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Variability and control of carbon consumption, export, and accumulation in marine communities

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Abstract

Elucidating the extent and controls of the routes followed by primary production in marine communities (i.e., consumption by herbivores, decomposition, transportation of plant material beyond the community boundaries—referred to as export—or accumulation as biomass or detritus) is essential to understand how much and why they differ in their capacity to fuel secondary production, both within or out of the community, and in their role as sinks in the oceanic carbon budget. Here, using an extensive compilation of published reports, I compare the magnitude of these routes across and within a wide range of community types, including oceanic and coastal phytoplanktonic communities, benthic microalgal communities, coral reef algal beds, macroalgal beds, seagrass meadows, marshes, and mangroves. Furthermore, I examine whether the variability in the magnitude of these routes among and within types is associated with that in the magnitude of primary production. In general, different community types showed similar levels of consumption by herbivores and export, in spite of substantial within-type variability. On the contrary, substantial differences in detritus decomposition and accumulation were found among types: coral reef algal beds and benthic microalgal communities tended to show the highest and lowest levels of decomposition, respectively, whereas marshes and oceanic phytoplanktonic communities tended to show the largest and smallest levels of detritus accumulation. The results also identify primary production as a robust (i.e., applicable to a wide range of environmental conditions and communities) control of the variability in herbivory and decomposition among marine communities. The role of primary production as a control of export and detritus accumulation is generally minor and only restricted to coastal phytoplanktonic and benthic microalgal communities, for export, and marshes and mangroves for detritus accumulation.

Marine primary production may follow a diverse fate. Herbivores may remove a variable percentage of production, from few percents in mangroves (Johnstone 1981; Li and Lee 1998) to a substantial fraction in oceanic phytoplanktonic communities (Welschemeyer and Lorenzen 1985). The amount of primary production not consumed by herbivores is accumulated as plant biomass, which eventually dies off and becomes detritus. In turn, detritus can be decomposed within the community or transported to neighboring systems through physical or biological agents (i.e., export, Mann 1988; Deegan 1993). The magnitude of export varies widely depending on detritus buoyancy and exposure to physical energy. For instance, communities of marine macrophytes and microalgae in sheltered embayments normally export a negligible percentage of production (Josselyn et al. 1983; Kilar and Norris 1988), whereas kelps exposed to intense wave scouring export most of their production (Marsden 1991). Finally, a small, albeit variable, fraction of detrital production eventually accumulates as recalcitrant material within the community (Schlesinger 1997).

The nature and extent of the routes followed by primary production have important implications for marine communities. For instance, the amount of production ingested by herbivores should set limits to the levels of herbivore production maintained in the community. Accordingly, past comparisons have documented that aquatic communities subject to higher levels of consumption support a larger herbivore biomass (Cyr and Pace 1993). Similarly, because most exported detritus is consumed into receiving communities (Mann 1988), the magnitude of detrital export should be indicative of the levels of secondary production maintained by the community beyond its boundaries. In addition, the amount of nonexported detritus decomposed within a community should impose a lower limit to the levels of detritivore production maintained within the community because imported detritus from neighboring communities can also be an important food resource for autochthonous consumers (Smith and Hollibaugh 1993). Finally, the accumulation of refractory detritus represents a carbon and nutrient sink. Both detrital export from and refractory accumulation within a community entail a loss of nutrients for the community (Hemminga et al. 1991). As a consequence, the percentage of primary production accounted for by these two routes should reflect the degree of dependence of the community on external nutrient supply.

Hence, elucidating the nature and controls of the fate of primary production in marine communities is important in understanding the extent of and variability in carbon consumption and preservation in marine ecosystems and their contribution to the marine and global carbon budget. However, no study has yet compared in concert the magnitude of absolute consumption, decomposition, export, and refractory accumulation across a broad range of marine communities. The only extensive study to date (Duarte and Cebrian 1996) compared the percentage of production represented by

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each of these routes in a wide range of community types, but it disregarded the absolute magnitude of the routes. Moreover, the controls of these routes are poorly known. Cyr and Pace (1993) showed that absolute consumption by herbivores was associated with net primary production when a wide range of aquatic community types, both freshwater and marine, were compared. However, whether absolute consumption and primary production are correlated across and within diverse types of marine communities is unknown. Similarly, decomposition and refractory accumulation are associated with primary production when aquatic and terrestrial communities are compared (Cebrian 1999), but no attempt to test this association for marine communities has been made. In addition, even though physical energy is a predominant control of detrital export out of marine communities (Bach et al. 1986; de Jonge and Colijn 1994), the association between export and primary production across marine communities remains to be examined.

In this paper I first examine, through an extensive compilation of published data, the variability in absolute consumption by herbivores, decomposition, export, and refractory accumulation within and among diverse types of marine communities (i.e., oceanic and coastal phytoplanktonic communities, benthic microalgal and macroalgal communities, coral reef algae, seagrass meadows, marshes, and mangroves). I then explore the importance of primary production as a control of the differences in consumption, decomposition, export, and refractory accumulation within and across community types. I conclude by discussing how the results improve our understanding of the role of marine communities in the oceanic carbon budget and how human-induced environmental perturbations may alter that role.

Methods

I compiled published values of primary production, consumption by herbivores, decomposition, export, and refractory accumulation in oceanic and coastal phytoplanktonic communities, benthic microalgal communities, coral reef algal communities, macroalgal beds (other than those in coral reefs), seagrass meadows, marshes, and mangroves. Oceanic (i.e., offshore) phytoplanktonic communities were typically dominated by small flagellates (<20 μm), whereas coastal communities were normally composed of larger cells, with diatoms often being a predominant group. The communities encompassed a wide geographical range, from tropical to boreal latitudes. Microphytobenthic communities lived within (endolithic) or attached (epilithic) to hard surfaces (other than coral reef algae, *see below*), or attached to unconsolidated sediments (epipelic). They were most commonly dominated by diatoms, chlorophytes, and cyanobacteria, and also spread across a broad latitudinal range. Algal communities associated with coral reefs (here referred to as ‘‘coral reef algae’’) were composed of large fleshy turf and encrusting calcareous and endolithic algae in a variable relative percentage depending on factors such as grazing intensity and the degree of exposure to physical action. Macroalgal communities other than those within coral reefs (here referred to as ‘‘macroalgal beds’’) and seagrass meadows expanded across a broad latitudinal range, including many diverse tropical and temperate environments, such as coastal embayments, estuaries, and rocky shores. Accordingly, the type of dominant producer within these communities varied widely, from small filamentous to kelp species for macroalgae and from small, fast-growing to large, slow-growing species for seagrasses. Marsh communities covered a broad latitudinal gradient, expanding from subtropical to subartic environments. They also exhibited a variable composition depending on factors such as latitude and exposure to tidal action. The range of mangrove communities encompassed, in terms of exposure to tidal action (fringe or scrub), structure (dwarf or large species) and composition, was also broad.

Few reports examined all the routes of production in concert, with most of them addressing one or two routes. In total, 180 publications, reporting data for 378 communities, were compiled. The data set is further described and available in Web Appendix 1 at http://www.aslo.org/lo/toc/vol_47/issue_1/0011a1.pdf. I only considered reports that met the following criteria: (1) they included the most abundant producers and consumers and were thus representative of the community studied; if focused on one species, they were considered only if the species accounted for most ($>50\%$) of the total community production; (2) they referred to natural conditions, with all communities clearly altered by human activities being excluded; (3) they covered at least 1 year of observations or the growing season for annual producers (i.e., producers showing most growth during a relatively short period, the so-called growing season, and negligible growth during the rest of the year).

Primary production represents the net fixation of CO_2 into autotrophic biomass through photosynthesis. It thus corresponds to the excess of total CO_2 fixation over autotrophic respiration (i.e., net primary production = gross primary production − autotrophic respiration). In most microalgal reports, it was measured directly using ^{14}C techniques. Some authors used clear/dark incubations in situ or in the lab to estimate gross primary production as the sum of oxygen evolution between clear and dark containers. They then calculated primary production as the difference between gross primary production and autotrophic respiration (i.e., respiration by microalgae), which was estimated directly or taken from the literature. Whenever the authors reported gross primary production, but not net primary production, I estimated the latter from the mean values ($\pm$SE) of the percentage of gross primary production represented by autotrophic respiration ($35.4 \pm 2.3\%$ for phytoplankton, and $26.4 \pm 2.9\%$ for microphytobenthos) compiled by Duarte and Cebrian (1996). About 40% of the production values for phytoplankton, and 30% for microphytobenthos, were estimated like that. Given the low SE of these mean values, their impact on the reliability of the final estimates, and on the results and conclusions of the paper, should be minimal. Finally, some other authors estimated microalgal production as the biomass increment in the absence of loss processes (i.e., grazing, horizontal and vertical advection, natural mortality), although that approach somewhat underestimated production since some losses, such as metabolical exudation, were often disregarded.

