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REPORT

Chemistry of the consumption and excretion of the bumphead parrotfish (*Bolbometopon muricatum*), a coral reef mega-consumer

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Abstract *Bolbometopon muricatum* are ecologically unique mega-consumers in coral reef ecosystems. They primarily divide their dietary intake between living scleractinian corals and coral rock, a substrate richly colonized by non-coral biota. Here we examine how the chemical, structural, and energetic content of these two main classes of forage material may influence *B. muricatum* feeding behavior and selectivity. We then also examine nutrient content, pH, and alkalinity of the carbonate-rich feces of *B. muricatum* as a step toward understanding how *B. muricatum* defecation could affect reef nutrient dynamics and localized seawater chemistry. Our results suggest that by most measures, coral rock constitutes a richer food source than living corals, exhibiting higher levels of eight biologically relevant elements, and containing approximately three times greater caloric value than living corals. Additionally, the two forage types also presented distinct mineralogy, with the coral rock resembling a Mg-enriched carbonate phase in contrast to the primarily aragonitic live corals. Despite the fact that individual *B. muricatum* excrete tons of macerated coral annually, the low measured concentrations of *N* and *P* in feces suggest that this excretion may have relatively minor effects of reef macronutrient budgets. We also observed negligible local-scale impacts of *B. muricatum* feces on seawater pH and alkalinity. The approaches applied here integrate perspectives from marine biogeochemistry, materials science, and ecology. Collectively, these results provide preliminary insight into how reef chemistry could shape foraging of this dominant and vulnerable coral reef consumer and how it, in turn, might affect the chemistry of these reefs.

Keywords Parrotfish · Coral · Reef · Nutrients · Calorimetry · Carbonates · *Bolbometopon* · pH

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Introduction

Large-bodied consumers often exert disproportionately strong impacts on the ecology and chemistry of the ecosystems they inhabit because they frequently consume large volumes of food and redistribute much of this intake in new forms and in new locations (Owen-Smith 1988; Bonaldo et al. 2014; Roman et al. 2014; Estes et al. 2016). The influence of these large consumers on material transfer is amplified in cases where they meet their energy demands via the intake of large volumes of low-quality foods. African elephants, for example, consume > 5 tons yr^{-1} of

well-defended foods (e.g., grasses and trees) and subsequently excrete the majority of this low-quality biomass intake. This high volume consumption and excretion have a defining influence on the morphology and biodiversity of African savannas (Jones et al. 1994; McCauley et al. 2006; Pringle et al. 2007; Asner 2009). Understanding how high-throughput mega-consumers select among available food sources and what the biochemical implications are of the large quantities of waste they generate can improve our view of system chemistry and ecosystem ecology.

Here we report upon the biogeochemical characteristics of the intake and fecal production of an understudied, but potentially important marine mega-consumer: *Bolbometopon muricatum*, the bumphead parrotfish (Fig. 1). Reaching 1.4 m in total length, *B. muricatum* is the largest parrotfish in the world and among the largest coral reef fishes (Choat et al. 2006). *B. muricatum* was once considered abundant or common throughout tropical and subtropical reefs in the Pacific and Indian Oceans, but this widespread species is now considered uncommon or rare in much of that range (Donaldson and Dulvy 2004). *B. muricatum* feed

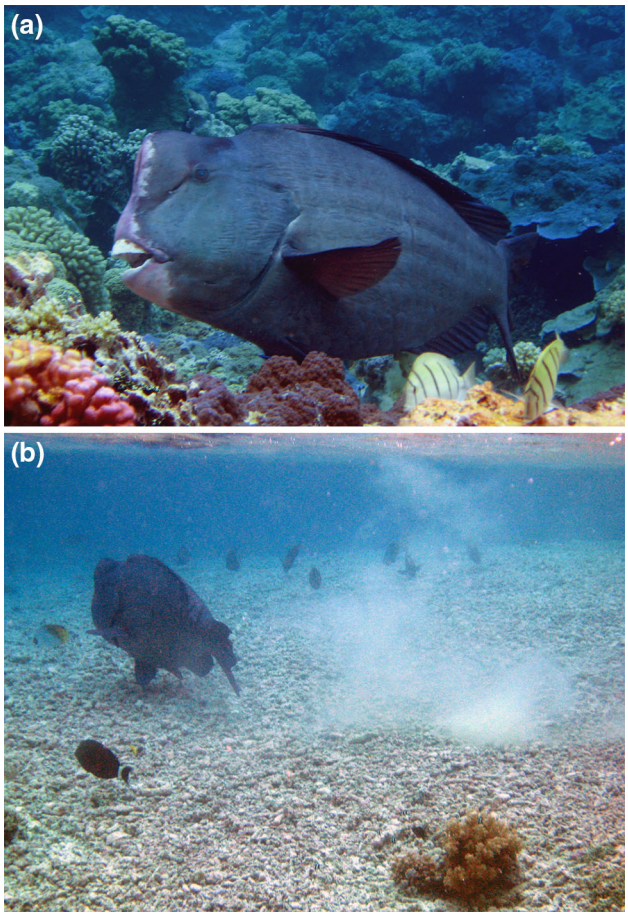

Fig. 1 *Bolbometopon muricatum* pictured here **a** delivering a bite upon a living scleractinian coral colony and **b** having just released feces, both at Palmyra Atoll. Photograph credit D. McCauley

principally on living corals and recolonized coral substrate—food items that, in respect to mass, are mostly composed of indigestible coral-derived calcium carbonates (McCauley et al. 2014). Because of this especially low-quality diet, *B. muricatum* must consume very high volumes of these foods. It is estimated that a *B. muricatum* individual takes in between 4.48 and 5.69 tons of reef material annually (Bellwood et al. 2003; McCauley et al. 2014; Hoey and Bellwood 2008). While foraging on coral rock material (i.e., reef bench lacking living coral but colonized by a diverse assemblage of other biota) is a common feeding mode in many parrotfish and acanthurids (Bellwood and Choat 1990; Choat et al. 2002), the heavy reliance of *B. muricatum* on live corals is relatively unique (Rotjan and Lewis 2006; Bonaldo et al. 2014). It is not known whether the inclusion of this live coral represents a shift toward increased optimality in resource acquisition. Understanding why this diet partitioning occurs is especially important in the case of *B. muricatum,* as intense predation of live corals by *B. muricatum* may alter patterns of coral abundance and diversity on reefs (McCauley et al. 2014). Likewise, the consumption of coral substrate without live coral polyps present (e.g., coral pavement, rubble) may serve as a major agent of bioerosion and can influence the physical structure of reef environments (Bellwood et al. 2003; Perry et al. 2015).

