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Selective feeding by the giant barrel sponge enhances foraging efficiency

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Abstract

Foraging theory predicts the evolution of feeding behaviors that increase consumer fitness. Sponges were among the earliest metazoans on earth and developed a unique filter-feeding mechanism that does not rely on a nervous system. Once thought indiscriminate, sponges are now known to selectively consume picoplankton, but it is unclear whether this confers any benefit. Additionally, sponges consume dissolved organic carbon (DOC) and detritus, but relative preferences for these resources are unknown. We quantified suspension feeding by the giant barrel sponge *Xestospongia muta* on Conch Reef, Florida, to examine relationships between diet choice, food resource availability, and foraging efficiency. Sponges consistently preferred cyanobacteria over other picoplankton, which were preferred over detritus and DOC; nevertheless, the sponge diet was mostly DOC (~70%) and detritus (~20%). Consistent with foraging theory, less-preferred foods were discriminated against when relatively scarce, but were increasingly accepted as they became relatively more abundant. Food uptake was limited, likely by post-capture constraints, yet selective foraging enabled sponges to increase nutritional gains.

Introduction

The necessity of obtaining food from the environment is recognized as "the primary driving force of all animals" (Elton 1927) and as such is a strong selective pressure for the evolution of diverse consumer adaptations for food acquisition (Hughes 1990, 1993). Consumer behavior has a strong influence on foraging efficiency and ecologists have long sought to explain and predict foraging behaviors such as the choice of which food types to eat and the allocation of time to different patches (Pyke et al. 1977; Stephens and Krebs 1986). Much of this work, however, was performed on vertebrates with complex nervous systems and has not considered invertebrate suspension feeders, which were historically viewed as simple mechanical sieves incapable of complex behaviors.

Suspension feeding is a major feeding mode in marine and freshwater ecosystems, especially among the benthos, and plays important roles in benthic-pelagic coupling, organic matter cycling and nutrient cycling (Gili and Coma 1998). It is now generally understood that feeding behavior plasticity is a common strategy among benthic suspension feeders to exploit heterogeneous planktonic food resources (Okamura 1990). One such strategy involves discrimination among available food and the selection of preferred resources (Ward and Shumway 2004; Maldonado et al. 2012). Diet selection has significant implications for energy acquisition (Stephens and Krebs 1986), the abundance, structure and composition of plankton communities (Pernthaler 2005), and the functional roles of benthic suspension feeders in marine ecosystems (Gili and Coma 1998).

Sponges are dominant components of marine ecosystems that efficiently filter a variety of food types from the water column, including living and nonliving (detritus) particulate organic matter (POM) (Ribes et al. 1999a; Yahel et al. 2003; Hadas et al. 2009) and dissolved organic matter (DOM) (Reiswig 1981; Yahel et al. 2003; de Goeij et al. 2008b). Increasingly, evidence suggests that sponges can feed selectively from living POM (LPOM), which consists mostly of picoplankton (0.2–2 μm) (Yahel et al. 2006; Hanson et al. 2009; Maldonado et al. 2010). Because all incurrent picoplankton must pass through the highly efficient choanocyte filter (Riisgård and Larsen 2010), variation in the retention of different picoplankton prey has suggested that food selection is an active process by the sponge that involves individual prey recognition and sorting (Frost 1980; Ribes et al.

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1999a; Yahel et al. 2006). Temporal changes in the retention of the same prey types (Ribes et al. 1999a; Hanson et al. 2009; Perea-Blázquez et al. 2013) further suggest that food selection involves active processes. Foraging theory predicts feeding behaviors that increase consumer fitness (Pyke et al. 1977; Stephens and Krebs 1986), however the factors that mediate changes in diet selection are not understood and it is unclear if selective foraging confers any benefit for sponges.

Here, we examined whether the frequencies of food types in the diet of the Caribbean giant barrel sponge *Xestospongia muta* were proportional to relative food abundance. For the first time, selection for the full spectrum of planktonic food resources available to sponges, including LPOM, DOM, and detritus, was determined from their differential presence in incurrent vs. excurrent sponge flow. Further, we tested the prediction from foraging theory that sponge behavioral plasticity in food selection confers an ability to increase nutritional gains.

X. muta is a dominant benthic organism on Caribbean coral reefs (McMurray et al. 2010, 2015) and is the second most abundant sponge in the Caribbean on the basis of percent cover (Loh and Pawlik 2014). Moreover, populations can filter a water-column 30 m deep every 2.3–18 d (McMurray et al. 2014); hence, suspension feeding by *X. muta* may have considerable influence on coral reef ecosystem function. Because details of the sponge filtration mechanism are not well-understood, we made no assumptions about the behavioral mechanisms used to select prey, but rather used descriptive models to test for frequency-dependent selection (Gendron 1987).

Methods

Picoplankton

Suspension feeding by *X. muta* on picoplankton was investigated in situ using SCUBA in May of 2012 on Conch Reef [24′56.996 N; 80′27.223 W], Key Largo, Florida. The abundance and community structure of picoplankton over Conch Reef are known to vary temporally and spatially (Pile 1997; Lesser 2006); therefore, to examine sponge feeding over a large natural range of picoplankton prey abundances, 10 single-osculum individuals were haphazardly selected for study at both 15 m and 30 m depths on 07 May 2012 and 08 May 2012 (total of 40 sponges).

Paired 5 mL incurrent (ambient) and excurrent seawater samples from each sponge were collected with 5 mL syringes. Incurrent seawater samples were collected approximately 5 cm from the ostia (inhalant apertures) lining the sponge surface tissue and excurrent samples were slowly collected from approximately 5 cm below the osculum (exhalant aperture) within the spongocoel (inner empty space) of each sponge and at a rate lower than the velocity of water expelled by the sponge to avoid contamination from ambient seawater. Samples were preserved in electron microscopy grade glutaraldehyde (Tousimis) at a final concentration of 0.1% in cryovials and, after 10 min, quickly frozen in liquid nitrogen and stored at −80°C until analysis.

Following seawater sample collection, the velocity of excurrent seawater from each sponge was measured using a Sontek Micro acoustic Doppler velocimeter (ADV) mounted on a tripod following the methods of McMurray et al. (2014). The ADV probe was positioned vertically over each sponge and excurrent velocity was measured at the osculum centerline for 3 min at 2 Hz. Subsequently, the dimensions of each sponge were measured with a flexible plastic measuring tape and sponge biomass estimates were obtained by approximating the morphology of *X. muta* as a frustum of a cone (McMurray et al. 2008).

Phytoplankton (*Prochlorococcus* (Pro), *Synechococcus* (Syn), and photosynthetic picoeukaryotes (Peuk)) in seawater samples were enumerated using a BD FACSCalibur Flow Cytometer using a syringe pump to quantitatively deliver sample (up to 500 μL) as previously described (Johnson et al. 2010; Lin et al. 2013). Briefly, cells were excited with a 488 nm laser (15 mW Ar) and inelastic forward (<15°) scatter, inelastic side (90°) scatter (SSC), green (530 ± 30 nm) fluorescence, orange fluorescence (585 ± 42 nm), and red fluorescence (> 670 nm) emissions were measured. Population geometric mean properties (scatter and fluorescence) were normalized to 1.0 μm yellow green polystyrene beads (Polysciences, Warrington, Pennsylvania, U. S. A.) and typically have excellent reproducibility (5–10% CV). Phytoplankton and detritus were classified based on their characteristic flow cytometric signatures relative to standard fluorescent microspheres following standard population gating schemes (Cavender-Bares et al. 1998; Lindstrom et al. 2002). Bacterioplankton (high nucleic acid bacteria (HNA) and low nucleic acid bacteria (LNA)) were similarly quantified by staining the samples with Sybr Green-I as previously described (Marie et al. 1997) and relative cellular DNA quantified assuming stoichiometric dye binding. Carbon (C) content of each type of picoplankton was estimated using standard cell conversions used in previous studies of sponge feeding on Conch Reef (e.g., Pile 1997; Lesser 2006 and references therein). Cell conversions used were 53 fg C cell^{-1} for Pro, 470 fg C cell^{-1} for Syn, 20 fg C cell^{-1} for HNA and LNA bacteria, and pg C = 0.433 × (biovolume)$^{0.866}$ for Peuk.

Dissolved organic carbon and detritus

To investigate sponge feeding on dissolved organic carbon (DOC) and detritus relative to picoplankton prey and to compare carbon consumed from all food types, additional incurrent and excurrent samples were collected from five sponges at 20 m depth on Conch Reef in May, 2013. A total of 1 L of both incurrent and excurrent seawater was collected from sponges with paired 100 mL syringes. Samples thus represent an integration of approximately 5 min of sponge feeding. Following seawater sample collection, excurrent seawater velocity

was measured with an ADV and the dimensions of each sponge were measured as previously described. To facilitate comparisons of DOC feeding by *X. muta* with similar studies (e.g., Yahel et al. 2003; Mueller et al. 2014), DOC was operationally defined as the organic carbon passing through a combusted GF/F glass fiber filter (Hansell and Carlson 2002).

