrient inputs needed to maintain the NPP of these systems may be less than those expected from the carbon losses. Similarly, use of the exported carbon in neighboring ecosystems dominated by nutrient-rich primary producers (e.g. phytoplankton) may require additional nutrient inputs. Conversely, the import of particulate organic matter derived from nutrient-rich primary producers to systems dominated by nutrient-poor primary producers (e.g. seagrasses; cf. Duarte 1992) may increase both heterotrophic carbon use and, particularly, local primary production once the nutrients are remineralized.

These arguments show that predictions of ecosystem functioning cannot be reliably derived from examinations of local carbon budgets alone and that such predictions must consider the continuity between marine ecosystems. For example, carbon export from marine ecosystems does not necessarily represent a large loss of carbon, and only the carbon stored in sediments may represent, when effectively buried, a net carbon sink. Based on examination of different ecosystem types, we attempted to scale our results to the global ocean by first calculating the fate of the total carbon produced by different marine ecosystems and then compounding these calculations into a carbon budget for the global ocean similar to that described by Eq. 1. The product of the average NPP of different types of marine ecosystems by the area they cover in the global ocean allowed an estimate of their global NPP. Phytoplankton production in the open ocean by far dominates ($\sim 80\%$) marine NPP. Less than 20% of total marine NPP is contributed by all other ecosystems, of which coastal

microalgae and macroalgae are the main contributors (Table 1). The amounts of total NPP consumed by herbivores and decomposed in different ecosystem types were proportional to the contribution of these ecosystems to total NPP (Table 1). Most (88%) herbivory in the sea takes place in the open ocean and represents a greater percentage of the open ocean NPP (56.9%, Fig. 2) than that of coastal NPP (34%, Table 1). Assuming a similar efficiency in the transformation of herbivore production into harvestable biomass for the coastal and open ocean, these calculations suggest that the fraction of NPP available for fisheries harvest should be roughly equal for the open and coastal ocean and that the harvestable production should be about 10-fold higher in the open ocean. Therefore, the report that the fraction of NPP required to support coastal fisheries is about 10–15 times greater than that in the open ocean (Pauly and Christensen 1995) cannot be accounted for on the basis of differential efficiencies in the conversion of NPP into harvestable biomass. Instead, these differences suggest a much greater capture efficiency in the coastal ocean than in the open ocean, where the fish biomass is diluted in a much thicker water column.

Unlike decomposition and herbivory, the total NPP stored by different marine ecosystems is independent of their total production (Table 1), as is expected from the general independence between detrital carbon storage and ecosystem primary production (Cebrián and Duarte 1995). In particular, marine ecosystems dominated by angiosperms (seagrasses, marsh plants, and mangroves) are responsible for $\sim 30\%$ of the total NPP stored in the ocean, whereas they contribute only $\sim 4\%$ of the total NPP (Table 1). Moreover, because carbon burial efficiency (i.e. the fraction of the carbon stored that remains buried over the long term) is much greater for coastal than for deep-sea

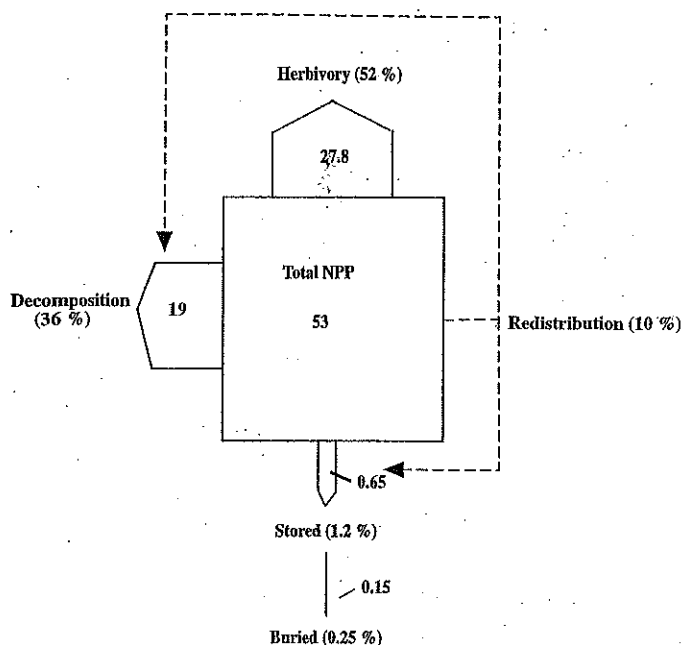


Fig. 3. A budget for the total marine net primary production. All values inside box and arrows are in Pg C yr^{-1} . Box construction as in Fig. 2. Dotted lines represent the redistribution of NPP that is exported from one ecosystem to another and that must eventually be decomposed or buried elsewhere.

sediments ($\sim 30\%$ and 3% , respectively; cf. Berner 1982; Lein 1984; Henrichs and Reeburgh 1987), the NPP buried in the coastal ocean is likely to be much greater than that buried in the deep ocean ($\sim 0.145 \text{ Pg C yr}^{-1}$ and $0.005 \text{ Pg C yr}^{-1}$, respectively, as calculated from Table 1).