The coral forage consumed by *B. muricatum* is pulverized in their pharyngeal mill, reducing this often structurally complex intake into fine particulate matter. As so little of this consumed material can be assimilated, *B. muricatum* excretes an estimated 4.8 tons of feces, largely as inorganic calcium carbonate particulate, back upon reefs annually (McCauley et al. 2014; Perry et al. 2015). Feces from other fish and vertebrates have been shown to have important effects on the biochemistry and ecology of ecosystems in a broad variety of contexts (Bray et al. 1981; Meyer and Schultz 1985; Young et al. 2010). The high fraction of inorganic calcium carbonate generally found in parrotfish feces differentiates it from other reef fish feces; however, parrotfish feces has been found to contain measurable volumes of lipids and proteins and to host diverse bacterial assemblages that can be quite biologically active (Bailey and Robertson 1982; Smriga et al. 2010). It remains unknown whether and how the especially large volume of feces generated by *B. muricatum* may influence reef biogeochemical processes. Nutrient enrichment is not the only avenue through which fecal deposition by *B. muricatum* could influence reefs. As crushed calcium carbonate is known to have a strong buffering capacity in other settings (Pytkowicz 1967), the constant, large volume of calcium carbonate-rich feces generated by *B. muricatum* could potentially influence the alkalinity and pH of seawater at localized scales, or in regions with restricted water

flow. Given great concern about the effects of rapidly changing pH levels in coral reefs, it is imperative to understand whether changes in abundance of *B. muricatum* and ecologically similar species may further impact pH in these systems.

We consider two main questions in this report. First we ask: What properties of *B. muricatum* forage may influence their feeding? To answer this question we identified differences in the chemical, mineralogical, and energetic content of its two principal food classes: living corals and other coral material lacking visible living coral. We use this information to interpret why *B. muricatum* partitions its feeding between these two major food sources. Second we ask: What are the biogeochemical implications of the high volume of fecal output of this species? To measure the potential effects of this excretion, we examined the nutrient content of field-collected *B. muricatum* feces and examined the influence of *B. muricatum* feces on seawater alkalinity and pH. Leveraging diverse toolkits from chemistry and material science, we gain understanding of the biogeochemical characteristics of these reef processes and identify feedbacks of this consumption on their surrounding ecosystems, rather than simply enumerating bulk rates of intake and output. Resolving these issues in the case of *B. muricatum* is particularly important because (1) *B. muricatum* is part of a globally imperiled Tribe whose numbers appear to be rapidly declining (Dulvy and Polunin 2004; Comeros-Raynal et al. 2012) and (2) *B. muricatum* is one of the most ecologically important benthic consumers in the coral reef communities where it exists, and it is predicted to shape the diversity, abundance, and size structure of corals in these communities as well as general dynamics of bioerosion and reef persistence (Bellwood et al. 2003; Bonaldo et al. 2014).

Materials and methods

Study site

Field data were collected at the Palmyra National Wildlife Refuge (5°52′N, 162°04′W). *B. muricatum* has been much depleted by fishing across its range (Dulvy and Polunin 2004; Comeros-Raynal et al. 2012), but it, and numerous other large reef fish, remains relatively abundant at Palmyra (Stevenson et al. 2007; McCauley et al. 2010, 2012). All sampling was conducted in backreef sites (landward side of reef crest; depth 1–5 m) of the atoll.

Elemental, energetic, and mineralogical content of *B. muricatum* forage

B. muricatum feed primarily on living and coral rock material (McCauley et al. 2014). "Living coral" will be used throughout to refer to macroscopic living scleractinian corals. Here we define "coral rock" to mean all materials consumed from reef substrates that contained no visible (> 25 mm) adult living corals. These coral rock reef substrates are highly biodiverse and highly biologically active. They can host a diverse assemblage of surface-colonizing and endolithic biota including turf and encrusting algae, crustose coralline algae, endolithic algae, boring reef invertebrates, newly settled microscopic coral recruits, and biofilms.

To understand more about how the properties of these two major forage classes guide feeding selectivity in *B. muricatum*, we measured the elemental composition, mineral structure, and energetic content of live corals and coral rock material. Samples were removed from the feeding areas of *B. muricatum* at Palmyra Atoll, placed in sterile containers, and frozen. Live coral fragments (living tissue plus skeleton) were removed from the living scleractinian corals in the following three genera: $n = 13$ *Pocillopora*, $n = 3$ *Acropora*, and $n = 2$ *Montipora*. Each of these genera is known to be consumed by *B. muricatum*. *Pocillopora*, in particular, has been previously observed at Palmyra to be preferentially consumed by *B. muricatum* (McCauley et al. 2014), and has been found elsewhere to be fed upon in proportion to its availability (Hoey and Bellwood 2008).

Live coral pieces were removed using a chisel or pliers. All coral rock samples were removed using a chisel. Live coral and coral rock samples were collected in such a way as to mimic the size, shape, and depth of material that *B. muricatum* take from each of these two forage classes, with field removal of samples performed adjacent to a known *B. muricatum* bite wherever possible (McCauley et al. 2014). The average size of these divot-type coral rock bites was measured in the field ($n = 64$) during focal follows of *B. muricatum* to be 3.7 length × 2.6 width × 0.4 depth cm (SE ± 0.2 × 0.2 × 0.05, respectively) (McCauley et al. 2014), and calipers were used to help match the size of coral rock sample collections to these natural mean dimensions. In the laboratory, living coral and coral rock materials were freeze-dried, milled to a fine powder in a SPEX mill using polymethacrylate balls, and thoroughly homogenized.

The percent *N* of living and deal coral samples was measured via elemental analyzer (Carlo-Erba NA 1500; $n = 18$ live coral; $n = 17$ coral rock). A subset of these samples was then analyzed to determine the abundance of a suite of twenty-three additional physiologically and

ecologically important elements using energy-dispersive X-ray fluorescence (XRF; $n = 4$ live *Pocillopora*, $n = 2$ live *Acropora*, and $n = 2$ live *Montipora*; $n = 8$ coral rock) with an XEPOS spectrometer. Finely powdered samples for XRF measurement were placed in a Teflon cup over a Prolene membrane. X-ray fluorescence spectra were acquired using an XEPOS spectrometer from four spots on each cup, and results were averaged, following normalization to the Compton scattering-background. We also analyzed a subset of samples ($n = 6$ live *Pocillopora*, $n = 1$ live *Acropora*, and $n = 1$ live *Montipora*; $n = 7$ coral rock) following wet-digestion (HNO_3/H_2O_2), using an inductively coupled plasma emission spectrometer (ICP; Thermo 6300, both axial- and radial-viewing geometry), which provides greater sensitivity when analyzing the abundance of elements with lower atomic numbers, allowing us to examine B and P more accurately. Samples were interspersed with processed blanks and QA/QC standards created from NIST-traceable SPEX ICP standards.

To compare the calorimetric content of live coral versus coral rock samples, we analyzed both food types using differential scanning calorimetry (DSC) on a TA Instruments DSC Q100 (V9.9, Build 303). Samples of live coral and coral rock ($n = 6$ live *Pocillopora*, $n = 2$ live *Acropora*, and $n = 2$ live *Montipora*, $n = 10$ coral rock) of between 8.00 and 12.00 mg were weighed in crimped-Al combustion pans, and the reference pan was filled with a comparable mass of laboratory-synthesized amorphous calcium carbonate (ACC). We selected ACC as a reference material to remove complicating endothermal transitions observed in biogenic carbonates during pilot runs with empty reference pans. Researchers have identified ACC as a common precursor to carbonate minerals in coral and other marine species (Addadi et al. 2003; Michel et al. 2008; Radha et al. 2010). The DSC temperature program heated samples (in hydrocarbon-free air at 40 ml min^{-1}) from room temperature to 105 °C at a rate of 25 °C min^{-1}. Samples were then heated to 465 °C at a rate of 10 °C min^{-1}. In the interval 110–465 °C, a slower rate of heating allowed greater resolution of potential exothermic/endothermic transitions, since this is the interval at which most organic substances digested by *B. muricatum* demonstrate exothermic transitions. Finally, samples were heated to 550 °C at a rate of 50 °C min^{-1}. Thermograms produced by the DSC were analyzed by integrating under the largely exothermic curve from 200 to 465 °C, obtaining a standardized enthalpy of combustion for each sample on TA's Universal Analysis 2000 software.