A 5 mL subsample from both incurrent and excurrent seawater samples was preserved and frozen for flow cytometry analysis to enumerate the five picoplankton prey types described above and to estimate total live particulate organic carbon (LPOC) available. To quantify total POC (LPOC + detritus), the remaining seawater from each sample was filtered through a 100 μm mesh and subsequently through a precombusted (500°C for 4 h) GF/F glass fiber filter. Filters were individually wrapped in aluminum foil and frozen until analysis. After filtration, a 5 mL subsample from the filtrate of each seawater sample was preserved and frozen for flow cytometry analysis to quantify any LPOC that was not retained by the filter. To quantify DOC, 20 mL of the filtrate from each sample was transferred to an EPA precleaned glass vial, acidified in the field with 100 μL of 50% phosphoric acid, and stored at 4°C until analysis. DOC concentrations were measured using high temperature catalytic oxidation with a Shimadzu TOC 5050 analyzer. To quantify POC, filters were dried at 50°C and subsequently exposed to hydrochloric acid fumes for 24 h. POC was then measured using a CE Elantech NC2100 elemental analyzer. All glassware and aluminum foil used to process samples was combusted prior to use and all plastic used for sample collection was acid washed before use (Tupas et al. 1994).

For excurrent seawater samples, it is impossible to distinguish sponge-generated detritus from incurrent detritus that has passed through the sponge uneaten; therefore, we used an indirect calculation to estimate detritus consumed [detritus consumed = (total POC incurrent) − (total POC excurrent) − (LPOC incurrent) + (LPOC excurrent)] (Ribes et al. 1999a; Hadas et al. 2009). Quantification of DOC and total POC for each sample were corrected for the carbon contained in the LPOC not retained by the GF/F filter using the per cell carbon estimators as above (Hadas et al. 2009).

Data analysis

Differences in the $\log_{10}$-transformed incurrent abundances of picoplankton prey were tested with a 3-way mixed effects model ANOVA with sampling date as a random factor and prey type and depth as fixed factors. The quantity of each food resource consumed was calculated as the difference between incurrent and excurrent food concentrations. Retention efficiency of each food resource was calculated as:

$$\mathrm{RE} = \left(\frac{C_{\mathrm{in}} - C_{\mathrm{ex}}}{C_{\mathrm{in}}}\right) \times 100$$

where RE is retention efficiency (%), and C_{in} and C_{ex} are the incurrent and excurrent food concentrations (cells or C mL^{-1}), respectively. Ordinary least squares (OLS) regression was used to describe the relationship between *RE* and $\log_e$-transformed incurrent food concentration for each food resource.

The mean excurrent seawater velocity for each sponge was corrected for the uneven velocity distribution across the osculum and volume flow through each sponge was estimated following McMurray et al. (2014). The filtration rate for each food resource was calculated as:

$$\mathrm{FR} = (C_{\mathrm{in}} - C_{\mathrm{ex}}) \times Q$$

where FR is the filtration rate (cells or C s^{-1}) and Q is volume flow (mL s^{-1}). Reduced-major-axis (RMA) regression was used to examine how filtration rates for each prey type and total cells scaled with sponge size. Data was $\log_{10}$-transformed and the T statistic was used to test the actual slope against an isometric slope of $\beta = 1$ (McArdle 1988). Specific filtration rates (cells or C s^{-1} mL^{-1}) were obtained by standardizing *FR* by sponge tissue volume. For each food resource, the relationship between specific filtration rate and incurrent food abundance was described by OLS regression.

Selectivity for each food resource was calculated using Chesson's (1983) selectivity index, α, which is a measure of the proportion of each food resource in the diet if all food types were equally abundant:

$$\hat{\alpha}_i = \mathrm{RE}_i \left(\sum_{i=1}^{m} \mathrm{RE}_i\right)^{-1}$$

where m is the number of food types and RE_i is the retention efficiency for the ith food type. Importantly, α does not change with food concentration unless consumer behavior changes (Chesson 1983); thus, we investigated the relationship between food preference and $\log_e$-transformed incurrent food concentration for each food type with OLS regression.

Results indicated that there was a direct relationship between selectivity and food availability for some food resource types, which implied that selectivity for a given food resource may vary as a function of the availability of other food resources. To examine if foraging effort varied with the relative abundance of food, OLS regression was used to describe the relationship between the proportion of each food resource in the sponge diet vs. the proportion of food resource available. The slope of each regression was tested against a slope of 1 using a *t*-test to examine if each food type was consumed in proportion to relative abundance. To test if relative foraging effort between food resources varied as a function of the relative availability of multiple food types, $\log_{10}$-transformed ratios of food consumed were regressed against $\log_{10}$-transformed ratios of food concentration for all food type combinations (Greenwood and Elton 1979; van Leeuwen et al. 2013). The y-intercept of these regressions indicates the relative proportion of each food resource consumed when food types are equally abundant and is

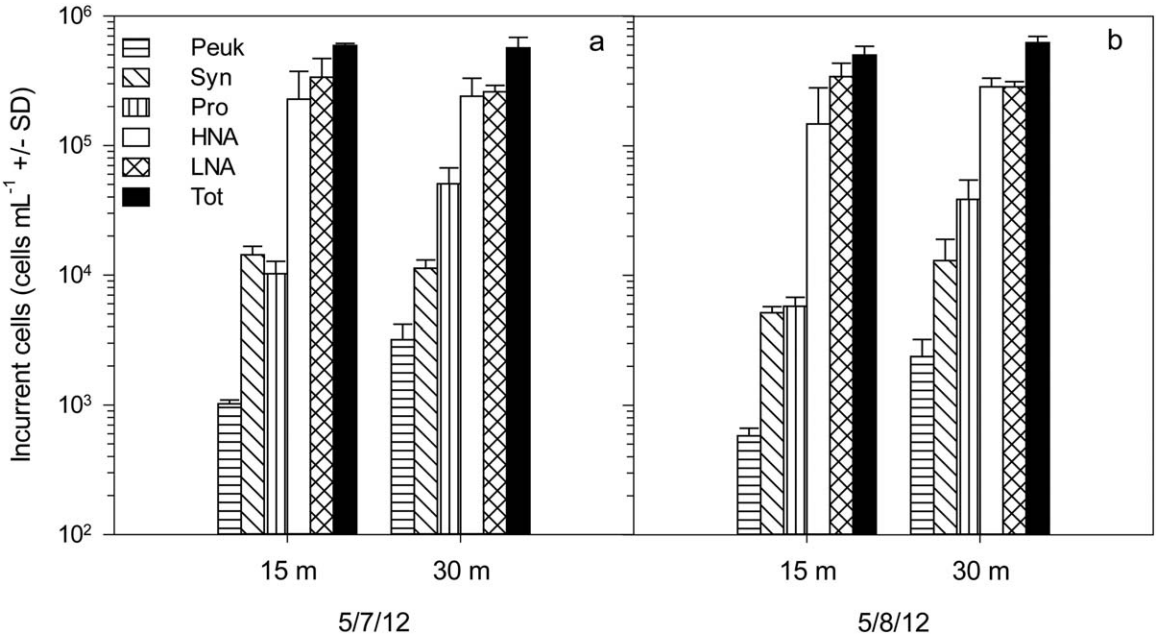

Fig. 1. Mean abundance of picoplankton prey at 15 m and 30 m depths on Conch Reef, Key Largo, FL, over the two day study period (A and B). Peuk = picoeukaryotes, Syn = *Synechococcus*, Pro = *Prochlorococcus*, HNA = high nucleic acid bacteria, LNA = low nucleic acid bacteria, and Tot = total cells. $n = 10$ for each prey type.

therefore a measure of food preference. The slope of these regressions is a measure of the strength of frequency-dependent consumption; a positive slope indicates that disproportionately more of the more abundant food resource is consumed, a negative slope indicates that disproportionately less of the more abundant food resource is consumed, and a slope of 1 implies that food consumption is proportional to food availability (Greenwood and Elton 1979; van Leeuwen et al. 2013). The *y*-intercept of each regression was tested against 0 with a *t*-test to investigate preference between food types at equality and we tested the slope of each regression against a slope of 1 using a *t*-test to examine frequency-dependent consumption. For all analyses, assumptions of normality and homogeneity of variances were checked with box and residual plots and data were transformed as needed. Analyses were conducted with SPSS (version 19 for Windows; IBM) statistical software. All means are reported with ± SD unless otherwise stated.

