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In situ grazing on plankton <10 µm by the boreal sponge *Mycale lingua*

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ABSTRACT: Ultraplankton, heterotrophic and autotrophic plankton <5 µm, are the most abundant food source in the world's oceans, yet their role as a food source for macroinvertebrates is largely unexamined. We quantified *in situ* feeding on heterotrophic and autotrophic plankton <10 µm by the boreal sponge *Mycale lingua* using measurements that quantified sponge feeding efficiencies, pumping rates, and abundance to determine the contribution of plankton <10 µm to sponge carbon intake. Using dual-beam flow cytometry we identified 5 populations of plankton <10 µm: heterotrophic bacteria, *Prochlorococcus*, *Synechococcus*-type cyanobacteria, autotrophic eucaryotes <3 µm, and autotrophic eucaryotes 3 to 10 µm. *Mycale lingua* nonselectively grazed on all types of plankton <10 µm. *Prochlorococcus* was filtered with the highest efficiency (93%), followed by *Synechococcus*-type cyanobacteria (89%), autotrophic eucaryotes 3 to 10 µm (86%), heterotrophic bacteria (74%), and autotrophic eucaryotes <3 µm (72%). We conservatively estimate that *M. lingua* at naturally occurring densities can obtain 29 mg C d^{-1} m^{-2} feeding on plankton <10 µm, with 74% resulting from ultraplankton, suggesting that ultraplankton are an important overlooked component of benthic-pelagic coupling.

KEY WORDS: Ultraplankton · Sponges · Suspension feeding · Benthic-pelagic coupling · *Mycale lingua* · Gulf of Maine

INTRODUCTION

Planktonic cells less than 5 µm in size, ultraplankton, are responsible for a large share of the primary and secondary production in marine ecosystems (Stockner & Anita 1986, Hobbie 1988) yet the role of ultraplankton in benthic-pelagic coupling remains uninvestigated. Although there are a variety of macroinvertebrates that have the capability to feed on ultraplankton (Rubenstein & Koehl 1977, Jørgensen 1983, Jørgensen et al. 1984), the most conspicuous component of marine benthic communities that has previously been shown to feed primarily on ultraplankton are the sponges (Reiswig 1971a).

Sponges are ubiquitous to both freshwater and marine ecosystems, constituting the dominant active suspension feeding macroinvertebrate in many communities from freshwater streams to the world's oldest, deepest lake (Lake Baikal, Siberia, Russia) (e.g. Frost & Williamson 1980, Sand-Jensen & Pedersen 1994, Pile et al. 1996), tropical to Arctic waters (e.g. Reiswig 1973, Dayton et al. 1974, Wilkinson 1987), and from the deep sea to estuaries (e.g. Koltun 1970, Pomponi & Meritt 1990, Vacelet et al. 1994). The unique ability of these organisms to adapt to all ecosystems by utilizing a variety of food sources ranging from dissolved organic material (DOM; Reiswig 1990) to small crustaceans (Vacelet & Boury-Esnault 1995) suggested to us that they may be able to exploit ultraplankton as a primary food source.

Globally, sponges feed primarily on picoplankton (plankton <2 µm) with efficiencies as high as 99% (Reiswig 1971a, 1990, Huysecom et al. 1988, van de Vyver et al. 1990, Pile et al. 1996). Yet, we are aware of only 3 studies that utilized *in situ* techniques to determine the natural diet of sponges (Reiswig 1971a, 1990,

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Pile et al. 1996), one of which was conducted in temperate marine communities (Reiswig 1990). Accurately quantifying ultraplankton makes such studies difficult. These difficulties have been recently overcome with the application of laser-based technologies, such as dual-beam flow cytometry, to accurately identify and enumerate heterotrophic and autotrophic ultraplankton simultaneously (Campbell et al. 1994). Single-beam flow cytometry has been employed to quantify suspension feeding in bivalves, tunicates, and gastropods on autotrophic plankton greater than 3 µm in laboratory studies (Cucci et al. 1985, Shumway et al. 1985, Lesser et al. 1992). Yet, many macroinvertebrates in a variety of taxa have the capability to remove particles much smaller than 3 µm and dual-beam flow cytometry is a more effective tool to accurately identify and quantify suspension feeding on both heterotrophic and autotrophic plankton in all size classes (Campbell et al. 1994, Pile et al. 1996).

