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Trophic effects of sponge feeding within Lake Baikal's littoral zone. 2. Sponge abundance, diet, feeding efficiency, and carbon flux

Abstract—Endemic freshwater demosponges in the littoral zone of Lake Baikal, Russia, dominate the benthic biomass, covering 44% of the benthos. We measured in situ sponge abundance and grazing and calculated sponge-mediated fluxes of picoplankton (plankton <2 μm) for two common species, *Baikalospongia intermedia* and *Baikalospongia bacillifera.* By means of dual-beam flow cytometry, we found retention efficiencies ranging from 58 to 99% for four types of picoplankton: heterotrophic bacteria, *Synechococcus*-type cyanobacteria, autotrophic picoplankton with one chloroplast, and autotrophic picoplankton with two chloroplasts. By using a general model for organism-mediated fluxes, we conservatively estimate that through active suspension feeding, sponges are a sink for 1.97 g C d^{-1} m^{-2}, mostly from procaryotic cell types. Furthermore, grazing by these extensive sponge communities can create a layer of picoplankton-depleted water overlying the benthic community in this unique lake.

Planktonic cells <5 μm in size (ultraplankton) are responsible for a large share of the primary and secondary production in freshwater and marine ecosystems (Stockner and Antia 1986; Hobbie 1988; Stockner 1988), yet the role of ultraplankton in benthic–pelagic coupling remains uninvestigated. Many benthic invertebrates from a variety of phyla have the capability to feed on this component of the water column community (Rubenstein and Koehl 1977; Jørgensen 1983; Jørgensen et al. 1984). Sponges are the most conspicuous component of freshwater and marine benthic communities that has previously been shown to feed primarily on ultraplankton.

Sponges are the most common benthic invertebrates in some freshwater lakes (Bailey et al. 1995) and ponds (Frost et al. 1982), second to corals in abundance in reef communities (e.g. Wilkinson 1987), and can cover 21–90% of the available habitat in temperate marine communities (Pomponi and Meritt 1990; Witman and Sebens 1990). All sponges are heterotrophs, but sponges with endosymbiotic cyanobacteria or algae have a phototrophic component to their nutrition (Wilkinson 1983). Sponges consume a variety of plankton, generally bacterioplankton and autotrophic plankton <2 μm (picoplankton) (Reiswig 1971b, 1975; van de Vyver et al. 1990). Although they are active suspension feeders, sponges can passively filter water via induced flow by currents (Vogel 1974, 1977) and have been estimated to filter the water over their communities every 24–48 h (Reiswig 1971a; Savarese et al. 1997).

Lake Baikal is the world's deepest (1,637-m max depth), largest by volume (23,000 km³), and oldest (~25 × 10⁶ yr) body of freshwater (Zhadin and Gerd 1963). Unlike most lakes, the littoral zone has extensive sponge communities, and three species dominate the rocky substrate—*Baikalospongia bacillifera, Baikalospongia intermedia,* and *Lubomirskia baicalensis,* which have globose, encrusting, and branching forms, respectively. All three species are brilliant green owing to their endosymbiotic relationship with zoochlorellae. Surprisingly, sponge abundance, diet, and the impact of sponges on water column communities have never been assessed.

