

Comparative analysis of foraging behavior and bite mechanics reveals complex functional diversity among Caribbean parrotfishes

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ABSTRACT: Parrotfishes are a diverse group of herbivores that can influence benthic community dynamics and ecosystem function on coral reefs. Different species and size classes of parrotfishes vary in their feeding ecology and can impact reef ecosystems in distinct ways. We documented differences in the feeding ecology of 9 species of parrotfishes in the Florida Keys National Marine Sanctuary (FKNMS). Many of the key differences can be summarized by assigning species to functional groups (e.g. scrapers, excavators, croppers, macroalgae browsers), which are differentially responsible for carrying out specific ecological processes. For example, we found that *Sparisoma viride*, *Scarus coelestinus*, *Sc. guacamaia*, *Sc. taeniopterus*, and *Sc. vetula* feed on short turfs with few sediments, while *Sp. aurofrenatum*, *Sp. chrysopterus*, and *Sp. rubripinne* feed on longer sediment-laden turfs in addition to macroalgae. Further, parrotfishes use distinct bite types that indicate contrasting impacts on the benthos. Species that feed on short turfs scrape and excavate epilithic and endolithic algae, while species that feed on longer turfs and macroalgae tend to tear or crop algae from the reef. These distinct feeding behaviors result in different rates of algae removal, carbonate erosion, and sediment production. Recognizing that different species of parrotfishes interact with the benthos in fundamentally different ways will enable scientists and managers to better predict how changes in the structure of parrotfish assemblages may affect benthic communities and ecosystem processes.

KEY WORDS: Herbivory · Coral reef · Niche partitioning · Bioerosion · Turf algae · Macroalgae · Ecosystem-based management · Functional groups

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INTRODUCTION

Parrotfish are key herbivores on coral reefs that carry out a number of important ecological processes, including the removal of algae, bioerosion of the reef matrix, and the production and transport of sediment (Bonaldo et al. 2014). On many coral reefs, parrotfishes are the dominant herbivores by biomass and are among the key species influencing the dynamics of algae and corals (Williams & Polunin 2001,

Mumby 2006, Burkepile & Hay 2008, Adam et al. 2011). Their unique beak-like jaws allow parrotfishes to access a wide range of food resources, and many species have fast growth rates and can achieve high population densities in environments with very low standing crops of algae (Choat 1991, van Rooij et al. 1998, Gust et al. 2001, Taylor & Choat 2014). Parrotfishes also support local fisheries, which can reduce their abundance and alter their species composition and size structure (McClanahan 1994, Hawkins &

Roberts 2004a, Taylor et al. 2015), ultimately impacting reef benthic dynamics (Bellwood et al. 2012, Humphries et al. 2014, Jackson et al. 2014, Bozec et al. 2016). While parrotfishes have often been considered a single ecological guild, there are significant morphological and ecological differences among species and size classes that likely result in different foraging behaviors, diets, and impacts on the benthos (Bellwood et al. 2004, Bonaldo & Bellwood 2008, Burkepile et al. 2018). Understanding the level of functional diversity present among parrotfishes is therefore critical for a better understanding of the role of herbivory on reefs (Adam et al. 2015a).

Parrotfishes have generally been assigned to 1 of 3 functional groups based on their feeding ecology, functional morphology, and resulting impacts on benthic communities (Bellwood et al. 2004, Green & Bellwood 2009): (1) browsers, which primarily crop erect macroalgae; (2) scrapers, which scrape diminutive algal turfs and associated detritus, microbes, and infauna from carbonate surfaces (often referred to as the epilithic algal matrix or EAM); and (3) excavators, which excavate crustose and endolithic algae and microbes from within the reef framework. Excavators and scrapers both feed on epilithic and endolithic algae and both act as bioeroders. However, excavators differ from scrapers by taking deeper more powerful bites, which allows them to harvest more endolithic algae, and also results in more bioerosion and slower rates of algal regrowth (Bellwood & Choat 1990, Bruggemann et al. 1994b, 1996, Bonaldo & Bellwood 2009). In contrast, browsers often crop algae without making contact with the reef substrate, which results in little bioerosion and faster regrowth of algae. In addition, the functional roles of many parrotfishes change ontogenetically; for example, small individuals of bioeroding species lack the bite force required for significant bioerosion (Bellwood et al. 2012).