Considering that freshwater sponges have removal efficiencies of ultraplankton up to 99% (Pile et al. 1996) coupled with sponges' ability to process copious volumes of water (Reiswig 1971b, Gerrodette & Flechsig 1979, Riisgård et al. 1993, Savarese et al. 1996) suggests that under some conditions sponges can substantially reduce the ultraplankton components of the water column community. We investigated the grazing of the boreal sponge *Mycale lingua* on plankton <10 µm using a series of *in situ* measurements coupled with the power of dual-beam flow cytometry to identify plankton <10 µm and found that this macroinvertebrate is extremely efficient at removing ultraplankton during active suspension feeding.

METHODS

Sponge-mediated 'living' carbon flux was calculated from empirical measurements employing the following model that can be used to determine organism-mediated fluxes for active suspension feeders and stated verbally as:

$$\text{organism-mediated flux} = \frac{\Delta\text{water column property}}{\text{volume processed}} \times \frac{\left(\frac{\text{volume processed}}{\text{pumping unit}}\right)}{\text{time}} \times \frac{\text{number of pumping units}}{\text{benthic surface area}} \quad (1)$$

where Δwater column property is the change in cell number as a unit volume is filtered by the organism and the pumping unit is 1 osculum. We conducted *in situ* measurements on 6 *Mycale lingua* at Ammen Rock Pinnacle, in the Gulf of Maine (northwest Atlantic Ocean. 42° 51' 25" N, 68° 57' 11" W), from September 15–19, 1994 that quantified (1) sponge feeding on plankton <10 µm using dual beam flow cytometry, (2) instantaneous sponge pumping rate using a heated microthermistor flowmeter, and (3) sponge abundance using photo quadrats.

Mycale lingua is a yellowish-white sponge with a pillow-like shape that is common on rock walls at Ammen Rock Pinnacle (Witman & Sebens 1990). Individuals are multioscular and, when fully expanded, oscula have diameters ranging from 13 to 23 mm. Observations of sponges indicate that individual oscula respond negatively to touch by closing. Care was taken during all sampling to avoid touching the sponges with the experimental apparatus. During this study we observed periods when all the oscula of an individual closed and water transport through the sponge, visualized with fluorescein dye, was at a minimum indicating periods of pumping inactivity. These events were rare and asynchronous between individuals and locations.

Sponge feeding on plankton <10 µm was quantified using dual-beam flow cytometry at the University of Hawai'i Flow Cytometry Facility (Honolulu, HI, USA) with an EPICS 753 flow cytometer (Coulter Electronics Corporation, Hialeah, FL, USA). 1 ml water samples were collected by SCUBA divers with 1 cc tuberculin syringes from 6 *Mycale lingua* at a depth of 30 m at 2 locations at Ammen Rock Pinnacle (n = 28). Five samples were taken from the exhalent current of different oscula within a sponge and 5 from ambient water at 0 m and 0.25 m (n = 20) from the bottom at each location with the average at these 2 depths comprising the ambient water concentrations and preserved for flow cytometry using standard protocols (Campbell et al. 1994). Samples were spiked with 0.59 and 0.98 µm polystyrene beads and 50 µl of sample illuminated with 1 W of the 488 nm line of a 6 W argon laser, and a 225 mW UV laser focused through confocal optics. Orange fluorescence (from phycoerythrin), red fluorescence (from chlorophyll *a*), and blue fluorescence (from DNA stained with Hoechst 33342) (Monger & Landry 1993) were collected through band pass interference filters at 575, 680, and 450 nm, respectively. Samples were then spiked with 10 µm polystyrene beads and the discriminators reset to include the 10 µm beads, and another 50 µl of sample processed as previously described so that larger plankton could be quantified. The 5 measured parameters, forward- and right-angle light scatter (FALS and RALS), orange, red, and blue fluorescence were recorded on 3-decade logarithmic scales, and sorted in list mode. Plankton populations were analyzed and enumerated with custom-designed software (CYTOPC; Vaulot 1989). Plankton populations were identified to the general cell types of heterotrophic bacteria, *Prochlorococcus*, *Synechococcus*-type cyanobacteria, picoeucaryotes (autotrophic