Most ($>50\%$ in coral reef algae and $>90\%$ in the rest of communities) of the production values compiled for macrophytic communities (i.e., all except microalgal communities) were directly provided in the reports. Clear/dark chambers were used to estimate primary production in most coral reef algal and macroalgal communities, and some seagrass communities, as explained for microalgal communities. Alternatively, the production of kelp communities was estimated with the punching technique presented by Mann (1972). Some authors also used biomass accumulation in the absence of the most important losses (i.e., grazing and wave scouring) as an estimate of primary production in coral reef algal communities. Most seagrass reports used the traditional marking technique (Zieman and Wetzel 1980). For marshes, production was commonly estimated as biomass accrual once losses, such as herbivory or senescence, are prevented (through, for instance, the deployment of exclosure cages and/or detrital traps; de la Cruz 1973; Hopkinson et al. 1978). Surveys of tree abundance and size in conjunction with regressions between tree biomass and size were used to estimate production in most mangrove communities (Lugo et al. 1988). When direct values were not reported, primary production was estimated as the product between the mean biomass (gC (unit area)$^{-1}$) directly provided by the authors and the mean turnover rate (time^{-1}) for the given type of community, which was obtained from the extensive compilation presented in Cebrian (1999). For some coral reef algal communities, I estimated net primary production as the difference between gross primary production and autotrophic respiration, which was estimated as 14.1 ± 3.4% (mean ± SE) of the gross primary production (Duarte and Cebrian 1996). Because these indirect calculations only represented a small percentage of the production values compiled and the SE's of the mean turnover values were small (Cebrian 1999), I do not believe they affected significantly the results and conclusions of the paper. Most reports of seagrasses and marshes ($>$80%) included both the belowground and aboveground compartments, but most reports for mangroves ($>$90%) were limited to the aboveground compartment. The potential impact of this limitation on the results obtained is discussed below (*see discussion*).

Consumption corresponds to the ingestion of autotrophic biomass by herbivores. All values in the data set were provided as such in the reports. Methods included the dilution technique (Landry and Hassett 1982) and grazer evacuation rates (Kiorbe and Tiselius 1987) for phytoplanktonic communities and herbivore enclosure/exclosures for the rest of communities (Valentine and Heck 1991; Heck et al. 2000). Some estimates of herbivory on macroalgae, seagrasses, and mangroves were based on the number and size of herbivore bites imprinted on thalli or leaf blades (Ogden 1990). Other authors combined models of herbivore metabolism with counts of natural densities (Jacobs et al. 1981) or estimated herbivory by default as the missing term in carbon budgets (Zieman et al. 1993). Some other authors provided rather qualitative estimates of herbivory based on existing evidence or observations for similar communities, which I uncritically accepted.

Decomposition represents the degradation of autotrophic detritus by decomposers, which can be microbes or detrital macroconsumers. Few papers (15%) reported direct estimates of decomposition for microalgal communities, which were derived by following detrital mass loss and/or oxygen consumption in field or laboratory incubations. Alternatively, I compiled reports of gross primary production (the sum of oxygen evolution in clear and dark incubations) and community respiration (oxygen evolution in dark incubations) for these communities and estimated decomposition as presented by Duarte and Cebrian (1996) and Cebrian (1999). This approach is based on the fact that community respiration (R_c) measured in the incubation chambers corresponds to (Valiela 1995)

$$R_c = R_a + R_g + R_d \tag{1}$$

where R_a, R_g, and R_d denote autotrophic respiration (respiration by primary producers) and respiration by the grazers (microzooplankton for phytoplanktonic communities, and microfauna and meiofauna for microphytobenthic communities) and decomposers enclosed in the dark incubation chamber. Therefore, R_d, which is a proxy for decomposition (Begon et al. 1996), can be estimated as $R_c - R_a - R_g$. In turn, when unavailable from the authors, I estimated R_a as the product of gross primary production, which was directly provided in the report, and the percentage of gross primary production represented by autotrophic respiration in the given community, which I took from Duarte and Cebrian (1996). Likewise, when not provided by the authors, R_g was estimated to be 50 ± 30% (mean ± SE) of the total respiration of the entire grazer community (i.e., both micrograzers enclosed in the incubation chamber and macrograzers left outside). This conversion factor was also obtained by Duarte and Cebrian (1996). A few of the reports compiled provided direct estimates of total grazer respiration. Others reported values of total microalgal consumption by grazers (i.e., by both micrograzers and macrograzers) and, in that case, total grazer respiration was estimated from models of grazer metabolism (Begon et al. 1996). Alternatively, and most often, if direct estimates of total consumption were unavailable, I estimated total consumption as the product between net primary production (i.e., which was either directly provided or estimated from the percentage of gross primary production respired by autotrophs) and the mean percentage of primary production consumed by grazers for the given community type, which I obtained from Cebrian (1999). Finally, the decomposition of sedimenting phytoplankton beyond the mixing layer, assumed to represent 17% (Martin et al. 1987) of the net primary production in the community, was added to the estimates of decomposition for phytoplanktonic communities obtained from the incubation chambers.

I did not find any reports with direct estimates of decomposition in coral reef algal communities. I therefore followed a similar approach to the one described above for microalgal communities. I compiled reports of gross primary production and community respiration for coral reef algal communities and, because the metabolism incubation chambers used in these communities typically enclose a small percentage of the total grazer community (Mann 1985), R_d was estimated as $R_c - R_a$. Some authors provided direct estimates of R_a, which was otherwise estimated as 14.1 ± 3.4% (mean ± SE) of the gross primary production (Duarte and Cebrian 1996).

The percentage of direct values (i.e., provided as such by the reports) of decomposition for macrophytic communities was variable, ranging from 25% for seagrasses to 50% for marshes and mangroves, and to 80% for macroalgae. Direct values were derived by following the mass loss of detritus enclosed in mesh bags (Harrison 1989) or oxygen consumption in field or lab detrital incubations (Mateo and Romero 1996). The rest of decomposition values (D) for macroalgae, marshes, mangroves, and some seagrasses, were derived from the equation

$$D = (\mathrm{DP} - E) \times (1 - e^{-kt}) \qquad (2)$$

where DP and E denote the cumulative detrital production (i.e., primary production − consumption by herbivores − biomass accrual) and detrital export over the duration of the study (in g DW m^{-2} (study duration)$^{-1}$), k is the decomposition rate (in d^{-1}), and t represents the duration of the study (d). Decomposition rates were taken from the extensive compilation presented by Enriquez et al. (1993). This approach was used only in communities with a steady pool of degradable detritus over the study duration (i.e., which ranged from one to a few years) and where all fresh detrital production is exported, decomposed, or incorporated into the refractory pool (Cebrian 1999). Finally, the rest of seagrass decomposition values were derived from measurements of gross primary production and community respiration in the same way as for coral reef algae. When autotrophic respiration was not provided directly by the authors, it was estimated to be 57.1 ± 5.7% (mean ± SE) of gross primary production (Duarte and Cebrian 1996).

Export corresponds to the transportation of autotrophic material (biomass and/or detritus) beyond the community boundaries. All values in the data set were given as such in the reports. When directly measured, it was estimated as the amount of autotrophic material carried out of the system through physical agents, such as waves and currents (Bach et al. 1986), or from mass balance models based on the comparison of expected detrital pools under nonexport and realized observations (Romero et al. 1992). No report accounted for export mediated through consumer migration (i.e., consumers defecating the ingested material out of the system). In some other cases, authors arrived at qualitative estimates of export, based on previous observations, or provided enough evidence to set reasonable limits to the magnitude of export. I uncritically accepted those approximations. Moreover, as many authors acknowledged, community geographical boundaries were often difficult to define. It is thus possible that a fraction of the so-called exported material did not actually traverse the limits of the community, but instead settled down and underwent decomposition within the community. This is particularly so for microphytobenthic communities, where export was mostly derived as resuspension in the water column and subsequent washing off. I arbitrarily considered export out of oceanic phytoplanktonic communities to be nil because horizontally advected oceanic phytoplankton was never transported out of the limits of the community. Moreover, I did not consider the sedimentation of detrital phytoplankton beyond the mixing layer as export, but rather as decomposition through the water column and further decomposition and preservation as refractory detritus in the sediment.