Much of the detailed work on parrotfish feeding ecology has focused on Pacific species (Green & Bellwood 2009). This work indicates that functional groups have a strong phylogenetic basis. For example, on Pacific reefs, macroalgal browsers and scraping and excavating parrotfishes belong to separate monophyletic clades (the *Sparisoma* [formerly Sparisomatinae] and *Scarus* [formerly Scarinae] clades, respectively). In addition, excavating parrotfishes in the Pacific belong to one of several genera (*Bolbometopon*, *Cetoscarus*, and *Chlorurus*) which have special morphological adaptations (e.g. strong jaw musculature, heavily cemented teeth with uneven cutting edges, etc.) that allow them to harvest endolithic algae (Streelman et al. 2002).

The situation is different in the Caribbean, where species in the *Sparisoma* clade appear to perform a mix of browsing, scraping, and excavating (Bonaldo et al. 2014, Adam et al. 2015a). For example, *Sp. viride* is an important excavator and bioeroder (Bruggemann et al. 1994b). In contrast, other members of the *Sparisoma* clade frequently browse macroalgae (Lewis 1985, McAfee & Morgan 1996), often without making contact with the substrate (Cardoso et al. 2009). Common parrotfishes, such as *Sp. rubripinne* and *Sp. aurofrenatum*, have been variously described as macroalgal browsers, excavators, or scrapers (Bellwood 1994, Bruggemann et al. 1996, Bernardi et al. 2000, Bellwood et al. 2004, Cardoso et al. 2009, Adam et al. 2015b), but it is unlikely that they serve all of these roles. Developing a better understanding of the functional roles of different parrotfishes will give us a clearer picture of the patterns of functional diversity and redundancy on Caribbean reefs. This information is essential for predicting how changes in parrotfish assemblages that result from fishing or disturbances may affect ecological processes and benthic community dynamics (Adam et al. 2015a).

Here, we explored the functional roles of 9 species of Caribbean parrotfishes. We used a combination of behavioral observations, detailed descriptions of individual bites, and video analysis of bite mechanics to document the foraging behavior and feeding impacts of the following 9 species: *Scarus coelestinus* (midnight parrotfish), *Sc. coeruleus* (blue parrotfish), *Sc. guacamaia* (rainbow parrotfish), *Sc. taeniopterus* (princess parrotfish), *Sc. vetula* (queen parrotfish), *Sparisoma aurofrenatum* (redband parrotfish), *Sp. chrysopterus* (redtail parrotfish), *Sp. rubripinne* (yellowtail parrotfish), and *Sp. viride* (stoplight parrotfish). These species are among the most abundant herbivores on many Caribbean reefs and represent 9 of the 10 species of parrotfishes commonly found on shallow, high-relief reefs throughout the Caribbean. Our objective was to quantify differences in foraging ecology among species, and to evaluate how these differences may result in unique functional roles.

MATERIALS AND METHODS

Study sites

We conducted fieldwork in the Florida Keys National Marine Sanctuary (FKNMS) during summer 2013 and 2014 off of Key Largo, FL, USA. The Florida Keys Reef Tract is a large bank reef system located ~8 km offshore of the Florida Keys, parallel to the island

chain. The FKNMS is a prime location for this study since fishing pressure on parrotfishes is very low (Bohnsack et al. 1994) and there are large populations of several species of parrotfishes that are rare or absent in many other locations (Hawkins & Roberts 2004a, Paddack et al. 2006, Adam et al. 2015b). All observations were conducted between ~5 and 12 m depth at 1 of 5 sites: Molasses, French, Elbow, Carysfort, and Conch. At each site, all fish species were observed in the same general habitats across the same depth range.