eucaryotes 2 to 3 µm diameter), and nanoeucaryotes (autotrophic eucaryotes 3 to 10 µm diameter) (Fig. 1) because there is limited information on the identification of picoplankton from the Gulf of Maine using dual-beam flow cytometry. Cell types were visually confirmed, except for *Prochlorococcus*, and cell diameters measured for picoeucaryotes and nanoeucaryotes using epifluorescence microscopy.

Differences between cell counts from ambient and exhalent current water of each type of picoplankton were analyzed using 2-sample *t*-tests with a Bonferroni transformed experimentwise experimental α of 0.01 to determine the effects of sponges on picoplankton (Sokal & Rohlf 1981). The mean feeding efficiency for each sponge was calculated as [(mean cell count ambient water – mean cell count exhalent current water)/mean cell count ambient water] × 100 for each type of picoplankton and analyzed as a function of type of plankton using 1-way analysis of variance (ANOVA) models and Ryans *Q*-test employed to determine differences between means (Underwood 1981, Day & Quinn 1989). The assumption of homogeneity of variance was tested with Bartlett's test. In order to maintain homogeneity of variance for the test of the effect of sponges on picoplankton, all cell counts for ambient and exhalent water were $\log(x+1)$ transformed and data back transformed for graphical representation. In all other instances, either the variances were homogeneous, or the hypotheses were rejected at α-values lower than the p-values of the test for homogeneity of variance when homogeneity of variance could not be achieved using any type of transformation (Underwood 1981).

Instantaneous sponge pumping was quantified using a heated microthermistor flowmeter (modified from LaBarbera & Vogel 1976). 45 s records were obtained by placing the microthermistor within the exhalent current perpendicular to the flow after water samples were collected for the feeding study (n = 28). The output of the flowmeter was encoded on a tape recorder using a frequency to voltage converter. Recordings were later converted to voltage and sampled at 10 Hz using a GW Instruments Model 411 A/D converter connected to an Apple Macintosh Plus. Mean velocity for 10 s segments was determined from the recordings using a program written in the software Mathematica (Wolfram Research, Inc., Champaign, IL, USA). Sponge oscula were videotaped immediately following the use of the heated microthermistor flowmeter and oscular area determined from digitized images using NIH Image 1.52. Volume processed per unit time was calculated using $Q = uA$ where Q is volume flow (ml s^{-1}), u is velocity (cm s^{-1}), and A is the oscular area (cm^2). This estimate of volume processed assumes a model of plug flow, or that the velocity profile of exhalent current is rectangular, rather than laminar pipe flow in which the velocity profile is parabolic. This assumption is supported by the shape of exhalent currents in ascidians (Fiala-Medioni 1973, 1978) and it is most likely true for sponges (Savarese et al. 1996).