During August 1993, we measured sponge-mediated fluxes of picoplankton at two locations in Lake Baikal (Fig. 1) by using an integrated set of in situ measurements. Sponge-mediated fluxes of picoplankton were calculated from em-
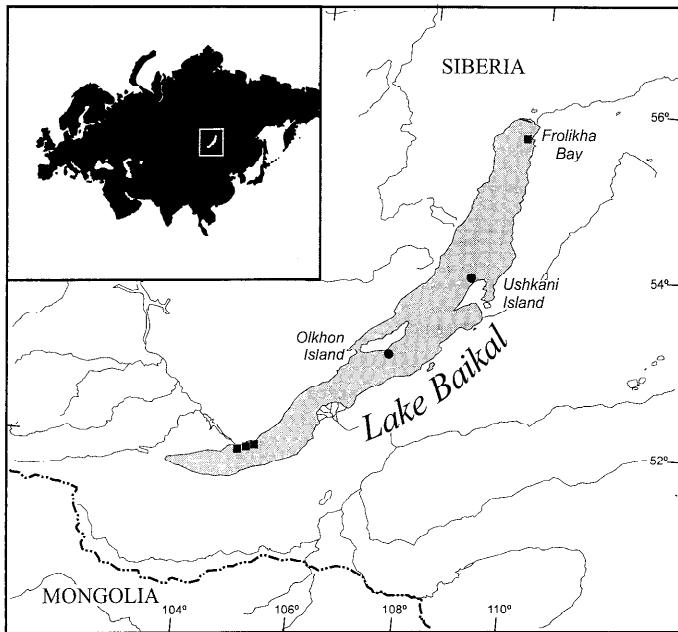
Fig. 1. Map of Lake Baikal, Russia, showing the locations of the video transects (■) and the feeding studies (●).

pirical measurements by means of a generalized model for active suspension feeders that incorporates organismal and community measurements and can be stated as

organism-mediated flux

$$= \frac{\Delta \text{water-column property}}{\text{vol. processed}} \times \frac{\left(\dfrac{\text{vol. processed}}{\text{pumping unit}}\right)}{\text{time}}$$
$$\times \frac{\text{no. of pumping units}}{\text{benthic surface area}}. \tag{1}$$

In this case, the water-column property is picoplankton concentration and the pumping units are sponge oscula. Sponge pumping was determined by use of in situ measurements and is reported elsewhere (Savarese et al. 1997). Our paper encompasses the remaining two components—sponge diet and abundance—and examines the sponge-mediated fluxes of heterotrophic and autotrophic picoplankton by two species, *B. bacillifera* and *B. intermedia*.

Previous researchers have had difficulty accurately quantifying suspension feeding on ultraplankton when using techniques such as radiolabeling of plankton, direct counts, and colony counts (Reiswig 1971b; Wilkinson 1978; Huysecom et al. 1988). Studies have accounted for 17–100% of the metabolic requirements of the sponges (Reiswig 1971b; van de Vyver et al. 1990), and Reiswig (1971b) suggested that sponges may be using dissolved organic carbon or plankton that could not be resolved with conventional methods. Recent advances in laser-based technologies have resulted in more accurate methods for the quantification of ultraplankton. Single-beam flow cytometry has been used to quantify suspension feeding by macroinvertebrates on particles >3 μm (Cucci et al. 1985; Shumway et al. 1985; Lesser et al.

1992); however, the application of dual-beam flow cytometry to quantify both heterotrophic and autotrophic picoplankton (e.g. Monger and Landry 1993; Campbell et al. 1994) has yet to be used to quantify suspension feeding in organisms that are known to feed primarily on ultraplankton. We used dual-beam flow cytometry to quantify suspension feeding by sponges on heterotrophic and autotrophic picoplankton because sponges are most likely to feed on this component of the water column community, and all previous research on freshwater and marine ecosystems indicates that most of the water-column productivity is within this size range. We do not suggest that this is the only component of plankton within the water-column community or the only component that sponges affect.

To quantify sponge suspension feeding, scuba divers collected 1-ml water samples with 1-ml tuberculin syringes from 10 *B. intermedia* and 10 *B. bacillifera* at a depth of 12 m. Five samples were taken from water adjacent to a sponge and five from the exhalent current of a sponge osculum. Additionally, divers collected five 1-ml samples at depths of 0, 0.5, and 1 m from the bottom, as well as 1 and 5 m from the surface, to quantify water-column picoplankton at each location. Picoplankton samples were preserved for flow cytometry by standard protocols (Campbell et al. 1994) and held in either liquid nitrogen, dry ice, or at −80°C until processing.

