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# Benthic grazing and carbon sequestration by deep-water glass sponge reefs

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## *Abstract*

Glass sponges are conspicuous members of the deep-sea fauna, but in the northeastern Pacific they form unusual reefs covering kilometers of seafloor. Individual sponges in fjords can process up to 10 $m^3$ water $d^{-1}$ $osculum^{-1}$; sponge reefs must therefore process considerable volumes and could significantly affect local water properties. We measured, in situ, the flux of carbon and nitrogen through *Aphrocallistes vastus*, the dominant reef-building species on Fraser Ridge reef, and calculated the energetics of feeding for all reefs in the Strait of Georgia, British Columbia. Sponges removed up to 90% of bacteria from the water and released ammonium. Because of the high density of sponges, high volumetric flow rates (up to 210 ± 35 $m^3$ $m^{-2}$ $d^{-1}$, mean ± standard error, 95% confidence interval (CI) 132–288 $m^3$ $m^{-2}$ $d^{-1}$), and the efficient extraction of bacteria, we calculate a grazing rate of 165 ± 29 $m^3$ $m^{-2}$ $d^{-1}$ (95% CI 102–228 $m^3$ $m^{-2}$ $d^{-1}$) for sponge reefs, the highest benthic grazing rate of any suspension-feeding community measured to date. Reefs of *A. vastus* extract seven times more carbon (3.4 ± 1.4 g C $m^{-2}$ $d^{-1}$) than can be supported by vertical flux of total carbon alone and therefore require productive waters and steady currents to sustain their strong grazing. We calculate that modern sponge reefs in the northeastern Pacific remove $2.27 \times 10^5 \pm 0.91 \times 10^5$ kg of bacterial carbon daily, nearly an order of magnitude less than the $1.38 \times 10^6 \pm 0.55 \times 10^6$ kg removed by past sponge reefs estimated to have covered the continental shelf.

Feeding by large communities of benthic suspension feeders, known as benthic grazing, can greatly affect water column properties and forms an important component of benthic–pelagic coupling in lakes and oceans (Gili and Coma 1998). Benthic grazing rates quantify the mass transfer from the water column to the benthos (Genin et al. 2009) and are used to understand the effect of suspension feeders on the surrounding water. Grazing rates are well quantified for nearshore, shallow-water communities; however, the effect of grazing by dense deep-water communities is less well studied. A better understanding of the energetics of suspension-feeding communities is especially needed in light of growing evidence of the removal of these communities by deep-water trawling in the ocean (Heifetz et al. 2009; Puig et al. 2012).

In many regions, sponges (Phylum Porifera) dominate benthic communities and, because sponges are particularly effective at removing suspended particulates, they are often implicated in water quality control (Gili and Coma 1998). Where sponges dominate shallow benthic communities their grazing can affect overlying water (Pile et al. 1997). Glass sponges (Class Hexactinellida) are deep-sea animals that occur in large numbers on seamounts, in the Southern Ocean, and on continental slopes and fjords in several oceans (Hogg et al. 2010). They pump water through numerous small pores (ostia) on the dermal surface where it passes via canals to chambers of flagellated collar cells, choanocytes. Particles are sieved by a mesh on the collar and water and wastes are expelled via canals and out of an apical osculum. Glass sponges are abundant on hard substrata throughout the north Pacific (Leys et al. 2004) but also form unusual reefs that cover hectares of seafloor on the continental shelf of the northeast Pacific (Conway et al. 2005a). Over the last two decades, we have built a body of knowledge about glass sponge physiology (Leys and Mackie 1997; Leys et al. 2007; Tompkins-MacDonald and Leys 2008), feeding (Yahel et al. 2007), distribution and densities (Chu and Leys 2010a; Du Preez and Tunnicliffe 2011), and their requirements for silica and water flow (Chu et al. 2011; Leys et al. 2011). We now seek to calculate fluxes through entire reefs to understand the magnitude of their grazing from and excretion into

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overlying water. Glass sponge reefs are built by three species, *Aphrocallistes vastus, Heterochone calyx*, and *Farrea occa*, all of which form fused (dictyonine) skeletons of silica. Over the last 6000–9000 yrs, they have constructed bioherms on glacially carved ridges where water flow is high and sediment accumulation low (Conway et al. 2005a) and, over time, the sponge skeletons become cemented together by sediment into a semisolid substratum. Young sponges settle and grow upon the skeletons of older generations to form the reefs (Conway et al. 2005a).

Glass sponge reefs form one of the densest communities of deep-water suspension feeders known, with up to 40 large oscula (each representing a pumping unit) in a square meter and hundreds of thousands of oscula across a hectare of reef (Chu and Leys 2010a). Like coral reefs, sponge reefs form a habitat for many animals (Du Preez and Tunnicliffe 2011) and, because of their large filtration capacity, they may also have an important role in benthic-pelagic coupling. However, the deep habitat of the sponge reefs, well below the photic zone, is typically poor in planktonic cells, and bacteria ($10^5$ $mL^{-1}$) are the primary food of the sponges (Yahel et al. 2007). Although bacteria could be enriched in bottom waters by sediment resuspension or internal waves (Clark et al. 2010), the source of sufficient bacteria to sustain the reported growth rates of 1–6 cm $yr^{-1}$ (Leys and Lauzon 1998) and of such large communities as the sponge reefs is not evident.

One glass sponge reef on Fraser Ridge near Vancouver, British Columbia, is well studied and serves as a model for understanding other dense glass sponge communities, including hundreds of square kilometers of known sponge reefs (Conway et al. 2005a) and dense sponge populations in the Antarctic and on continental slopes and seamounts. Reefs in the Strait of Georgia, a marginal sea near Vancouver, British Columbia, are nearly monospecific, with the species *A. vastus* (hereafter *Aphrocallistes*) forming approximately 86% of individuals in a reef. Here we combine measurements of individual grazing and excretion rates of *Aphrocallistes* with sponge size and density data to develop reef-wide estimates of the community metabolism and the effect of these animals on overlying waters. Our results indicate that glass sponge reefs have grazing rates and water processing capacity up to an order of magnitude higher than other suspension-feeding communities. Our results also provide insight into the conditions needed to sustain such a dense community of suspension feeders. As conservation of cold-water sponge and reef habitats is a pressing issue, we examine the ecosystem functions of these large glass sponge communities in shelf ecosystems, both present and past.