The 5 study sites differed somewhat in topographic complexity and benthic community composition. Molasses, Elbow, Carysfort, and French are topographically complex, high-relief spur and groove reefs while Conch is less topographically complex. The dominant substrates at all sites were multi-species turf assemblages (also known as the EAM), foliose and calcareous macroalgae (primarily *Dictyota* spp. but also *Galaxaura* spp., *Halimeda* spp., among others), and crustose coralline algae (CCA). The relative proportions of these algal groups varied among sites (for more information see Figs. S1–3 in the Supplement at www.int-res.com/articles/suppl/m597p207_supp/). Following the algal functional group classification of Steneck & Dethier (1994), we use 'macroalgae' to refer to large (thallus size generally >1 cm), complex algae and 'turf algae/EAM' to refer exclusively to filamentous turf assemblages.

Turf assemblages (i.e. EAM) were composed of multiple species of short (generally <1 cm) filamentous algae, including *Polysiphonia* spp., *Laurencia* spp., *Gelidiella* spp., *Gelidium* spp., and *Ceramium* spp. (amongst others). These turfs often harbored a thick layer of sediment (up to ~1 cm) trapped among the algae. Foliose (e.g. *Dictyota* spp.) and calcareous (e.g. *Halimeda* spp., and articulated coralline algae such as *Galaxaura* spp. and *Amphiroa* spp.) macroalgae were also generally short (usually <3 cm in height) and grew intermingled with turf assemblages. Turf assemblages also harbor many other organisms, including young/small stages of macroalgae that were not visible to us.

Behavioral observations to determine foray size

During summer 2013, we conducted 20 min focal behavioral observations at 3 sites (Molasses, Elbow, and Carysfort). Approximately 18 individuals of each of the 9 species of parrotfishes (range = 16 to 19) were observed for 20 min each, with observations evenly distributed across sites and time of day. All observa-

tions were conducted between 10:00 and 16:00 h, which corresponds to peak feeding time of herbivorous fishes on coral reefs (Bruggemann et al. 1994b). We focused on quantifying bite rates and behavior of large adults. For strongly sexually dimorphic species, we limited observations to initial phase (IP) individuals (see Fig. S4 in the Supplement for more information on the sizes and stages of fish observed).

We haphazardly selected focal individuals using criteria that ensured that different species were observed in the same general locations while minimizing the potential for resampling of the same individuals (see Adam et al. 2015b for further details on selection criteria). A SCUBA diver slowly approached focal fish and allowed ~2 to 3 min for the fish to acclimate to the presence of the diver while estimating their total length (TL) to the nearest cm. Upon acclimation, a diver followed a fish closely for a period of 20 min, recording the fish's behavior on an underwater slate. In addition to quantifying bite rates and the food items targeted by focal fish (reported in Adam et al. 2015b), we also quantified the number of bites taken in individual feeding forays (discrete feeding events with no discernable interval between successive bites, as defined by Bellwood & Choat 1990). Previous work found that foray size (i.e. the number of bites taken in a foray) varies in a predictable way among different parrotfish functional groups (Bellwood & Choat 1990, Bruggemann et al. 1994b). For each species, we then calculated the total proportion of bites that were taken in forays of different sizes and plotted these separately for *Scarus* and *Sparisoma* parrotfishes.

Detailed description of individual bites

During summer 2014, we described in detail individual bites by each species of parrotfish at 4 sites (Molasses, Carysfort, French, and Conch), with samples distributed as evenly as possible across the sites (Table 1). At each site, we haphazardly selected focal fish using similar criteria to that used during our 20 min behavioral observations, except that we sampled both IP and terminal phase (TP) individuals over a wide range of sizes (see Fig. S5 in the Supplement). After selecting a fish, we slowly approached it and allowed it time to acclimate to our presence while we estimated its TL to the nearest cm. We then randomly selected a single bite to describe. For each bite, we described the food item(s) targeted as well as characteristics of the substrate (e.g. hard bottom versus other common substrates such as sponges, gorgoni-