Plankton <3 μm were quantified at the University of Hawaii Flow Cytometry Facility using an EPICS 753 flow cytometer (Coulter Electronics Corp.). Samples were quick-thawed, spiked with 0.57-μm Polysciences Fluoresbrite standard beads, diluted 1:9 with filtered deionized water, and stained with Hoechst 33342 according to Monger and Landry (1993). Samples (50 μl) were illuminated with 1 W of the 488-nm line of a 5-W argon laser and a 225-mW UV laser focused through confocal optics. Orange fluorescence (from phycoerythrin), red fluorescence (from Chl a), and blue fluorescence (from DNA stained with Hoechst 33342) were collected through band pass interference filters at 575, 680, and 450 nm, respectively. The five measured parameters (forward-angle light scatter, right-angle light scatter, and orange, red, and blue fluorescence) were recorded on 3-decade logarithmic scales, sorted in list mode, and analyzed with custom-designed software (CYTOPC, by Daniel Vaulot). Picoplankton populations were identified to general cell type, heterotrophic bacteria, *Synechococcus*-type cyanobacteria, autotrophic picoplankton with one chloroplast (APP I), and autotrophic picoplankton with two chloroplasts (APP II), and visually confirmed with epifluorescence microscopy.

Differences between cell counts from ambient and exhalent current water of each type of picoplankton were analyzed by means of paired t-tests for each sponge with a Bonferroni-transformed experimentwise α of 0.00625 to determine the effects of sponges on picoplankton (Sokal and Rohlf 1981). The mean feeding efficiency for each sponge was calculated as [(mean cell count ambient − mean cell count exhalent)/mean cell count ambient] × 100 for each type of picoplankton and analyzed as a function of sponge species (*B. bacillifera* vs. *B. intermedia*) by means of paired t-tests with a Bonferroni-transformed experimentwise α of 0.0125 (Sokal and Rohlf 1981).

Total sponge percentage cover and mean number of sponge oscula for *B. intermedia* and *B. bacillifera* were determined from underwater video transects ($n = 12$). Three 8-m, haphazardly selected transects at a depth of 12 m were videotaped at three locations (Fig. 1) by scuba divers with a Panasonic V-99 video camera in an Ikelite underwater housing. At the fourth location, three 8-m transects were videotaped by using a remotely operated vehicle. Twenty randomly selected 1-m² quadrants from each transect were analyzed for percentage cover of the bottom by the sponges *B. intermedia*, *L. baicalensis*, and *B. bacillifera*, a filamentous red algae, rock, and uninhabitable substrate (sand). Mean numbers of sponge oscula per square meter for *B. intermedia* and *B. bacillifera* were determined by directly counting oscula within the randomly selected quadrats, thereby eliminating the effects of size of individuals as well as the three-dimensional nature of hard bottom communities in the flux equation.

Sponge-mediated fluxes of "living carbon" were conservatively estimated by converting the mean number of picoplankton cells removed or expelled by an oscula to an equivalent grams of carbon. Cell conversion factors of 20 fg cell^{-1} for heterotrophic bacteria and 470 fg cell^{-1} for *Synechococcus*-type cyanobacteria were selected as they are for cells with mean diameters that are equal to or greater than those found during this study. Carbon in the form of the eucaryotic cells of APP I and APP II were determined from the formula fg C $= 433 \times$ [biovolume $(\mu m^3)]^{0.866}$, with APP I and APP II having biovolumes of 0.35 and 0.50 μm^3 as determined from epifluorescence microscopy (Campbell et al. 1994 and references therein).

Instantaneous and diel pumping rates were determined for *B. bacillifera* by Savarese et al. (1997) and are comparable to those of other sponges (Reiswig 1971*a*, 1974; Savarese et al. 1997). Additional pumping measurements were conducted on *B. intermedia*, and although values were comparable to *B. bacillifera*, small sample sizes precluded statistical comparison. Therefore, we used the mean pumping rate of *B. bacillifera* [0.13 ml s^{-1} oscula^{-1} (plug flow model)] in flux calculations for both species (Savarese et al. 1997). In contrast to tropical marine sponges (Reiswig 1971*a*), these sponges demonstrated no diel variation in pumping during the period of this study (Savarese et al. 1997). However, we used the assumption that all the oscula pumped actively for 12 h each day to obtain a *conservative* estimate of sponge activity.