## Methods

### Study site

Samples and measurements were collected from Fraser Ridge reef in July 2005. The Fraser Ridge is a relict glacial deposit of boulders and gravel with its base at about 200 m. The ridge lies roughly perpendicular to the prevailing northerly currents in the central Strait of Georgia (SoG), British Columbia (Conway et al. 2005a; Bedard 2011). The Fraser Ridge reef covers about 170,000 $m^2$ (Conway et al. 2005b) on the northern and western edges of the ridge (49°9′15.7″N, 123°23′3.7″W; Fig. 1A). The reef ranges from 150 m to 180 m depth beneath the outflow of the Fraser River, which is the source of 73% of the freshwater and 64% of particles entering the Strait (Johannessen et al. 2003). Strong southward riverine outflow from the Fraser River creates stratification that limits downwelling of surface waters and induces a northerly flow of water at the bottom (Masson 2002). Current speeds through Fraser Ridge reef are very high, reaching up to 92 cm $s^{-1}$ during flood tides (Leys et al. 2011), but follow a mixed semidiurnal tide schedule so currents vary throughout each tide cycle. Mean northward currents amplify flood tides and dampen currents during ebb tides (Bedard 2011) so that the flow over the ridge is almost always to the north.

### Water sampling

The remotely operated vehicle (ROV) *ROPOS* carried out nine dives to gather samples. A pumping conductivity, temperature, depth (CTD) instrument (SBE19plus, Seabird) mounted on the ROV continuously recorded water conditions to produce a vertical profile of salinity, density, temperature, oxygen concentration (SBE43), and transmissivity (SeaStar). Water samples were collected with precision positioning beside the sponges (zero meters above bottom, mab) and from the sponge excurrent flow using custom designed paired samplers (SIPs) that can be manipulated by the ROV and draw water in at a rate lower than the excurrent velocity, as described by Yahel et al. (2007). Ambient water conditions at and above the reef were determined from samples collected with Niskin bottles. During four separate dives, one Niskin attached to the ROV was triggered at each of 5 m, 10 m, and 20 m above the reef and water from each Niskin was divided for analysis of dissolved nutrients (ammonium, nitrate, dissolved silica, and phosphate), bacteria, and total organic carbon (TOC) concentrations.

Previous work has shown that *Aphrocallistes* pumps continuously unless disturbed by sediment (Tompkins-MacDonald and Leys 2008). To confirm that each sponge was actively filtering prior to sampling with SIPs, fluorescein dye was released beside each sponge to visualize filtration by dye uptake and release from the osculum (Fig. 1D). We collected a total of 22 paired samples (ambient water [in] and water filtered by the sponge [ex]). When sampling water from a sponge in situ, the sampling tube must be well inside the osculum and must not touch the sponge to prevent contamination by ambient water or sponge tissue; we checked video records of each sample collection to confirm SIP samplers did not touch the sponge and were inserted sufficiently into

