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Phytoplankton growth, microzooplankton grazing, and carbon cycling in marine systems

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Abstract

We present an analysis of the global impact of microplanktonic grazers on marine phytoplankton and its implications for remineralization processes in the microbial community. The data were obtained by an extensive literature search that yielded 788 paired rate estimates of autotrophic growth (μ) and microzooplankton grazing (m) from dilution experiments. From studies in which phytoplankton standing stock was measured in terms of carbon equivalents, we show that the production estimate from dilution experiments is a reasonable proxy ($r = 0.89$) for production determined by the standard ^{14}C method. The ratio $m:\mu$, the proportion of primary production (PP) consumed by micrograzers, shows that microzooplankton consumption is the main source of phytoplankton mortality in the oceans, accounting for 67% of phytoplankton daily growth for the full data set. This ratio varies modestly among various marine habitats and regions, with data averages ranging from 60% for coastal and estuarine environments to 70% for the open oceans, and from ~59% for temperate–subpolar and polar systems to 75% for tropical–subtropical regions. Given estimates for the metabolic requirements of micrograzers and assuming they consume most bacterial production, regionally averaged estimates of the protistan respiration are 35–43% of daily PP for the first level of consumer or 49–59% of PP for three trophic transfers. The estimated contributions of microbial grazers to total community respiration are of the same magnitude as bacterial respiration. Consequently, potential ecosystem differences in micrograzer activity or trophic structure are a large uncertainty for biogeochemical models that seek to predict the microbial community role in carbon cycling from bacterial parameters alone.

Although old and new paradigms of community structure and trophic interactions are strongly integrated in contemporary views of the marine plankton (e.g., Sherr and Sherr 1988; Legendre and Rassoulzadegan 1996), classical and microbial pathways remain a useful dichotomy for distinguishing the alternate fates of primary production (PP). The production originated as large classical diatoms, e.g., is the portion most efficiently transferred to higher levels of the food web, like fish, by a short chain of consumers (Ryther 1969) or exported from the euphotic zone as the fecal pellets of large grazers or the mass sinking of cell aggregates (Turner 2002). In contrast, production generated or consumed within the microbial community is largely lost to multiple trophic transfers and remineralization within the euphotic zone, with the exception of energy transfer through fine-particle suspension feeders (e.g., appendicularians). The fraction of community production diverted through the microbial components of the food web is thus a characteristic that could potentially vary among regions and ecosystem types, with implications for carbon cycling, biogeochemical fluxes, trophic ecology, and potential fishery yield (e.g., Mann 1993; Legendre and Rassoulzadegan 1996).

In recent studies, two different perspectives have emerged on the losses of PP through microbial components of the food web. The first is based on the role of microzooplankton (i.e., the <200-μm herbivores, dominated by protists) as consumers of phytoplankton. To quantify this trophic pathway, relevant assessments of phytoplankton growth and microzooplankton grazing have been systematically conducted in a variety of oceanic habitats as part of the JGOFS (Joint Global Ocean Flux Studies) Program, and often with contemporaneous measurements of mesozooplankton grazing, sinking, and advective losses (e.g., Landry et al. 1997; Le Borgne and Landry in press). Such results indicate that microzooplankton tend to dominate mesozooplankton as primary consumers, especially in the open oceans, and that their grazing impact often accounts for most of the measured phytoplankton production.

The second perspective is based on the biogeochemical mass balance of production and respiration processes. As elucidated by Rivkin and Legendre (2001), this view highlights the importance of bacterial respiration to total community utilization of PP. Bacterial production rates and bacterial growth efficiencies thus become the critical constraints on carbon cycling and export in the oceans rather than the portion of PP consumed by microzooplankton. Nonetheless, if these bacterial parameters are to be usefully applied as community respiration proxies for estimating regional and global patterns in carbon cycling, as Rivkin and Legendre (2001) have proposed, it is important to examine whether

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interregional variability in microzooplankton grazing losses complements or confounds their trends. After all, in regions where protistan zooplankton may consume almost all PP, they cannot at the same time be inconsequential to community respiration and carbon remineralization processes.