Refractory accumulation is the amount of nonexported detrital production that is not decomposed over the study period. Because most studies encompassed from one to a few years, these values represent detrital accumulation over relatively short-term scales and disregard long-term losses such as diagenetic processes (Schlesinger 1997). Direct values (i.e., provided as such by the reports) ranged from 10% in mangroves to 80% in phytoplanktonic communities. Direct values were obtained from measurements of sediment accumulation rates and organic content (Anderson et al. 1994) or as the excess of detrital input over sediment respiration (Smith 1992). Alternatively, I estimated refractory accumulation as the excess of nonexported detrital production over decomposition through the study duration (DP − D), where decomposition (D) was estimated following Eq. 2 as explained above (k was provided by the authors in a few cases, but I mostly used the community-specific mean values in Enriquez et al. 1993). In addition, for a number of coral reef algal communities, I estimated refractory accumulation as the difference between measurements of nonexported gross primary production and total system respiration over large spatial (i.e., including most of the area, producers and heterotrophs of the community) and long temporal (i.e., covering several seasons) scales.

The estimates of decomposition from measurements of community respiration heavily rely on the use of mean values calculated from other communities. In some cases, the SE of those mean values is small (for instance, the percentage of gross primary production respired by autotrophs), but large in some other cases (for instance, the percentage of total grazer respiration represented by the grazers enclosed in incubation chambers for microalgal communities). Moreover, the estimate that decomposition of sedimenting phytoplankton represents on the average 17% of the community net primary production is a vast generalization because this percentage may vary notably among oceanic regions (Muller and Suess 1979; Suess 1980). In addition, the use of plant-specific mean k values in Eq. 2 may involve significant bias in the estimates of decomposition and refractory accumulation because decomposition rates can vary substantially in relation to abiotic factors (such as temperature, humidity, and redox conditions) independent of plant-specific characteristics (i.e., internal nutrient and lignin concentrations). It is difficult to assess the total degree of uncertainty entailed by the use of all these mean values. It may seem substantial because the variance of the final estimates would result from multiplying the errors of all the terms involved in their derivation (i.e., error propagation, Tsokos 1972). Moreover, some values of consumption and export directly provided by the authors are qualitative estimates (i.e., low = 10%; moderate = 25%; intermediate = 50%; high = 75%, when expressed as percentage of primary production), which adds to the level of uncertainty in the final data set.

Nevertheless, I believe all the uncertainty generated by the use of mean values and qualitative nature of some data does not compromise the results and conclusions of the paper. I base this contention on three arguments. First, the error associated with the mean values and qualitative data is small

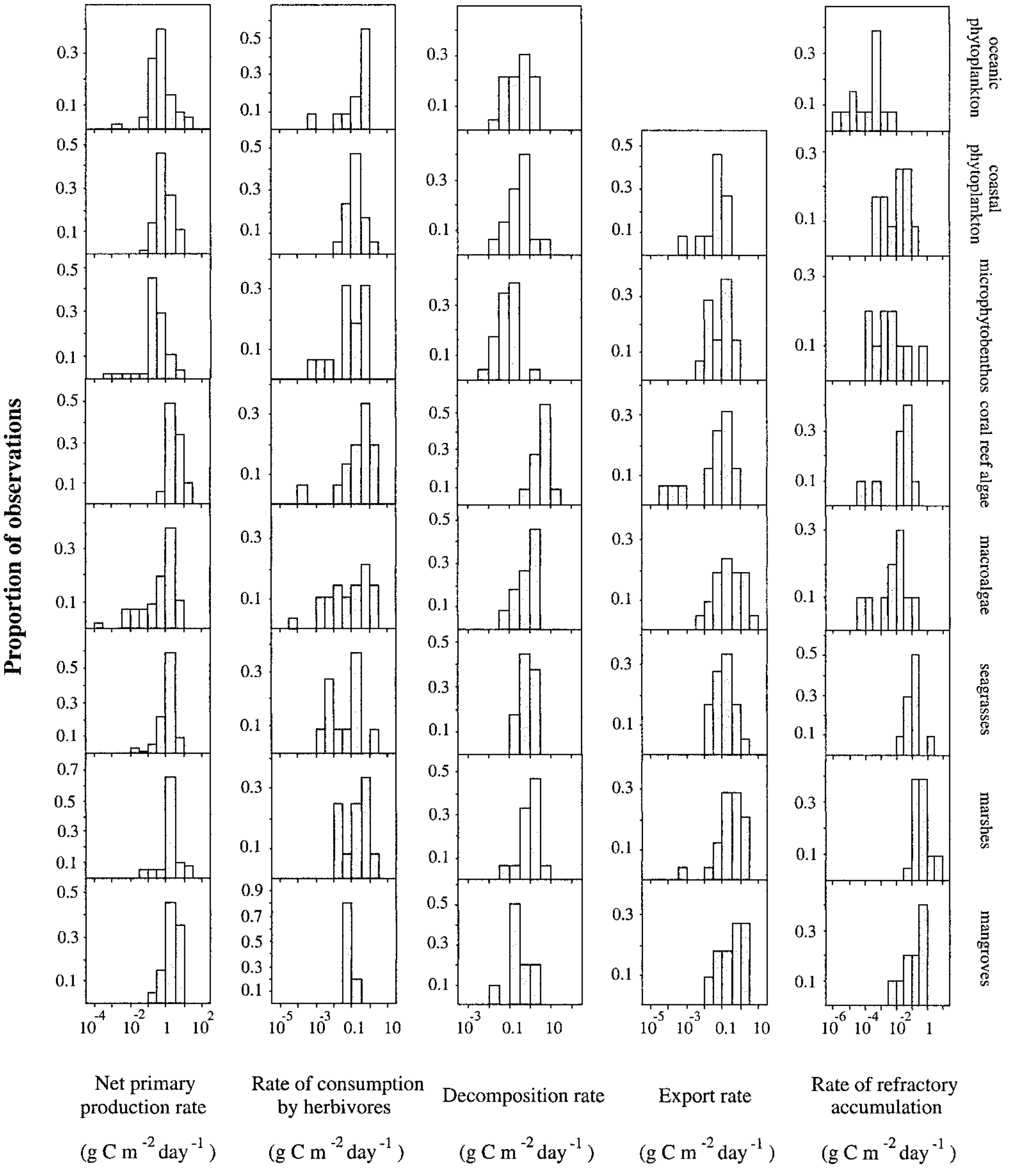

Fig. 1. The distribution of net primary production, consumption by herbivores, decomposition, export, and refractory accumulation in the community types considered.

when compared with the wide range in herbivory, decomposition, export, and refractory accumulation across and within community types (i.e., several orders of magnitude) encompassed by the data set. Therefore, that error should not affect significantly the patterns found within and across community types (*see results*). Second, the same approaches have been used in the past and shown to yield reliable, consistent estimates of herbivory, decomposition, export, and refractory accumulation (Cebrian and Duarte 1994; Duarte and Cebrian 1996; Cebrian et al. 1998; Cebrian 1999). Finally, because the estimates of herbivory, decomposition, export, and refractory accumulation for each type of community are generally independent (i.e., very few reports provide estimates for more than two trophic routes), the methodological bias of the data set should be unimportant if the percentages of net primary production represented by these routes sum up to a value not different from 100 for each community type. The results obtained were (sum ± SE) 97.0 ± 8.3 for oceanic phytoplankton; 101.6 ± 7.9 for coastal phytoplankton; 99.8 ± 9.5 for microphytobenthos; 115.5 ± 8.2 for coral reef algae; 129.3 ± 13.6 for macroalgae; 105.2 ± 8.9 for seagrasses; 114.5 ± 10.4 for marshes, and 97.8 ± 12.6 for mangroves. None of these values is significantly different from 100 (t-test, $p = 0.04$ for macroalgal beds and $p > 0.05$ for the rest of community types).