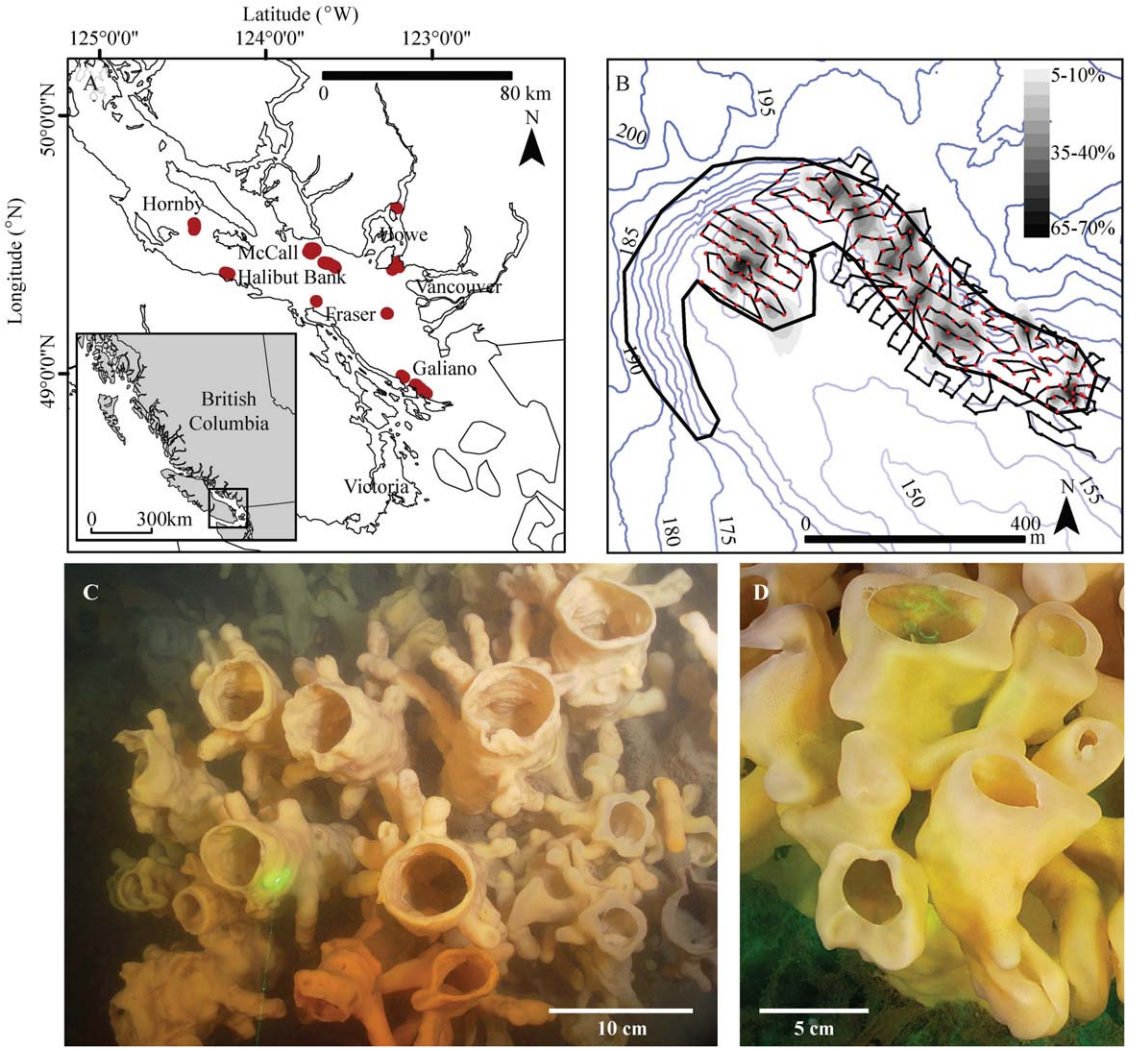


**Fig. 1.** Glass sponges form dense reef habitats in the northeastern Pacific. (A) Locations of sponge reefs in the Strait of Georgia. Sampling was conducted at Fraser Ridge reef and fluxes were compared with populations from Galiano Ridge and Howe Sound reefs. All the three reefs lie on the continental shelf between Vancouver Island and mainland Canada. (B) A map showing the reef at Fraser Ridge and the extent of the surveys in 2005 and 2007 (gray gradients are interpolated reef live percent cover), with survey tracks set to overlap with the area predicted to be reef from multibeam mapping (black outline). Survey points outside (black dots) and inside (red dots) of the predicted reef area. (C, D) Sponge reefs are dense associations of live sponges growing on the skeletons of previous dead generations. The large openings are the excurrent oscula and are approximately 5–10 cm across in these photos. (D) Green fluorescein dye was used to verify the sponges were pumping water.

the osculum. Our previous data showed the sponges filter with up to 95% efficiency (Yahel et al. 2007), so samples with less than 25% filtration efficiency (5 of 22 samples collected) were considered contaminated with ambient seawater due to improper position of the sampler.

SIP water samples were processed for nutrient analysis (as above), TOC and total nitrogen (TN), as well as for flow cytometry for bacteria removal following Yahel et al. (2007). Pieces of each sponge from which water was sampled were collected to verify species identification by spicule composition. Of 243 samples collected to date, 86% have been *Aphrocallistes*; all sponges we sampled water from in this study were *Aphrocallistes*.

**Sponge respiration**

Dissolved oxygen in ambient and excurrent water from 24 individuals was measured using a long tube connected to a pumping CTD with an attached oxygen sensor (SBE 43, Seabird). For each sponge, the tube was positioned inside the osculum and, once the CTD record stabilized, a 2-min time series was recorded at 4Hz. This procedure was repeated adjacent to the sponge to measure the ambient oxygen concentrations. We took the difference between the two measurements to be an estimate of sponge respiration in $\mu$mol $O_2$ per liter processed. Flow visualization with fluorescein dye was carried out before collecting respiration samples to ensure the sponge was pumping.

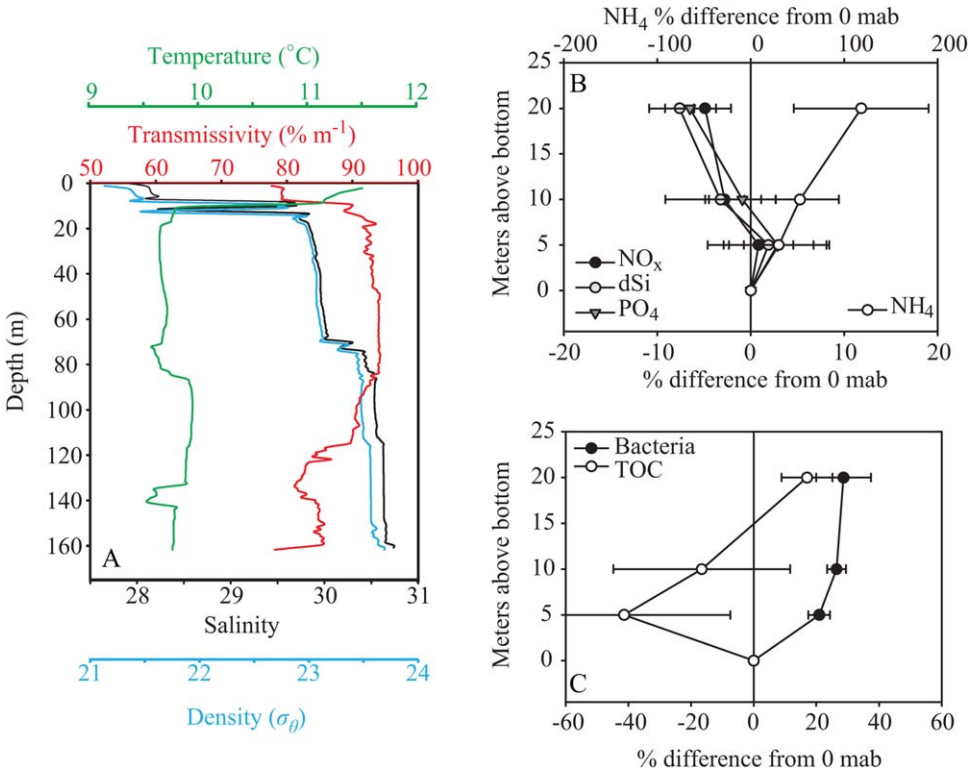


**Fig. 2.** Water characteristics above Fraser Ridge reef. (A) Depth profiles of temperature, salinity, density, and transmissivity from July 2005 during one ROV ascent from the reef. Bottom depth was 160 m. (B) Nutrient profiles above the seafloor. Data are presented as the difference from the average value measured among the sponges ($n$=17). Three Niskin bottles were triggered during each ROV dive, at 5 m, 10 m, and 20 m above the sponges. Niskin samples and SIP samples from water surrounding the sponges were analyzed to compare bottom water conditions. Error bars: SE. (C) Vertical profiles of bacteria and TOC concentration above the reef presented as the average percent difference from their concentration among the sponges. Error bars: SE.