Both sponges were highly efficient at removing picoplankton by active suspension feeding, with efficiencies ranging from 58 to 99%. *B. bacillifera* significantly reduced concentrations of all types of picoplankton (Fig. 2A). In contrast, *B. intermedia* significantly reduced heterotrophic bacteria and *Synechococcus*-type cyanobacteria from ambient levels, whereas APP I and APP II were significantly increased by 37 and 12 times above ambient levels (Fig. 2A). The feeding efficiency for *B. bacillifera* on heterotrophic bacteria was 84%, which was significantly higher than the feeding efficiency of 71% for *B. intermedia* (*t*-test, $t_{17} = -2.82$, $P = 0.011$). The mean feeding efficiencies of 66 and 58% for *B. bacillifera* and *B. intermedia* on *Synechococcus*-type cyanobacteria were not significantly different (*t*-test, $t_{17} = -0.95$,
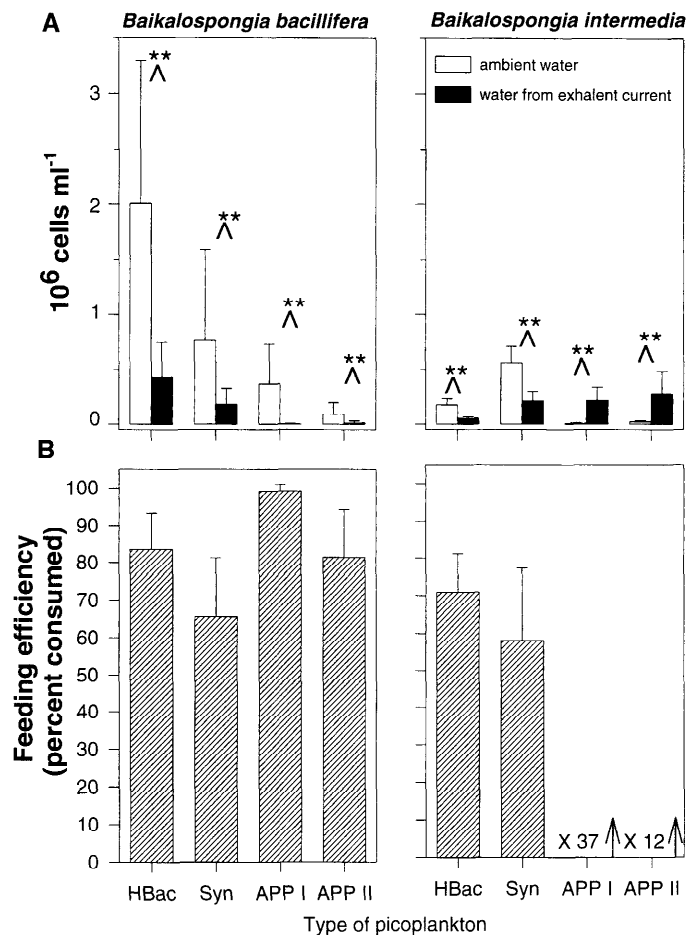

Fig. 2. A. Concentration of each type of picoplankton in the ambient water and water from the exhalent currents of the globose sponge *B. bacillifera* and the encrusting sponge *B. intermedia*. B. Feeding efficiencies (mean±SD, $n = 10$). HBac—heterotrophic bacteria, Syn—*Synechococcus*-type cyanobacteria, APP I—autotrophic picoplankton with one chloroplast, APP II—autotrophic picoplankton with two chloroplasts. White bars denote ambient water; black bars, water from the exhalent current (mean±SD, $n = 50$). All cell concentrations between ambient water and exhalent current water within cell types were significantly different as determined with paired *t*-tests with a Bonferroni-transformed experimentwise experimental α of 0.00625 (**).

$P = 0.36$). The contribution of APP I and APP II by *B. intermedia* was significantly different than the respective removal efficiencies of 99% (*t*-test, $t_{17} = -40.3$, $P < 0.001$) and 81% (*t*-test, $t_{17} = -33.7$, $P < 0.001$) by *B. bacillifera* (Fig. 2B).