I expressed all variables in gC m^{-2} d^{-1} by dividing the cumulative values (i.e., values integrated over the duration of the study) by the duration of the study and using standard conversion factors (Wiebe 1988; Gasol et al. 1997). Owing to the nonnormal nature of the data compiled, the overall variability in primary production, consumption by herbivores, decomposition, export and refractory accumulation

Table 1. Multiple comparisons (Q-test) of primary production (PP) and decomposition (D) (upper panel), and export (E) and refractory accumulation (RA) (lower panel). Letters denote a significant difference at $\alpha = 0.05$ and the symbols ">" or "<" the direction of the difference where the row community type is on the left side of the symbol (for instance, coral reef algae have higher production than oceanic phytoplankton).

	Oceanic phytoplankton	Coastal phytoplankton	Microphytobenthos	Coral reef algae	Macroalgae	Seagrasses	Marshes
Coastal phytoplankton							
Microphytobenthos							
Coral reef algae	PP(>), *D*(>)	PP(>), *D*(>)	PP(>), *D*(>)				
Macroalgae			*D*(>)	PP(<)			
Seagrasses	PP(>)		PP(>), *D*(>)	PP(<), *D*(<)			
Marshes	PP(>)	PP(>)	PP(>), *D*(>)		PP(>)		
Mangroves	PP(>)	PP(>)	PP(>)	*D*(<)			

	Oceanic phytoplankton	Coastal phytoplankton	Microphytobenthos	Coral reef algae	Macroalgae	Seagrasses	Marshes
Coastal phytoplankton							
Microphytobenthos							
Coral reef algae							
Macroalgae							
Seagrasses	RA(>)						
Marshes	RA(>)	RA(>)	RA(>)	*E*(>), RA(>)	RA(>)		
Mangroves	RA(>)						

among all community types was analyzed with the nonparametric Kruskal-Wallis statistic, and specific types were compared with a nonparametric multiple comparison Q-test (Zar 1984). The dependence of consumption by herbivores, decomposition, export, and refractory accumulation on primary production across and within types was examined with techniques of least-squares regression after log-transforming the variables to comply with the assumptions of these techniques.

Results

Net primary production differed among community types (Fig. 1; Kruskal-Wallis, $p < 0.05$), with microalgal communities (phytoplankton and microphytobenthos) showing a lower production than most macrophytic communities (Table 1). Coral reef algae were more productive than most other community types (Table 1). There was also substantial variability within types, with values ranging over four orders of magnitude within oceanic phytoplankton, microphytobenthos and macroalgae, and over two orders of magnitude within the rest of types (Fig. 1). On the contrary, consumption by herbivores did not differ among community types (Fig. 1; Kruskal-Wallis, $p > 0.05$), but it ranged over three orders of magnitude within some types.

The differences in decomposition among community types were similar to those in primary production (Fig. 1; Kruskal-Wallis, $p < 0.05$). Microphytobenthic communities showed lower values than most macrophytic communities, whereas coral reef algae displayed the highest values (Table 1). Yet the variability in decomposition within types was generally smaller than that in primary production, consumption by herbivores, export, and refractory accumulation, with values ranging less than three orders of magnitude within all types (Fig. 1).

Export was also found to differ significantly among community types (Fig. 1; Kruskal-Wallis, $p < 0.05$), but this result was driven by the only significant difference between specific communities, i.e., that marshes had higher export values than coral reef algae (Table 1). Refractory accumulation also differed among community types (Fig. 1; Kruskal-Wallis, $p < 0.05$). Oceanic phytoplankton showed lower values than seagrasses, marshes, and mangroves, whereas marshes displayed higher values than any other community type except seagrasses and mangroves (Table 1). Within-type variability in both export and refractory accumulation was substantial, with values ranging over three orders of magnitude within most types (Fig. 1).

Across community types, differences in consumption by herbivores were associated with differences in primary production, with the tendency toward increased consumption with larger production explaining 65% of the variability (Fig. 2a, Table 2). In addition, the slope of the regression equation adjusted in log-transformed units was smaller than one (t-test, H_0: slope = 1, $p < 0.05$), indicating that consumption represents a lower percentage of production in more productive communities when all types are compared. Within types, increased consumption was strongly associated ($R^2 > 0.7$) with larger production within pelagic and benthic microalgal, macroalgal, and seagrass communities, but only weakly related within marshes or independent within communities of coral reef algae and mangroves (Fig. 2b, Table 2). Herbivores consumed a smaller percentage of production in more productive communities of coastal phytoplankton and benthic microalgae (Table 2).

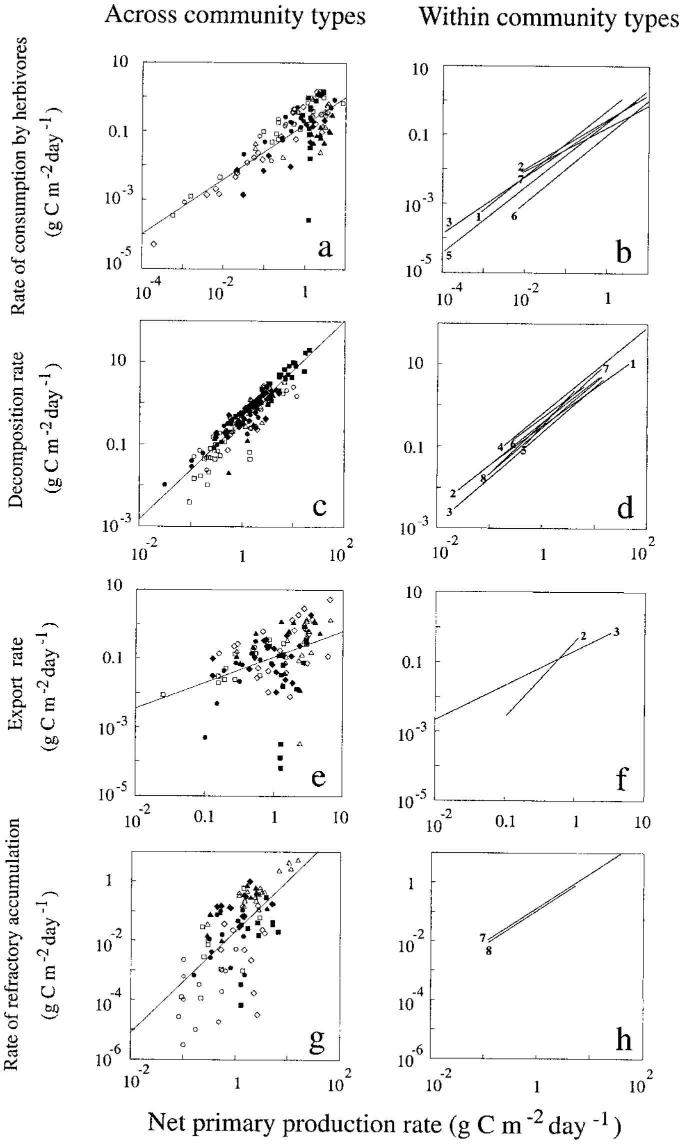

Fig. 2. Relationships across and within community types between consumption by herbivores, decomposition, export, and refractory accumulation as dependent variables and net primary production as independent variable. Lines represent significant equations adjusted with least-square regression analyses (*see Table 2*). Data are log-transformed to comply with the requirements of this analysis. Symbols and numbers denote community type: oceanic phytoplankton, 1 or open circles; coastal phytoplankton, 2 or solid circles; microphytobenthos, 3 or open squares; coral reef algae, 4 or solid squares; macroalgae, 5 or open diamonds; seagrasses, 6 or solid diamonds; marshes, 7 or open triangles; mangroves, 8 or solid triangles.

Increased decomposition was associated with larger production both across and within all community types (Fig. 2c,d, Table 2). The associations were generally strong, with the percentage of variance explained ranging from 45% to 90%. Across community types, decomposition represented a higher percentage of production in more productive communities, but an unchanged percentage within all community types (Table 2).

On the contrary, the association between increased export and higher production across community types was poor, with export ranging over four orders of magnitude for similar values of production (Fig. 2e, Table 2). Within types, increased export was associated with higher production only within communities of coastal phytoplankton and benthic microalgae (Fig. 2f). In addition, export represented a higher percentage of primary production in more productive communities of coastal phytoplankton (Table 2).