Results

Sponge feeding on picoplankton

Picoplankton prey available for consumption by sponges significantly varied over the study (depth by date interaction: $F_{1,180} = 13.8$, $p < 0.001$); variation in the relative composition of the picoplankton community was either significant or marginally significant (prey type by date interaction: $F_{4,180} = 2.4$, $p = 0.05$; prey type by depth interaction: $F_{4,4} = 10.5$, $p = 0.021$; prey type by depth by date interaction: $F_{4,180} = 2.2$, $p = 0.07$). Mean (± SD) total picoplankton prey abundances at 15 m and 30 m depths were $5.9 \times 10^5 \pm 2.2 \times 10^4$ cells mL^{-1} and $5.6 \times 10^5 \pm 1.2 \times 10^5$ cells mL^{-1} on the first sampling date and $5.0 \times 10^5 \pm 8.4 \times 10^4$ cells mL^{-1} and $6.2 \times 10^5 \pm 7.3 \times 10^4$ cells mL^{-1} on the second date, respectively (Fig. 1). The most abundant cells were generally LNA (55.3 ± 19.0%), followed by HNA (37.9 ± 18.0%), *Prochlorococcus* (Pro) (4.6 ± 3.8%), *Synechococcus* (Syn) (1.9 ± 0.8%), and photosynthetic picoeukaryotes (Peuk) (0.3 ± 0.2%).

Retention efficiency was found to significantly increase as a direct positive logarithmic function of incurrent prey abundance for all prey types and total prey (Fig. 2; Supporting Information Table S1). Retention efficiencies were generally the greatest for Pro (mean: 97.2 ± 1.7%) and Syn (96.6 ± 1.1%), followed by HNA (87.4 ± 14.6%), Peuk (84.1 ± 3.9%), and LNA (62.4 ± 11.2%); the mean retention efficiency for total prey was 77.2 ± 5.6%. Filtration rates for all prey types and total prey increased isometrically with increasing sponge volume and were found to be reliably predicted from sponge size (Supporting Information Table S2). Similarly, the filtration rate for total carbon increased isometrically with increasing sponge volume ($T = 0.36$, df = 28, $r^2 = 0.91$, $p < 0.001$).

There was a significant positive linear relationship between specific filtration rates and incurrent prey abundance for all cell types (Fig. 3; Supporting Information Table S3), but not for total cells ($p = 0.128$) (Fig. 4a; Supporting Information Table S3). Specific filtration rates were generally greatest for LNA (mean: 4219 ± 2849 cells s^{-1} mL^{-1}) and HNA (4137 ± 3410 cells s^{-1} mL^{-1}), followed by Pro

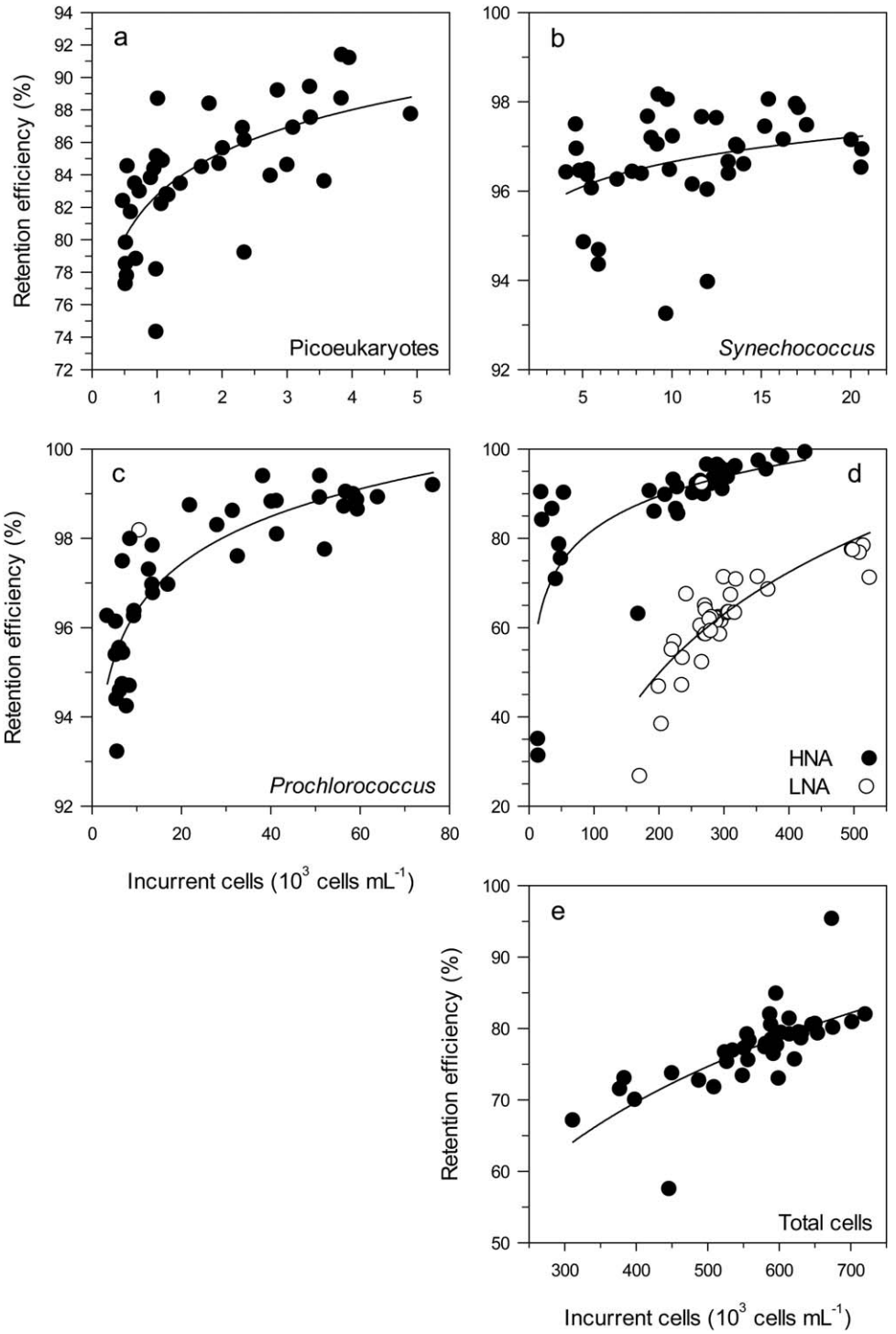

Fig. 2. Relationship between sponge retention efficiency for picoplankton prey and prey availability for (A) picoeukaryotes, (B) *Synechococcus*, (C) *Prochlorococcus*, (D) high nucleic acid and low nucleic acid bacteria, and (E) total cells. Regression coefficients for fitted lines are provided in Supporting Information Table S1.

(476 ± 431 cells s^{-1} mL^{-1}), Syn (219 ± 146 cells s^{-1} mL^{-1}), and Peuk (29 ± 23 cells s^{-1} mL^{-1}). The mean specific filtration rate of total cells was 9080 ± 4458 cells s^{-1} mL^{-1}. When total cells were converted to carbon, the specific filtration rate of total carbon increased linearly with incurrent carbon available ($r^2 = 0.35$, $p < 0.001$; Fig. 4b).

The relationship between selectivity and incurrent prey abundance varied between prey types (Fig. 5). Selectivity for