In the present study, we consider the role of microzooplankton as consumers of phytoplankton based on a synthesis of 20 years of experimental studies by the dilution technique (Landry and Hassett 1982). Our focus is not on a critical review of each data product or of the approach per se, but rather on general trends, the extent to which they vary among tropical to polar regions and near-coastal to oceanic habitats and what they imply about the fates of PP in the oceans.

Methods

The data were obtained by an extensive literature search for all studies in which rates of phytoplankton growth and microzooplankton grazing were estimated by the dilution technique (Landry and Hassett 1982). Only data from experiments dealing with natural marine ecosystems were used, including an open-ocean iron-enrichment experiment (IronEx II; Landry et al. 2000) but excluding research with artificial mesocosms. The resulting data set includes 788 paired observations of autotrophic growth and grazing mortality obtained from 66 studies spanning four orders of magnitude of chlorophyll concentration. The full data set is available in Web Appendix 1 at http://www.aslo.org/lo/vol_49/issue_1/0051a1.pdf. Of the data pairs, 510 (65%) are from oceanic (open-ocean waters) habitats, with the remainder divided about equally between coastal (overlying the continental shelf = 142) and estuarine (including coastal embayments = 136) habitats. In terms of major water mass types, 259 data pairs (33%) are from tropical–subtropical regions, 435 (55%) from temperate–subpolar regions, and 94 (12%) from polar systems, principally Antarctic waters.

As the primary strategy for analysis, we used the whole data set with minimal modification and selection. Nonetheless, several modest changes were made to facilitate the calculations. First, we assumed that photoacclimation responses of the phytoplankton to experimental incubation conditions and/or day-to-day variations in light levels would produce offsetting positive and negative errors in the growth-rate estimates, but that some negative estimates would be expected by this process. A total of 29 negative, but generally small, growth-rate estimates were found in the data set and corrected to $+0.01$ d^{-1}. The slight positive number was essential to avoid division by zero (see below). Second, negative rate estimates for microzooplankton grazing were set equal to zero. This affected 20 estimates, 10 of which the original authors had determined were not statistically different from zero, and 5 of which were not tested for significance. Of the remaining five significantly negative estimates, four were from a single study (Zhang et al. 2001) and thus likely reflected some methodological deficiency. The original authors did not use these data in their interpretations of ecosystem characteristics, and we elected to do the same (these also included 4 of the 29 cases of negative growth-rate estimates, which were thereby reduced to 25).

As a secondary strategy for data analysis, we selected a priori a subset of the studies (reduced data set) that followed the established protocol for using nutrient-amended dilution treatments to determine grazing estimates and no nutrient controls for the growth-rate estimates (e.g., Landry et al. 1998). Experiments conducted under natural conditions of high nutrients were also included in this reduced composite of 392 data pairs, or about half of the total. The purpose of this secondary analysis was to assess whether potential methodological variations in the larger data set had a substantial impact on our conclusions.

To assess the grazing impact of microzooplankton (G) in terms of the proportion of primary production (PP) consumed, we used the formulas from Landry et al. (2000),