Uninhabited substrate, or rocks, was the most common component of the benthos, comprising 45% of the surface area, whereas sand only accounted for 11%. *B. intermedia* was the most abundant sponge, covering 36% of the benthos; *L. baicalensis* and *B. bacillifera* covered only 6 and 2% of the benthos. The only other noncryptic component of the benthic community was a filamentous red algae, which covered 2% of the benthos (Fig. 3). Because none of the three noncryptic sponges were found living on any portion of the bottom not covered by hard substrate, sediment is considered
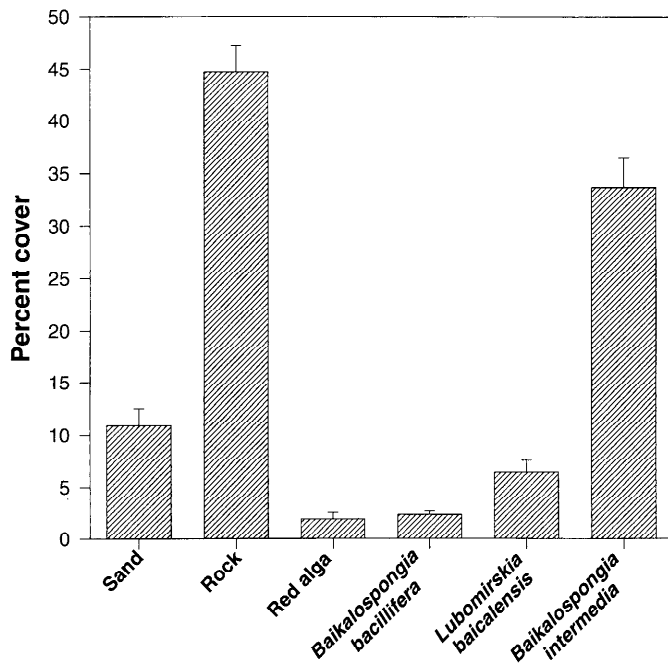
Fig. 3. Mean percentage cover at 12 m of the sponges *B. intermedia, B. bacillifera,* and *L. baicalensis,* a filamentous red algae, rock, and sand.
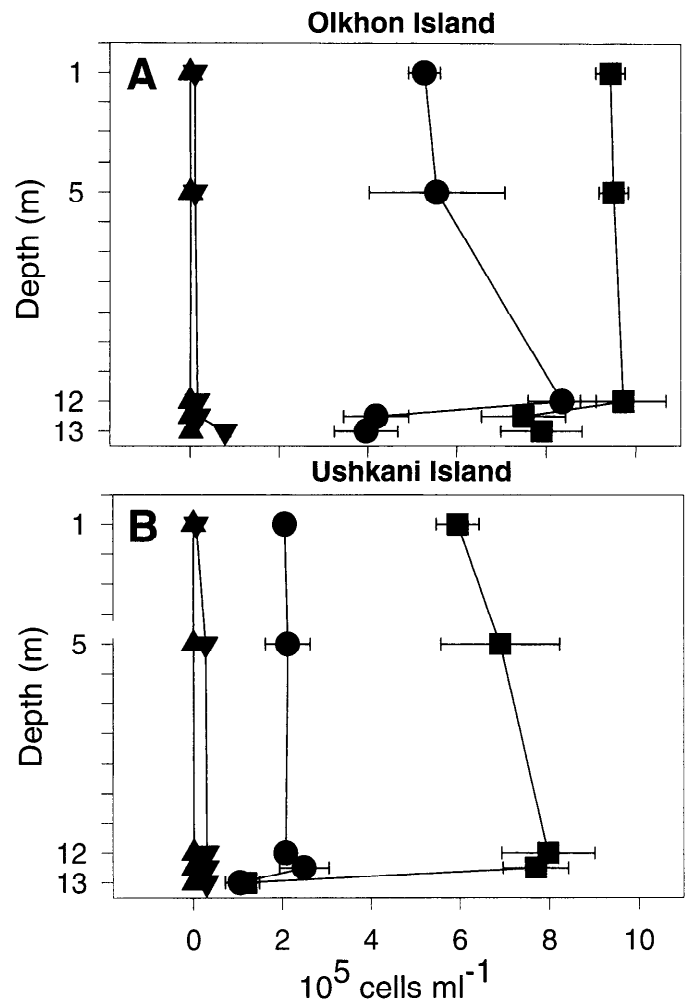