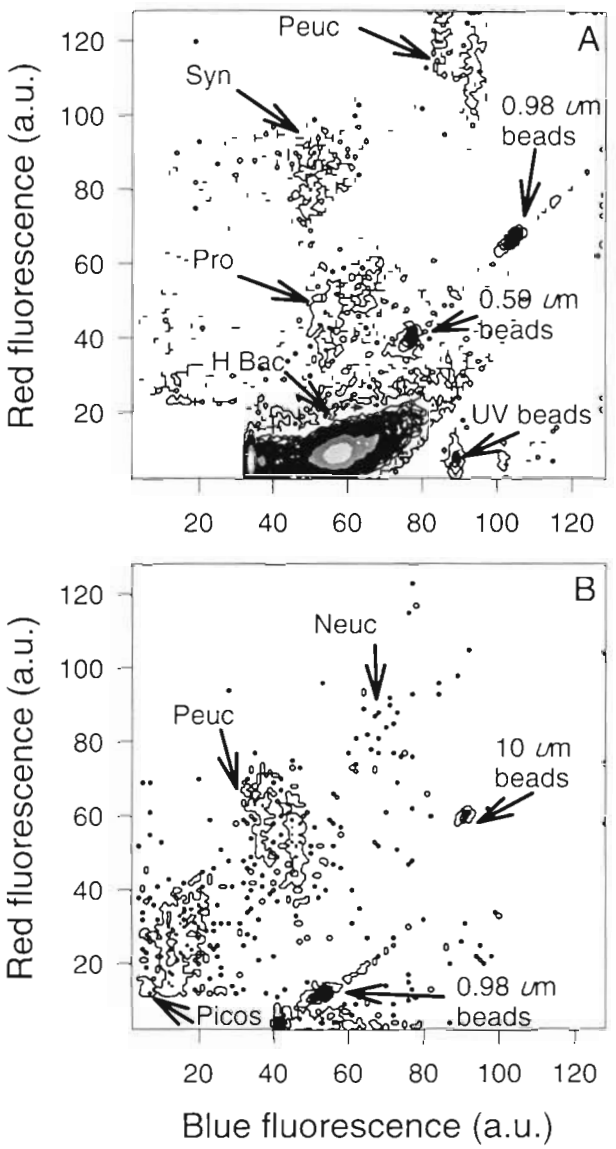

Fig. 1. Contours of cell abundance in ambient water from Ammen Rock Pinnacle (Gulf of Maine, northwest Atlantic Ocean) in 50 µl samples. Red fluorescence results from chlorophyll *a* excitation and blue fluorescence from DNA stained with Hoechst 33342. (A) Picoplankton with HBac: heterotrophic bacteria; Pro: *Prochlorococcus*; Syn: *Synechococcus*-type cyanobacteria; Peuc: autotrophic eucaryotes 2 to 3 µm cell diameter. (B) Pico- and nanoeucaryotes with Peuc: autotrophic eucaryotes 2 to 3 µm cell diameter; Neuc: autotrophic eucaryotes 3 to 10 µm cell diameter; and Picos: all types of hetero- and autotrophic picoplankton. Note that in (B) the blue and red fluorescence have relatively higher settings, shifting the relative position of the 0.98 µm beads and clustering all types of picoplankton together. a.u.: arbitrary units

Sponge percent coverage and mean number of sponge oscula m^{-2} were determined from 4 permanent transects consisting of 92, 0.25 m^2 photo quadrats at 30 to 35 m depth. The percent cover of sponges in the photo quadrats was determined by projecting each photographed quadrat onto a grid of 200 random dots (2 mm diameter). Sponges with dots falling on them were identified, summed per quadrat, and expressed as percent of 200 dots. Oscula of *Mycale lingua* were enumerated within each quadrat. Mean percent cover and number of sponge oscula m^{-2} were then calculated as the average of 92 quadrats.