$$\mathrm{PP} = \mu \cdot C_\mathrm{m}$$

$$G = \mathrm{m} \cdot C_\mathrm{m}$$

$$C_\mathrm{m} = C_\mathrm{o}[e^{(\mu-\mathrm{m})t} - 1]/(\mu - \mathrm{m})t$$

where μ = the instantaneous rate of phytoplankton growth (day^{-1}), C_m is mean phytoplankton concentration during the incubations, m = rate of phytoplankton mortality attributable to microzooplankton grazing (day^{-1}), t is incubation time (days), and C_0 is the initial phytoplankton concentration in terms of carbon. Experimental rate estimates for dilution experiments are typically based on measured changes in chlorophyll (Chl) *a*. Thus, for C_0 = initial Chl *a*, the percentage of Chl standing stock consumed day^{-1} is calculated as $G \cdot 100/\mathrm{Chl}_0$. Although C_0 is rarely given as carbon units in the dilution literature, one can readily see that the ratio of interest (G : PP), the fraction of production consumed, reduces simply to the rate ratio of grazing to growth (i.e., G : PP = m : μ) whether C_m is expressed in terms of carbon or pigment (i.e., the concentration terms cancel). Moreover, where C_0 carbon biomass has been determined from microscopical estimates of cell biovolume (BV) and established C : BV conversions, as for example in experiments conducted in the equatorial Pacific (Landry et al. 2000), the Arabian Sea (Brown et al. 2002), and the Southern Ocean (Landry et al. 2002); the derived parameter, PP, is well related ($r = 0.89$) to contemporaneous estimates of PP by the ^{14}C-uptake method (Fig. 1). Thus, the m : μ ratio $\times$ 100 is taken to be a reasonable proxy for the percentage of ^{14}C PP consumed by microzooplankton. Laws et al. (2000) provide a more detailed analysis of the relationship between the dilution growth rate μ and the measured rate of ^{14}C production.

For data-plotting purposes and for computing regional averages of the m : μ ratio, we first transformed the ratio estimates for individual experiments to their arctangent values. This has the effect of reducing the impact of large ratios (i.e., large m relative to μ) on computed averages and making the data distribution more normal. Arctangent averages and standard errors were converted back to percent production consumed using the inverse function, tangent(x).

Results and discussion

Data trends and regional averages—The relationships between rate estimates for grazing mortality (m) and phyto-

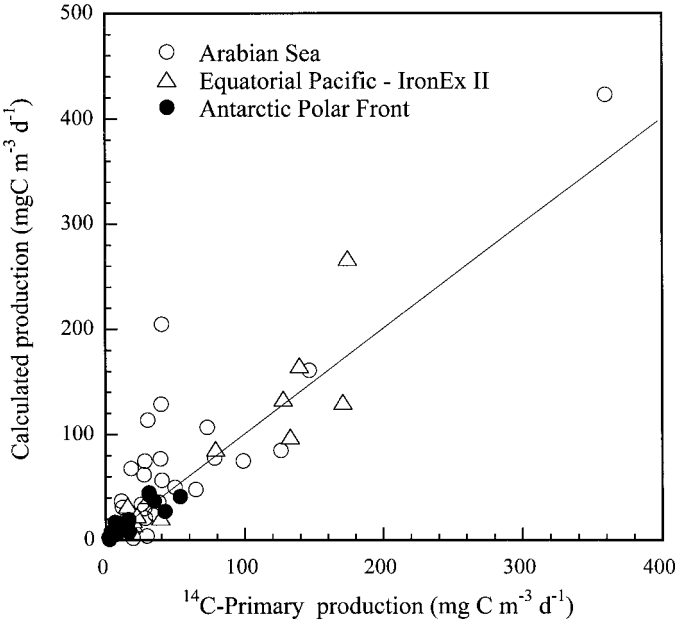

Fig. 1. Relationship between calculated and ^{14}C-based estimates of primary production from dilution experiments conducted in three ocean regions. Calculated primary production was obtained by multiplying phytoplankton growth rates times mean phytoplankton concentration expressed in terms of carbon. Carbon conversion was obtained from volumetric estimates of the phytoplanktonic community and established carbon to biovolume conversions. Equatorial Pacific data from Landry et al. (2000), Arabian Sea data from Brown et al. (2002) and Southern Ocean data from Landry et al. (2002). The line represents a 1 : 1 relationship.