### Calculating grazing and excretion rates

We estimated whole-reef fluxes using previously published data for the average excurrent velocity (2.8 ± 0.4 cm $s^{-1}$, mean ± standard error, SE, range 0–5.2 cm $s^{-1}$; Leys et al. 2011) and sponge oscula diameter and density (Chu and Leys 2010a) for each of three reefs that occur in the SoG region: Fraser Ridge, Galiano Ridge, and Howe Sound (Fig. 1A). We propagated error to calculate SE and 95% confidence intervals (CI) using the exact method of Goodman (1962) for grazing rates and excretion rates per $m^2$. Relative error approximations were used for scaling up calculations beyond 1 $m^2$ by adding each SE—normalized by its respective mean—for each variable in a product (Taylor 1997). Sponge reefs in British Columbia have been identified by multibeam mapping, providing an outline of past (buried) and present (living and dead) glass sponges (Conway et al. 2005b). In order to calculate fluxes for only live (actively filtering) reef, we first calculated the fluxes through an average 1 $m^2$ of reef using published estimates of osculum density (Chu and Leys 2010b), and then applied that number to the percent cover of live sponges in reefs. Previous work by Chu and Leys (2010a) estimated live sponges to occupy 14% of the area surveyed at Fraser Ridge, but the survey areas in that study extended beyond the boundaries of area predicted to be reef by multibeam mapping (Conway et al. 2005b); therefore, some areas surveyed had no reef, and in two instances, the reef extended beyond the predicted area. To account for patchiness of the reefs and estimate the live sponge cover more accurately at the Fraser Ridge reef and other reefs in the SoG, we used two datasets: the area predicted to be reef based on multibeam sonar (177,486 $m^2$, courtesy of K. Conway), and images by ROV that surveyed a grid of 593 1 $m^2$ plots, of which 98 $m^2$ or 16.5% showed live reef structure (Fig. 1B). We extended this approach to determine the area predicted to be reefs by multibeam mapping in the SoG (1.8 × $10^6$ $m^2$ live cover from 1.1 × $10^7$ $m^2$ predicted) and from Alaska to southern British Columbia (6.6 × $10^7$ $m^2$ live cover from 4.0 × $10^8$ $m^2$ predicted).

## Results

### Ambient conditions at Fraser Ridge

Full water column profiles reflected the strong influence of the Fraser River outflow on temperature, salinity, density,

**Table 1.** Concentrations of ammonium, nitrate + nitrite ($NO_x$), dissolved silica (dSi), phosphate ($PO_4$), and total organic carbon (TOC), and bacterial concentrations at 0m, 5m, 10m, and 20 meters above Fraser Ridge Reef. Mean ± SE.

| Meters above bottom | Ammonium (nmol $L^{-1}$) | $NO_x$ ($\mu$mol $L^{-1}$) | dSi ($\mu$mol $L^{-1}$) | $PO_4$ ($\mu$mol $L^{-1}$) | TOC ($\mu$mol $L^{-1}$) | Bacteria (cells $mL^{-1}$) |
|---|---|---|---|---|---|---|
| 0 | 571±110 | 25.8±0.4 | 49±1 | 2.24±0.07 | 65±3.3 | $6.7\times10^5\pm3.5\times10^4$ |
| 5 | 625±184 | 26.0±0.6 | 49±2 | 2.31±0.09 | 69±1.1 | $8.3\times10^5\pm5.0\times10^4$ |
| 10 | 708±170 | 25.1±0.2 | 47±2 | 2.22±0.05 | 73±8.2 | $8.7\times10^5\pm4.5\times10^4$ |
| 20 | 993±271 | 24.6±0.3 | 45±1 | 2.10±0.12 | 75±4.2 | $8.8\times10^5\pm3.9\times10^4$ |