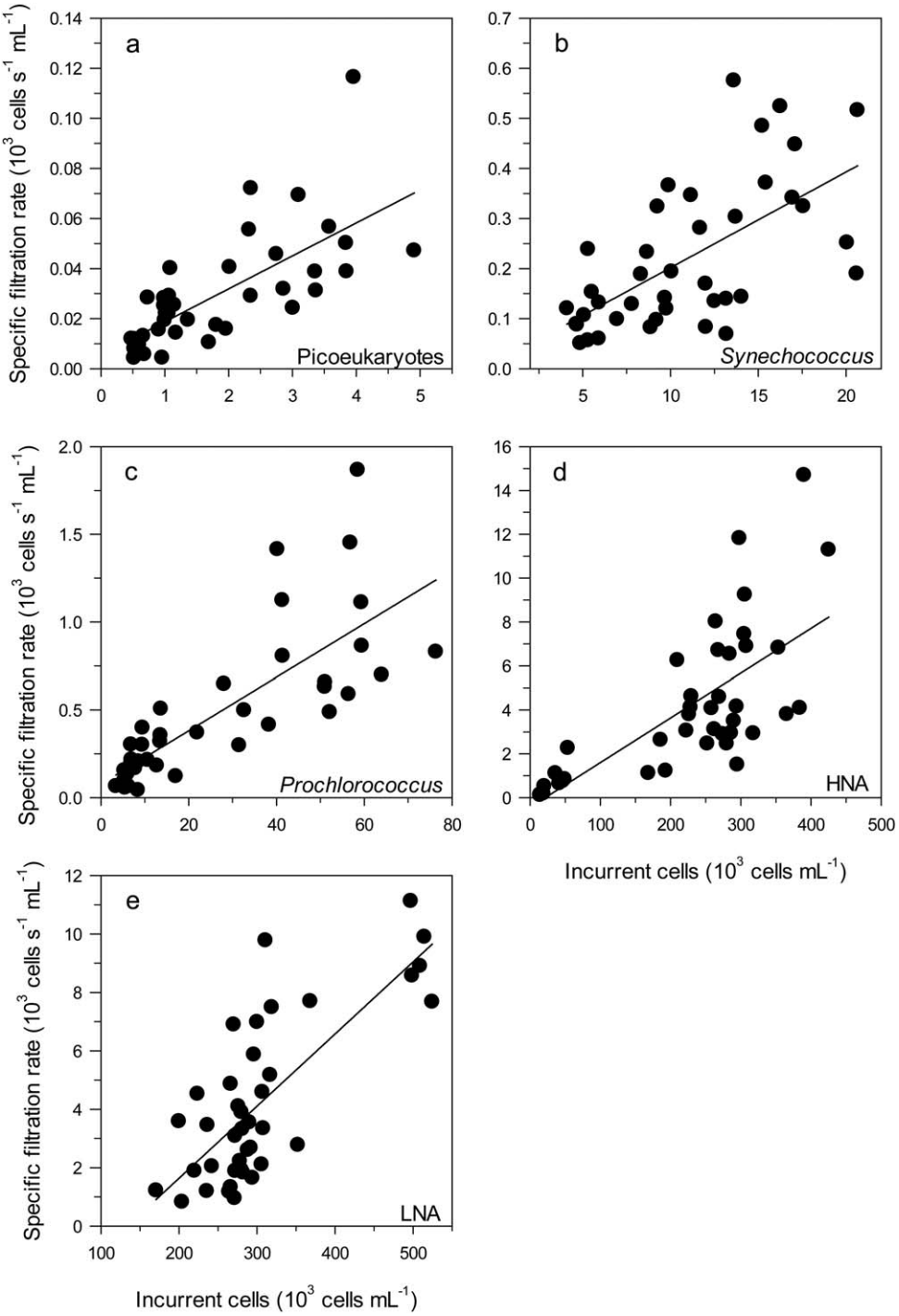

Fig. 3. Specific filtration rate vs. prey abundance for (A) picoeukaryotes, (B) *Synechococcus*, (C) *Prochlorococcus*, (D) high nucleic acid (HNA) bacteria, and (E) low nucleic acid (LNA) bacteria. Regression coefficients for fitted lines are in Supporting Information Table S3. $n = 40$ for each prey type.

Peuk, HNA, and LNA was found to significantly increase as a logarithmic function of increasing incurrent abundance of each prey type (Peuk: $r^2 = 0.15$, $p = 0.014$; HNA: $r^2 = 0.55$, $p < 0.001$; LNA: $r^2 = 0.68$, $p < 0.001$) (Supporting Information Table S4). Peuk were generally selected against, but became preferred prey at high incurrent abundances (Fig. 5a). There was relatively strong (i.e., large deviation in Chesson's α from 0.20) negative selectivity for HNA at low incurrent abundances and strong preference for HNA at high abundances (Fig. 5d). LNA were generally strongly unpreferred, but at

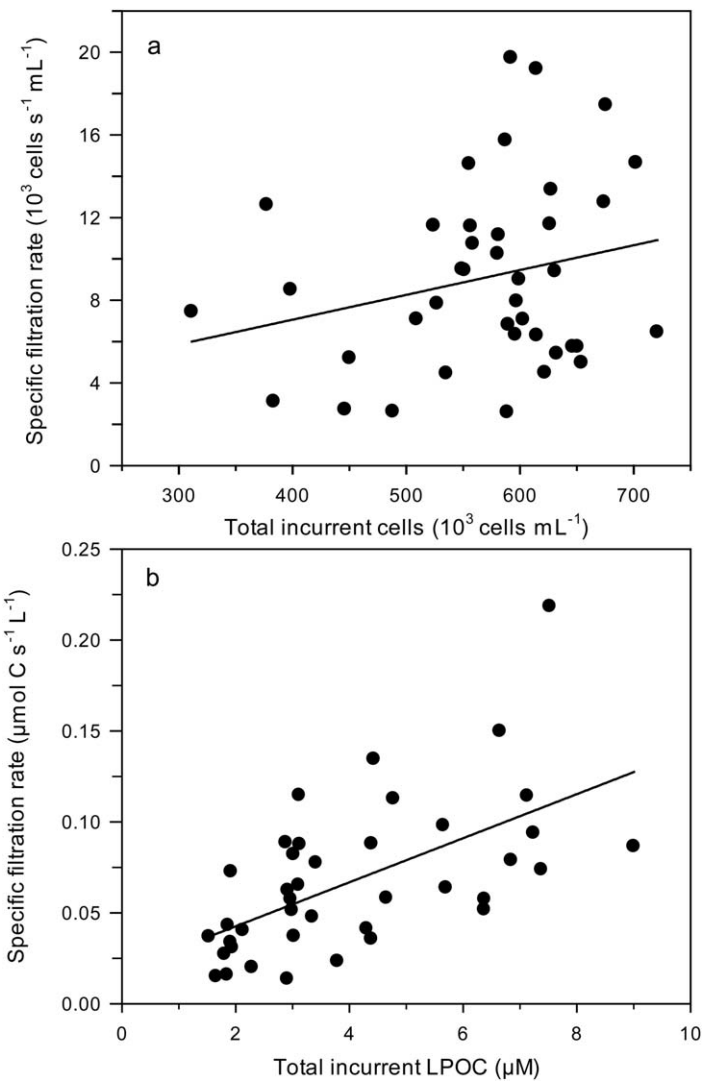

Fig. 4. Specific filtration rate vs. food abundance for (a) total picoplankton, and (b) total picoplankton converted to live particulate organic carbon (LPOC). $n = 40$.

the highest measured incurrent abundances selectivity for LNA became neutral (Fig. 5d). Both Pro and Syn were consistently strongly preferred prey and the magnitude of this preference did not change with the incurrent abundance of these prey types ($p > 0.05$ for both regressions) (Fig. 5b,c; Supporting Information Table S4).

The proportion of each prey type in the diet of *X. muta* increased disproportionately with increasing relative abundance of each prey type (Fig. 6; Supporting Information Table S5). The proportions of Pro and Syn in the sponge diet were generally always greater than the relative availability of these prey types, while the proportion of LNA in the sponge diet was generally less than the relative availability of LNA (Fig. 6b–d). Peuk and HNA contributed less than expected to the sponge diet at low relative abundances and more than expected at high relative abundance (Fig. 6a,e). Regressions of relative consumption vs. the relative incurrent abundance of prey for all possible two prey type combinations revealed that Pro and Peuk were consumed in proportion to their relative abundance, but for all other prey type comparisons consumption increased disproportionately with increasing relative prey abundance, indicating positive frequency-dependent consumption (Fig. 7; Table 1). There was no preference for Pro vs. Syn at equality and the more abundant prey type was always over-consumed. Pro and Syn were generally always preferred to other prey types (Fig. 7b–g). Peuk were preferred to HNA at high relative abundances of Peuk to HNA and HNA were preferentially consumed at low relative abundances of Peuk to HNA (Fig. 7h). Peuk were generally preferred to LNA, but at the lowest relative abundances of Peuk to LNA both prey were consumed in proportion to their relative abundance (Fig. 7i). HNA were generally preferred to LNA, but LNA were preferred at the lowest relative abundances of HNA to LNA (Fig. 7j).

Sponge feeding on DOC and detritus relative to picoplankton

A large proportion of the carbon available in incurrent seawater was in the form of DOC and nonliving particulate organic carbon (i.e., detritus) (Fig. 8). Incurrent concentrations of DOC ranged from 61.9 μM to 123.5 μM and accounted for a mean of $84.1 \pm 2.5\%$ of the incurrent total organic carbon (TOC). Detritus accounted for a mean of $10.2 \pm 1.6\%$ of the incurrent TOC and concentrations ranged from 7.9 μM to 12.6 μM. Incurrent LPOC was largely in the form of Peuk ($47.2 \pm 6.6\%$) and Syn ($39.0 \pm 3.7\%$), followed by LNA ($5.6 \pm 1.9\%$), Pro ($4.7 \pm 0.6\%$), and HNA ($3.6 \pm 1.3\%$).

One sponge was a net source of DOC, but all other individuals ($n = 4$) were net sinks of DOC. Additionally, despite flow cytometric observations of detritus in excurrent seawater, all sponges measured were net sinks of detritus. With the exclusion of the sponge that was found to release DOC, the mean proportions of DOC, detritus, and LPOC in the diet of sponges were $70.2 \pm 7.7\%$, $20.0 \pm 5.7\%$, and $9.8 \pm 2.4\%$, respectively.

There was a positive, logarithmic relationship between the concentration of DOC in incurrent seawater and DOC retention efficiency ($r^2 = 0.80$, $p = 0.041$) and specific filtration rates ($r^2 = 0.94$, $p = 0.007$) (Supporting Information Fig. S1). DOC retention ranged from −8.8 (i.e., the release of DOC) to 46.1%. Detritus specific filtration rates increased linearly with increasing detritus availability ($r^2 = 0.83$, $p = 0.033$) (Supporting Information Fig. S2b). The relationship between detrital retention efficiency and the incurrent concentration of detritus was not significant ($r^2 = 0.65$, $p = 0.098$) (Supporting Information Fig. S2a) and sponges retained a mean of $79.2 \pm 10.7\%$ of the incurrent detritus.

