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Microzooplankton production in the oceans

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A literature synthesis of phytoplankton growth (μ) and grazing (m) rate estimates from dilution experiments reveals that microzooplankton account for most phytoplankton mortality in the oceans, averaging 60–75% of daily phytoplankton production (PP) across a spectrum of open-ocean and coastal systems. For reasonable estimates of gross growth efficiency (GGE = 30–40%), such impacts imply that secondary production rates of microzooplankton ($MP_{2°}$) are typically in the range 21–34% of PP. However, multiple trophic transfers within the microbial community can further enhance total microzooplankton production by an additional third to a half (MP_{tot} = 28–55% of PP). These estimates are 2–5 times typical values for bacterial production (10–15% of PP). Thus, in aggregate and on average, microzooplankton consume substantially more (6–7 times) production from phytoplankton than from heterotrophic bacteria. High grazing impacts and relatively high GGEs are consistent with population growth rates for microzooplankton and phytoplankton that are roughly equivalent under ambient conditions, which may be requisite for grazing regulation. Transfer efficiencies of microzooplankton production to mesozooplankton depend critically on the number of predatory interactions among microconsumers, and may be one way in which systems differ substantially. Overall, the ability to quantify microzooplankton production in terms of more broadly measured rates of PP provides a potential avenue for broadening our understanding of ocean community dynamics through remote sensing and modelling.

Keywords: grazing, growth, heterotrophic protists, phytoplankton, production.

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Introduction

Over the past decade, oceanographic field investigations have established that "microzooplankton", broadly the protistan-dominated <200-μm size fraction of pelagic consumers, comprise the primary grazers of phytoplankton in the open oceans (e.g. Landry *et al.*, 1993, 1997, 1998; Verity *et al.*, 1993; Quevedo and Anadón, 2001; Liu *et al.*, 2002). Micro-herbivores also appear frequently as grazing dominants in coastal ecosystems (e.g. Gallegos *et al.*, 1996; Lehrter *et al.*, 1999). In addition, protistan microzooplankton are increasingly viewed as a major component of mesozooplankton nutrition, filling shortfalls in metabolic requirements not met by phytoplankton alone or representing outright the primary food resource (Stoecker and Capuzzo, 1990; Gifford, 1993; Prestidge *et al.*, 1995; Van Wambeke *et al.*, 1996; Roman and Gauzens, 1997; Klein Breteler *et al.*, 1999). Despite the now obvious importance of microzooplankton as trophic intermediaries in the marine foodweb, the magnitude of their production remains poorly characterized. There are, in fact, no established protocols for making such rate measurements from ships or satellites, and there have certainly been no systematic studies on the subject. Regardless, given the theme of the 3rd International Symposium on Zooplankton Production, it seems appropriate, both in time and place, to address this long neglected topic.

We take the view here that more can be surmised about the general magnitude of microzooplankton community production in the oceans than is presently apparent from the dearth of its discussion in the literature. The information remains to be extracted from the relevant data on related processes, augmented with appropriate assumptions, and presented in an organized context. Our goal is therefore to develop a reasonable logic for extending from what we know about microzooplankton rate processes in the oceans, namely grazing impact on phytoplankton, to what we would like to know about their production. To do this, we first briefly review the database for microzooplankton grazing. We then consider the principles and the relatively simple computations through which grazing estimates can

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be related to microzooplankton secondary production, total production, instantaneous rates of population growth, and production transfer to mesozooplankton. The central thread of this discussion is that each of these manifestations of microzooplankton production can be reasonably expressed in terms of the rates of primary production, for which there exist an extensive database, global models, and remote measurement capabilities. These connections thus provide a potential avenue through which our theoretical and practical understanding of plankton community dynamics might be tested and advanced.

Data set and analytical methods

The present analysis is based on a synthesis of paired estimates for the instantaneous rates of phytoplankton growth (μ, d^{-1}) and phytoplankton grazing mortality by microzooplankton (m, d^{-1}) from studies employing the dilution technique (Landry and Hassett, 1982). As noted in the primary synthesis (Calbet and Landry, 2004), the data set comprises 788 experiments from 66 studies, which we have partitioned in two ways: according to *oceanic*, *coastal* (overlying the continental shelf) and *estuarine* (including coastal bays) habitats; and according to *tropical–subtropical*, *temperate–sub-polar*, and *polar* (principally Antarctic) regions.