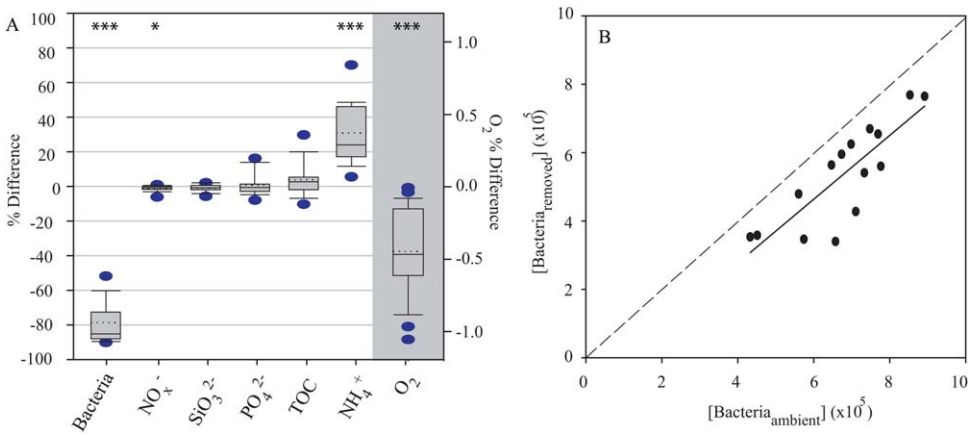


**Fig. 3.** Sponge pumping efficiencies and behavior. (A) Percent differences of bacteria, nutrients, TOC, ammonia, and oxygen between ambient water and the water emerging from the exhalent osculum; samples collected by SIPs as described by Yahel et al. (2007). Boxes encompass 25th and 75th percentiles and contain medians (solid lines) and means (dotted lines); whiskers encompass 10th and 90th percentiles. Outliers are shown as dots. Asterisks indicate statistically significant *p*-values from paired *t*-tests of water sampled from ambient and excurrent water (* for $p<0.05$, *** for $p<0.0005$). (B) Removal of bacteria by a sponge is plotted as a function of bacteria availability in ambient water. "Ambient" refers to water immediately adjacent to the sponge.

and transmissivity at the surface (Fig. 2A). Closer to the seafloor, measurements made from water collected at 0 m, 5 m, 10 m, and 20 m above the sponges were variable because replicates were collected across different days, times, and stages of the tide (Table 1). On an average, however, nutrient concentrations (nitrate, phosphate, and dissolved silica) showed a peak 5 m above the reef rather than among the sponges (Fig. 2B). Average ammonium concentration was lower among the sponges than at all depths above (Fig. 2B), and while bacteria concentrations were also reduced among the sponges compared to all other depths, TOC was greater among the sponges than above the reef (Fig. 2C); there was low variability in bacterial concentration across all Niskin samples.

Ambient water among the sponges (zero mab) was moderately low in oxygen and highly enriched with dissolved silica, nitrate, and phosphate (Table 1). Dissolved inorganic nitrogen formed nearly 89% (26.1 ± 0.74 $\mu$mol $L^{-1}$, mean ± SE) of the TN. Dissolved organic carbon made up 85% of TOC in the water. The concentration of particulate organic matter (POM) at the sponge reef habitat was low (10.5 ± 4.2 $\mu$mol C $L^{-1}$) and the POM was nitrogen poor (C:N ratio 8.5 ± 1.9). The POM component consisted partly of picoplankton of which bacteria dominated whereas picoeukaryotes were much less abundant than other picoplankton constituents (714 ± 213 cells $mL^{-1}$, $n = 17$).

### Feeding and excretion

Comparisons of water samples before and after filtration by *Aphrocallistes* show removal of bacteria with up to 90% efficiency (78.6% ± 3.20% mean ± SE, paired *t*-test, $t = 14.063$, degrees of freedom (df) = 14, $p < 0.001$; Fig. 3A). Sponges also removed small populations of nonphotosynthetic larger cells that we isolated through flow cytometry but could not identify unambiguously. Numbers of bacteria removed by individual sponges increased linearly with ambient bacteria concentrations (a Type I functional response; $r^2 = 0.69$, $p < 0.0005$; Fig. 3B). Ammonia was the major nitrogenous waste product with 0.17 ± 0.02 $\mu$mol ammonium $L^{-1}$ of water filtered (paired *t*-test, $t = -7.37$, df = 14, $p < 0.001$; max 70% difference from ambient). Oxygen

**Table 2.** Component fluxes mediated by the sponges on Fraser Ridge, Galiano Ridge, and Howe Sound reefs based on in situ measurements of osculum size and density from Chu and Leys (2010a, 2010b) and excurrent flow speeds from Leys et al. (2011). Mean-SE. Dashes indicate values that were not measured.

| | Reef | | |
|---|---|---|---|
| **Component** | **Fraser** | **Galiano** | **Howe** |
| *Osculum size ($cm^2$) | 38.2±1.9 | 22.7±0.8 | 14.6±0.5 |
| *Osculum density ($m^{-2}$) | 23.0±1.7 | 46.3±3.7 | 30.9±3.0 |
| †Excurrent flow speed (cm $s^{-1}$) | 2.8±0.40 | — | — |
| Volumetric pumping rate ($m^3$ $m^{-2}$ $d^{-1}$) | 210±35 | 252±42 | 108±19 |
| Benthic grazing rate ($m^3$ $m^{-2}$ $d^{-1}$) | 165±29 | 198±34 | 85±15 |
| Bacteria (cells $m^{-2}$ $d^{-1}$) | $1.1\times10^{14}\pm0.25\times10^{14}$ | $1.4\times10^{14}\pm0.29\times0^{14}$ | $5.8\times10^{13}\pm1.3\times10^{13}$ |
| ‡Bacterial carbon (g C $m^{-2}$ $d^{-1}$) | 3.4±1.4 | 4.1±1.6 | 1.8±0.7 |
| ‡Bacterial nitrogen (g N $m^{-2}$ $d^{-1}$) | 0.66±0.31 | 0.79±0.37 | 0.34±0.16 |
| Oxygen ($\mu$mol $m^{-2}$ $d^{-1}$) | 32.8±13.3 | 39.3±15.6 | 16.8±6.99 |
| Ammonia (mmol $m^{-2}$ $d^{-1}$) | 39±17 | 47±20 | 20±9 |

*Data from Chu and Leys (2010a).
†Data from Leys et al. (2011). $n$ = 9 sponges, 13 measurements.
‡Using bacterial carbon and nitrogen values of 30.2 fg $cell^{-1}$ and 5.8 fg $cell^{-1}$, respectively. From Fukuda et al. (1998).

removal was slight but significant, 0.56 ± 0.37 $\mu$mol $L^{-1}$ (0.45%; ambient [$O_2$] 126.39 ± 3.57 $\mu$mol $L^{-1}$, $n$ = 24).

*Aphrocallistes* did not take up or excrete notable amounts of dissolved nutrients (phosphate, silica), or total carbon (Fig. 3A). It should be noted that the small sample size ($n$ = 15 pairs), dictated by the logistics of deep-sea work, resulted in low statistical power (< 0.5) of the paired $t$-tests we used.