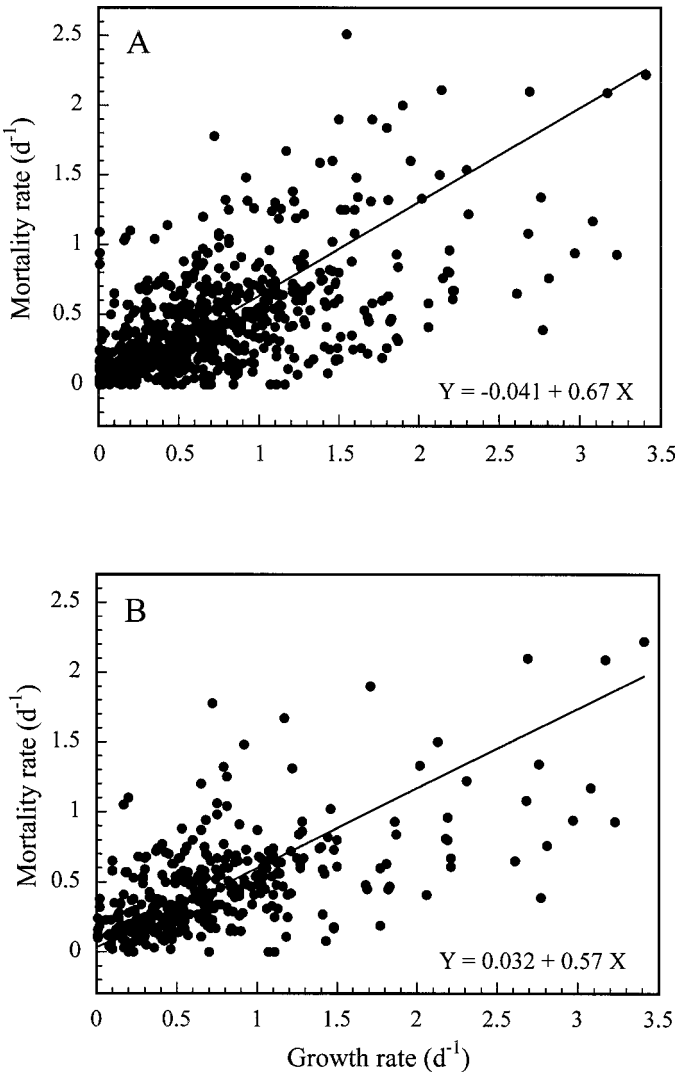

Fig. 2. Scatter plots of paired rate estimates for phytoplankton grazing mortality and phytoplankton growth from dilution experiments. (A) Full data set, (B) reduced data set. The lines and relationships are for Model II linear regressions by reduced major axis ($r = 0.6$ in both cases).

plankton growth (μ) are presented for the full and reduced data sets in Fig. 2A,B, respectively. As judged by the slopes of the linear regressions of m versus μ, microzooplankton consumption accounts on average for 67% of phytoplankton growth in the full data set and a lower 57% in the constrained data set. These slopes can be deceptive, however, because they are forced largely by high-end data extremes, whereas most of the rate estimates, and arguably the more reliable portion, are densely packed in the parameter space <2 cell doublings per day (i.e., 1.4 d^{-1}). As observed in Fig. 3, there is no apparent trend for the transformed m : μ ratios as a function of initial concentration of Chl *a*. At the very high end of the chlorophyll values, the data are dominated by a single study (Ruiz et al. 1998; Mundaka Estuary). These are plotted at 62 μg Chl *a* L^{-1}, the mean chlorophyll estimate, because concentrations were not reported for individual experiments. Because such values are clearly very rare even for rich marine systems, the relatively large number of experiments for this particular ecosystem results in a disproportionate representation of extreme (estuarine) conditions in the data set. On an areal basis, coastal and particularly open-ocean systems are underrepresented, even though they comprise the majority of data available.

For a less biased interpretation of the data trends, we present separate averages of the system characteristics for different divisions of the data by habitat type (Table 1). Characterizing the habitats as oceanic, coastal, or estuarine strongly organizes the data by relative richness of Chl *a*. The richer estuarine/bay systems have higher mean rates of phytoplankton growth (0.97 d^{-1} vs. 0.59 d^{-1} for the open ocean) as well as higher mean rates of microzooplankton grazing mortality (0.53 d^{-1} vs. 0.39 d^{-1}, respectively). Because grazing rates vary proportionately less than phytoplankton growth rate among these habitat categories, however, a higher percentage of PP is consumed in the open-ocean systems. According to these data, approximately 70% of ^{14}C production is consumed on average by microherbivores in oceanic habitats and about 60% in coastal and estuarine systems. Interestingly, because the mean grazing mortality coefficient is higher for estuarine habitats relative

Table 1. Regional comparisons of system characteristics from the full data set of dilution experiments. Data are distinguished among oceanic, coastal (overlying the continental shelf), and estuarine habitats in the upper table and among tropical/subtropical, temperate/subpolar, and polar habitats in the lower table. Mean values (± standard errors) are given for initial Chl *a*, phytoplankton growth rate (μg), grazing mortality (m), % Chl *a* grazed day^{-1}, and % primary production (PP) grazed day^{-1}. Growth and mortality rate averages are significantly different among zones and climates ($p < 0.05$, Tukey–Kramer test), except for oceanic and coastal (μm and m), and for tropical and temperature (μ).