For analysis, we used the whole data set with minimal modification and selection. Of 20 negative rate estimates for microzooplankton grazing, only 5 were evaluated as significantly different from zero by the original authors, and 4 of these were from the same study (Zhang *et al.*, 2001). Since the estimates from these four experiments likely reflected some (undefined) methodological deficiency, we excluded them from the data analysis. The remaining negative grazing estimates were taken to be zero. For calculation purposes, we also adjusted 25 negative rate estimates for phytoplankton growth to $+0.01\ d^{-1}$. These negative numbers were generally very small and, since the rate estimates were based on measured changes of chlorophyll *a*, they were assumed to represent day-to-day photoacclimation responses of phytoplankton pigments and/or pigment adjustments to the incubation light levels. The slight positive number avoids division by zero in computing the percent of production consumed, as described below.

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):

$$PP = \mu \times C_m$$

$$G = m \times C_m$$

$$C_m = C_o(e^{(\mu - m)t} - 1)/(\mu - m)t$$

where C_m is mean phytoplankton concentration during the incubations, "t" is incubation time (d), and C_o is the initial phytoplankton concentration in terms of carbon. Although the phytoplankton concentration measurements for dilution experiments are more typically made as chlorophyll *a*, the ratio of interest (G:PP = the fraction of production consumed) reduces to the rate ratio of grazing to growth (i.e. $G/PP = m/\mu$) regardless of whether C_m is expressed as carbon or pigment. In studies where C_o 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 to contemporaneous estimates of primary production by the ^{14}C-uptake method (Calbet and Landry, 2004). Thus, the m:μ ratio $\times$ 100 is taken to be a reasonable proxy for the percentage of ^{14}C primary production consumed by microzooplankton.

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 percentage production consumed using the inverse function, tangent(x).

Microzooplankton grazing impact and secondary production

As noted above, the m:μ rate ratios from dilution experiments provide instantaneous estimates of the proportion of primary production (PP) consumed by microzooplankton. Such ratios can vary broadly for individual experiments, indicating little or no grazing on one extreme to grazing several times in excess of daily production on the other (Calbet and Landry, 2004). The precision of individual ratio estimates, however, is relatively good (mean coefficient of variation = 30%), as established from 42 fully replicated experiments (separate water collection, set-up, incubation, and processing) from the equatorial Pacific, Arabian Sea, and Southern Ocean (Brown, 2001). Thus, the high variability appears to reflect the daily dynamics of predator and prey, as well as daily light-dependent adjustments of pigment content. Such temporal fluctuations are assumed to offset one another when averaged over the reasonably large numbers of experiments conducted in broadly defined hydrographic regions of the oceans (Table 1).

According to the dilution data synthesis, direct consumption by micro-herbivores accounts for the majority of the loss of phytoplankton production across the full spectrum of major pelagic marine habitats. As expected by the dominance of relatively small phytoplankton in open-ocean and particularly tropical/subtropical ecosystems, the portion of PP consumed by micro-grazers is highest in such habitats, 70% and 75%, respectively (Table 1). Nonetheless, even

Table 1. Regional comparisons of system characteristics from dilution experiments. Data are distinguished among *Oceanic*, *Coastal* (overlying the continental shelf), and *Estuarine* (including coastal bays) habitats in the upper table and among *Tropical/Subtropical*, *Temperate/Sub-polar*, and *Polar* regions in the lower table. Mean values (± standard errors) are given for initial Chl *a*, phytoplankton growth rate (μ), grazing mortality (m), and percentage primary production grazed d^{-1}. Exp = number of experimental estimates averaged for the region, out of a total of 788.