Sponges had a consistent negative preference for DOC, but selectivity was found to increase as a logarithmic

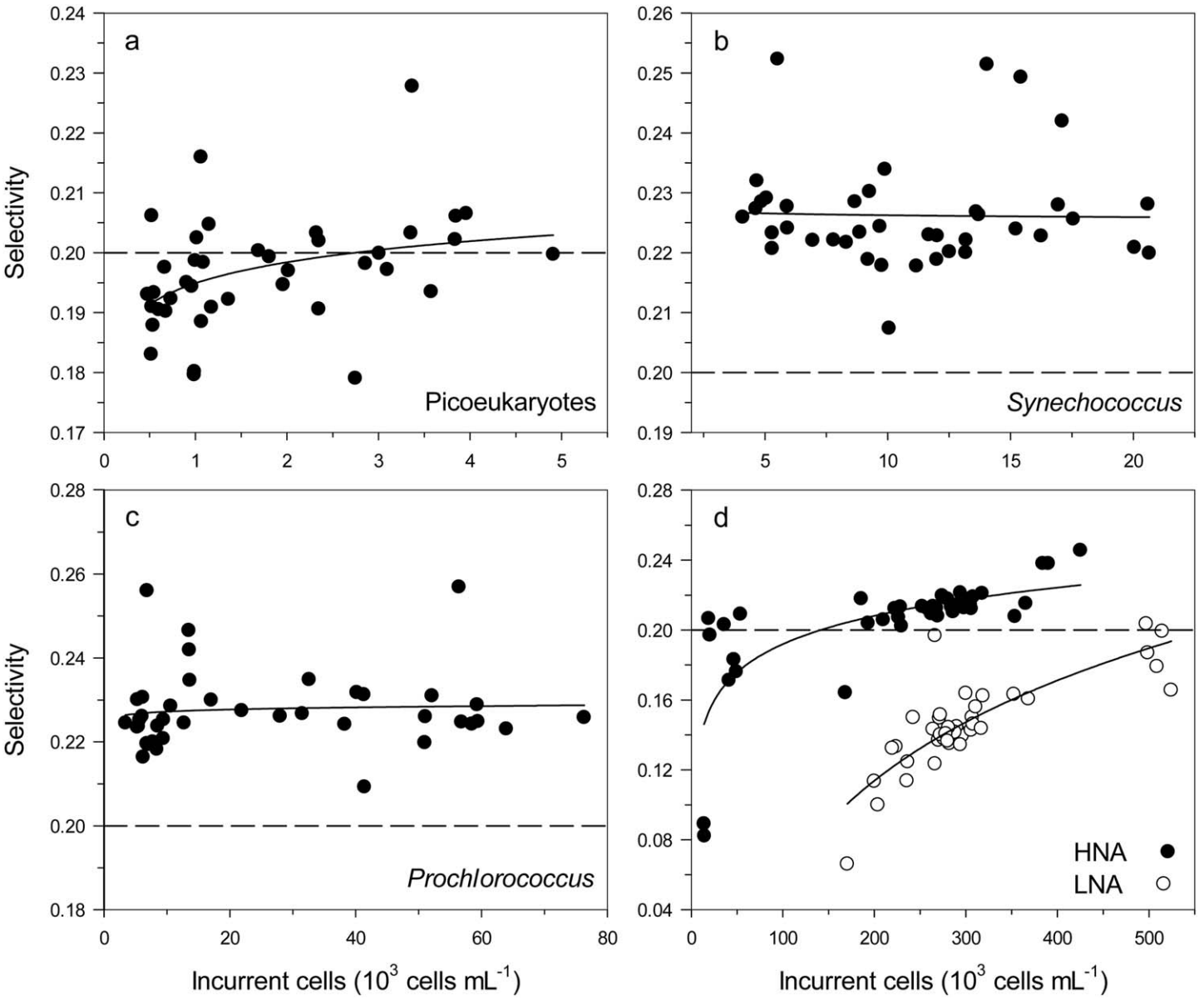

Fig. 5. Relationship between selectivity (Chesson's α) and prey abundance for (a) picoeukaryotes, (b) *Synechococcus*, (c) *Prochlorococcus*, and (d) high nucleic acid (HNA) and low nucleic acid (LNA) bacteria. Dashed horizontal lines indicate the value of α obtained if cell types were selected at random (0.20); values above and below this threshold indicate positive and negative preferences, respectively. Regression coefficients for fitted lines are provided in Supporting Information Table S4. $n = 40$.

function of increasing DOC concentrations ($r^2 = 0.80$, $p = 0.042$) (Fig. 9a). Sponges had both negative and positive preferences for detritus and there was no relationship between selectivity and incurrent detritus concentrations ($r^2 = 0.35$, $p = 0.294$) (Fig. 9b). Regressions of the relative consumption of food types vs. relative abundance indicated that sponges preferred LPOC over detritus at equality and detritus, LPOC, and POC were preferred over DOC (Supporting Information Fig. S3; Table 2). Sponges consumed detritus and DOC in proportion to their relative abundance; however positive frequency-dependent consumption occurred between LPOC and DOC, total POC and DOC, and LPOC and detritus (Supporting Information Fig. S3; Table 2).

Discussion

The sponge diet

X. muta retained picoplankton at high efficiencies (62–97%); however, the sponge diet was largely composed of DOC (70% of TOC) and detritus (20% of TOC). Consistent

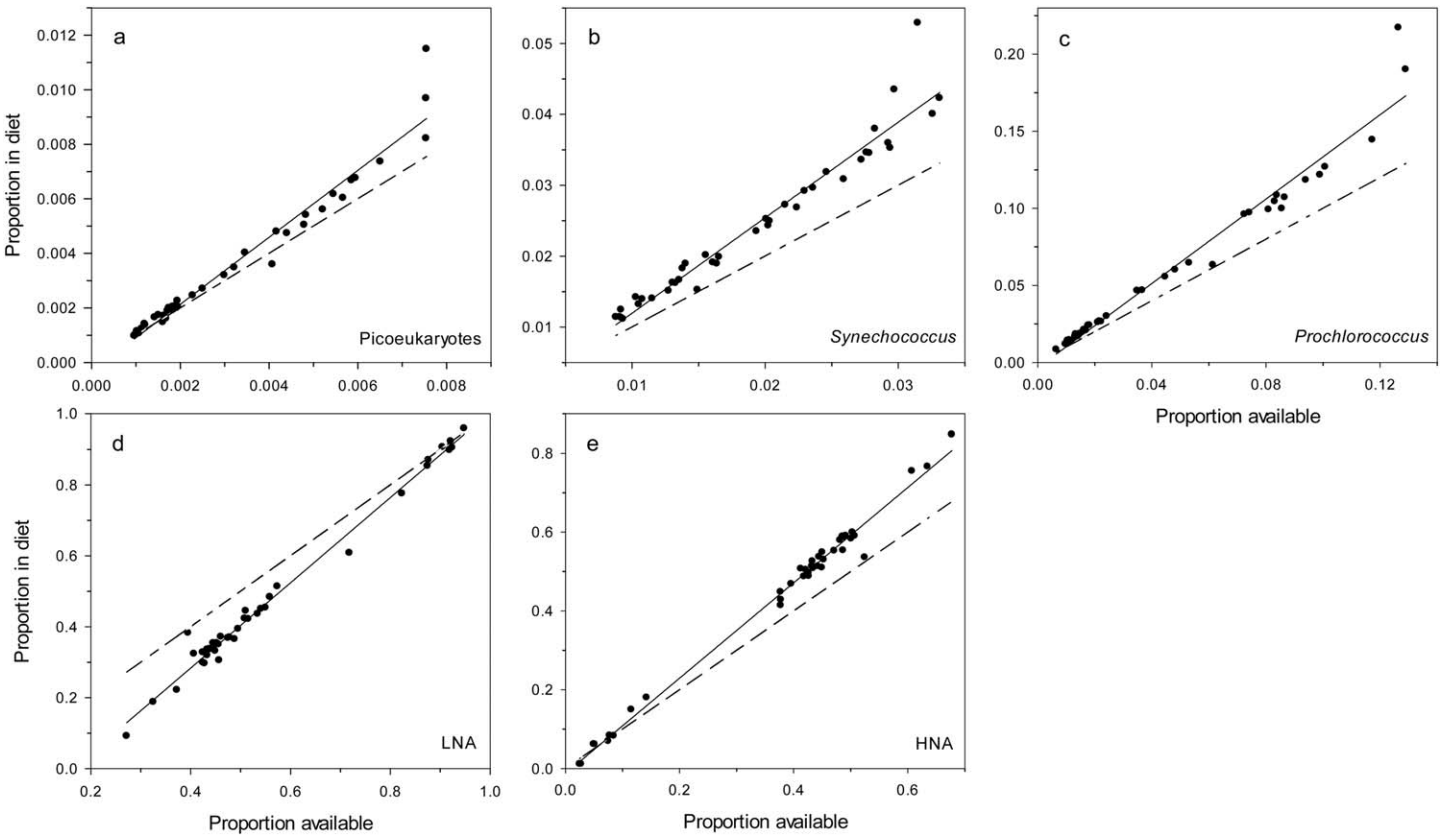

Fig. 6. Relationship between the relative contribution of each prey type to the sponge diet and the relative abundance of each prey type in incurrent seawater. (a) picoeukaryotes, (b) *Synechococcus*, (c) *Prochlorococcus*, and (d) low nucleic acid (LNA) bacteria, and (e) high nucleic acid (HNA) bacteria. Regression coefficients for fitted lines are provided in Supporting Information Table S5. Dashed lines indicate relative consumption that is proportional to relative abundance. $n = 40$.