### Flux through the reef

We calculated the volume processed by each osculum each day for 1 $m^2$ of seafloor using flow rate, osculum area, and density on Fraser reef reported in Table 2. Each osculum processes 9140 ± 1750 L $osculum^{-1}$ $d^{-1}$ and thus 1 $m^2$ processes 210 ± 35 $m^3$ $d^{-1}$ (95% CI: 132–288 $m^3$ $m^{-2}$ $d^{-1}$). Although Howe Sound reef covers a larger area, the sponge density is lower and therefore this reef filters the least water per unit area, 108 ± 19 $m^3$ $m^{-2}$ $d^{-1}$ (95% CI 65–150 $m^3$ $m^{-2}$ $d^{-1}$). Galiano reef sponges, in contrast, are the most dense and therefore process the most water at 252 ± 42 $m^3$ $m^{-2}$ $d^{-1}$ (95% CI 158–345 $m^3$ $m^{-2}$ $d^{-1}$; Table 2).

### Reef metabolism

Grazing rates ($\alpha$) reflect the efficiency of removal of particles or nutrients from a volume of water, and can be compared across suspension-feeding communities to determine effectiveness of extraction. For Fraser Ridge reef, we calculated that the benthic grazing rate on bacteria, the primary food item extracted by sponges, was 165 ± 29 $m^3$ $m^{-2}$ $day^{-1}$ (95% CI 102–228 $m^3$ $m^{-2}$ $d^{-1}$)—that is, the volume from which 100% of bacteria are cleared. Since bacteria concentrations in water near the sponges were $6.9 \times 10^6 \pm 3.0 \times 10^4$cells $mL^{-1}$, this equates to $1.2 \times 10^{14} \pm 2.36 \times 10^{13}$ bacterial cells $m^{-2}$ $d^{-1}$ removed by 1 $m^2$ reef sponges. We calculated the total bacterial carbon and nitrogen removed by reef sponges based on the amount of bacteria consumed. Assuming 30.2 ± 12.3 fg C $cell^{-1}$ and 5.8 ± 1.5 fg N $cell^{-1}$ for coastal bacteria (Fukuda et al. 1998), each square meter of reef at Fraser Ridge consumes 3.4 ± 1.4 g C $m^{-2}$ $d^{-1}$ and 0.7 ± 0.3 g bacterial N $m^{-2}$ $d^{-1}$ (Table 2). The rate of excretion of nitrogenous waste was comparable to the rate of uptake of bacterial nitrogen (0.04 ± 0.02 mol ammonium $m^{-2}$ $d^{-1}$, or 0.55 ± 0.23 g N $m^{-2}$ $d^{-1}$).

Not all of the area mapped by remote sensing (multibeam mapping) has exposed reef structure today—some is buried under mud—however, we were able to use the area surveyed by ROV (Chu and Leys 2010b) to estimate how much of the area mapped by multibeam consists of sponge cover today at Fraser Ridge reef. Thus, 16.5% of the area identified by multibeam mapping at Fraser Ridge (177,486 $m^2$, data courtesy of K. Conway) has live sponge cover today, giving a total filtering reef size of 29,242 $m^2$. This area alone consumes $1.00 \times 10^5 \pm 3.99 \times 10^4$ g C $d^{-1}$ (Table 3). Parts of Galiano and Howe reefs have been mapped in detail as well, allowing us to also calculate their grazing rate. The area of reef mapped by multibeam in Howe Sound was larger than Fraser (898,541 $m^2$, data courtesy of K. Conway) so, although ROV surveys showed it had fewer, larger sponges (11.6% live reef cover, Chu and Leys 2010a), because of its size it is calculated to consume more carbon, $1.83 \times 10^5 \pm 7.46 \times 10^4$ g C $d^{-1}$ from 104,231 $m^2$ of live reef. Galiano reef extends north and south along a long ridge, and multibeam mapping estimates suggest it is as large as Howe (862,799 $m^2$). It also has greater reef cover (26% live reef cover, Chu and Leys 2010a) and more dense oscula, so live cover is estimated to be greater than Howe (224,328 $m^2$) and to consume more carbon, $9.20 \times 10^5 \pm 3.67 \times 10^4$ kg C $d^{-1}$.

Multibeam mapping has identified 10 additional reefs in the SoG (Conway et al. 2005b). Although we have not yet surveyed these using ROV and video, by using the estimate of average sponge cover calculated for Fraser Ridge reef (16.5%), we estimate that all live sponges at SoG reefs (including Fraser, Galiano, and Howe) cover $1.84 \times 10^6$ m$^2$ and remove $6.3 \times 10^6 \pm 2.5 \times 10^6$ g C d$^{-1}$ (Table 3).

## Discussion

Glass sponges are effective ecosystem engineers by constructing a three-dimensional habitat for other animals (Beaulieu 2001; Du Preez and Tunnicliffe 2011). Our work now highlights the important role glass sponges have in in filtering enormous volumes of water each day, removing bacteria and oxygen, and releasing ammonium. Our calculations show that the sponge reefs have an unusually high grazing rate in comparison to all known benthic suspension-feeding communities due to their density, efficient capture of bacteria, and high water processing rates making them a potential carbon sink in Canadian shelf waters.