To obtain a conservative estimate of 'living carbon' fed upon by sponges, mean number of cells removed ml^{-1}, as determined using flow cytometry, was converted to mg C for each of the 5 types of plankton <10 µm using standard cell conversions. Cellular conversions to carbon were 20 fg C $cell^{-1}$ for heterotrophic bacteria (Ducklow et al. 1993), 53 fg C $cell^{-1}$ for *Prochlorococcus* (Morel et al. 1993), and 470 fg C $cell^{-1}$ for *Synechococcus* (Campbell et al. 1994). Values for eucaryotes were computed using pg C = 0.433 × (biovolume)$^{0.866}$ (Verity et al. 1992) with the mean biovolumes of 10.3 and 82.4 μm^3, respectively, as determined from measurements of the cells using epifluorescence microscopy. Further, we assumed that *Mycale lingua* was actively pumping at the mean instantaneous rate for 12 h d^{-1} Some tropical marine sponges have a diel periodicity in pumping activity that results in 18 h d^{-1} of active pumping while some freshwater and marine sponges do not demonstrate any periodicity in pumping activity (Reiswig 1971b, 1974, Gerrodette & Flechsig 1979, Riisgård et al. 1993, Savarese et al. 1996). Further, by assuming a 12 h pumping period we are most likely underestimating the volume processed daily by *M. lingua*.

It is of interest to determine if *Mycale lingua* is selectively grazing on any of the components of the plankton community <10 µm. Selectivity indices require the probability that a particle in a given size category will be retained by the filtering apparatus and ingested (Vanderploeg & Scavia 1979). This is generally empirically calculated from microscopic measurements of the filtering apparatus and is unavailable for *M. lingua*. Therefore, to determine if *M. lingua* is grazing selectively on any proportion of the plankton community <10 µm, the percent of carbon in the diet of sponges was compared to the percent of carbon in the plankton component using a Kolmogorov-Smirnov 2-sample test (Sokal & Rohlf 1981).

RESULTS

Heterotrophic bacteria were the most abundant food available followed by *Prochlorococcus*, *Synechococcus*-type cyanobacteria, picoeucaryotes, and nanoeucaryotes (Table 1). *Mycale lingua* significantly decreased all 5 types of plankton <10 µm (Table 1, Fig. 2A) from ambient concentrations at feeding efficiencies ranging from 72 to 93% (Fig. 2B). *M. lingua* was most efficient (93%) feeding on *Prochlorococcus*, *Synechococcus*-type cyanobacteria (89%), and nanoeucaryotes (87%). Although not statistically different from each other, feeding efficiencies on *Prochlorococcus*, *Synechococcus*-type cyanobacteria, and nanoeucaryotes were significantly higher than the feeding efficiencies on heterotrophic bacteria (74%) and picoeucaryotes (72%) which were not different from each other (ANOVA, $F_{4,25} = 14.27$, $p < 0.0001$) (Fig. 2B).

Table 1. Summary of the effect of individual *Mycale lingua* on the 5 types of plankton <10 µm. Mean cells ml^{-1} (SD) in the ambient water and the exhalent current and *t*-values from 2-sample *t*-tests employing a Bonferroni transformed experimentwise $\alpha = 0.01$

Type of plankton	Ambient	Exhalent	*t*
Heterotrophic bacteria	6.79×10^5 (1.81×10^5)	1.79×10^5 (0.72×10^5)	9.22••••
Prochlorococcus	5.16×10^4 (3.28×10^4)	0.34×10^4 (0.15×10^4)	5.09•••
Synechococcus-type cyanobacteria	3.15×10^4 (3.00×10^4)	0.33×10^4 (0.16×10^4)	3.24••
Autotrophic eucaryotes <3 µm	6.68×10^3 (5.82×10^3)	1.86×10^3 (0.77×10^3)	2.85••
Autotrophic eucaryotes 3–10 µm	832 (557)	113 (71)	4.45•••

••$p < 0.01$, •••$p < 0.001$, ••••$p < 0.0001$

The mean velocity of the exhalent currents was 14.0 cm s^{-1} (SD = 9.7 cm s^{-1}) with a mean oscular diameter of 0.12 cm^2 (SD = 0.07 cm^2) resulting in a mean sponge pumping rate of 1.6 ml s^{-1} $oscula^{-1}$ (SD = 1.4 ml s^{-1}). Sponges on rock walls at 30 to 35 m depth at Ammen Rock Pinnacle cover 21% of the available benthic surface area, with *Mycale lingua* covering only 8.9% of the benthic surface area, resulting in 7.6 oscula m^{-2} (SD = 33.6 oscula m^{-2}).