	Exp (% total)	Chl *a* ($\mu g\, l^{-1}$)	μ (d^{-1})	m (d^{-1})	% PP grazed
Oceanic	510 (65%)	0.58 ± 0.03	0.59 ± 0.02	0.39 ± 0.01	69.6 ± 1.5
Coastal	142 (18%)	3.06 ± 0.53	0.67 ± 0.05	0.40 ± 0.04	59.9 ± 3.3
Estuarine	136 (17%)	13.0 ± 1.8	0.97 ± 0.07	0.53 ± 0.04	59.7 ± 2.7
Tropical	259 (33%)	1.01 ± 0.21	0.72 ± 0.02	0.50 ± 0.02	74.5 ± 2.0
Temperate	435 (55%)	5.18 ± 0.66	0.69 ± 0.03	0.41 ± 0.02	60.8 ± 1.8
Polar	94 (12%)	0.62 ± 0.06	0.44 ± 0.05	0.16 ± 0.01	59.2 ± 3.3

relatively rich coastal and estuarine systems and the colder, more seasonally dynamic temperate and polar regions show high, as well as similar, mean ratios of micro-herbivory. For all of the habitat categories considered, PP consumption by microzooplankton ranges only from ~60% to 75%. The same upper limit (75%) is found by selectively averaging only the results from experiments conducted in waters that are both tropical and open ocean.

Since nanoflagellates typically comprise the first grazing step in the microbial loop for the biomass produced by heterotrophic bacteria (Azam *et al.*, 1983), it is reasonable to include an additional grazing term for the transfer of this resource to the microzooplankton assemblage. According to Anderson and Ducklow (2001), bacterial production (BP) generally ranges from 10% to 15% of PP for a variety of ocean habitats. We take the lower value ($0.1 \times$ PP) as our estimate of grazed BP, allowing that some BP is lost to viral lysis (viral loss may also account in part for the low estimates of bacterial GGE used to compute BP). In subsequent equations, the expression $(m : \mu + 0.1) \times PP$ thus represents the combined rates of consumption of PP and BP by microzooplankton.

First-order estimates of microzooplankton secondary production ($MP_{2\circ}$) can be derived from community grazing (ingestion) rates according to the equation:

$$MP_{2\circ} = GGE \times (m : \mu + 0.1) \times PP$$

where GGE (gross growth efficiency) is the decimal fraction of ingested carbon incorporated into growth. In applying this equation, we assume that GGE is roughly constant, averaged over *regionally adapted assemblages* of microzooplankton. This assumption is based, in part, on the low basal metabolic requirements of protistan consumers (Fenchel and Finlay, 1983), which make their individual GGEs less sensitive to varying food availability compared to larger mesozooplankton. The compositional plasticity of micro-herbivore assemblages also contributes to relative GGE constancy. Thus, while some protists (e.g. large ciliates) may be at or below food thresholds for positive growth in the oligotrophic oceans, such conditions naturally select for more efficient dominants, namely flagellates and mixotrophs. The GGE synthesis of Straile (1997) indicates that 30% would be a reasonable average estimate for mixed protistan communities. However, Rivkin and Legendre (2001) suggest even higher efficiencies (~40%). For the sake of comparison, we use both of these GGE estimates for our calculations of $MP_{2\circ}$.

Given mean grazing estimates in Table 1 and the assumptions above, the magnitude of microzooplankton secondary production ($MP_{2\circ}$) can be readily constrained as a percentage of primary production (Table 2). For GGE = 30%, the mean estimates of $MP_{2\circ}$ vary narrowly among the ocean regions and habitats compared, from ~21% to 25% of PP. Trivially, $MP_{2\circ}$ estimates for GGE = 40% (~28–34% of PP) are exactly one-third higher than those for GGE = 30% because of the direct multiplicative effect of the GGE assumed.

For clarity, we emphasize that the production estimates in Table 2 apply only to the first step of trophic pathways in which microzooplankton serve as the "primary consumers" of phytoplankton and bacterial production. We have not distinguished the relative amounts of PP consumption that come from eukaryotic versus prokaryotic primary producers, the latter (e.g. *Prochlorococcus* and *Synechococcus* spp.) being particularly important in the oceanic tropical

Table 2. Calculated estimates of microzooplankton secondary production ($MP_{2\circ}$) as a percentage of daily primary production. Calculations are based on the mean regional/habitat estimates of microzooplankton grazing on phytoplankton from Table 1 with assumed gross growth efficiencies (GGEs) of 30% and 40%.