Table 1. Number of parrotfish bites observed for each species at each site

Species	Carysfort	Conch	French	Molasses	Total
<i>Scarus coelestinus</i>	60	27	83	70	240
<i>Scarus coeruleus</i>	63	43	51	26	183
<i>Scarus guacamaia</i>	27	46	81	50	204
<i>Scarus taeniopterus</i>	63	16	34	40	153
<i>Scarus vetula</i>	78	35	73	68	254
<i>Sparisoma aurofrenatum</i>	80	102	59	72	313
<i>Sparisoma chrysopterus</i>	21	87	66	44	218
<i>Sparisoma rubripinne</i>	83	79	62	58	282
<i>Sparisoma viride</i>	87	83	70	64	304

ans, etc.) at the precise location of the bite. Our goal was to determine, to the highest taxonomic resolution possible, the precise food items bitten and ingested by each fish. For hard substrates, we recorded whether a bite was on a convex, concave, or flat surface. In addition, we framed each bite within a 5 × 5 cm microquadrat and measured the depth of the sediment and height of the algae at several points to determine the average sediment depth and algal height within the vicinity of the bite. We then photographed the microquadrat with a digital camera (Olympus Stylus Tough TG-3) using the underwater macro setting; photographs were taken both before and after the manual removal of sediments. Following the removal of sediments, for every bite, we determined whether or not the fish left a distinct grazing scar where calcium carbonate had been removed from the reef framework in addition to epilithic algae. For *Scarus guacamaia* and *Sc. coelestinus*, we measured the area of each grazing scar from photographs using the image analysis program ImageJ (US National Institute of Health). We used a general linear model with a numeric and categorical predictor to estimate the relationship between bite area and fish size (TL²) and to test whether this relationship varied between the 2 species. We excluded photographs with multiple bites taken in the same location since the area of a single bite could not be determined.

We determined that fishes were taking different types of bites, which we described as scraping/excavating, cropping, and tearing. During scraping/excavating bites, fishes exerted a downward force as they applied their jaws to the reef. These bites resulted in a visible grazing scar (where algae and reef carbonate had been removed) and almost always made a scraping sound. In contrast to scraping/excavating bites, some fishes cropped algae without making contact with the substrate. These bites did not make an audible sound or leave a distinct mark on the ben-

thos. Finally, other fishes fed by tearing algae from the reef. During a tearing bite, fish would rotate onto their side, accelerating their head away from the substrate following jaw closure. Similar to cropping bites, tearing bites generally did not make an audible scraping sound and rarely left a visible mark on the reef (see Videos 1–4 in the Supplement for representative examples of each bite type).

We used hierarchical cluster analysis (with Ward's linkage on Curtis-Bray distance matrices from square-root transformed data) to identify unique functional

groups based on the data on diet (i.e. the food items targeted during the detailed description of individual bites) and data on bite type (e.g. scraping/excavating, cropping, tearing). Because previous work on herbivorous fishes has shown that foraging behavior can be context-dependent, varying with resource availability (e.g. Hanmer et al. 2017), competitor and predator abundance (e.g. Catano et al. 2014), and reef structural complexity (e.g. Catano et al. 2016), we first built separate distance matrices and ran separate cluster analyses for each site (given that these context-dependent factors likely differ across sites). However, visual inspection of the site-specific dendrograms indicated that classifications were similar across sites. To test this more rigorously, we used Mantel tests to examine pairwise correlations of the site-specific distance matrices. All matrices were highly correlated ($p < 0.001$ for all cases, with Mantel's r ranging from 0.72 to 0.92 for bite type and 0.68 to 0.85 for diet), indicating that classifications were highly congruent among sites (see Figs. S6 & S7 in the Supplement for more information). Thus, for the final analyses we pooled data across sites.

We hypothesized that fishes employing particular bite types were doing so in order to target specific food items. Thus, we tested whether functional groups based on bite type and diet were congruent using a Mantel test. A significant positive correlation between the 2 matrices would indicate that fishes that use similar bite types have similar diets. We used ANOVA on log-transformed data to test whether sediment depth and the height of the turf algae within the EAM differed among species and sites, and whether any differences among species were consistent across sites (i.e. we tested for a site × species interaction). We also tested whether fish length (i.e. TL) was a significant predictor of diet by using logistic regression to test whether the probability of targeting macroalgae varied with length for

each species. In addition, for fish that targeted EAM, we used linear regression to test whether TL was a significant predictor of the sediment depth or turf height of the turf assemblages targeted. Because foraging patterns may be context-dependent, based on resource availability, competitor abundance, etc., we also tested for a site \times size interaction in all models. Finally, we used a chi-squared contingency test to determine whether different species targeted substrates with different topography (e.g. convex vs. concave vs. flat surfaces).