	Chl *a* (μg L^{-1})	μ (day^{-1})	m (day^{-1})	% Chl *a* grazed	% PP grazed
Oceanic	0.58±0.03	0.59±0.02	0.39±0.01	41.5±1.4	69.6±1.5
Coastal	3.06±0.53	0.67±0.05	0.40±0.04	47.3±4.4	59.9±3.3
Estuarine	13.0±1.8	0.97±0.07	0.53±0.04	78.7±7.3	59.7±2.7
Tropical	1.01±0.21	0.72±0.02	0.50±0.02	55.1±2.3	74.5±2.0
Temperate	5.18±0.66	0.69±0.03	0.41±0.02	51.4±2.9	60.8±1.8
Polar	0.62±0.06	0.44±0.05	0.16±0.01	19.5±2.1	59.2±3.3

to coastal and oceanic systems, the daily turnover of phytoplankton standing stock by micrograzers is higher on average where the chlorophyll standing stock is greater (79% d^{-1} vs. 42% d^{-1} for estuarine and open-ocean systems, respectively). One would probably not have anticipated such a difference intuitively.

Dividing the data into tropical (including subtropical), temperate (including subpolar), and polar habitats implicitly organizes the analysis according to mean environmental temperature (not shown because it was not always measured). The temperate systems have the highest mean chlorophyll concentration, but differences in system richness are not as strongly expressed as that for the gradient from estuarine to oceanic habitats. Phytoplankton growth rates are comparable, on average, for tropical and temperate systems (~0.7 d^{-1} = 1 cell doubling d^{-1}), but drop off sharply, as expected, for studies in polar regions (0.4 d^{-1}). Each of the other parameters presented is highest for the tropical regions and lowest for the polar regions. Both the mean rates of grazing mortality (0.16–0.5 d^{-1}) and the mean daily percentage of Chl grazed (19.5–55%) vary by about a factor of three among regions. However, the percentages of PP grazed are not so different, varying from ~60% for studies from temperate and polar systems to ~75% for tropical studies. The latter does not increase significantly (74.8% vs. 74.5%) for experimental sites that are both tropical/subtropical and open ocean. Thus, this appears to be a relatively robust estimate of the mean maximum percentage of PP consumed by micrograzers for ocean conditions where the microbial portion of the food web most strongly dominates.

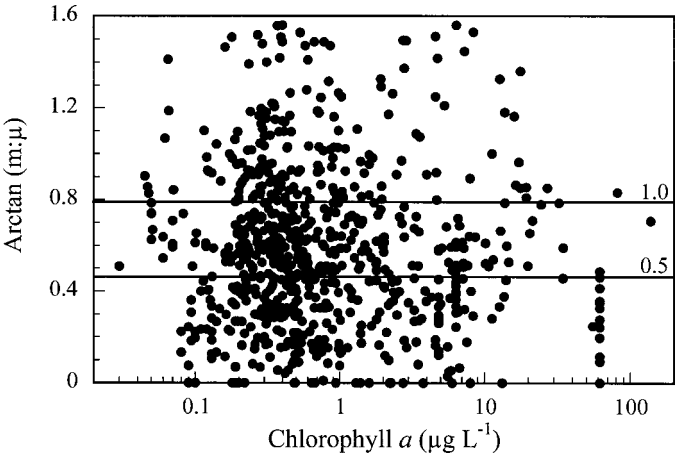

Fig. 3. Scatter plot of the proportion of primary production consumed by micrograzers as a function of initial chlorophyll concentration. Data is derived as the ratio of grazing mortality to growth rate (m : μ) from dilution experiments and arctangent transformed for a more normal distribution. For reference, the lines labeled 1.0 and 0.5 refer, respectively, to grazing mortalities equal to 100% and 50% of concurrent estimates of phytoplankton growth.