	GGE = 0.3	GGE = 0.4
Oceanic	23.9	31.8
Coastal	21.0	28.0
Estuarine	20.9	27.9
Tropical	25.4	33.8
Temperate	21.2	28.3
Polar	20.8	27.7

and subtropical waters. Nor have we made allowances for shallow, eutrophic coastal systems where heterotrophic bacterial production may be strongly decoupled from PP by alternate sources of organic matter (i.e. BP > 0.1PP). Given these caveats, however, it is instructive to note that the relative magnitudes of the microzooplankton grazing fluxes from phytoplankton and heterotrophic bacteria differ by a factor of 6–7, on average, for the major ocean subregions considered. From this we conclude that microzooplankton nutrition is, at least in the euphotic zone, many times more dependent on the consumption of phytoplankton than bacterial production.

Total production and mean growth rates of the microzooplankton

Owing to the predatory interactions among component populations of the microzooplankton, total microzooplankton production (MP_{tot}) can be significantly higher than we have computed above as true "secondary" production. The total estimate depends on the number of trophic transfers (n) within the microzooplankton, beginning with n = 1 for the primary consumers of phytoplankton and bacteria up to the mean number of subsequent steps before microzooplankton are lost as food to >200-μm consumers (e.g. mesozooplankton). Accordingly, for i = 1 to n,

$$MP_{tot} = (m : \mu + 0.1) \times PP \times \Sigma GGE^{i}$$

Production estimates for this calculation are given in Table 3 with the individual regional/habitat averages from previous tables now expressed as a range of values. For example, the production range for primary consumers (n = 1) and GGE = 30% in Table 3 (MP_{tot} = 21–25% PP) is the same as that represented for the individual regional/habitat groups in Table 2. An additional two trophic transfers within the microzooplankton (n = 3) elevates MP_{tot} by more than one-third, from 28% to 35%, but there is little further gain to be had by considering more steps. As intuition would suggest, the effect of the additional trophic transfers is magnified by using the higher GGE (=40%); for n = 3, MP_{tot} is enhanced by more than 50% over $MP_{2\circ}$. For open-ocean and tropical ecosystems, where microzooplankton consume the highest amount of PP and where the tiny size of dominant primary producers leads to many levels of protistan consumers (Calbet *et al.*, 2001), MP_{tot} should average about 35% and >50% of PP for GGE = 30% and 40%, respectively. Such estimates are 2–5 times the mean production rates of heterotrophic bacteria for these regions (Anderson and Ducklow, 2001).

In principle, it would be useful to be able to determine the instantaneous growth rates of the primary consumers of phytoplankton and bacteria, but this is difficult without knowing the exact biomass of microzooplankton to which $MP_{2\circ}$ applies. Thus, MP_{tot} is the appropriate production term for estimating a mean growth rate for the microzooplankton assemblage. We do this by recognizing that MP_{tot} at steady state can be expressed as the product of an instantaneous growth rate and a mean biomass; $MP_{tot} = \mu_{\mu Zoo} \times B_{\mu Zoo} = (m : \mu + 0.1) \times PP \times \Sigma GGE^{i}$. Letting $X = (m : \mu + 0.1) \times \Sigma GGE^{i}$ (i.e. the values in Table 3 for various n and GGE) and substituting the identity $PP = \mu_{phyto} \times B_{phyto}$ yields the following relationship between biomass and growth rate ratios for phytoplankton and microzooplankton grazers

$$\mu_{\mu Zoo} = X \times \mu_{phyto} \times (B_{phyto}/B_{\mu Zoo})$$

We illustrate the calculation of $\mu_{\mu Zoo}$ in Table 4 using mean estimates of μ_{phyto} and B_{phyto}:$B_{\mu Zoo}$ ratios from experiments conducted in the Arabian Sea (Brown *et al.*, 2002) and the Southern Ocean (Landry *et al.*, 2002). For GGE = 30% and a realistic number of trophic transfers (n = 2 or 3), the data are consistent with mean instantaneous growth rates for the microzooplankton community that are roughly comparable to those for their phytoplankton prey. Although GGE values are assumed in these examples, rather than independently measured, one can readily appreciate that, with reasonable growth efficiencies, microzooplankton are in a position to exert a significant