with our findings, DOC has been found to account for 76 to > 90% of the TOC in the diets of other sponge species (Yahel et al. 2003; de Goeij et al. 2008b; Mueller et al. 2014). Consumption of detritus by sponges, however, is not well understood and consumption estimates can be confounded by the release of detritus. Hadas et al. (2009) found that detritus constituted 54% of the POC consumed by the sponge *Negombata magnifica*, while detritus utilization appears to be negligible for other species (Ribes et al. 1999a; Yahel et al. 2003).

Importantly, this is the first report of a sponge species able to consume all components (LPOC, detritus, DOC) of TOC. In marine ecosystems, the biomass of detritus in the size fraction available to benthic suspension feeders often exceeds that of LPOC (Ribes et al. 1999b; Coma et al. 2001; Hadas et al. 2009) and much of the TOC available is in the form of DOC (Ribes et al. 1999b; Yahel et al. 2003; de Goeij et al. 2008b). In this study, approximately 84 and 10% of the TOC available in the water column was in the form of DOC and detritus, respectively. The capability of *X. muta* to use several food resources may allow a generally constant level of food uptake throughout the year despite seasonal fluctuations in plankton communities (Ribes et al. 1999a). Moreover, by consuming the large organic carbon pools available in DOC and detritus, *X. muta* is able to access large quantities of carbon, with sponge-mediated TOC specific filtration rates ranging from 15 nmol min^{-1} mL^{-1} to 265 nmol min^{-1} mL^{-1}. Comparable TOC flux estimates for species previously found to consume DOC range from 30 nmol min^{-1} mL^{-1} (Yahel et al. 2003) to 273 nmol min^{-1} mL^{-1} (de Goeij et al. 2008b). Given the high abundance and large biomass of *X. muta* (McMurray et al. 2010, 2015), populations likely play a significant role in benthic pelagic coupling on Caribbean coral reefs.

Selective suspension feeding

While *X. muta* exhibited a wide diet breadth, food types were not retained similarly. Among the picoplankton food sources, *X. muta* preferred the relatively rarer phytoplankton to the numerically dominant heterotrophic bacteria, and these results are largely consistent with those for other sponge species in recent investigations (Maldonado et al. 2012). Pro and Syn were equally and consistently preferred over all other cell types. Peuk were preferred over HNA and LNA at equality, and HNA were preferred over LNA. The

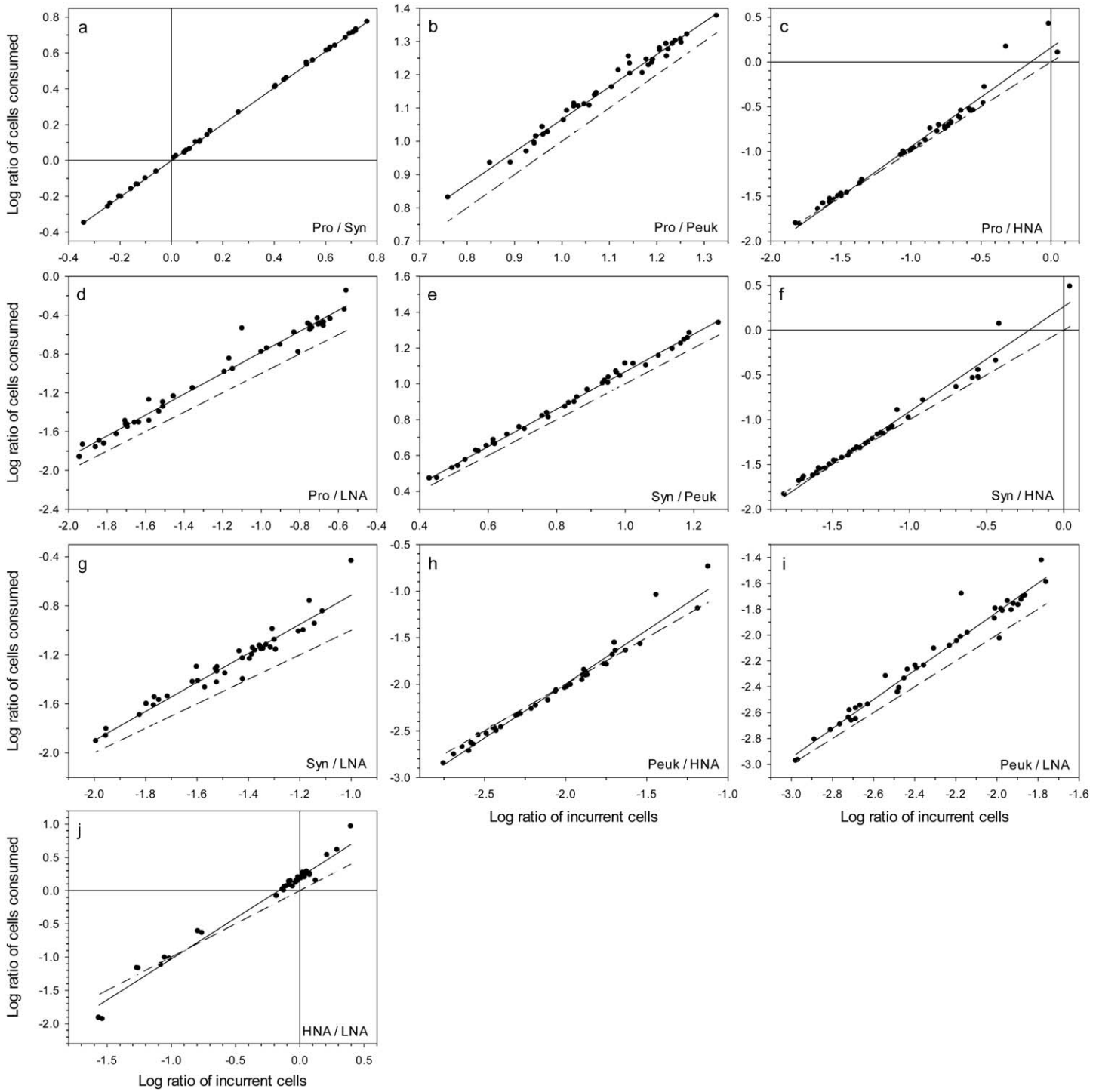

Fig. 7. Relationship between relative foraging effort on two prey types and relative prey abundance. Log-log plots of sponge feeding on (a) *Prochlorococcus* and *Synechococcus*, (b) *Prochlorococcus* and picoeukaryotes, (c) *Prochlorococcus* and high nucleic acid bacteria (HNA), (d) *Prochlorococcus* and low nucleic acid bacteria (LNA), (e) *Synechococcus* and picoeukaryotes, (f) *Synechococcus* and HNA, (g) *Synechococcus* and LNA, (h) picoeukaryotes and HNA, (i) picoeukaryotes and LNA, and (j) HNA and LNA. Regression coefficients for fitted lines are provided in Table 1. Dashed lines indicate relative consumption that is proportional to relative abundance. $n = 40$.

Table 1. Regression equations for $\log_{10}$ cell consumption ratios vs. $\log_{10}$ incurrent cell concentration ratios.