To better understand how potential differences in the mineralogy of live coral versus coral rock materials shape *B. muricatum* feeding, we analyzed both forage types using X-ray powder diffraction (XRD, SSRL beamline 11-2, $\lambda = 0.9744$ Å) in Debye–Scherrer geometry. Diffraction rings were integrated using the software Fit2D (ESRF) by comparing to a laboratory standard of the salt LaB_6. Live coral (composited from 2 *Pocillopora* samples) and coral rock (likewise composited from two samples) samples (collected and prepared as above) were analyzed. The XRD patterns obtained in these analyses were queried against the PDF/4 + database of the International Centre for Diffraction Data (ICDD 2015), including major lines to identify calcite, aragonite, and dolomite.

To reinforce XRD measurements, the two major classes of *B. muricatum* forage materials ($n = 4$ live *Pocillopora*, $n = 2$ live *Acropora*, and $n = 1$ live *Montipora*; $n = 7$ coral rock) were analyzed using Fourier transform infrared spectroscopy (FTIR) on a Thermo-Nicolet Nexus 470 (Madison WI) spectrometer. Ball-milled live coral and coral rock powders were mixed at 1% (w/w) with spectral-grade potassium bromide, pressed into mulls, and spectra collected in transmission-mode using FTIR over the frequency range of 5000–400 cm^{-1} (2–25 μm wavelength) at a resolution of 2 cm^{-1} and co-addition of 512 interferograms. Raw spectra were auto-corrected for the presence of ambient CO_2 and H_2O vapor in the sample compartment using OMNIC software. Spectra were converted into absorbance by rationing single-beam spectra with a blank KBr mull, as described in Raab and Vogel (2004). To confirm the FTIR spectral assignments, one composited sample from two each live coral and coral rock were compared over the range 50–2000 cm^{-1} for their FT-Raman spectra using a Thermo-Nicolet DXR Raman microscope and 532 nm laser-excitation at the Lawrence Berkeley National Lab, BL 5.4.1. FT-Raman spectral assignments followed Urmos et al. (1991).

Nutrient content of *B. muricatum* feces

To evaluate the possible effects of *B. muricatum* defecations on reef nutrient cycling, we assayed the *N* and *P* content of *B. muricatum* feces. For these tests, subsamples of fresh feces were collected using 100-ml sterile syringes immediately after feces has been defecated by *B. muricatum* and had settled onto a relatively clean portion of the substrate (Smriga et al. 2010). Effort was taken to minimize the collection of benthic substrate or detritus that might contaminate the sample of feces. The feces and seawater collected by this method were stored frozen. To measure P concentrations ($n = 15$), samples were filtered in the laboratory onto pre-leached ash-less filter papers (Whatman #40), freeze-dried, ground to a fine powder (as above), homogenized, Kjeldahl-digested, and analyzed on a continuous flow autoanalyzer (Alpkem Flow Solution IV). Percent N was measured from a separate set of samples of *B. muricatum* feces ($n = 22$) collected using the

same methods as above, prepared using methods described above for coral, and analyzed on an elemental analyzer.

Effects of *B. muricatum* excretion on seawater alkalinity and pH

To determine whether the calcium carbonate-rich feces of *B. muricatum* have any influence on core parameters of local water chemistry, we measured the total alkalinity and pH of seawater in *B. muricatum* feces produced in the field (feces $n = 14$, reference $n = 14$). Water samples containing an ambient mix of feces and seawater were collected in acid-washed glass bottles in the densest portion of the cloud of feces defecated by *B. muricatum*. Reference samples containing only seawater were collected at the same water depth in like fashion in an area 5 m outside of the region where *B. muricatum* defecated. Mercuric chloride was added as a preservation agent to all feces and reference samples, and samples were sealed in airtight glass bottles, and then stored in a cool, dark location until analyzed.

The TA of the samples was evaluated from the proton balance at the alkalinity equivalence point, 4.5, at 25 °C using an open-cell titration. This method utilized a multipoint hydrochloric acid titration of seawater (Dickson 1981). The instrument program used a Levenberg–Marquardt nonlinear least-squares algorithm to calculate the TA from the potentiometric titration data. The program was patterned after those developed by Dickson (1981), Dickson et al. (2007) and Johansson and Wedborg (1982). The least-squares algorithm of the potentiometric titrations also gave initial pH as calculated from the initial electromotive force (EMF), the standard potential of the electrode system (E°). The semi-automated system consisted of a Metrohm 765 Dosimat titrator, an Orion 720A pH meter with a ROSS glass pH electrode (Orion, model 810100), and a double junction Ag/AgCl reference electrode (Orion, model 900200), and a water-jacketed pen titration cell (Millero et al. 1993). The system used $\sim$ 60 g of sample, which was determined gravimetrically to $\pm$ 0.003 g. The seawater samples were equilibrated to a constant temperature of 25 $\pm$ 0.1 °C with a water bath (NESLAB, RTE-10). A typical titration records the stable solution EMF (deviation less than 0.09 mV) and adds enough acid to change the voltage a pre-assigned increment ($\sim$ 13 mV). The electrode was calibrated for each titration as part of the fitting procedure, using certified reference material Batch 112 provided by A. Dickson (Scripps Institution of Oceanography). We determined instrument precision at $\sim$ 2 µmol/kg, with average value measured at 2222.8 ($n = 2$) and the certified value at 2223.26.

Statistical analyses

A MANOVA was used to assess differences in ICP and XRF-derived elemental concentrations. Other differences in the elemental and nutrient concentrations and caloric content of coral foods of *B. muricatum*, as well as differences in the total alkalinity and pH between feces and reference samples were compared using Welch's two-sample *t* tests. Statistics were computed in Program R (R Core Team 2012) and MINITAB version 14.

Results

Elemental, energetic, and mineralogical composition of forage

Comparisons of the nutrient content of live coral and coral rock foods consumed by *B. muricatum* revealed unique patterns of enrichment and depletion. Eleven of the twenty-four elements measured were significantly different between live coral and coral rock samples (Table 1). Eight of these were higher in coral rock material than in live corals and three elements were higher in living coral. IR spectroscopy confirmed that the lack of difference in N content detected through EA was paralleled by low detectability of protein. Though the IR spectra point to differences in the average chain length of lipids between live coral and coral rock materials, no qualitative differences in abundance could be seen, and we found low detectability of carbohydrates.

Measurements of caloric content of *B. muricatum* potential food sources demonstrated that coral rock materials had a caloric content (as referenced to ACC) that was approximately three times greater than values observed for live corals (Fig. 2; $t = 6.4$; $df = 14.6$, $P < 0.001$).