Fig. 4. Water-column profiles for two locations overlying sponge communities. HBac (●)—heterotrophic bacteria, Syn (■)—*Synechococcus*-type cyanobacteria, APP I (▲)—autotrophic picoplankton with one chloroplast, APP II (▼)—autotrophic picoplankton with two chloroplasts (mean±SD, n = 5). Benthic topography at Olkhon Island (53°3.99′N, 107°18.99′E), located on the western shore, is characterized by a gentle slope away from shore; Ushkani Island (53°52.46′N, 109°00.94′E) (Fig. 1), on the eastern shore, is a wall. Both locations have a decrease in HBac and Syn within 1 m of the benthic community. At Olkhon Island (A), a site dominated by *B. intermedia,* there is an increase in APP II within 0.5 m of the benthic community.

an area uninhabitable by sponges. When percentage cover was recalculated to that of habitable benthic surface area, total sponge cover rose to 47%. Mean oscula m^{-2} for *B. intermedia* was 154.9 and for *B. bacillifera* was 21.4.

Both *B. bacillifera* and *B. intermedia* obtained most of the carbon in their diet (an integrated removal of 1.87 g C d^{-1} m^{-2}) from procaryotic cell types (Table 1). Although eucaryotes were removed by *B. bacillifera,* the addition of APP I and APP II to the water column by *B. intermedia* resulted in a net production of 0.75 g C d^{-1} m^{-2}. During this study we were unable to determine whether the APP I and APP II coming from *B. intermedia* were viable, or nonviable organisms that would contribute to the detrital biomass. Our results suggest that relative to the water column, sponges are a carbon sink for procaryotes but a carbon source for eucaryotes.

Water-column profiles at the two study sites reflect the net decrease and increase in cell types (Fig. 4) creating food-depleted (or enhanced) layers overlying these extensive sus-

Table 1. Estimated mean daily grams of carbon removed from (−) or added to (+) the picoplankton community by the globose sponge *Baikalospongia bacillifera* and the encrusting sponge *Baikalospongia intermedia* occupying 1 m^2 of the benthos in Lake Baikal's littoral zone at naturally occurring densities. Estimates were computed assuming that sponges were actively pumping for 12 h each day. Integrated effect is the net effect of *B. bacillifera* and *B. intermedia* on the picoplankton community. (not applicable—na.)

Picoplankton component	Sponge-mediated flux (g C d^{-1} m^{-2})				
	B. bacillifera	% Diet	*B. intermedia*	% Diet	Integrated effect
Procaryotes					
HBac	−0.04	8	−0.03	2	−0.07
Syn	−0.37	72	−1.43	98	−1.80
Total	−0.41	80	−1.46	100	−1.87
Eucaryotes					
APP I	−0.08	15	+0.32	na	+0.24
APP II	−0.02	5	+0.53	na	+0.51
Total	−0.10	20	+0.85	na	+0.75
Total of all cell types	−0.51	100	−0.61	100	−1.12

HBac—heterotrophic bacteria, Syn—*Synechococcus*-type cyanobacteria, APP I—autotrophic picoplankton with one chloroplast, APP II—autotrophic picoplankton with two chloroplasts.

pension-feeding communities. Both heterotrophic bacteria and *Synechococcus*-type cyanobacteria were depleted within 1 m of the benthos at both locations despite the dramatically different topography of the benthic communities. Olkhon Island has a gentle sloping littoral zone, whereas Ushkani Island is a steep, almost vertical wall. Furthermore, the Olkhon Island location was dominated by *B. intermedia* (Pile and Patterson pers. obs.) with a resultant increase in APP II near the bottom.