Table 3. Calculated estimates of microzooplankton total production (MP_{tot}) as a percentage of daily primary production. Calculations are based on the ranges of regional/habitat estimates for microzooplankton secondary production ($MP_{2\circ}$) in Table 2 for different numbers (n) of predatory levels within the microplankton assemblage.

n	GGE = 0.3	GGE = 0.4
1	20.8–25.4	27.7–33.8
2	27.0–33.0	38.8–47.3
3	28.4–34.6	42.9–52.4
4	29.1–35.5	45.0–54.9

Table 4. Calculated estimates of microzooplankton growth rate ($\mu_{\mu Zoo}$) based on phytoplankton growth (μ_{phyto}) and phytoplankton–microzooplankton biomass ratios (B_{phyto}:$B_{\mu Zoo}$) from dilution experiments conducted in the Arabian Sea (Brown *et al.*, 2002) and the Southern Ocean (Antarctic Polar Front; Landry *et al.*, 2002). All rate estimates are d^{-1}. Calculations assume a gross growth efficiency (GGE) = 30% for different numbers (n) of predatory levels within the microplankton assemblage.

			$\mu_{\mu Zoo}$ for n grazer levels		
	μ_{phyto}	B_{phyto}:$B_{\mu Zoo}$	1	2	3
Arabian Sea	0.79	3.8	0.64	0.83	0.87
Southern Ocean	0.28	2.2	0.18	0.24	0.25

regulatory influence on phytoplankton by virtue of their comparable growth rates and large grazing impact. Inversely, if the ability to grow at rates comparable to the phytoplankton is taken as a requisite regulatory characteristic for the micro-grazer assemblage, this condition cannot be met, given observed B_{phyto}:$B_{\mu Zoo}$ ratios, when either microzooplankton grazing impact or GGE is low. These results thus provide an internally consistent perspective on the biomass structure and dynamics of phytoplankton and their dominant consumers.

Production transfer to mesozooplankton

In considering the potential role of microzooplankton as a food resource for larger animals (e.g. mesozooplankton) in the oceans, it is important to recognize that neither secondary ($MP_{2\circ}$) nor total (MP_{tot}) production may be fully available. Since predators within the microbial community compete for these resources, the transfer production estimate must take these losses into account. For n = the mean number of trophic transfers involving micro-grazers, the residual production available to mesozooplankton is

$$MP_{meso} = GGE^{n} \times PP \times (m : \mu + 0.1)$$

Among the various representations of microzooplankton production considered above, MP_{meso} is clearly the most sensitive to n (Table 5). Relatively large amounts of production (21−34% of PP depending on region and GGE) are potentially available to mesozooplankton under conditions where they can directly exploit the primary microconsumers. For example, because the Subarctic Pacific is dominated by very large suspension-feeding copepods (*Neocalanus* spp.) with fine feeding appendages, this may be one open-ocean region where much of the secondary production of microzooplankton ($MP_{2\circ}$) can make its way to higher levels (Miller *et al.*, 1991; Gifford, 1993). In contrast, the tiny flagellate consumers and long trophic pathways of oligotrophic subtropical waters are clearly incompatible with an efficient transfer of microzooplankton production to higher levels (e.g. Calbet and Landry, 1999).

Table 5. Calculated estimates of microzooplankton production transfer to mesozooplankton (MP_{meso}) as a per cent of daily primary production. Calculations are based on the ranges of regional/habitat estimates for microzooplankton secondary production ($MP_{2\circ}$) in Table 2 for different numbers (n) of predatory levels within the microplankton assemblage.