Regression	r^2	F	α (S.E.)	t	β (S.E.)	t
$\log_{10}$ (Pro/Syn consumed) = β $\log_{10}$ (Pro/Syn incurrent) + α	0.99	165,331*	−0.002 (0.001)	-1.44^{NS}	1.016 (0.002)	8.00*
$\log_{10}$ (Pro/Peuk consumed) = β $\log_{10}$ (Pro/Peuk incurrent) + α	0.98	2305*	0.090 (0.022)	4.05*	0.975 (0.020)	-1.25^{NS}
$\log_{10}$ (Pro/HNA consumed) = β $\log_{10}$ (Pro/HNA incurrent) + α	0.97	1318*	0.160 (0.033)	4.85*	1.107 (0.031)	3.45†
$\log_{10}$ (Pro/LNA consumed) = β $\log_{10}$ (Pro/LNA incurrent) + α	0.97	1353*	0.297 (0.038)	7.73*	1.078 (0.029)	2.69‡
$\log_{10}$ (Syn/Peuk consumed) = β $\log_{10}$ (Syn/Peuk incurrent) + α	0.99	9139*	0.022 (0.010)	2.31‡	1.046 (0.011)	4.18*
$\log_{10}$ (Syn/HNA consumed) = β $\log_{10}$ (Syn/HNA incurrent) + α	0.98	1663*	0.262 (0.037)	7.06*	1.171 (0.029)	5.90*
$\log_{10}$ (Syn/LNA consumed) = β $\log_{10}$ (Syn/LNA incurrent) + α	0.93	535*	0.417 (0.077)	6.16*	1.185 (0.051)	3.63*
$\log_{10}$ (Peuk/HNA consumed) = β $\log_{10}$ (Peuk/HNA incurrent) + α	0.97	1315*	0.316 (0.067)	4.71*	1.157 (0.032)	4.91*
$\log_{10}$ (Peuk/LNA consumed) = β $\log_{10}$ (Peuk/LNA incurrent) + α	0.96	1015*	0.425 (0.083)	5.14*	1.124 (0.035)	3.54†
$\log_{10}$ (HNA/LNA consumed) = β $\log_{10}$ (HNA/LNA incurrent) + α	0.98	1643*	0.203 (0.017)	11.7*	1.231 (0.030)	7.70*

Peuk = picoeukaryotes, Syn = *Synechococcus*, Pro = *Prochlorococcus*, HNA = high nucleic acid bacteria, LNA = low nucleic acid bacteria. *t*-tests were used to test β against a slope of 1 and α against an intercept of 0 for all regressions. $n = 40$ for all regressions.
*$p < 0.001$
†$p < 0.01$
‡$p < 0.05$
NS not significant.

ability of *X. muta* to discriminate between heterotrophic bacteria populations is also consistent with findings for other species studied to date: the sponge *Callyspongia* sp. was found to generally prefer HNA over LNA (Hanson et al. 2009), and two hexactinellid species were found to selectively feed from among three populations of heterotrophic bacteria, although preferences for each type varied over time (Yahel et al. 2006). For the first time, we also considered feeding preferences for DOC and detritus. Interestingly, again, the rarer carbon pools that constituted a relatively small proportion of the sponge diet were preferred over larger carbon pools: LPOC was preferred over DOC and detritus, and both detritus and total POC were preferred over DOC.

Similar to other studies of sponge feeding (Ribes et al. 1999a; Hanson et al. 2009; Perea-Blázquez et al. 2013), food preferences and the diet of *X. muta* were not consistent over space and time. Importantly, we found that this variation was largely explained by the relative abundance of available food types. Consistent with predictions from foraging theory (Lehman 1976; Stephens and Krebs 1986), less-preferred foods were generally discriminated against when preferred foods were relatively abundant, but increasingly accepted as the relative abundance of preferred foods decreased. Pro and Syn were generally preferred relative to other prey types at all abundances measured, but the relative preference for less-preferred prey types (i.e., HNA, LNA, and Peuk) increased as the relative abundance of Pro and Syn decreased (Fig. 7; Table 1). To our knowledge, this is the first study to document frequency-dependent consumption by a benthic suspension feeder in situ. Perea-Blázquez et al. (2013) concluded that retention efficiency was independent of ambient particle concentration for three common sponges off New Zealand; however, the analyses from which this conclusion was based only considered the slopes (β) of correlations between the number of cells retained ($C_{in} - C_{ex}$) vs. the ambient concentration of cells (C_{in}) and did not consider the *y*-intercept (α), which, if not zero, indicates that retention changes with food availability (i.e., RE $\propto \beta - \alpha/C_{in}$). Temporal changes in the diets of three sessile Mediterranean suspension feeders, including one sponge species, suggested that planktonic foods were consumed in proportion to their availability, however the relationship between relative consumption and food abundance was not explicitly tested (Coma et al. 2001).

How do sponges select among food types?

Interspecific differences in sponge feeding have been attributed to variations in feeding methods, aquiferous system complexity, choanocyte numbers, and life history strategies (Turon et al. 1997; Weisz et al. 2008; Poppell et al. 2013). The mechanism of intraspecific prey selection by sponges is less understood, but may be partially explained by differences in food capture systems (Maldonado et al. 2010). Food selection may result from either passive processes, in which the physical properties of the sponge filter lead to differential uptake of picoplankton cell types, or active processes, in which food selection is mediated by sponge behavior (Jürgens and Demott 1995).

Although the current study did not consider the mechanism of selection, our findings provide support for the notion that sponge food selection involves active processes by the sponge; however we are unable to exclude the potential for co-occurring passive processes. First, the high retention observed for some picoplankton types (>99%) supports the view that filtration is highly efficient and that selection occurs post-capture (Frost 1980; Ribes et al. 1999a; Yahel et al. 2006). Further, consistent with other work (Yahel et al. 2006; Hanson et al. 2009; Maldonado et al. 2010) (but see

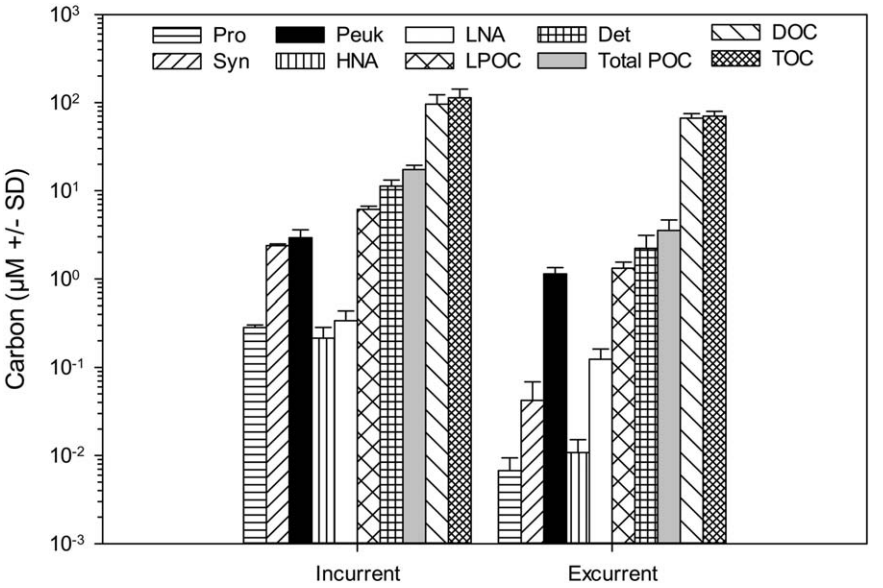

Fig. 8. Mean carbon of each food type in incurrent and excurrent seawater samples. Pro = *Prochlorococcus*, Syn = *Synechococcus*, Peuk = picoeukaryotes, HNA = high nucleic acid bacteria, LNA = low nucleic acid bacteria, LPOC = total live particulate organic carbon, Det = detritus, Total POC = total particulate organic carbon (LPOC + detritus), DOC = dissolved organic carbon, TOC = total organic carbon (Total POC + DOC). $n = 5$.

Ribes et al. 1999a; Hadas et al. 2009; Topçu et al. 2010) we found no relationship between picoplankton size and selectivity, as the preferred prey Pro and Syn are intermediate in size relative to less-preferred LNA and Peuk that are smaller and larger, respectively. Moreover, the strong relationship observed between picoplankton selectivity and ambient abundance suggests that sponge behavior changes with food availability. We did not detect any differences in the phenotypes of each picoplankton type (e.g., size) over the course of the study to suggest that passive selection may explain such variation in selectivity. Finally, we found that such behaviors have direct implications in the uptake of carbon, further suggesting that food selection is an active process that enables *X. muta* to increase foraging efficiency (see below).

The selection of DOC and detritus is more difficult to evaluate because the physical and chemical composition and nutritional value of these food resources is highly heterogeneous (Lenz 1977; Hansell and Carlson 2002). Further, only the small labile fraction of DOC appears to be available to sponges (Yahel et al. 2003; de Goeij et al. 2008b) and it is unknown if sponges can use the entire detrital pool. In this respect, selection of these food resources is likely to be partly passive and it is not surprising that LPOC was preferred over DOC and detritus. Moreover, many sponges, including *X. muta*, host large assemblages of microbes, and the relative DOC uptake by microbes vs. sponge cells remain unknown (de Goeij et al. 2008a). Nonetheless, similar to our findings for picoplankton selection, we found that selectivity for DOC increases with DOC availability, further suggesting that

Table 2. Regression equations for $\log_{10}$ food type consumption ratios vs. $\log_{10}$ incurrent food concentration ratios.