Employing the model for organism mediated fluxes (Eq. 1) and the carbon equivalent of the mean number of cells eaten ml^{-1}, mean sponge pumping rate per oscula, and mean number of oscula m^{-2}, we conservatively estimate that for this benthic environment, 29 mg C d^{-1} m^{-2} is captured by *Mycale lingua* through active suspension feeding. Carbon acquisition is evenly distributed between procaryotic and eucaryotic plankton <10 µm (Table 2) and not statistically different from those of the water column community (Kolmogorov-Smirnov 2 sample test, $D_{5,5} = 36$, $p < 0.01$). We are aware of the limitations of making such calcu-

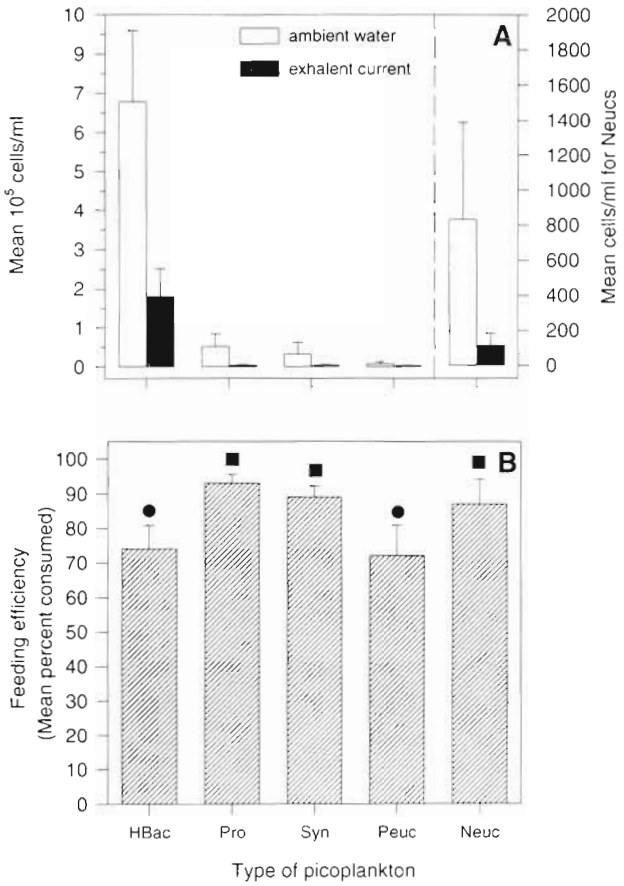

Fig. 2. Effect of *Mycale lingua* on plankton <10 µm: (A) concentration of each type of picoplankton in the ambient water and water from the exhalent currents of the sponge *M. lingua* and (B) feeding efficiencies. The abscissa is the same for both graphs, with abbreviations as in Fig. 1 (A) Pooled cell concentrations of ambient water and water from the exhalent current. All sponges significantly reduced concentrations of all types of plankton <10 µm and samples pooled and back transformed for graphical representation. White bars denote ambient water ($\bar{x}$ ± SD, n = 20) and black bars denote water from the exhalent current ($\bar{x}$ ± SD, n = 28). *Y*-axis for Neuc in (A) is on the right. (B) Pooled feeding efficiencies ($\bar{x}$ ± SD, n = 6) of all the sponges on plankton <10 µm. Bars sharing a symbol are not significantly different

lations and the data are presented in such a manner that, should better cell conversions become available, sponge-mediated fluxes can be recalculated.