Differences in refractory accumulation across community types were partially associated with those in primary production (Fig. 2g, Table 2). More productive communities tended to accumulate more refractory detritus, but this tendency only explained 40% of the variability. Moreover, the increase in refractory accumulation was exponential, indicating that, when diverse community types are compared, more productive communities tend to store a greater percentage of production as refractory detritus. Within types, increased accumulation was associated with higher production only in marshes and mangroves (Fig. 2h, Table 2).

Discussion

The results offer a synthetic view of the nature and variability of the fate of production in marine communities. They also point to important consequences for the consumption, recycling, and storage of organic carbon in these communities. For instance, in spite of substantial within-type variability, the magnitude of autotrophic carbon transferred to herbivores does not differ significantly among the types of community examined here. Provided the efficiency of herbivore production (i.e., ratio of growth to consumption) does not vary systematically among different types of marine communities, which seems possible (Schroeder 1981), that result would imply that the magnitude of herbivore production does not vary significantly among these community types. In contrast, the magnitude of autotrophic carbon transferred to detritivores is high in communities of coral reef algae and low in communities of benthic microalgae, in relation to most other community types. Hence, total secondary production (the sum of herbivore and detritivore production) should be large in the former communities and small in the latter, when compared to other communities. Accordingly, coral reefs often maintain a high abundance of consumers (Lewis 1977; Crossland et al. 1991), whereas consumer abundance in communities dominated by benthic microalgae tends to be much lower (Miller et al. 1996; Middelburg et al. 2000). In addition, coral reefs have elevated structural complexity and offer high levels of shelter and refuge to consumers in comparison with microphytobenthos-dominated sediment flats (Mann 1985), which can also contribute to the variability in consumer abundance.

Moreover, my results show that the magnitude of autotrophic carbon exported out of the community does not differ among the types compared here, with the exception that marshes export a larger magnitude than do coral reef algae. It is interesting to notice that microalgal-dominated communities, such as coastal phytoplankton and benthic microalgal beds, export on the whole as much autotrophic material

Table 2. Results of the least-square regression analyses between consumption by herbivores, decomposition, export, and refractory accumulation as dependent variables, and primary production as the independent variable across (overall) and within community types. Intercepts and slopes (±SE) are provided only for significant equations. All variables have been log-transformed to comply with the assumptions of least-square regression analyses. Asterisks signify the slope of the regression equation is different from one (*t*-test, $P <$ 0.05). Bold relationships are based on <50% direct values of decomposition or refractory accumulation (i.e., directly provided by the reports, *see methods*).

	Consumption by herbivores					Decomposition				
	n	R^2	*p*	Intercept	Slope	*n*	R^2	*p*	Intercept	Slope
Overall	120	0.65	<0.00001	−0.77 (±0.05)	0.80 (±0.05)*	**179**	**0.84**	**<0.00001**	**−0.43 (±0.02)**	**1.20 (±0.04)***
Oceanic phytoplankton	11	0.88	<0.0001	−0.29 (±0.12)	0.97 (±0.11)	**23**	**0.86**	**<0.00001**	**−0.51 (±0.05)**	**0.94 (±0.08)**
Coastal phytoplankton	17	0.74	<0.0001	−0.58 (±0.06)	0.73 (±0.11)*	**30**	**0.90**	**<0.00001**	**−0.41 (±0.03)**	**1.03 (±0.06)**
Microphytobenthos	16	0.91	<0.00001	−0.59 (±0.08)	0.82 (±0.07)*	**23**	**0.52**	**<0.0001**	**−0.67 (±0.13)**	**1.12 (±0.23)**
Coral reef algae	15	0.12	0.12			**22**	**0.84**	**<0.00001**	**−0.20 (±0.09)**	**1.07 (±0.10)**
Macroalgae	28	0.91	<0.00001	−0.64 (±0.07)	0.94 (±0.06)	11	0.59	<0.01	−0.48 (±0.14)	1.42 (±0.36)
Seagrasses	11	0.76	<0.001	−1.02 (±0.14)	0.99 (±0.17)	**45**	**0.78**	**<0.00001**	**−0.31 (±0.02)**	**0.95 (±0.08)**
Marshes	12	0.32	<0.05	−0.78 (±0.16)	0.64 (±0.26)	15	0.72	<0.0001	−0.43 (±0.08)	1.21 (±0.20)
Mangroves	10	0.24	0.09			10	0.46	<0.05	−0.54 (±0.14)	1.11 (±0.37)

as do macrophyte-dominated communities. Therefore, previous generalizations that macrophyte-dominated communities often exhibit higher levels of export (Duarte and Cebrian 1996; Cebrian 1999) than microalgal communities seem to be an oversimplification. Because the magnitude of autotrophic carbon exported does not differ among the community types compared here, I suggest that all these types potentially have a similar importance in fuelling allochthonous (i.e., out of the community) secondary production, although the nutritional quality of the material exported (internal nutrient concentration) needs also be considered (Sterner and Hessen 1994).

The results also identify marshes as a larger organic carbon trap than the other community types, with the exception of seagrass beds and mangroves, because they accumulate a greater magnitude of refractory detritus. This is probably due to the sediment anaerobic conditions and high values of belowground production typical of marshes (Howes et al. 1985). Because refractory accumulation often entails a loss of nutrients, albeit small, for the community (i.e., nutrients are bound to recalcitrant carbon and unavailable for further recycling, Schlesinger 1977; White and Howes 1994), the percentage of primary production fuelled by nutrients imported from allochthonous sources should in general be greater in marshes than in microalgal and macroalgal communities. Accordingly, marshes often import substantial amounts of nutrients from neighboring communities (Nixon 1980; Childers et al. 1993), atmospheric precipitation (Valiela and Teal 1979; White and Howes 1994), and nitrogen fixation (Bazely and Jefferies 1989; DeLaune et al. 1989). Oceanic phytoplanktonic communities, on the other hand, accumulate a small magnitude of refractory detritus in comparison with most macrophyte-dominated communities because most phytoplanktonic detritus is decomposed in the surface waters and during sedimentation to the bottom (Suess 1980; Jahnke 1996). These differences, however, refer to a m^2 basis. When the total area covered by each type of community in the world's oceans is accounted for, oceanic phytoplankton stand out as the greatest trap of organic carbon in the global marine budget because they cover the largest area (Duarte and Cebrian 1996).

I demonstrate that primary production is a consistent control of absolute decomposition across and within community types, with more productive communities tending to support higher levels of decomposition regardless of the type of community compared. This is so in spite of the wide range of abiotic (i.e., temperature, sediment redox condition, light) and biotic (i.e., size of detrital particles, detritus source and associated nutritional quality, nature of detritivore populations) controls of decomposition (Tenore et al. 1982; Enriquez et al. 1993; Schlesinger 1997) encompassed by the data set. In fact, Tenore et al. (1982) reviewed existing evidence to show that detritus origin, by determining its nutritional quality and availability to different trophic levels in the detrital food web, may condition the nature and extent of trophic transfer though the detrital food chain and magnitude of absolute decomposition. For instance, vascular plant (seagrasses, marshes, and mangroves) detritus often undergoes reduced decomposition in comparison with macroalgal detritus because the former typically has lower nutrient concentrations and higher concentrations of lignin and phenols, which depresses the activity of decomposers. Similarly, Enriquez et al. (1993) and Cebrian (1999) compiled extensive data sets and reported that phytoplanktonic detritus generally exhibits faster decomposition rates than macroalgal detritus, which in turn decompose faster than vascular plant detritus, and attributed these differences to the tendency toward increased internal nutrient concentrations from vascular plants to macroalgae to microalgae.

I believe that absolute decomposition is consistently and strongly associated with primary production across and within community types because, at the time scale covered by the reports examined (i.e., from one to a few years) and in spite of the variability induced by all the abiotic and biotic factors mentioned above, most primary production in marine communities is generally decomposed (Duarte and Cebrian 1996; Cebrian 1999). Furthermore, and more importantly, the variability in the percentage of production decomposed

Table 2. Extended.