Regression	r^2	F	α (S.E.)	t	β (S.E.)	t
$\log_{10}$ (LPOC/Det consumed) = β $\log_{10}$ (LPOC/Det incurrent) + α	0.99	248.66*	0.133 (0.026)	5.11‡	1.513 (0.096)	5.34‡
$\log_{10}$ (Det/DOC consumed) = β $\log_{10}$ (Det/DOC incurrent) + α	0.97	65.27‡	1.146 (0.211)	5.42‡	1.833 (0.227)	3.67NS
$\log_{10}$ (LPOC/DOC consumed) = β $\log_{10}$ (LPOC/DOC incurrent) + α	0.99	245.36†	1.698 (0.164)	10.4†	2.099 (0.134)	8.20‡
$\log_{10}$ (POC/DOC consumed) = β $\log_{10}$ (POC/DOC incurrent) + α	0.98	80.25‡	1.061 (0.162)	6.56‡	1.926 (0.215)	4.31‡

Det = detritus, LPOC = live particulate organic carbon, DOC = dissolved organic carbon, POC = total particulate organic carbon (detritus + LPOC). *t*-tests were used to test β against a slope of 1 and α against an intercept of 0 for all regressions. $n = 4$–5 for all regressions; one sponge was found to be a net source of DOC and was therefore omitted from analysis.

*$p < 0.001$

†$p < 0.01$

‡$p < 0.05$

NS not significant.

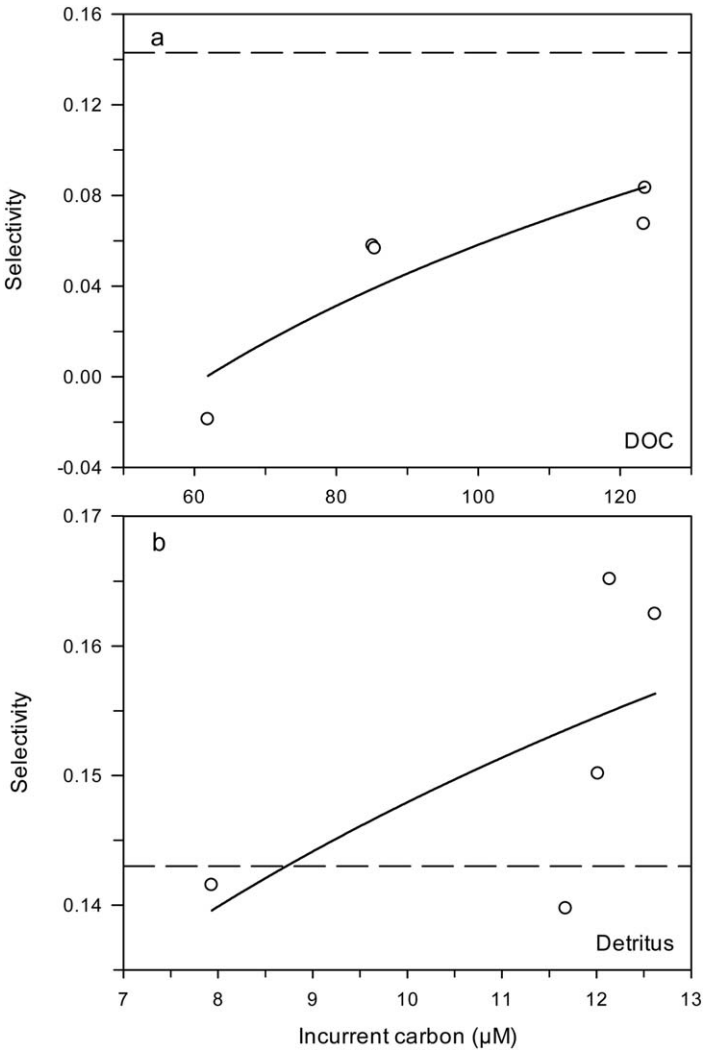

Fig. 9. Relationship between selectivity (Chesson's α) and the abundance of each food type for (a) dissolved organic carbon (DOC), and (b) detritus. Dashed horizontal lines indicate the value of α obtained if food types were selected at random (0.143); values above and below this threshold indicate positive and negative preferences, respectively. $n = 5$

food selection involves active processes mediated by the sponge.

Active selection requires food recognition and sorting and there is evidence that sponges are capable of such behaviors. Sponges are able to discriminate between bacterial prey and bacterial symbionts (Wilkinson et al. 1984) and selectively uptake spermatozoa for transfer to the oocyte (Riesgo et al. 2007). More recently, sponges have been found to contain an unusually large and diverse suite of nucleotide-binding domain and Leucine-rich repeat containing genes (NLRs) belonging to a family of pattern recognition receptors that can recognize microbial ligands and thus may play a role in discriminating between planktonic food resources (Degnan 2014). Although the mechanism of food selection in sponges remains unresolved, we hypothesize that the ability to select amongst food types is likely a widespread feature among Porifera given the consistency in the design of the sponge filter among the major classes of sponges.

Why select among food types?

Although a number of studies have examined selective feeding by sponges, the role of this foraging behavior has remained unaddressed. We propose that the variable food conditions characteristic of the plankton (Ribes et al. 1999b) and digestive constraints limiting the total cells filtered may be strong selective pressures favoring the evolution of flexible sponge foraging behaviors. Foraging theory proposes that evolution will favor feeding behaviors that increase fitness (Pyke et al. 1977; Stephens and Krebs 1986) and it has been hypothesized that sponge behavioral plasticity in food selection may confer an ability to increase net nutritional gains from heterogeneous planktonic food (Hanson et al. 2009; Massaro et al. 2012). Although energetic costs of food handling and digestion by sponges are unknown, our results on the foraging by *X. muta* support the hypothesis that food selection confers increased nutritional gains. The total number of cells filtered did not vary with total incurrent picoplankton available (Fig. 4a), yet carbon consumption was found to increase with increasing availability of carbon (Fig. 4b), suggesting that selective behaviors enable sponges to exploit temporal patches of high food availability.

The lack of a relationship between total cells available and total cells filtered indicates that cell uptake is limited by post-capture constraints (e.g., digestion). For example, it has been found that digestion rates may vary between some bacterial types (e.g., *Escherichia coli* vs. *Vibrio anguillarum*; Maldonado et al. 2010). Because of the high efficiency of picoplankton filtration, it has been hypothesized that, after capture, preferred prey are transferred into food vacuoles, while unpreferred prey are transported and released into excurrent canals (Yahel et al. 2006). But why is it favorable to release less-preferred prey that is already captured? According to foraging theory, decisions about which food resources to digest can be assessed by comparing the opportunity cost of each food resource ("principle of lost opportunity" (Stephens and Krebs 1986)). No opportunity is lost by digesting favorable foods; however, the digestion of inferior foods represents a loss of opportunity to do better (Stephens and Krebs 1986). Given this framework, net carbon uptake by *X. muta* would be predicted to increase by selectively excluding inferior foods from food vacuoles that may otherwise be occupied by favorable foods, as has been found for other suspension feeders (Jürgens and Demott 1995). Consistent with this hypothesis and optimal diet models for suspension feeders (Lehman 1976), we found that less-preferred foods were discriminated against when preferred foods were relatively abundant, but were increasingly

accepted as the relative abundance of preferred foods decreased. In retrospect, such feeding behavior plasticity should be expected for a feeding mode dependent upon the variable food conditions characteristic of the plankton.

Implications, limitations, and future directions

Given our results, there is a strong need to consider varying food availability as a covariate in the experimental design and interpretation of work on the functional role of sponges as benthic suspension feeders. For example, to date, most work on sponge diet selection has only considered interspecific and intraspecific comparisons of mean selectivities for included food types (Maldonado et al. 2012). Although the temporal scale of the present study was limited, there was considerable variation in the incurrent abundance and composition of food resources measured, and a clear pattern of food selection that was explained by this variability. However, diel and yearly variability of planktonic foods available to sponges can be much greater (e.g., Ribes et al. 1999a) and it remains to be seen whether the patterns of sponge diet selection reported here are generalizable to potential cycles of food availability. Additionally, sponge metabolism may vary over broader temporal scales not considered here and it is unknown whether sponge physiological condition or reproductive status may influence patterns of diet selection.

More broadly, if diet selection is common among the Porifera, how may this affect planktonic food webs and the cycling of carbon in marine ecosystems? Selective suspension feeding by protozoans has been recognized to regulate the biomass and structure of plankton communities (Pernthaler 2005). Thus, in systems where sponges dominate the benthos, such as on Caribbean coral reefs (Loh and Pawlik 2014), selective sponge foraging may have a similarly strong influence on picoplankton communities. Recently, it has been proposed that sponges are fundamental in the cycling of carbon on coral reefs by making DOC available to higher trophic levels as detritus; a process termed the "sponge loop" (de Goeij et al. 2013). Our results only partially support the sponge loop as it was originally proposed—*X. muta* was found to uptake large quantities of DOC from the water-column, however sponges released relatively little detritus and were net carbon sinks. Maldonado (2015) has predicted that sponge detritus production will vary with differences in sponge communities and the relative abundance of particulate and dissolved carbon available between habitats. Given our results on sponge diet selection, we hypothesize that the flux of carbon to higher trophic levels via the sponge loop may additionally vary with food availability.

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