DISCUSSION

Mycale lingua is highly efficient at grazing on heterotrophic and autotrophic plankton <10 µm with feeding efficiencies comparable to those of other marine (Reiswig 1971a, 1975, Stuart & Klumpp 1984) and freshwater demosponges (Huysecom et al. 1988, van de Vyver et al. 1990, Pile et al. 1996). More importantly, the use of dual-beam flow cytometry has allowed us to accurately quantify the diet of *M. lingua*, including the previously undocumented feeding of any macroorganism on *Prochlorococcus*.

Table 2. Estimated mean mg C removed from the picoplankton community daily by the sponge *Mycale lingua* occupying 1 m^2 of the benthos at Ammen Rock Pinnacle at naturally occurring densities. Estimates were computed assuming that sponges were actively pumping for 12 h each day. ‰ diet was calculated assuming all cells removed were consumed and % plankton component was calculated as the proportion of total 'living carbon' of plankton <10 µm in the ambient water

Picoplankton component	Sponge-mediated flux		
	mg C m^{-2} d^{-1}	‰ diet[a]	% plankton component[a]
Procaryotes			
Heterotrophic bacteria	5	18	20
Prochlorococcus	1	5	5
Synechococcus-type cyanobacteria	6	22	19
Total procaryotes	13	45	44
Eucaryotes			
Picoeucaryotes (2 to 3 µm)	8	29	32
Nanoeucaryotes (3 to 10 µm)	8	26	24
Total eucaryotes	16	55	56
Total of all cell types	29	100	100

[a]Kolmogorov-Smirnov 2-sample test indicates distributions are not significantly different ($p < 0.01$)

Prochlorococcus are photoautotrophic, procaryotic picoplankton typically <0.8 µm in diameter that can only be distinguished from heterotrophic bacteria using flow cytometry (Chisholm et al. 1988, Olson et al. 1990, Li et al. 1992, Veldhuis & Kraay 1993, Campbell et al. 1994). Although they are extremely abundant (ca 10^5 ml^{-1}), contributing up to 35% of the total biomass of plankton <20 µm, and found in all of the world's oceans, their abundance and distribution are highly variable (Chisholm et al. 1988, Olson et al. 1990, Li et al. 1992, Veldhuis & Kraay 1993, Campbell et al. 1994). They appear to increase in abundance at lower latitudes and with distance from land margins (Chisholm et al. 1988, Olson et al. 1990, Li et al. 1992, Veldhuis & Kraay 1993, Campbell et al. 1994).

Prochlorococcus is an integral component of the picoplankton in coral reefs (Pile 1996) and other ecosystems (Chisholm et al. 1988, Olson et al. 1990, Li et al. 1992, Veldhuis & Kraay 1993, Campbell et al. 1994) dominated by pelagic and benthic macroorganisms with filters designed to capture particles 0.8 µm or smaller (Rubenstein & Koehl 1977, Jørgensen 1983, Jørgensen et al. 1984). The diet of these taxa may have been incorrectly identified using conventional methods and total carbon flux underestimated using traditional methods

to identify plankton. Grazing on *Prochlorococcus* by both micro- and macroorganisms needs to be further quantified using dual-beam flow cytometry to resolve the flow of carbon in marine ecosystems.

Instantaneous pumping rates for *Mycale lingua* are on the higher end of the range of those of other sponges (Reiswig 1971b, Gerrodette & Flechsig 1979, Riisgård et al. 1993, Savarese et al. 1996). Previous researchers have estimated the effect of sponges on water column communities by determining the time for a community of sponges to process the entire overlying water column (turnover rate) (Reiswig 1974, Riisgård et al. 1993, Savarese et al. 1996). They have extrapolated the pumping rates with the fictitious assumption of a well mixed water column. Despite the inherent problems with these types of calculations we estimate that at Ammen Rock Pinnacle, *M. lingua* at naturally occurring densities processes a column of water 0.532 m high each day, taking 56.2 d to turn over the entire 30 m water column. A turnover rate of 56.2 is much higher than previously determined near-daily turnover times for other shallower sponge dominated communities (Reiswig 1974, Savarese et al. 1996). However, it is highly unlikely that sponges can affect the water column community more than 1 m from the substrate and that shear velocity, bottom roughness, and the strength of horizontal flow play an important role in providing unfiltered water to the benthic community.