Export					Refractory accumulation				
n	R^2	*p*	Intercept	Slope	*n*	R^2	*p*	Intercept	Slope
115	0.14	<0.0001	−0.96 (±0.07)	0.73 (±0.16)	**96**	**0.40**	**<0.00001**	**−1.73 (±0.11)**	**1.71 (±0.21)***
					13	0.06	0.21		
11	0.65	<0.01	−0.40 (±0.26)	2.18 (±0.49)*	12	0.00	0.42		
14	0.74	<0.0001	−0.67 (±0.11)	1.00 (±0.16)	10	0.27	0.07		
16	0.03	0.24			10	0.28	0.07		
21	0.10	0.09			10	0.00	0.62		
18	0.05	0.19			10	0.00	0.63		
24	0.05	0.15			**21**	**0.79**	**<0.00001**	**−0.86 (±0.08)**	**1.18 (±0.14)**
11	0.00	0.44			**10**	**0.48**	**<0.05**	**−0.93 (±0.15)**	**1.18 (±0.39)**

among communities of the same or different types is generally smaller than the variability in primary production (Duarte and Cebrian 1996; Cebrian 1999). As a consequence, and because absolute decomposition results from multiplying primary production and the percentage decomposed, absolute decomposition remains closely associated with primary production across or within marine community types. Nevertheless, because of the paucity of reports with direct estimates, most decomposition values for microalgal communities and all for coral reef algae were derived from measurements of community respiration (*see methods*). In addition, for some of those communities, primary production was estimated as a given percentage of gross primary production (*see methods*). Because the magnitude of gross primary production and community respiration are normally correlated in microalgal and coral reef algal communities (Duarte and Agusti 1998), it may thus be possible that the associations between decomposition and net primary production across community types and within communities of microalgae and coral reef algae are somewhat affected by a spurious codependence resulting from the methodology used. I have provided arguments to support that this effect should be minimal and should not invalidate the results (*see methods*).

The nature of the increase in decomposition with higher primary production depends on the range of community types compared. Across types, decomposition increases as an increasing percentage of production but as an unchanged percentage within any of the types considered here. Higher percentages of production decomposed imply that decomposers play a greater role in nutrient recycling (Legendre and Rassoulzadegan 1995; Sterner et al. 1997) and in limiting the size of the detrital pool (Cebrian and Duarte 1995; Cebrian 1999). Therefore, it seems that detritivores become a more prominent control of nutrient recycling and carbon storage in more productive communities when different types are compared. This hypothesis, however, would not hold when communities of the same type are compared.

Increasing consumption by herbivores is associated with higher primary production across community types, but the association does not hold within all types. Moreover, the nature of the association depends on the type of community examined: consumption increases as a constant percentage of production within communities of oceanic phytoplankton, macroalgal beds, seagrass meadows, and marshes, but as a decreasing percentage across community types and within communities of coastal phytoplankton and microphytobenthos. Therefore, it seems that the importance of herbivores as a control of organic carbon recycling and storage as autotrophic biomass, which is reflected by the percentage of primary production consumed (Cebrian and Duarte 1994; Sterner et al. 1997; Cebrian 1999), decreases in more productive communities when different types or only communities of coastal phytoplankton or microphytobenthos are compared. Previous comparisons of planktonic communities also suggest this hypothesis (Eppley 1981; Elser and Goldman 1991). Moreover, because it seems possible that the efficiency of herbivore production does not vary systematically among different types of marine communities (Schroeder 1981), herbivore production may be expected to increase as a decreasing percentage of primary production across community types or within communities of coastal phytoplankton and microphytobenthos. These hypotheses, however, do not apply to the rest of community types compared here. Elucidating why the strength and nature of the relationship between consumption by herbivores and production depends on the community type considered deserves more research.

Primary production is not a consistent, robust control of the magnitude of export out of marine communities because the two variables are poorly associated across community types and only for microalgal communities at the within-type level of analyses. These results indicate that the influence of primary production on export, by setting an upper limit to the magnitude of organic matter than can be carried out of the community, is blurred by more influential factors, such as the buoyancy of autotrophic material (Zieman et al. 1979; Alongi 1998) or exposure to physical energy (Bach et al. 1986; Barranguet et al. 1998), when communities of diverse or the same type, other than microalgal communities, are compared. Differences in refractory accumulation across types are also poorly associated with those in primary production. Within types, the association is only significant for marshes and mangroves, although not strong. Accordingly, when terrestrial and aquatic communities are compared, the variability in refractory accumulation is poorly related to that in primary production (Cebrian et al. 1998; Cebrian 1999). Detritus nutritional quality (Enriquez et al. 1993; Cebrian and Duarte 1995), redox sediment conditions (Romero et al. 1994; Schlesinger 1997), sediment accumulation rates (Canfield 1989), and temperature (Valiela 1995) appear to be more important controls of refractory accumulation in marine communities. Nevertheless, the regression analyses between refractory accumulation and production within most community types is based on a small sample size (i.e., limited statistical power). Thus, it is possible that the data set of this paper, albeit extensive, is still too limited to detect a significant relationship between refractory accumulation and primary production within most community types.

The patterns identified here bear a number of limitations that merit discussion. The following arguments justify that in general the nature, strength, and applicability of my results are not compromised by those limitations. First, the data set, albeit extensive, is not exhaustive. Many environments, such as the Arctic and Antarctic water column and sediments, are underrepresented due to the paucity of original data or failure to comply with the selection requirements (*see methods*). Moreover, the data set contains the inevitable geographical bias generated by available reports. For instance, I found few suitable reports of seagrasses in Asia, and none in Africa, in spite of the great importance seagrasses have in those continents. In any case, I believe the results obtained should be representative of general patterns because all the variables compiled cover a broad range (i.e., several orders of magnitude) for each of the community types examined and, hence, the probability for new values to significantly disrupt the tendencies described here is minimal.

Secondly, the estimates of refractory accumulation only integrate a time span ranging from one to a few years. Long-term losses, such as slow anaerobic decomposition and diagenesis (Canfield 1989, Schlesinger 1997), are disregarded. Hence, the values of refractory accumulation presented here are gross overestimates of the actual amount of carbon preserved in marine ecosystems over long time scales (i.e., millennia). Nevertheless, because long-term losses usually amount to 90–95% of short-term refractory accumulation in open ocean sediments, whereas they only amount to 70–75% in coastal sediments (Berner 1982; Lein 1984), the differences in carbon preservation between oceanic phytoplankton and coastal macrophytic communities (i.e., marshes) reported here should also hold on the long term. I also expect the dependence of carbon preservation on primary production shown here for marshes and mangroves to hold at longer time scales because the percentage of detritus lost through long-term processes should not vary greatly among the communities compared (Schlesinger 1997). The potential effects of including long-term losses on the relationship between short-term refractory accumulation and primary production across community types are uncertain. The relationship is poor, and it may be nonsignificant on the long term.

Finally, few reports ($<10\%$) of mangroves included the belowground compartment, which may be responsible for a substantial percentage of total biomass and primary production (Lugo and Snedaker 1974). Because few grazers feed on mangrove belowground material and most of it undergoes decomposition (Lugo and Snedaker 1974; Lugo et al. 1988), including the belowground compartment would increase the values of primary production and decomposition but not consumption by herbivores, export, and refractory accumulation for mangroves. At any rate, the increment represented by the incorporation of the belowground compartment would be small (i.e., twofold, at the most, Lugo and Snedaker 1974) in comparison with the range encompassed by the trends shown here (i.e., several orders of magnitude), and, thus, should not affect them significantly.

Hence, my results may help predict the impact of human-induced changes in the extension and primary production of marine communities on local and global carbon budgets. For instance, about 35% of the world's area covered by mangroves, or 47,839 km^2, has been lost over the last 20 yr due to coastal deforestation generated by human activities (Valiela et al. unpubl. data). Using the mean values of consumption by herbivores, decomposition, export, and refractory accumulation for mangroves derived from the data set, I estimate that such a decline in mangrove extension represents a cumulative loss of 2.1×10^{13} gC consumed per year (the sum of consumption by herbivores, decomposition and export) and 4.5×10^{12} gC accumulated as refractory detritus per year in the oceans. I also estimate, from a mean (±SE) plant biomass in mangrove communities equivalent to $7{,}990.9 \pm 1{,}049.0$ gC m^{-2} that has been compiled from references in the data set and others (Golley et al. 1962; Golley 1968; Lugo and Snedaker 1974; Christensen 1978; Suzuki and Tagawa 1983; Putz and Chan 1986; Lugo et al. 1988; Robertson and Daniel 1989; Gong and Ong 1990; Ong 1993; Steinke et al. 1995; Li and Lee 1997), that 3.8×10^{14} gC stored as mangrove plant biomass have been lost over the last 20 yr. This is a gross underestimate of the total drop in carbon storage associated with mangrove decline because belowground biomass and detrital mass are not included in the values averaged.