X-ray diffraction of live coral versus coral rock showed considerable overlap in calcite- and aragonite-derived bands, but in the case of coral rock, additional lines associated with magnesian calcites appeared as well, principally at *d*-spacings of 2.9791, 2.3648 and 1.811 Å. Dolomite was not observed. In Supplemental Figure 1, whole diffractograms are shown, as well as best library matches for each.

FTIR spectra for replicate live coral versus coral rock showed some overlap: a combination of aragonite- and calcite-associated IR absorptions at 713 and 700 cm^{-1}, the ν_1 line of aragonite (1083 cm^{-1}), and additional organic absorptions features near 2620 cm^{-1} (Fig. 3). IR spectra from coral rock showed three principal differences from live coral: (1) calcite ν_2 absorptions showed clear splitting of the main 856 cm^{-1} peak/843 cm^{-1} shoulder to include a band at 873 cm^{-1}; (2) the ν_4 absorptions (known to be

Table 1 Nutrient content of live coral and coral rock, principal food sources of *Bolbometopon muricatum*

	Live coral	Coral rock	*P* value	Method
Macroelement				
Ca (%)	35.9 ± 0.47	31.0 ± 0.74	0.001	XRF
K (%)	0.083 ± 0.0083	0.282 ± 0.050	0.001	XRF
Mg (%)	0.52 ± 0.16	3.20 ± 0.36	0.001	XRF
Na (%)	0.92 ± 0.38	2.96 ± 0.37	0.007	XRF
N (%)	0.178 ± 0.016	0.163 ± 0.013	ns	EA
P (%)	0.0174 ± 0.0031	0.0291 ± 0.0034	ns	ICP
S (%)	0.35 ± 0.017	0.60 ± 0.06	0.001	XRF
Microelement				
Mn (ppm)	17.9 ± 2.2	8.43 ± 0.89	0.009	XRF
Ni (ppm)	24.6 ± 1.2	28.3 ± 1.2	ns	XRF
B (ppm)	84 + 2.9	98 ± 13	ns	ICP
Co (ppm)	7.10 ± 5.2	7.52 ± 3.7	ns	XRF
Cu (ppm)	11.6 ± 4.7	10.5 ± 3.0	ns	XRF
Fe (ppm)	867 ± 250	599 ± 60	ns	XRF
Mo (ppm)	2.89 ± 0.22	2.74 ± 0.33	ns	XRF
W (ppm)	2.65 ± 0.57	2.66 ± 0.45	ns	XRF
Zn (ppm)	12.5 ± 1.5	11.5 ± 1.7	ns	XRF
Trace elements				
Br (ppm)	27 ± 5.1	235 ± 22	0.001	XRF
Cl (%)	2.50 ± 0.28	0.96 ± 0.23	0.002	XRF
I (ppm)	3.7 ± 2.5	142 + 13	0.001	XRF
Cd (ppm)	3.3 ± 0.3	2.9 ± 0.2	ns	XRF
Se (ppm)	1.4 ± 0.3	1.7 ± 0.2	ns	XRF
Coral indicator elements				
Sr (%)	0.45 ± 0.034	0.68 ± 0.008	0.001	XRF
U (ppm)	16.8 ± 1.8	22.8 ± 0.6	0.012	XRF
Pb (ppm)	61 ± 44	15.1 ± 1.3	ns	XRF

Values reported as mean ± standard error; $n = 8$, $m = 8$. Measurements reported either as percent of dry weight or parts per million (as indicated). Tests were conducted using X-ray-fluorescence (XRF), inductively coupled plasma emission-spectrometry (ICP), or an elemental analyzer (EA). The significance of differences between coral food sources were compared by MANOVA, except for *N*, for which a *t* test was used

sensitive to Mg^{++} substitution; Luzinova et al. 2011) possessed a weak shoulder at 718 cm^{-1}; and (3) altered lipid composition as judged by ratios of several bands between 2980 and 2820 cm^{-1} (Supplemental Figure 2). Together these bands arise from the acyl chains of lipids; the ratio of methylene (> CH_2) spacers to terminal methyl (–CH_3) provides a bulk estimate of lipid chain lengths. While overall intensity of the lipid absorbances is not very different between live coral and coral rock material, average chain lengths differ, consistent with contrasting

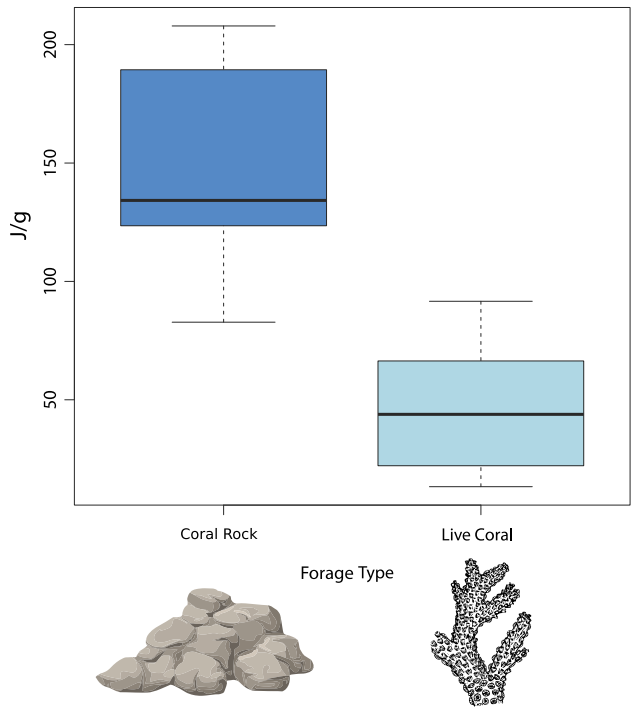

Fig. 2 Comparisons of the energy content of living coral and coral rock—major diet items of reef consumer *Bolbometopon muricatum*. This box and whisker plot shows the median energetic content at the bolded line, with the range of the box representing 25th and 75th quartiles, and whiskers extending to minimum and maximum values observed

biological colonization. In the context of the differing mineralogy of the two substrates, we include a spectrum for the laboratory-synthesized ACC used as a reference in the DSC measurements for this manuscript (Supplemental Figure 3); comparison of this standard material suggests ACC as a minor component of these coralline materials.

Nutrient content of feces and impacts on seawater properties

The nitrogen and phosphorus contents of field-collected *B. muricatum* feces were overall very low (mean % $N = 0.34$, SE ± 0.02; mean % $P = 0.0002$, SE ± 0.002).

Total alkalinity levels measured in *B. muricatum* feces (mean = 2216 µmol kg^{-1}, SE ± 5) and reference (mean = 2221 µmol kg^{-1}, SE ± 6) water samples were not significantly different ($t = -1.16$, $df = 3$, $P = 0.27$). A minor, but statistically significant, difference was observed in pH between the feces (mean = 7.99, SE ± 0.009) and reference (mean = 8.00, SE ± 0.008) water samples ($t = -2.77$, $df = 13$, $P = 0.02$).