The extensive sponge community of Lake Baikal's littoral zone can create a picoplankton depleted layer of water within 1 m of the benthos (Pile et al. 1996) while other benthic communities dominated by suspension feeding macroinvertebrates result in similar food depleted layers (Glynn 1973, Buss & Jackson 1981, Peterson & Black 1987, Fréchette et al. 1989, Butman et al. 1994). Mean flow speeds during this study period were 0.20 m s^{-1} (J. D. Witman & M. R. Patterson unpubl. data) which were 3 times as high as those found in Lake Baikal (Savarese et al. 1996) and would most likely preclude the development of a food depleted boundary layer over Ammen Rock Pinnacle. To understand the effect of sponges on ultraplankton communities a more accurate descriptor is to determine the percentage of water that passes over the Ammen Rock Pinnacle daily that can be filtered by *Mycale lingua*. Ammen Rock Pinnacle has a benthic surface area of 160 m^2 (J. D. Witman unpubl. data), and a volume of 1730 m^3 d^{-1} passes over the pinnacle that is available to sponges. Using the assumption that the sponges are only actively pumping for 12 h d^{-1}, *M. lingua* can conservatively process 5% of the water that passes over Ammen Rock Pinnacle. The integrated feeding efficiency on ultraplankton (all procaryotes + picoeucaryotes) is 76%. *M. lingua* has a gross daily grazing effect of removing 4% of the ultraplankton from the near bottom water. The incorporation of the remaining suite of benthic invertebrates that feed primarily on ultraplankton and are common at Ammen Rock Pinnacle (Witman & Sebens 1988), such as the remaining sponges, ascidians (Riisgård et al. 1980, Stuart & Klumpp 1984), juvenile and adult bivalves (Riisgård et al. 1980, Stuart & Klumpp 1984), and bryozoans (Winston 1978), will substantially increase the percentage of water that is grazed by suspension and filter feeders and most likely significantly impact near bottom, water column communities. More importantly, in shallower near shore ecosystems the effect of grazing by benthic invertebrates on water column communities will be greater.

Previous estimates of tropical sponge, daily carbon metabolic requirements range between 80 and 1800 mg C d^{-1} m^{-2}, which was met by a diet that consisted of bacteria and unresolvable particulate organic carbon (most likely other types of picoplankton) (Reiswig 1971a). Sponges in Lake Baikal's littoral zone can obtain 1970 mg C d^{-1} m^{-2} through active suspension feeding on both heterotrophic and autotrophic plankton <3 µm (Pile et al. 1996). Our estimates of areal carbon flux of 29 mg C d^{-1} m^{-2} for *Mycale lingua* are lower than that previously described and this sponge is less abundant by an order of magnitude (Reiswig 1973, Pile et al. 1996). Considering this, *M. lingua* obtains carbon from plankton <10 µm at rates similar to other sponges.

Mycale lingua obtained carbon in nearly equal proportions from procaryotic and eucaryotic plankton <10 µm. This is in contrast to the freshwater sponges in Lake Baikal's littoral zone where a majority of carbon was obtained from *Synechococcus*-type cyanobacteria (Pile et al. 1996) and tropical marine sponges where 80% of captured carbon was obtained from bacterioplankton and unresolvable particulate organic carbon (Reiswig 1971a). None of the sponges examined with flow cytometry were selectively feeding on any component of the plankton community (Pile et al. 1996, this study) suggesting that the composition of the plankton community is an important factor in a sponge's ability to meet metabolic carbon requirements. Ultimately, variability in water column community composition at many temporal scales (e.g. seasonal, diurnal, and short term physical events such as internal waves and storms) can affect sponge nutrition.

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