The estimates presented may underestimate by as much as 50% the NPP of coastal plants buried if only 10% of the NPP exported by coastal plants (i.e. $\sim 0.2 \text{ Pg C yr}^{-1}$) is stored and subsequently buried (i.e. $\sim 0.06 \text{ Pg C yr}^{-1}$) in deep-sea sediments. The 3-fold difference between NPP stored in coastal vs. deep marine sediments is quite substantial, and that between the NPP buried in coastal vs. deep marine sediments is even larger (~ 30 -fold). The conservative estimate of total NPP burial in the ocean derived from these calculations ($0.15\text{--}0.21 \text{ Pg C yr}^{-1}$) is close to available estimates of this rate ($0.13 \text{ Pg C yr}^{-1}$, Berner 1982). Carbon storage, however, is a small fraction (1.2%) of the total marine NPP, most of which is consumed by herbivores or decomposed (88%; Table 1, Fig. 3). The budget of total marine NPP obtained shows a dominance of herbivory in the use of marine NPP (52%), which is greater than microbial use of total NPP (36% of NPP; Table 1, Fig. 3). However, the excess carbon is only $\sim 1\%$ of the total NPP, three-fourths of which is consumed by diagenetic processes in the sediments, so that only $\sim 0.25\%$ of the total marine NPP is buried in the sediments (Fig. 3).

Burial of marine NPP represents an estimate of the excess autotrophic production in the ocean and, therefore, the size of the carbon sink associated with marine photosynthesis. Our results identify angiosperms growing in

the sea as major contributors to the carbon sink associated with marine photosynthesis ($\sim 30\%$ of the total sink). This excess of marine photosynthetic carbon does not imply that the ocean is a net autotrophic system. Burial of marine photosynthetic carbon ($\sim 0.15 \text{ Pg C yr}^{-1}$) is much less than the input of organic carbon from terrestrial ecosystems, which is ~ 4 -fold greater (0.4 Pg C yr^{-1} from rivers, $0.15 \text{ Pg C yr}^{-1}$ from direct sewage inputs, and $0.10 \text{ Pg C yr}^{-1}$ as atmospheric deposition of land-derived organic carbon; Schlesinger 1991; Smith and Hollibaugh 1993). Hence, use by marine heterotrophs of only 25% of the organic carbon derived from land would render the ocean a net heterotrophic system, as suggested by previous analyses (Smith and Mackenzie 1987; Smith and Hollibaugh 1993). Of course, the input of land-derived organic carbon to the ocean is not uniformly distributed, so its importance in driving the systems toward net heterotrophy must be greater in the coastal ocean (Smith and Hollibaugh 1993).

The data presented here help us to evaluate the role of different marine plant types in local carbon budgets by establishing trends in the average fraction of their net primary production that is channeled to heterotrophs through grazing or decomposition of photosynthetic carbon, as well as trends in the excess carbon stored in the sediments or exported to adjacent ecosystems. From the results presented, we can identify a decline in the fractions of the net primary production used within the systems and consumed by herbivores, as well as an increment in the fraction of NPP stored in sediments, from phytoplankton to angiosperm-dominated ecosystems. Communities dominated by higher plants tend to be net autotrophic and to act as carbon sinks, suggesting that their autotrophic production should be largely controlled by resources. In contrast, planktonic communities should have a close balance between autotrophic and heterotrophic metabolism. Consumers are therefore likely to exert a close control on the autotrophic production of planktonic communities, which should be largely supported by recycled nutrients. Our results provide a basis for formulating and testing hypotheses on the functioning of marine ecosystems and the global ocean. Extrapolation of these results to the global ocean identifies marine higher plants, which only contribute 4% of total ocean NPP, as major contributors of the NPP stored in marine sediments (30% of total ocean carbon storage) and subsequently buried in the ocean. Future attempts to estimate the potential of marine photosynthesis to sequester atmospheric carbon must therefore consider marine angiosperms as important contributors to this process.

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