The application of dual-beam flow cytometry to quantify picoplankton proved to be a powerful new tool for the quantification of suspension feeding by macroinvertebrates on heterotrophic and autotrophic picoplankton. This is the first record of grazing by freshwater macroinvertebrates on *Synechococcus*-type cyanobacteria. Both *B. bacillifera* and *B. intermedia* were highly effective at grazing on picoplankton, with efficiencies ranging from 58 to 99%. These efficiencies are comparable to those of other freshwater and marine sponges (Reiswig 1971*b*; van de Vyver et al. 1990; Riisgård et al. 1993), but many studies of efficiency were conducted in the laboratory and used artificial water-column assemblages, yeast, or large eucaryotic algae as an artificial food source (Huysecom et al. 1988; Riisgård et al. 1993). The in situ techniques we used are preferable to laboratory experiments with artificial food sources because they accurately reflect the organisms' ability to graze on natural assemblages of picoplankton.

Baikalospongia intermedia was an unexpected source for two types of picoeucaryotes, APP I and APP II. Although pelagic organisms have been found to be a source of bacterial plankton (Nealson et al. 1984; Lee and Ruby 1994), this is the first evidence that a benthic macroinvertebrate is a source of autotrophic plankton to the water column. Nealson et al. (1984) found that release of symbiotic luminescent bacteria by shallow-water species of monocentrid and anomalopid fishes had an irregular pattern, and Lee and Ruby (1994) found that release of episymbiotic luminescent bacteria from the light organs of squid occurred at dawn, when they were no longer needed by their hosts. Because doubling times of bacteria in the light organs of the host can be half those in seawater, Lee and Ruby suggested that expulsion is a form of population regulation. Additionally, they found that the luminescent bacterium *Vibrio fischeri* was a component of bacteria plankton communities only in areas with populations on the host squid.

Like many sponges, *B. intermedia* has a thick mucus coating that can either inhibit or enhance the growth of episymbionts (Becerro et al. 1994). Given the magnitude of the increases above ambient levels, we suggest that APP I and APP II could be expelled by the sponge after living within the mucus layer on the exterior or within the aquiferous system of the sponge via the exhalent currents, similar to a mechanism described by Ducklow and Mitchell (1979*a,b*) for bacteria and coral. Ducklow and Mitchell demonstrated that bacteria living within the external mucus coating of corals use the mucus as a source of nutrients and can be released from the corals to the water-column community. Unfortunately, it is impossible to tell from their studies whether the APP I and APP II expelled from *B. intermedia* are living cells that would enter the carbon pool associated with the

water column or dead cells that would contribute to the detrital biomass, or whether there is any periodicity in production. However, we recently found two species of sponge common to coral reefs that are also a net source of autotrophic eucaryotic picoplankton, and neither sponge exhibited any diel variation in expulsion (Pile in press), suggesting that expulsion of episymbiotic autotrophs is most likely mediated by the pumping activity of the sponge.

Sponges dominated the littoral zone of Lake Baikal, covering 47% of the available surfaces. A percentage cover of 47% for sponges is unusual for a freshwater ecosystem and is difficult to compare with reported sponge biomass and occurrence for freshwater ecosystems (Frost et al. 1982; Bailey et al. 1995). However, such coverage is comparable to some coral reef (e.g. Wilkinson 1987), temperate marine (e.g. Witman and Sebens 1990), and nearshore Antarctic benthic communities (Dayton et al. 1974).