In summary, this report contributes to summarizing our knowledge of the nature and control of the fate of primary production in marine communities. The results identify differences among marine communities that have important implications for the consumption, recycling, and preservation of organic carbon in marine ecosystems. In turn, this information may be instrumental in understanding how much and why marine ecosystems differ in their role as sinks or sources in marine carbon budgets. However, this compilation also identifies a number of areas where more descriptive research is needed. For instance, I found very few reports with direct estimates of carbon decomposition in pelagic and benthic microalgal communities, and none in coral reef algal communities. The number of reports with direct estimates of refractory carbon accumulation was also low, except for phytoplanktonic communities. Although I have provided arguments as to why my indirect estimates of decomposition and refractory accumulation should not compromise the validity of the patterns arrived at, those patterns should be verified with direct, first-hand measurements.

References

Alongi, D. M. 1998. Coastal Ecosystem Processes, 1st ed. CRC.

Anderson, R. F., G. T. Rowe, P. F. Kemp, S. Trumbore, and P. E. Biscaye. 1994. Carbon budget for the mid-slope depocenter of the Middle Atlantic Bight. Deep-Sea Res. II **41:** 669–703.

Bach, S., G. Thayer, and M. LaCroix. 1986. Export of detritus from eelgrass (Zostera marina) beds near Beaufort, North Carolina, USA. Mar. Ecol. Prog. Ser. **28:** 265–278.

Barranguet, C., J. Kromkamp and J. Peene. 1998. Factors controlling primary production and photosynthetic characteristics of intertidal microphytobenthos. Mar. Ecol. Prog. Ser. **173:** 117–126.

Bazely, D. R., and R. L. Jefferies. 1989. Lesser snow geese and the nitrogen economy of a grazed salt marsh. J. Ecol. **77:** 24–34.

Begon, M., J. L. Harper, and C. R. Townsend. 1996. Ecology: Individuals, populations and communities. Blackwell.

Berner, R. A. 1982. Burial of organic carbon and pyrite sulfur in the modern ocean: Its geochemical and environmental significance. Am. J. Sci. **282:** 451–473.

Canfield, D. E. 1989. Sulfate reduction and oxic respiration in marine sediments: Implications for organic carbon preservation in euxinix environments. Deep-Sea Res. **36:** 121–138.

Cebrian, J. 1999. Patterns in the fate of production in plant communities. Am. Nat. **154:** 449–468.

———, and C. M. Duarte. 1994. The dependence of herbivory on growth rate in natural plant communities. Functional Ecology **8:** 518–525.

———, and ———.1995. Plant growth-rate dependence of detrital carbon storage in ecosytems. Science **268:** 1606–1608.

———, M. Williams, J. McClelland, and I. Valiela. 1998. The dependence of heterotrophic consumption and carbon accumulation on autotrophic content in ecosystems. Ecol. Lett. **1:** 165–170.

Childers, D. L., N. H. McKellar, R. F. Dame, F. H. Sklar, and E. R. Blood. 1993. A dynamic nutrient budget of subsystem interactions in a salt marsh estuary. Estuar. Coast. Shelf Sci. **36:** 105–131.

Christensen, B. 1978. Biomass and primary production of Rhizophora apiculata in a mangrove in Southern Thailandia. Aquat. Bot. **4:** 43–52.

Crossland, C. J., B. G. Hatcher, and S. V. Smith. 1991. Role of coral reefs in global ocean production. Coral Reefs **10:** 55–64.

Cyr, H., and M. L. Pace. 1993. Magnitude and patterns of herbivory in aquatic and terrestrial ecosystems. Nature **361:** 148–150.

de Jonge, V., and F. Colijn. 1994. Dynamics of microphytobenthos biomass in the Ems Estuary. Mar. Ecol. Prog. Ser. **104:** 185–196.

de la Cruz, A. A. 1973. The role of tidal marshes in the productivity of coastal waters. Assoc. Southeast. Biol. Bull. **20:** 147–156.

Deegan, L. A. 1993. Nutrient and energy transport between estuaries and coastal marine ecosystems by fish migration. Can. J. Fish. Aquat. Sci. **50:** 74–79.

DeLaune, R. D., T. C. Feijtel, and W. H. Patrick. 1989. Nitrogen flows in Louisiana Gulf Coast salt marsh: Spatial considerations. Biogeochemistry **8:** 25–37.

Duarte, C. M., and S. Agusti. 1998. The CO_2 balance of unproductive aquatic ecosystems. Science **281:** 234–236.

———, and J. Cebrian. 1996. The fate of marine autotrophic production. Limnol. Oceanogr. **41:** 1759–1766.

Elser, J. J., and C. R. Goldman. 1991. Zooplankton effects on phytoplankton in lakes of contrasting trophic status. Limnol. Oceanogr **36:** 64–90.

Enriquez, S., C. M. Duarte, and K. Sand-Jensen. 1993. Patterns in decomposition rates among photosynthetic organisms: The importance of detritus C : N : P content. Oecologia **94:** 457–471.

Eppley, R. W. 1981. Autotrophic production of particulate matter, p. 343–361. *In* A. R. Longhurst [ed.], Analysis of marine ecosystems. Academic.

Gasol, J. M., P. A. del Giorgio, and C. M. Duarte. 1997. Biomass distribution in marine planktonic communities. Limnol. Oceanogr. **42:** 1353–1363.

Golley, F. B. 1968. Mineral cycling in tropical forest ecosystems. Unpublished manuscript from the Institute of Ecology. University of Georgia.

———, H. Odum, and R. Wilson. 1962. The structure and metabolism of a Puerto Rican Red Mangrove Forest in May. Ecology **43:** 8–19.

Gong, W. K., and J. E. Ong. 1990. Plant biomass and nutrient flux in a managed mangrove forest in Malaysia. Estuar. Coast. Shelf Sci. **31:** 519–530.

Harrison, P. G. 1989. Detrital processing in seagrass systems: A review of factors affecting decay rates, remineralization and detritivory. Aquat. Bot. **23:** 263–288.

Heck, K. L., Jr., J. R. Pennock, J. F. Valentine, L. D. Coen, and S. A. Sklenar. 2000. Effects of nutrient enrichment and small predator density on seagrass ecosystems: An experimental assessment. Limnol. Oceanogr. **45:** 1041–1057.

Hemminga, M., P. G. Harrison, and F. van Lent. 1991. The balance of nutrient losses and gains in seagrass meadows. Mar. Ecol. Prog. Ser. **71:** 85–96.

Hopkinson, O., J. Gosselink, and R. Panardo. 1978. Aboveground production of seven marsh plant species in coastal Louisiana. Ecology **59:** 760–769.

Howes, B. L., J. W. H. Dacey, and J. M. Teal. 1985. Annual carbon mineralization and belowground production of Spartina alterniflora in a New England salt marsh. Ecology **66:** 595–605.

Jacobs, R., C. den Hartog, C. Braster, and F. Carrière. 1981. Grazing of the seagrass Zostera noltii by birds at Terschelling (Dutch Wadden Sea). Aquat. Bot. **10:** 241–259.

Jahnke, R. A. 1996. The global ocean flux of particulate organic carbon: Areal distribution and magnitude. Glob. Biogeochem. Cycles **10:** 71–88.

Johnstone, I. M. 1981. Consumption of leaves by herbivores in mixed mangrove stands. Biotropica **13:** 252–259.

Josselyn, M. N., G. Cailliet, T. Niesen, R. Cowen, A. Hurley, J. Conner, and S. Hawes. 1983. Composition, export and faunal utilization of drift vegetation in the Salt River submarine canyon. Estuar. Coast. Shelf Sci. **17:** 447–465.

Kilar, J., and J. Norris. 1988. Composition, export and import of drift vegetation on a tropical, plant dominated, fringing-reef platform (Caribbean Panama). Coral Reefs **7:** 93–103.

Kiorbe, T., and P. T. Tiselius. 1987. Gut clearance and pigment destruction in a herbivorous copepod, Acartia tonsa, and the determination of in situ grazing rates. J. Plankton Res. **9:** 525–534.

Landry, M. R., and R. P. Hassett. 1982. Estimating the grazing impact of marine micro-zooplankton. Mar. Biol. **67:** 283–288.