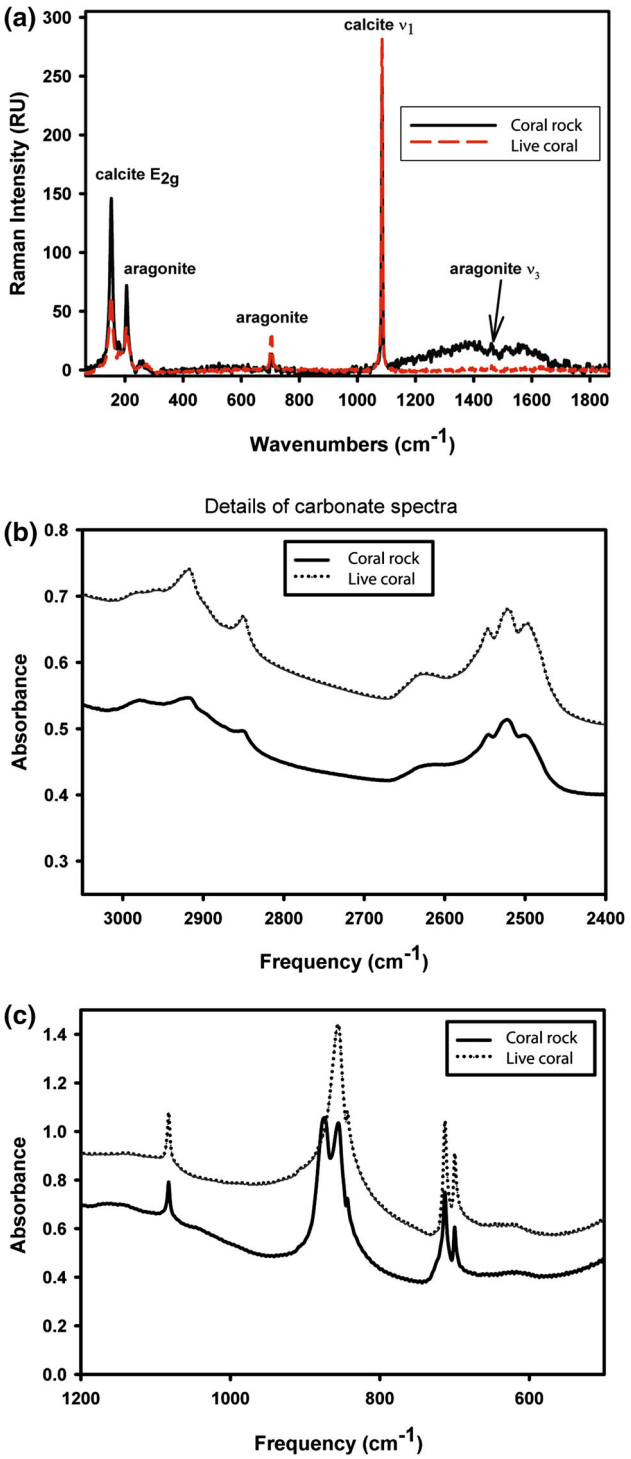

Fig. 3 FT-Raman and FTIR spectra identifying mineral matrices of live coral and coral rock materials ingested by *Bolbometopon muricatum.* FTIR spectra are mean of seven individual collections for each of the two dietary inputs, whereas each FT-Raman spectra are composited materials from three individual collections

Discussion

Nutritional and energetic quality of dominant foods

The large size and powerful feeding morphology of *B. muricatum* endow them with the unique mechanical capacity to consume and process large volumes of living scleractinian coral. Yet they divide their consumption relatively evenly between living corals and coral rock substrates colonized by other reef biota (McCauley et al. 2014).

Our assays of the energy content of live coral and coral rock materials suggested that coral rock contained approximately three times more caloric value than live corals (Fig. 2). Previous methods for measuring energy content of coral forage have focused on the caloric density of living tissues only and thus predictably yielded higher values than our measurements, which included both tissue and skeleton material (Glynn and Krupp 1986; Hourigan 1987; Tricas 1989; Haramaty 1991; Choat et al. 2002). However, since dietary value includes processing time and effort associated with non-living components, samples resembling whole bites are likely a more meaningful assay for determining the food preference of species that ingest skeleton along with living tissue.

Coupling previous estimates of intake rates of *B. muricatum* on live coral and coral rock (2140 and 2330 kg yr^{-1} indv, respectively, McCauley et al. 2014) with our calorimetry measurements, we estimate that an individual *B. muricatum* processes approximately 2752 kJ d^{-1} derived solely from coral-associated (i.e., live coral and coral rock) materials. These intake rates do not account for the energetic contributions obtained from the consumption of foods other than live coral and coral rock, although by mass such sources are estimated to comprise less than 0.5% of the diet of these fish. Such estimations must be viewed as upper bound estimates of caloric intake by *B. muricatum* for it is unknown what proportion of these calories estimated using these methods can in fact be digested by *B. muricatum*. Epilithic algal cell walls, for example, represent one class of materials found in coral rock that may not be digestible by *B. muricatum* and, consequently, would represent inaccessible calories.

The ostensible advantages of coral rock as a food pool is only moderately well reflected in the diet distributions of *B. muricatum.* Focal follows of *B. muricatum* at Palmyra, where these nutrient and energy measurements were taken, indicate that *B. muricatum* consumes coral rock in proportion to availability, while strongly preferring Pocilloporid live corals and avoiding macroalgae and other live corals (McCauley et al. 2014).

Although we found similarly low levels of macronutrients *N* and *P* in both forage types, we found elevated concentration of eight biologically important elements in the coral rock materials sampled relative to living corals (Table 1). The higher abundance of these specific nutrients in coral rock samples likely derives from the fact that the non-living skeletal matrix of the corals has been recolonized extensively, both superficially and interstitially, by a diverse array of algae, invertebrates, and microbes (e.g., turf and crustose coralline algae, endolithic algae, boring reef invertebrates, newly settled microscopic coral recruits, biofilms), that serve as rich sources of nutrients and energy, likely in forms of proteins and lipids (Campion-Alsumard et al. 1995; Clements et al. 2016). Parrotfish in other contexts have exhibited tendencies to feed preferentially on coral substrates with denser macroborer colonization (Rotjan and Lewis 2005). It remains, however, unknown and untested in the context of this research exactly which macronutrients and biologically important elements are directly detectable by *B. muricatum* during feeding or if and how the presence of these constituents can affect the longer-term evolution of feeding preferences for this species.

Traditional dietary trace metals were unlikely to be the selective agent for feeding, with no significant difference in levels of Cu, Ni, Mo, Co, Zn or Cd observed—with one exception, the micronutrient Mn, in which coral rock samples were depleted relative to live coral. Halogens are not usually considered in the context of nutrition, but Cl, Br, and I can play an important role in the physiology of marine organisms (e.g., in the context of defense compound/hormone production). XRF demonstrated coral rock to be highly enriched in both Br and I, when expressed as a molar ratio to [Cl]. This comparison of coral material [Br]/[Cl], [I]/[Cl] to mean ocean water values (1.57×10^{-3}; Davis et al. 1998; 3×10^{-6}; Winchester and Duce 1967) strongly suggests that organisms colonizing the coral rock substrates are bio-concentrating these elements from seawater. Marine algae are commonly associated with this bioaccumulation and production of complex halogenated secondary metabolites, with red algae being the most prolific (Cabrita et al. 2010; Bedke and Vanderwaal 2011). In addition, symbiotic cyanobacteria associated with sponges produce large quantities of halogenated secondary metabolites containing both chlorine and bromine (Unson et al. 1994). We found that iodine concentrations were particularly enriched, showing a nearly 20-fold increase in concentration in coral rock substrate as compared to live coral forage. The source of this iodine in the coral rock could be derived from sources such as turf or encrusting red or brown algae, sponges, or boring molluscs and other invertebrates (Das et al. 1981; Heyland and Moroz 2005). Though halogenated compounds are usually examined in the context of defense and toxicity (Hay et al. 1987), *B. muricatum* does not appear to present avoidance. If *B. muricatum* is capable of assimilating some portion of the halogenated compounds in this coral rock, then this food source may play an important role in its development and growth.