Our estimates of sponge-mediated fluxes of picoplankton, which incorporated in situ measurements of sponge grazing, sponge abundance, and sponge pumping, found that sponges in Lake Baikal's littoral zone are a net sink for procaryotic cells types but a net source for eucaryotic cell types. Sponges removed 1.97 g C d^{-1} m^{-2} from the water column, mostly in the form of procaryotic cell types. Although all types of picoplankton contributed to the daily sponge-mediated flux, *Synechococcus*-type cyanobacteria was by far the largest component, contributing 91% of the total daily flux. Previous estimates for tropical marine sponges found that 0.80–1.80 g C d^{-1} m^{-2} were necessary to meet metabolic carbon demands (Reiswig 1971*b*). Furthermore, Reiswig (1971*b*) found that 80% of the carbon flux by marine sponges was from unresolvable particulate organic carbon, most likely heterotrophic and autotrophic plankton that could not be identified with the methods then available. By using dual-beam flow cytometry to accurately quantify picoplankton and by converting direct counts of cells to carbon with standard conversion factors, we estimated a slightly higher sponge-mediated flux of 1.97 g C d^{-1} m^{-2}. Baikal sponges graze on a water column dominated by procaryotic cell types, similar to that of coral reef ecosystems (Ayukai 1995), but they comprise more of the benthos than do sponges on coral reefs (Reiswig 1971*b*) and thus they have a higher estimated sponge-mediated flux.

The grazing rates of these sponges were so high that food-depleted layers developed over the benthos. Food-depleted layers have been previously identified in a variety of other communities dominated by suspension feeders (Buss and Jackson 1981; Peterson and Black 1987; Fréchette et al. 1989), yet the ability of organisms that feed primarily on picoplankton to create food-depleted or enhanced layers had been undocumented. Food-depleted layers develop when removal of plankton by suspension feeders exceeds input of plankton from higher in the water column from turbulent vertical diffusivity and sinking (Fréchette et al. 1989; Butman et al. 1994; Savarese et al. 1997). We found picoplankton-depleted and -enhanced layers overlying both communities where feeding studies were conducted. Both days were calm, with little wind mixing of the water column, suggesting that horizontal flow of picoplankton-rich water over the

community is necessary to provide a heterotrophic food source for the sponges.

The extensive sponge communities in Lake Baikal's littoral zone significantly affect local picoplankton communities through active suspension feeding. Because of the large volume of water in the lake, it is unlikely that the sponge communities will affect the total picoplankton community. More importantly, in this study we have demonstrated that extensive macrobenthic communities can be supported by heterotrophic and autotrophic picoplankton. We recommend in situ measurements coupled with the power of dual-beam flow cytometry as a new tool for quantifying the grazing by macroinvertebrates on picoplankton. This technique promises a better understanding of the flow of carbon within closely coupled benthic–pelagic ecosystems such as those in shallow, nearshore communities in marine and freshwater ecosystems.

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Some aspects of the analysis of size spectra in aquatic ecology

Abstract—The established approach to model seston size distributions involves the grouping of particles within logarithmic size classes and the examination of the relationship between density, or normalized biomass, and the characteristic sizes of the classes. Here we examine the distributional basis of the established approach and draw a connection between the biomass size spectrum and the Pareto distribution, a model widely used in other disciplines dealing with size-structured systems. We provide efficient estimators of the parameters and also suggest that datasets exhibiting significant departures from a smooth power function decline can be adequately modeled using a Pareto type II distribution.

Current instrumental developments in the analysis of individual particles have fostered research approaches based on individual particles (rather than on volume-averaged compound samples) as the units of analysis in biological oceanography (Legendre and Le Fèvre 1991; Falkowski et al. 1991). This approach originated with the advent of automatic particle-sizers and the discovery of fundamental regularities in the size distribution of oceanic seston (Sheldon et al. 1972). These findings were followed by research, both experimental and theoretical, on the implications of the observed regularities in the size distribution of marine (e.g. Borgmann 1982, 1987; Rodríguez and Mullin 1986*a,b*) and freshwater seston (Sprules et al. 1983; Peters 1983, 1985) and benthos (Schwinghamer 1981; Hanson et al. 1989). The established approach to model seston size distribution involves grouping particles within logarithmic size classes and examining the relationships between their density, or biomass normalized to the width of each size class, and a characteristic value of the size classes (Platt and Denman 1978; Sprules and Munawar 1986). The distributional basis and implications of this procedure, however, have not been fully addressed (Ahrens and Peters 1991; Blanco et al. 1994).

Here we examine some mathematical properties of the so-called normalized biomass–size spectra (hereafter NB-SS) and discuss their effect on the inferences drawn from this model. We suggest that the description of plank-