The comparison of % PP grazed for the full and reduced data sets show the largest differences for the analysis of estuarine, coastal, and oceanic regions (Table 2). Because the restricted data set does not consider experiments conducted in nutrient-poor waters without the appropriate nutrient addition treatments and controls (e.g., Landry et al. 1998), it should better reflect the true relationship between grazing and growth in such systems. Thus, the mean estimate of % PP consumed is increased somewhat relative to the full data set. For the estuarine comparison, the reduced data analysis is strongly dominated by 38 experiments from the Ruiz et al. (1998) study, which exceed all other data combined. Because this very eutrophic system is atypical of estuarine and near-coastal waters generally, the available data are simply too limited to draw any insight from the substantial difference in the full and reduced data means for such habitats. Intuitively, however, we might expect that the role of micro-

Table 2. Comparisons of % primary production grazed day^{-1} for the full and reduced data sets of dilution experiments. Data are averages (±standard errors) for oceanic, coastal, and estuarine habitats in the upper table and for tropical/subtropical, temperate/subpolar, and polar habitats in the lower table.

Habitat	Full data	Reduced data
Oceanic	69.6±1.5	78.0±1.8
Coastal	59.9±3.3	56.6±2.9
Estuarine	59.7±2.7	38.6±2.5
Tropical/subtropical	74.5±2.0	71.3±2.3
Temperature/subpolar	60.8±1.8	68.8±2.3
Polar	59.2±3.3	65.2±3.7

zooplankton as consumers of phytoplankton production would be diminished in very shallow water systems where direct consumption by benthic filter feeders can be an important loss factor (e.g., Murrell and Hollibaugh 1998). For the tropical–temperate–polar region comparison, % PP grazed was more similar among the different regions in the reduced data analysis, varying only modestly from 65% to 71%. This is not particularly surprising, as the reduced data set is comprised mostly of open-ocean experiments. Nonetheless, it begs the question of whether fundamental differences exist among tropical, temperate, and polar open-ocean systems with respect to the fraction of PP consumed by microherbivores. One might expect this to be the case based on perceptions of the size differences of dominant primary producers in such systems, but the evidence thus far does not indicate a large effect.

Implications for grazing and respiration budgets—One obvious conclusion from the present analysis is that microzooplankton grazing represents the major loss term for phytoplankton cell growth and classically measured PP (^{14}C method) across a broad range of ocean regions and habitats. There are clearly times and places where microzooplankton do not consume the majority of phytoplankton production, just as there are circumstances where their grazing exceeds local contemporaneous production. However, none of the regional or ecosystem categories that we considered stands out as having an unusually low mean grazing impact of microzooplankton. In fact, the mean grazing impacts of microherbivores fall within a relatively narrow range, 59–75% of PP, for environments varying from estuarine to oceanic and from tropical to polar.

Tight control of phytoplankton production by micrograzers is a cornerstone of our understanding of how the central regions of the oceans function with respect to general system oligotrophy and iron limitation (e.g., Landry et al. 1997). However, the relatively important role of microzooplankton as primary consumers in more productive waters is somewhat surprising because large zooplankton have traditionally been considered the major grazers in such regions. Because they can grow and divide as rapidly as phytoplankton cells, protistan microherbivores derive considerable advantage over larger metazoans in their ability to exploit ephemeral changes in food availability (e.g., Miller et al. 1995). Their grazing pressure is thus better coupled to production processes relative to slow-responding metazoans. In addition, within the broad size range and diversity of protists, there is more capability (among dinoflagellates, in particular) for preying on large phytoplankton, including diatoms and cell chains, than generally appreciated (e.g., Strom and Buskey 1993; Hansen et al. 1994; see also Landry et al. 2000; Strom et al. 2001; Landry et al. 2002). Large metazoans are not rendered irrelevant by a more uniform dominance of microherbivory in the oceans (Calbet 2001), but their different roles—as exporters of euphotic zone production, as trophic connections to fish stocks, and structuring agents of the marine plankton—need to be kept in perspective. In addition, by virtue of their selective predatory impacts on the microherbivores, the indirect role of mesozooplankton in grazing processes may be substantial (Buskey et al. 2003).