The major diet types of *B. muricatum* also differed in respect to their structural chemistry. The coral rock, for example, exhibited greater substitution of Mg, K, Sr, and Na for Ca (significant at $P < 0.001$), an elemental signature akin to a 'high Mg' calcite. In addition, X-ray diffraction, FTIR spectroscopy, and X-ray-fluorescence collectively indicated that the mineral mass of coral rock *B. muricatum* forage reflected a Mg-calcite form different from the mixture found in the live coral samples of calcite and aragonite. Coral skeletons are known to be dominated by aragonite, with calcite pointing to the presence of other calcifying organisms in the sample (Goffredo et al. 2012). The difference in the structural composition of these food types may be attributed to the benthic colonizers themselves. Crustose coralline algae, which principally utilize Mg-calcite (de Vrind-de Jong and de Vrind 1997; Addadi et al. 2003) was likely present in the coral rock sampled, along with a diverse group of other colonizers. Mineral properties of forage have consequences for their consumers, with higher substitution of Mg in the calcite lattice resulting in a mechanically harder skeletal structure (Wang et al. 1997), while also having higher solubility (Woosley et al. 2012) once ground and digested.

Rationalizing food preference and diet composition is challenging, as the consumer is not only seeking to maximize nutrient and energy intake, but to also balance these benefits with other direct and indirect costs associated with foraging for and processing of each food item (Schoener 1971; Hughes 1980; Targett et al. 1986; Targett and Targett 1990; Gerking 1994; Hay et al. 1994). Surprisingly, we found that coral rock material was by most measures a richer food source than living corals, despite some living corals being actively targeted. Additional experimental work is necessary to determine which of the compounds we have examined or other characteristics of the forage are most critical to determining the diet choices of *B. muricatum*, including work to understand what is actually assimilated and thus contributes to nutrition. While some species of marine fish appear to strategically target diet items based primarily on nutrient or energy content (Lobel 1981; Tricas 1989), others appear to make diet selections based on other criteria (Hay et al. 1994; Rotjan and Lewis 2005). Moreover, the relative importance of energy versus specific nutrients may vary by species, ecological context, and even ontological stage of the consumer.

Impacts of feces on reef ecosystems

Feces from reef fishes other than *B. muricatum*, as well as reef invertebrate communities, have been reported previously to be particularly high in nutrient content (Pinnegar and Polunin 2006) and as such, to constitute a potentially important source of nutrients and energy for recipient organisms and ecosystems (Bray et al. 1981; Bailey and Robertson 1982; Geesey et al. 1984; Meyer and Schultz 1985; Tribollet 2008). Overall rates of fish excretion, for example, have been found in some systems to contribute 25 times more *N* to certain reefs than all other biotic and abiotic sources pooled (Burkepile et al. 2013). Our analyses of the nutrient content of *B. muricatum* feces shows, however, that it contains relatively little *N* and *P* (see Pinnegar et al. 2007: $\%N = 1.46$, $\%P = 1.73$). As such, even though individual *B. muricatum* output a large volume of feces onto reefs (approximately 4 tons or greater annually; Bellwood et al. 2003; McCauley et al. 2014), it does not seem likely that this input has the capacity to induce the same fertilizing impact on reef ecosystems that is hypothesized for other piscine feces (Meyer and Schultz 1985; Pinnegar and Polunin 2006). It is important to note, however, that a sizable fraction of *B. muricatum* feces consists of fine particulates; $\sim 25\% < 125$ um in *B. muricatum* feces sampled via gut contents analysis in the Great Barrier Reef (Hoey and Bellwood 2008). While smaller particulates were detected in the fecal samples we collected from reef substrates for nutrient analysis (e.g. $\sim 18\% < 75$ µm and $\sim 30\%$ 76–212 µm; McCauley et al. 2014), it is highly likely that some fraction of the smallest particles do not settle to the reef substrate and would not be collected using our fecal sampling methods. Consequently, our analysis may underrepresent total nutritional output contained in *B. muricatum* feces. Furthermore, the analysis of feces alone does not consider the potential contributions of other excretory products of fishes (i.e., urine) which have been shown to shape nutrient budgets (Allgeier et al. 2016).

Investigations of these *B. muricatum* feces deposits showed little influence on seawater total alkalinity and pH at localized scales. There was no difference in the total alkalinity of *B. muricatum* feces from ambient seawater, providing no evidence that excreted calcium carbonate has a significant buffering effect on localized areas. Additionally, differences in feces and ambient pH were minor (i.e., Δ 0.01 pH) and do not suggest that *B. muricatum* alters localized seawater pH conditions to an ecologically significant degree, especially when compared to natural diurnal fluctuations (Ohde and van Woesik 1999). Despite this lack of direct effect on seawater chemistry, feces production by *B. muricatum* may yet exert an important influence on overall carbonate dynamics in reef ecosystems. Bioeroding Holothuroidea, for example, has been shown to increase alkalinity and exhibit distinct effects on the coral reef; however, these studies were conducted with a specimen held in an aquarium for 24 h, rather than in a field setting under natural flow conditions (Schneider et al. 2011). The transformation of tons of reef-bound, structurally complex carbonates by *B. muricatum* into more mobile sediment forms may yet have an important influence on reef ecosystems, by increasing transport of carbonates across reef boundaries or otherwise altering reef carbonate budgets (Bellwood 1995; Perry et al. 2015). Calcium carbonate derived from fish feces inputs (this material produced as a result of gastrointestinal precipitation) has been documented to play a major role in marine carbonate dynamics in other contexts (Wilson et al. 2009). Evaluation of the importance of these potential impacts of *B. muricatum* excretion will require further investigation. Experiments tracking change in carbonate chemistry in areas where *B. muricatum* have been extirpated or recovered over time could, for example, provide more meaningful insight into the cumulative effects of *B. muricatum*.