Legendre, L., and F. Rassoulzadegan. 1995. Plankton and nutrient dynamics in marine waters. Ophelia **41:** 153–170.

Lein, A. Y. 1984. Anaerobic consumption of organic matter in modern marine sediments. Nature **312:** 148–150.

Lewis, J. B. 1977. Processes of organic production on coral reefs. Biol. Rev. **52:** 305–347.

Li, M. S., and S. Y. Lee. 1997. Mangroves of China: A brief review. For. Ecol. Manag. **96:** 241–259.

———, and ———. 1998. Carbon dynamics of Deep Bay, eastern Pearl River Estuary, China. I: A mass balance budget and implications for shorebird conservation. Mar. Ecol. Prog. Ser. **172:** 73–87.

Lugo, A. E., S. Brown, and M. M. Brinson. 1988. Forested wetlands in freshwater and salt-water environments. Limnol. Oceanogr. **33:** 894–909.

———, and S. C. Snedaker. 1974. The ecology of mangroves. Annu. Rev. Ecol. Syst. **5:** 39–64.

Mann, K. H. 1972. Ecological energetics of the seaweed zone in a marine bay on the Atlantic coast of Canada. II. Productivity of seaweeds. Mar. Biol. **14:** 199–209.

———. 1985. Ecology of Coastal Waters. Studies in Ecology, vol. 8, 2nd ed. Blackwell.

———. 1988. Production and use and detritus in various freshwater, estuarine and coastal marine ecosystems. Limnol. Oceanogr. **33:** 910–931.

Marsden, I. 1991. Kelp-sandhopper interactions on a sand-beach in New Zealand. I. Drift composition and distribution. J. Exp. Mar. Biol. Ecol. **152:** 49–62.

Martin, J. H., G. A. Knauer, D. M. Karl, and W. W. Broenkow. 1987. VERTEX: Carbon cycling in the northeast Pacific. Deep-Sea Res. **34:** 267–285.

Mateo, M. A., and J. Romero. 1996. Evaluating seagrass leaf litter decomposition: An experimental comparison between litter-bag and oxygen-uptake methods. J. Exp. Mar. Biol. Ecol. **202:** 97–106.

Middelburg, J. J., C. Barranguet, H. T. S. Boschker, P. M. J. Herman, T. Moens, and C. H. R. Heip. 2000. The fate of intertidal microphytobenthos carbon: An in situ ^{13}C-labeling study. Limnol. Oceanogr. **45:** 1224–1234.

Miller, D. C., R. J. Geider, and H. L. MacIntyre. 1996. Microphytobenthos: the ecological role of the ''Secret Garden'' of unvegetated, shallow-water marine habitats. II. Role in sediment stability and shallow-water food webs. Estuaries **19:** 202–212.

Muller, P. J., and E. Suess. 1979. Productivity, sedimentation rate, and sedimentary organic matter in the oceans. I. Organic carbon preservation. Deep-Sea Res. **26A:** 1347–1362.

Nixon, S. W. 1980. Between coastal marshes and coastal waters—a review of twenty years of speculation and research on the role of salt marshes in estuarine productivity and water chemistry, p. 437–525. *In* P. Hamilton and K. B. MacDonald [eds.], Estuarine and Wetland Processes. Plenum.

Ogden, J. C. 1990. Community structure and function: The influence of grazing, p. 177–182. *In* R. C. Phillips and C. P. McRoy [eds.], Seagrass research methods. Monographs on Oceanographic Methodology, 9. United Nations Educational.

Ong, J. E. 1993. Mangroves—a carbon source and sink. Chemosphere **27:** 1097–1107.

Putz, F. E., and H. T. Chan. 1986. Tree growth, dynamics, and productivity in a mature mangrove forest in Malaysia. For. Ecol. Manag. **17:** 211–230.

Robertson, A., and P. Daniel. 1989. Decomposition and the annual flux of detritus from fallen timber in tropical mangrove forests. Limnol. Oceanogr. **34:** 640–647.

Romero, J., M. Perez, M. A. Mateo, and E. Sala. 1994. The belowground organs of the Mediterranean seagrass Posidonia oceanica as a biogeochemical sink. Aquat. Bot. **47:** 13–19.

———, G. Pergent, C. Pergent-Martini, M. A. Mateo, and C. Regnier. 1992. The detritic compartment in a Posidonia oceanica meadow: Litter features, decomposition rates and mineral stocks. P.S.Z.N.I.: Mar. Ecol. **13:** 69–83.

Schlesinger, W. H. 1977. Carbon balance in terrestrial detritus. Annu. Rev. Ecol. Syst. **8:** 51–81.

———. 1997. Biogeochemistry: An analysis of global change, 2nd ed. Academic.

Schroeder, L. A. 1981. Consumer growth efficiencies: Their limits and relationships to ecological energetics. J. Theor. Biol. **93:** 805–828.

Smith, K. L., Jr. 1992. Benthic boundary layer communities and carbon cycling at abyssal depths in the Central North Pacific. Limnol. Oceanogr. **37:** 1034–1057.

Smith, S. V., and J. T. Hollibaugh. 1993. Coastal metabolism and the oceanic organic carbon balance. Rev. Geophys. **31:** 75–89.

Steinke, T. D., C. J. Ward, and A. Rajh. 1995. Forest structure and biomass of mangroves in the Mgeni Estuary, South Africa. Hydrobiologia **295:** 159–166.

Sterner, R. W., J. J. Elser, E. J. Fee, S. J. Guildford, and T. H. Chrzanowski. 1997. The light : nutrient in lakes: The balance of energy and materials affects ecosystem structure and process. Am. Nat. **150:** 663–684.

———, and D. O. Hessen. 1994. Algal nutrient limitation and the nutrition of aquatic herbivores. Annu. Rev. Ecol. Syst. **25:** 1–29.

Suess, E. 1980. Particulate organic carbon flux in the oceans: Surface productivity and oxygen utilization. Nature **288:** 260–263.

Suzuki, E., and H. Tagawa. 1983. Biomass of a mangrove forest and a sedge marsh on Ishigaki Island, South Japan. Jpn. J. Ecol. **33:** 231–234.

Tenore, K. R., L. Cammen, S. E. G. Findlay, and N. Phillips. 1982. Perspectives of research on detritus: Do factors controlling the availability of detritus to macroconsumers depend on its source? J. Mar. Res. **40:** 473–490.

Tsokos, C. P. 1972. Probability distributions: An introduction to probability theory with applications. Duxburry.

Valentine, J. F., and K. L. Heck, Jr. 1991. The role of sea urchin grazing in regulating subtropical seagrass meadows: Evidence from field manipulations in the northern Gulf of Mexico. J. Exp. Mar. Biol. Ecol. **154:** 215–230.

Valiela, I. 1995. Marine ecological processes, 2nd ed. Springer.

———, and J. M. Teal. 1979. The nitrogen budget of a salt marsh ecosystem. Nature **280:** 652–656.

Welschmeyer, N. A., and C. J. Lorenzen. 1985. Chlorophyll budgets: Zooplankton grazing and phytoplankton growth in a temperate fjord and the Central Pacific Gyres. Limnol. Oceanogr. **30:** 1–21.

White, D. S., and B. L. Howes. 1994. Long-term ^{15}N-nitrogen retention in the vegetated sediments of a New England salt marsh. Limnol. Oceanogr. **39:** 1878–1892.

Wiebe, P. H. 1988. Functional regression equations for zooplankton displacement volume, wet weight, dry weight, and carbon: A correction. Fish. Bull. **86:** 833–835.

Zar, J. H. 1984. Biostatistical analysis. Prentice Hall.

Zieman, D. A., P. K. Bienfag, K. W. Fulton-Bennett, W. Kottenmeier, and L. D. Conquest. 1993. Carbon budget for the spring bloom in Auke Bay, Alaska. Mar. Biol. **105:** 509–521.

Zieman, J. C., G. Thayer, M. Robblee, and R. Zieman. 1979. Production and export of seagrasses from a tropical bay, p. 21–34. *In* R. J. Livingston [ed.], Ecological processes in coastal and marine systems. Plenum.

———, and R. G. Wetzel. 1980. Productivity in seagrasses: Methods and rates, p. 87–116. *In* R. C. Phillips and C. P. McRoy [eds.], Handbook of seagrass biology: An ecosystem perspective. Garland STPM Press.

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