To account for the potential contribution of microzooplankton to community respiration, we must first consider the portion of their bulk food consumption lost to metabolic processes. A respiratory cost on the order of 50% of food ingested would be consistent with the general magnitude of gross growth efficiencies (GGE) for proto- and metazooplankton (~30%; Straile 1997), net growth-rate estimates based on allometric scaling of protistan growth and respiration rates (Fenchel and Findlay 1983), as well as direct assessments from protistan carbon budgets (e.g., Verity 1985). Applying this estimate to the mean percentages of PP grazed in Table 1, about 30–38% of production should be respired by protistan herbivores. To this, we can reasonably add 5% of PP to account for the feeding of bacterivorous protists on net bacterial production, which we take as 10–15% of PP (Anderson and Ducklow 2001), assuming that some goes to viral lysis.

One variable that is not considered in the present analysis, but which likely defines a major difference among ecosystems, is the average number of grazing links in the microbial food web before protists are consumed by larger metazoans. If we take 35–43% of PP as a reasonable estimate of respiratory loss by the primary level of protistan consumers and assume that their production can be passed to predators with an efficiency of 30%, then 46–55% of PP will be respired after two levels of protistan consumers and 49–59% after three levels. Although additional levels may be possible where PP is dominated by tiny prokaryotes (e.g., Calbet and Landry 1999; Calbet et al. 2001), relatively little new respiration is added with more transfers.

The above calculations illustrate that particle-feeding protists within the marine microbial food web can reasonably account for contributions to community respiration similar to those ascribed to bacteria (~50% of PP, Anderson and Ducklow 2001; 50–90%, Rivkin and Legendre 2001). In accounting for the respiratory contributions of micrograzers and bacteria, both of which may consistently exceed half of measured PP, it is important to keep in mind that the ^{14}C method does not measure all of the carbon fixed. Some is utilized and cycled during the incubation (e.g., Laws et al. 2000) and production of labeled dissolved organic carbon is often inadequately measured. For instance, Karl et al. (1998) have suggested that gross PP rates in the subtropical Pacific may be double that typically reported as ^{14}C-particulate uptake. This issue is also relevant to any approach that seeks to constrain the fluxes of PP to higher tropic levels and to export process by subtracting the losses to microbial recycling. We first need to establish the true total production to which these losses will be applied.

Rivkin and Legendre (2001) have suggested that, because bacterial respiration represents a large loss term relative to PP and because bacterial GGE appears to be well correlated with temperature, bacterial rate parameters might be predictable from satellite observations and usefully applied as

a proxy for total community respiration in global carbon models. As they have noted, however, this depends on bacterial respiration representing a relatively constant or predictable proportion of total community metabolism. If the present analysis is correct, respiratory losses to microbial particle grazers of about the same magnitude as bacterial respiration could provide a large source of unresolved error to such extrapolations. The relative constancy (on average) of phytoplankton production losses to microherbivores suggests that there may still be some utility to the Rivkin and Legendre (2001) approach if bacterial production and microherbivory both track PP in some predictable or common manner. As articulated above, however, there are likely to be substantial differences in the lengths of protistan predatory chains among different ocean regions. For example, there is evidence for long pathways that maximize protistan remineralization in the oligotrophic open oceans (e.g., Calbet and Landry 1999; Calbet et al. 2001). In contrast, systems in which the relatively large protistan herbivores may be consumed directly by large metazoans (e.g., *Neocalanus* feeding on ciliates in the subarctic Pacific; Miller et al. 1991) will lose much less matter to protistan respiration for approximately the same direct grazing impact on phytoplankton. According to the calculations above, the contribution of protistan consumers to community respiration could vary by about a factor of two (about 25% of PP) for these two conditions. This is a sizeable error if the goal is to predict export rates of about this magnitude or less. We thus believe that the structure of protistan grazing pathways needs to be better understood for various ocean regimes in order to account for carbon losses within the microbial community in global models.

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