In conclusion, this work allows us to develop a holistic characterization of how *B. muricatum* both shapes its environment, and how it's foraging behavior is shaped by the environment. Our analyses of the chemistry and structure of *B. muricatum*'s forage materials in the coral reef landscape where it feeds will help make more sense of the foraging decisions made by this species. Our examination of the in situ measured chemistry of its feces also shape our expectations of the influence it may have on nutrient budgets and patterns of ecosystem ecology. Similar combinations of integrated insight derived from material science, marine chemistry, and foraging ecology can likely be usefully applied to furthering our understanding of other marine mega-consumers or species with similarly influential roles in marine ecosystems.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

References

Addadi L, Raz S, Weiner S (2003) Taking advantage of disorder: Amorphous calcium carbonate and its roles in biomineralization. Adv Mater 15:959–970

Allgeier JE, Valdivia A, Cox C, & Layman CA (2016). Fishing down nutrients on coral reefs. Nat Comm 7:12461; https://doi.org/10.1038/ncomms12461

Asner GP (2009) Tropical forest carbon assessment: integrating satellite and airborne mapping approaches. Env Res Lett 4(3):034009

Bailey, TG, & Robertson, DR (1982). Organic and caloric levels of fish feces relative to its consumption by coprophagous reef fishes. *Marine Biology*, *69*(1), 45–50

Bedke DK, Vanderwaal CD (2011) Chlorosulfolipids: Structure, synthesis, and biological relevance. Nat Prod Rep 28:15–25

Bellwood DR (1995) Carbonate transport and within-reef patterns of bioerosion and sediment release by parrotfishes (family Scaridae) on the Great Barrier Reef. Mar Ecol Prog Ser 117:127–136

Bellwood DR, Choat JH (1990) A functional analysis of grazing in parrotfishes (family Scaridae): the ecological implications. Env Biol Fishes 28(1–4):189–214

Bellwood DR, Hoey AS, Choat JH (2003) Limited functional redundancy in high diversity systems: resilience and ecosystem function on coral reefs. Ecol Lett *6*(4):281–285

Bonaldo RM, Hoey AS, & Bellwood DR (2014). The ecosystem roles of parrotfishes on tropical reefs. *Oceanography and Marine Biology: An Annual Review*, *52*, 81–132

Bray RN, Miller AC, Geesey GG (1981) The fish connection: a trophic link between planktonic and rocky reef communities? Science 214:204–205

Burkepile DE, Allgeier JE, Shantz AA, Pritchard CE, Lemoine NP, Bhatti LH, Layman CA (2013). Nutrient supply from fishes facilitates macroalgae and suppresses corals in a Caribbean coral reef ecosystem. Sci Rep *3*: 1493

Cabrita MT, Vale C, Rauter AP (2010) Halogenated compounds from marine algae. Mar Drugs 8(8):2301–2317

Campion-Alsumard T, Golubic S, Hutchings P (1995) Microbial endoliths in skeletons of live and dead corals: *Porites lobata* (Moorea, French Polynesia). Mar Ecol Prog Ser 117:149–157

Choat JH, Clements KD, Robbins WD (2002) The trophic status of herbivorous fishes on coral reefs. 1. Dietary analyses. Mar Biol 140:613–623

Choat JH, Davies C, Ackerman J, Mapstone B (2006) Age structure and growth in a large teleost, *Cheilinus undulatus*, with a review of size distribution in labrid fishes. Mar Ecol Prog Ser 318:237–246

Clements KD, German DP, Piché J, Tribollet A, & Choat JH (2016). Integrating ecological roles and trophic diversification on coral reefs: multiple lines of evidence identify parrotfishes as microphages. Biol J Linnean Soc 120(4):729–751

Comeros-Raynal MT, Choat JH, Polidoro BA, Clements KD, Abesemis R, Craig MT, Lazuardi ME, McIlwain J, Muljadi A, Myers RF, Nanola CL, Pardede S, Rocha LA, Russell B, Sanciangco JC, Stockwell B, Harwell H, Carpenter KE (2012) The likelihood of extinction of iconic and dominant herbivores and detritivores of coral reefs: The Parrotfishes and Surgeonfishes. PLoS ONE 7:1–13

Das B, Mittal PK, Kamat SY (1981) Bromine and iodine content in sponges and algae of the Andaman Sea. Indian J Mar Sci 10:301–302

Davis SN, Whittemore DO, Fabryka-Martin J (1998) Use of chloride/bromide ratios in studies of potable waters. Groundwater 36(2):338–350

de Vrind-de Jong EW, & de Vrind, JP (1997). Algal deposition of carbonates and silicates. *Reviews in Mineralogy and Geochemistry*, *35*(1), 267–307

Dickson AG (1981) An exact definition of total alkalinity and a procedure for the estimation of alkalinity and total inorganic carbon from titration data. Deep Sea Part A – Oceanographic Res Papers 28:609–623

Dickson AG, Sabine CL, Christian JR (2007) Guide to Best Practices for Ocean CO2 Measurements PICES Special Publication 3, 191 pp

Donaldson, TJ, & Dulvy, NK (2004). Threatened fishes of the world: Bolbometopon muricatum (Valenciennes 1840)(Scaridae). *Environmental Biology of Fishes*, *70*(4), 373-373

Dulvy NK, Polunin NV (2004) Using informal knowledge to infer human-induced rarity of a conspicuous reef fish. Anim Conserv 7(4):365–374

Estes JA, Heithaus M, McCauley DJ, Rasher DB, Worm B (2016). Megafaunal Impacts on Structure and Function of Ocean Ecosystems. Annu Rev Environ Res 41:83–116

Geesey GG, Alexander GV, Bray RN, Miller AC (1984) Fish fecal pellets are a source of minerals for inshore reef communities. Mar Ecol Prog Ser 15(1):19–25

Gerking SD (1994) Feeding Ecology of Fish. Academic Press, San Diego

Goffredo S, Caroselli E, Mezzo F, Laiolo L, Vergni P, Pasquini L, Levy O, Zaccanti F, Tribollet A, Dubinsky Z, Falini G (2012) The puzzling presence of calcite in skeletons of modern solitary corals from the Mediterranean Sea. Geochimica et Cosmochimica Acta 15(85):187–199

Glynn P, Krupp D (1986) Feeding biology of a Hawaiian sea star corallivore, *Culcita novaeguineae* Muller & Troschel. J Exp Mar Biol Ecol 96:75–96

Haramaty L (1991) Reproduction effort in the nudibranch *Phestilla sihogae*: Calorimetric analysis of food and eggs. Pac Sci *45*(3):257–262

Hay ME, Fenical W, Gustafson K (1987) Chemical defense against diverse coral reef herbivores. Ecol 68(6):1581–1591

Hay ME, Kappel QE, Fenical W (1994) Synergisms in plant defenses against herbivores: interactions of chemistry, calcification, and plant quality. Ecol 75(6):1714–1726

Heyland A, Moroz LL (2005) Cross-kingdom hormonal signaling: an insight from thyroid hormone functions in marine larvae. J Exp Biol 208:4355–4361

Hoey AS, Bellwood DR (2008) Cross-shelf variation in the role of parrotfishes on the Great Barrier Reef. Coral Reefs, 27(1):37–47

Hourigan TF (1987) The behavioral ecology of three species of butterflyfishes (family Chaetodontidae). PhD Dissertation, University of Hawai'I, Manoa

Hughes RN (1980). Optimal foraging theory in the marine context. *Oceanogr Mar Biol Annu Rev*, *18*, 423–481

ICDD (2015) PDF-4+ 2015 (Database), edited by Dr. Soorya Kabekkodu, International Centre for Diffraction Data, Newtown Square, PA, USA