**Table 3.** Estimates of bacterial carbon consumption by glass sponge reefs. Mean ± SE.

| Reef | Live cover (m$^2$) | Bacterial C consumed (g C day$^{-1}$) |
|---|---|---|
| Fraser Ridge Reef | $2.9\times10^4$ | $1.0\times10^5\pm0.40\times10^5$ |
| All SoG reefs | $1.8\times10^6$ | $6.3\times10^6\pm2.5\times10^6$ |
| Reefs known from Alaska to southern British Columbia | $6.6\times10^7$ | $2.3\times10^8\pm0.91\times10^8$ |

### Grazing rates and bacterial supply

Within the glass sponge reefs in British Columbia, sponge densities and size are much higher than those seen in other glass sponge communities (Table S1). At Galiano Ridge reef, for example, oscula reach densities up to 46 m$^{-2}$ in dense patches of reef (Chu and Leys 2010a), more than 18 times greater than those seen in other glass sponge communities. Because each sponge removes on average >75% of the bacteria from the water as it passed through the aquiferous system, the reef functions as a highly efficient filtration system. Thus, sponge reefs have the highest grazing rates of any other suspension-feeding animal or community measured to date (Table 4). However, perhaps more important is what such a high grazing rate translates to in carbon consumption.

Filtration requires active beating of flagella to pull water through the fine passages in the sponge. The oxygen consumed by the sponge mainly reflects this energy expenditure

**Table 4.** Comparison of benthic grazing rate, water processing rate, and carbon consumed by suspension feeding communities (numbers come directly from the references unless indicated otherwise by footnotes).

| Habitat | Benthic grazing rate, $\alpha$ (m$^3$ m$^{-2}$ d$^{-1}$) | Water processing rate (m$^3$ m$^{-2}$ d$^{-1}$) | Carbon consumed (g C m$^{-2}$ d$^{-1}$) | Material consumed | Reference |
|---|---|---|---|---|---|
| Glass sponge reef | 85–198 | 108–252 | 1.8–4.1 | Bacteria | This study |
| Soft-bottom community, San Francisco Bay | 40–60 | 10.3* | 0.14–0.16 | Phytoplankton | Jones et al. 2009 |
| Tropical sponge community | 16.5–40 | — | — | Bacteria | Reiswig 1973; Reiswig 1974 |
| Coral reef in Eilat, Red Sea | 10–20 | 2.6[†] | 0.22 | Phytoplankton | Genin et al. 2009 |
| Bivalve: *Corbicula* in tidal lakes, Sacramento-San Joaquin river delta | 1–11 | —[‡] | 0.04–0.32 | Phytoplankton | Lucas et al. 2002 |
| Tropical demosponge: *Aplysina* (*Verongia*) *fistularis*[§] | 1.7 | 0.06 | 0.0070 | POC | Reiswig 1981 |
| Lake Baikal sponges | 1.4 | 1.98 | 1.12[#] | Prokaryotes, eukaryotes | Pile et al. 1997; Savarese et al. 1997 |

*Pumping rates presented in Table 4 (Jones et al. 2009).
[†]Calculated using the same scale-up approach as used here, but only for conspicuous pumping suspension feeders.
[‡]Water processing rates were not measured because grazing and carbon consumption were estimated using plankton biomass.
[§]All values were presented for an individual sponge (Reiswig 1981). Densities were assumed as an average of density of *Mycale lingua* and *Verongia gigantea* (Reiswig 1973). Retention efficiency was only for bacteria (97%). Particulate organic carbon (POC) consumption (16.7 $\mu$g POC L$^{-1}$) accounted for 14% of metabolic needs while DOC made up 86%.
[#]Includes carbon consumed or removed from the water and carbon released. Chloroplast-containing picoeukaryotes were found expelled from one species (*Baikalospongia intermedia*).

(Leys et al. 2011), so knowing the oxygen removal per liter of water filtered (0.013 ± 0.0017 mL $L^{-1}$) and assuming 0.46 mg C = 1 mL $O_2$ (Hadas et al. 2009) we calculated that each sponge osculum requires 0.0058 ± 0.0008 mg carbon per liter of water filtered. Considering the average bacteria removal of $5.36 \times 10^5$ cells $mL^{-1}$ (0.016 ± 0.004 mg carbon $L^{-1}$), there remains about 0.010 ± 0.005 mg carbon $L^{-1}$ available for growth. This suggests that 36% ± 14% of food energy consumed by actively pumping sponges is used toward metabolism, as estimated previously (Leys et al. 2011), and the most of this must be used for pumping water through the body for feeding and respiration. The remaining food energy is available for growth (and skeleton production), reproduction, maintenance, or is excreted as fecal pellets and waste (Reiswig 1981).

Each day, a square meter of reef clears bacteria from the equivalent volume of 165 m of water above it. This high grazing rate implies that large sponge reefs need particular hydrographic conditions to provide enough food for growth and to prevent the formation of a depleted boundary layer above the reef (Genin et al. 2009). Just north of Fraser Ridge, carbon delivery to the seafloor is 0.46 g C $m^{-2}$ $d^{-1}$ (Johannessen et al. 2003) whereas reef sponges extract 3.4 g C $m^{-2}$ $d^{-1}$, seven times more than total POC delivered by vertical flux. Therefore, there is a deficit which must be mitigated by lateral transport.

Organic matter comes from several sources in the highly productive SoG. Similar amounts of organic input arrive from terrigenous and phytoplankton sources, with about 80% of the carbon in dissolved form and so available to microbial production (Johannessen et al. 2008). The Fraser Ridge reef grows on the lee of a ridge. A topographically controlled bottom "jet" forms over the ridge with velocities up to 70 cm $s^{-1}$ during flood tides, thereby resuspending sediments (Bedard 2011) and associated organic matter. The Fraser sponge reef is located where a strong lee wave advances downslope as the northward jet forms over the tidal cycle. As most POC in the Strait settles in the southern SoG and is redistributed northward by currents (Johannessen et al. 2005), the reef placement is optimal to receive this material or more likely, the bacteria that thrive on it. This lateral delivery of bacteria to the reef seems to be the principal reason for the location of reefs on major topographic features that accelerate water flow such as canyons, shelf walls, and fjord sills (Conway et al. 2005a).