n	GGE = 0.3	GGE = 0.4
1	20.8−25.4	27.7−33.8
2	6.2−7.6	11.1−13.5
3	1.9−2.3	4.4−5.4
4	0.6−0.7	1.8−2.2

To evaluate the nutritional contribution of microzooplankton to higher level consumers, the relatively modest MP_{meso} fluxes in Table 5 need to be viewed relative to the direct exploitation of phytoplankton by the mesozooplankton, which is often inefficient due to size incompatibilities. Based on gut pigment assessments of herbivory, for example, grazing impacts of a few percent of phytoplankton standing stocks and production rates d^{-1} are fairly typical for the open ocean (e.g. Bautista and Harris, 1992; Dagg, 1993; Dam *et al.*, 1993, 1995; Landry *et al.*, 1994; Rollwagen Bollens and Landry, 2000). Moreover, measured feeding rates on phytoplankton are often insufficient to satisfy basal metabolic requirements of the mesozooplankton (e.g. Roman and Gauzens, 1997). Thus, for modest rates of mesozooplankton herbivory (2−10% of PP), even trophic path lengths of 2 or 3 steps can yield significant additional nutrition from microzooplankton production (Table 5). Clearly, however, when the food available through direct herbivory falls many times short of their metabolic demands, mesozooplankton would need to feed very close to the first level of microzooplankton consumers to make up the difference from this alternate resource.

Discussion

This presentation has explored how the accumulating database on microzooplankton community grazing in the oceans can be relevant to the virtually ignored and very difficult measurement problem of microzooplankton production. Micro-herbivores consume most primary production in the oceans, averaging 60−75% of PP for various habitats and regions. Realistic GGEs of 30−40% thus imply secondary production rates ($MP_{2\circ}$) on the order of 21−35% of PP, with even higher total production (MP_{tot}) when the grazing chain involves multiple steps. Such estimates exceed the expected rates of bacterial secondary production (BP) by twofold to fivefold. Consequently, while some components of the microzooplankton (e.g. small nanoflagellates) may subsist principally on bacteria, micro-grazers as a group derive substantially (6−7 times) more production by feeding directly on phytoplankton.

To provide numerical examples of the various computations of microzooplankton production, we have used broad regional averages of grazing impact and assumed constant values of GGE. These simplifications should be considered open issues or null hypotheses for future exploration. The present synthesis, for example, does not lend itself to a straightforward analysis of whether there might be substantial systematic differences among major ocean systems with respect to the grazing role of microzooplankton. What variability there is could be due to true system differences, to peculiar or atypical circumstances during the short periods when experiments were conducted, or to subtle differences in experimental technique among investigators. Nonetheless, select areas that have been studied fairly

extensively by many investigators (e.g. the Arabian Sea, the equatorial and Subarctic Pacific, the North Atlantic, and the Southern Ocean) may provide at least the beginning for an expanded analysis of variance. The hope is that any systematic differences will be reflected in other system characteristics (e.g. biomass structure), such that underlying relationships and mechanisms might be revealed.

In contrast to the dilution database on grazing impact, there is little information on microzooplankton GGEs for a variety of ocean habitats. Modest departures from a relatively robust mean value (e.g. 30%) would be of little consequence for production estimates, given the uncertainties in other terms. However, the differences in computed results for GGEs of 30% and 40% and the possibility of systematic variability related to trophic richness are substantial enough to merit attention. A reasonable investment of time and effort in determining growth efficiencies for a range of ocean conditions would clearly be very useful for resolving these uncertainties.

Broadly defined, the microzooplankton comprises a diverse assemblage of protists and metazoans of varying size, taxonomic groupings, trophic relationships, and nutritional strategies (including mixotrophy). Assessing even the biomass of this assemblage can be challenging, requiring different sampling, preservation, and enumeration techniques to optimize results for its various components. It is therefore unlikely that an all-encompassing methodology can be developed to measure microzooplankton production directly (e.g. in carbon terms) at the temporal and spatial scales needed to account for its importance in ocean energy flows and carbon cycling. The present approach provides one way in which a measurable rate estimate for the assemblage, in this case aggregate herbivory, can be extended to useful assessments of production, growth rate, and tropic transfer. Although the approach is computational and requires improved knowledge of growth efficiencies and microbial foodweb structure in natural ocean systems, it has the unique property of directly linking microzooplankton process rates to primary production. Given their fast growth potential and great functional and morphological diversity, we might reasonably expect that the structure and rate processes of microzooplankton assemblages would be rapidly responsive to the dynamics of phytoplankton prey, and thus predictable, in some sense, from optical-based technologies and/or regional and global models designed to assess primary production. Thus, the coupling of production and grazing processes in the ocean's microbial communities and the scales at which they adapt to regional and small-scale forcing phenomena need to be resolved in future research.

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