Johansson O, Wedborg M (1982) On the evaluation of potentiometric titrations of seawater with hydrochloric acid. Ocean Acta 5(2):209–218

Jones CG, Lawton JH, Shachak M (1994) Organisms as ecosystem engineers. Oikos 69:373–386

Lobel PS (1981) Trophic biology of herbivorous reef fishes: alimentary pH and digestive capabilities. J Fish Biol 19(4):365–397

Luzinova Y, Dobbs GT, Lapham L, Chanton JP, Mizaikoff B (2011) Detection of cold seep derived authigenic carbonates with infrared spectroscopy. Mar Chem 125:8–18

McCauley DJ, Keesing F, Young TP, Allan BF, Pringle RM (2006) Indirect effects of large herbivores on snakes in an African savanna. Ecol 87(10):2657–2663

McCauley DJ, Micheli F, Young HS, Tittensor DP, Brumbaugh DR, Madin EM, Holmes KE, Smith JE, Lotze HK, DeSalles PA, Arnold SN, Worm B (2010) Acute effects of removing large fish from a near-pristine coral reef. Mar Biol 157(12):2739–2750

McCauley DJ, Young HS, Dunbar RB, Estes JA, Semmens B X, Micheli F (2012). Assessing the effects of large mobile predators on ecosystem connectivity. Ecol Appl 22(6):1711–1717

McCauley DJ, Young HS, Guevara R, Williams GJ, Power EA, Dunbar RB, Bird DW, Durham WH, Micheli F (2014) Positive and negative effects of a threatened parrotfish on reef ecosystems. Cons Biol 28(5):1312–1321

Meyer JL, Schultz ET (1985) Migrating haemulid fishes as a source of nutrients and organic matter on coral reefs. Limn Ocean 30(1):146–156

Michel FM, Macdonald J, Feng J, Phillips BL, Ehm L, Tarabrella C, Parise JB, Reeder RJ (2008) Structural characteristics of synthetic amorphous calcium carbonate. Chem Mater 20:4720–4728

Millero FJ, Zhang J-Z, Lee K, and Campbell DM, Titration alkalinity of seawater, Mar Chem, 44, pp. 153–165 (1993)

Ohde S, & van Woesik R (1999) Carbon dioxide flux and metabolic processes of a coral reef, Okinawa. Bulletin of Marine Science, 65(2): 559–576

Owen-Smith RN (1988) Megaherbivores: The influence of very large body size on ecology. Cambridge University Press, Cambridge UK

Perry CT, Kench PS, O'Leary MJ, Morgan KM, Januchowski-Hartley F (2015) Linking reef ecology to island building: Parrotfish identified as major producers of island-building sediment in the Maldives. Geology 43(6):503–506

Pinnegar JK, Polunin NVC (2006) Planktivorous damselfish support significant nitrogen and phosphorus fluxes to Mediterranean reefs. Mar Biol 148(5):1089–1099

Pinnegar JK, Polunion NVC, Videler JJ, de Wiljes JJ (2007) Daily carbon, nitrogen and phosphorus budgets for the Mediterranean planktivorous damselfish *Chromis chromis*. J Exp Mar Biol Ecol 352:378–391

Pringle RM, Young TP, Rubenstein DI, McCauley DJ (2007) Herbivore-initiated interaction cascades and their modulation by productivity in an African savanna. Proc Nat Acad Sci 104(1):193–197

Pytkowicz RM (1967) Carbonate cycle and the buffer mechanism of recent oceans. Geochim Cosmochim Acta 31(1):63–73

Raab TK, Vogel JP (2004) Ecological and agricultural applications of synchrotron IR microscopy. Infr Phys Tech 45:393–402

R Core Team (2012) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

Radha AV, Forbes TZ, Killian CE, Gilbert PUPA, Navrotsky A (2010) Transformation and crystallization energetics of synthetic and biogenic amorphous caclcium carbonate. Proc Nat Acad Sci 107:16438–16443

Roman J, Estes JA, Morissette L, Smith C, Costa D, McCarthy J, Nation JB, Nicol S, Pershing A, Smetacek V (2014) Whales as marine ecosystem engineers. Front Ecol Environ 12(7):377–385

Rotjan RD, Lewis SM (2005) Selective predation by parrotfishes on the reef coral *Porites astreoides*. Mar Ecol Prog Ser 305:193–201

Rotjan RD, Lewis SM (2006) Parrotfish abundance and selective corallivory on a Belizean coral reef. J Exp Mar Biol Ecol 335:292–301

Schneider K, Silverman J, Woolsey W, Eriksson H, Byrne M, Caldeira K (2011) Potential influence of sea cucumbers on coral reef $CaCO_3$ budget: A case study at One Tree Reef. J Geophys Res 116:G04032

Schoener TW (1971) Theory of feeding strategies. Annu Rev Ecol Syst 2:369–404

Smriga S, Sandin SA, Azam F (2010). Abundance, diversity, and activity of microbial assemblages associated with coral reef fish guts and feces. FEMS Microbiology Ecol 73(1):31–42

Stevenson C, Katz LS, Micheli F, Block B, Heiman KW, Perle C, Weng K, Dunbar R, Witting J (2007) High apex predator biomass on remote Pacific islands. Coral Reefs 26(1):47–51

Targett TE, Targett NM (1990) Energetics of food selection by the herbivorous. Mar Ecol Prog Ser 66:13–21

Targett NM, Targett TE, Vrolijk NH, Ogden JC (1986) Effect of macrophyte secondary metabolites on feeding preferences of the herbivorous parrotfish *Sparisoma radians*. Mar Biol 92(1):141–148

Tribollet, A (2008) The boring microflora in modern coral reef ecosystems: a review of its roles. *Current developments in bioerosion,* (pp. 67–94). Springer, Berlin, Heidelberg

Tricas TC (1989) Prey selection by coral-feeding butterflyfishes: strategies to maximize the profit. *The butterflyfishes: success on the coral reef*, (pp. 171–186). Springer Netherlands

Unson MD, Holland ND, Faulkner DJ (1994) A brominated secondary metabolite synthesized by the cyanobacterial symbiont of a marine sponge and accumulation of the crystalline metabolite in the sponge tissue. Mar Biol 119(1):1–11

Urmos J, Sharma SK, Mackenzie FT (1991) Characterization of some biogenic carbonates with Raman spectroscopy. Am Mineral 76:641–646

Wang RZ, Addadi L, Weiner S (1997) Design strategies of sea urchin teeth: structure, composition and micromechanical relations to function. Phil Trans Royal Soc B: Biol Sci 352:469–480

Wilson RW, Millero FJ, Taylor JR, Walsh PJ, Christensen V, Jennings S, Grosell M (2009) Contribution of fish to the marine inorganic carbon cycle. Science 323:359–362

Winchester JW, Duce RA (1967) The global distribution of iodine, bromine, and chlorine in marine aerosols. Naturwissen 54:110–113

Woosley RJ, Millero FJ, Grosell M (2012) The solubility of fish-produced high magnesian calcite in seawater. J Geophys Res 117:C04018

Young HS, McCauley DJ, Dunbar RB, Dirzo R (2010) Plants cause ecosystem nutrient depletion via the interruption of bird-derived spatial subsidies. Proc Nat Acad Sci 107(5):2072–2077