### A carbon sink

The amount of carbon consumed by reefs in the SoG (Table 3) is only 0.8% ± 0.3% of the daily vertical flux of primary production to the seafloor in the SoG ($7.80 \times 10^8$ g C $d^{-1}$; Johannessen et al. 2003), so there is not a great effect on the mass balance of carbon in the SoG, which is a highly productive basin. Our calculations, however, stem from just a fraction of the area covered by known reefs and other dense stands of glass sponges in the northeast Pacific. If all other reefs mapped by remote sensing—from Hecate Strait, Queen Charlotte Strait, the Strait of Georgia, and southeastern Alaska (Conway et al. 2005b; Stone et al. 2013)—are included (Table 3); the amount of carbon consumed by sponge reefs may be considerably larger. Assuming the same relationship between reef cover and area mapped by multibeam sonar found at Fraser Ridge (16.5%) for all reefs identified by remote sensing (403 $km^2$), glass sponges cover a total of 66 $km^2$, process $1.4 \times 10^{10} \pm 2.3 \times 10^9$ $m^3$ water $d^{-1}$, and consume $2.27 \times 10^8 \pm 9.1 \times 10^7$ g C $d^{-1}$. Manned submersible dives since the 1980 s have documented that fjord walls and sills within straits also have dense communities of glass sponges (up to 24 $m^{-2}$; Leys et al. 2004) and as we do not include those sponges, our calculation of carbon consumption by glass sponges is an underestimate.

Sponges in other classes, especially Demospongiae which can be conspicuous inhabitants in tide pools to freshwater lakes, abyssal seafloors, and coral reefs, also consume large amounts of carbon, but still substantially less than glass sponge reefs (0.029–1.970 g C $m^{-2}$ $d^{-1}$) (Maldonado et al. 2012). While we are confident in our estimates of overall fluxes for glass sponges, generalizations beyond the Hexactinellida are difficult for two reasons. First, the Demospongiae may contain symbionts that cause them to feed on and excrete different carbon and nitrogen species (reviewed by Maldonado et al. 2012). Second, it is rare to get the full suite of measurements needed to scale up estimates, although there have been some attempts (reviewed in Maldonado et al. 2012).

### Ammonia excretion and ammonium

The sponges not only efficiently remove bacteria from the water but also excrete wastes as ammonia. Water sampled above the reef had five times more ammonium than water collected around solitary glass sponges growing in fjords in Barkley Sound (Yahel et al. 2007). The difference could be regional, but the voluminous water processing by the reef likely has a substantial effect. Vertical Niskin profiles show higher ammonium concentrations in water 5 m, 10 m, and 20 m above the reef sponges compared to water among the sponges; however, we do not imagine excretion by glass sponge reefs has a large effect on total primary production in this nutrient-rich basin. Reefs cover a small fraction of the total size of the SoG and their contribution to the SoG nitrogen budget is small relative to the dominant source: oceanic water brought in via the bounding Haro Strait ($3.0 \times 10^4$ mmol $yr^{-1}$; Sutton et al. 2013). This would not be the case, however, for more enclosed or less productive waters. Unlike the nitrate-rich waters in the SoG, ammonium is the favored and dominant nitrogen source for phytoplankton in other regions such as the Weddell Sea, where excretion by krill makes up nearly 80% of the ammonium taken up by phytoplankton for primary production (Whitehouse et al. 2011).

Likewise, glass sponges perched on seamounts may contribute to primary production in the photic zone through turbulent mixing and internal waves (Clark et al. 2010), transporting ammonia up to where it can fuel further productivity.

### Conservation issues: Implications of water processing by glass sponges

We measured nutrient and particle fluxes from sponges in a reef whose flow dynamics, density, and other features are well studied, resulting in first-order estimates of reef-wide fluxes. Multibeam mapping reveals reef structure, both past and present; therefore, if all areas identified by multibeam mapping to have been reef at some time in the past are considered, the potential total reef cover for all past reefs is 403 $km^2$, which could have resulted in consumption of $1.38 \times 10^9 \pm 5.5 \times 10^8$ g C $day^{-1}$. These figures indicate that sponge reefs have been a carbon sink, at least locally, for as long as they have been present.

Modern-day reefs occur from southern Alaska to British Columbia (Conway et al. 2005a; Stone et al. 2013) but we do not know their extent before trawling. Bottom trawling has damaged 21% of sponges in the Aleutian archipelago (Heifetz et al. 2009), with potential for greater damage where densities are high. Bottom trawling is common in Canadian waters, with glass sponges recorded in bycatch records since 1996. Trawl records from 1996 to 2001 find a catch per unit effort for sponges between 0.086 kg $min^{-1}$ and 6.041 kg $min^{-1}$ during trawls through reefs (Jamieson and Chew 2002). Each sponge damaged is one that is no longer sequestering bacterial carbon into its skeleton or recycling nitrogen. Prior to anthropogenic effects in the Northeast Pacific, dense assemblages of glass sponges may have had a substantial effect on nutrient dynamics in bottom waters.

Glass sponges may have served a similar role in prehistoric oceans and the ammonium they excreted may have been more important to the surrounding community; unlike the highly productive waters that reefs are found in today, ancient reefs in the Tethys Sea lived in oligotrophic waters (Leinfelder et al. 1996). Like modern-day oligotrophic habitats, recycled nutrients were very important in driving productivity in Jurassic oceans. Ancient reefs in the Jurassic were not monocultures (Leinfelder et al. 1996) and did not have fused skeletons, which enhance reef structure, as modern reefs do, but assuming that their filtration was similar to present-day reefs, prehistoric reefs were likely very important cyclers of carbon and nitrogen in ancient waters.

Sponges were predicted to be on the "winners" side of climate change after dramatic, episodic growth was observed following breakage of ice shelves in the Southern Ocean (Dayton et al. 2013; Fillinger et al. 2013). If this is true, then sponges may be one of many buffers against climate change as carbon concentrations in the ocean rise and subsequently become sequestered into sponge tissue.

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