Video analysis of bite mechanics

We used video analyses to gain further insight into the different bite types employed by the scraping and excavating species; bites by scraping parrotfishes tend to be much more rapid than the more powerful bites taken by excavating parrotfishes (Bellwood & Choat 1990). To determine bite speeds of scraping and excavating parrotfishes, we filmed parrotfish feeding on natural substrate *in situ* using underwater cameras (GoPro) deployed in the field (frame rate = ~ 30 frames s^{-1}). For each scraping and excavating species (species that frequently leave a grazing scar on the substrate) except *Sc. guacamaia* (for which we were unable to obtain high quality video) we analyzed multiple bites ($n = 9$ when possible) from 4 different individuals. For each bite, we recorded the bite duration as the time between when an individual's jaws initially contacted the substrate and the time when its jaws had completely closed and were no

longer in contact with the substrate. We determined time intervals through inspection of individual video frames using the free open source program Avidemux 2.6. We used a linear mixed effects model to test whether bite duration differed among species. Because we observed multiple bites from all individuals, we modeled individuals as a random effect with species modeled as a fixed effect. All analyses were conducted in R v.3.3.2 (R Core Team 2016).

RESULTS

Foraging behavior

Sparisoma parrotfishes fed in shorter forays with generally < 3 bites $foray^{-1}$, compared to *Scarus* parrotfishes (Fig. 1; Table 2). The 3 largest *Scarus* species (*Sc. coelestinus*, *Sc. coeruleus*, and *Sc. guacamaia*) fed in shorter forays with generally < 10 bites $foray^{-1}$ compared to the smaller species (*Sc. taeniopterus* and *Sc. vetula*) that often took > 10 bites $foray^{-1}$ (Fig. 1).

Diet

Our observations of 2151 individual bites revealed that parrotfishes fed primarily on macroalgae, filamentous turf assemblages (i.e. EAM), and CCA (Fig. 2). All species fed on turf assemblages, but only *Sparisoma aurofrenatum*, *Sp. chrysopterus* and *Sp. rubripinne* frequently fed on macroalgae. In addition to turf algae, these macroalgae-browsing species fed

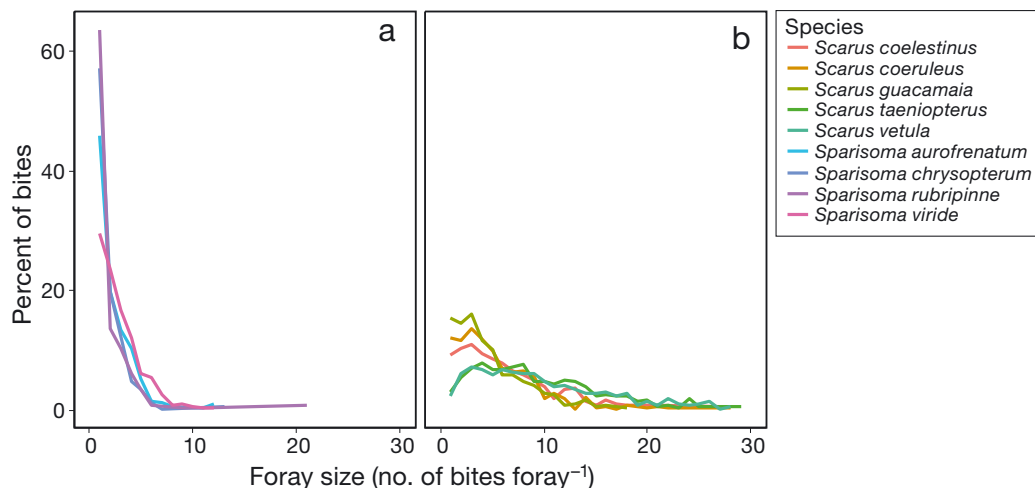


Fig. 1. Distribution of foray sizes from 20 min behavioral observations of parrotfishes from 2 genera, (a) *Sparisoma* and (b) *Scarus*, expressed as the percentage of total bites taken ($n = 16$ to 19 ind. for each species). Forays are discrete feeding events with no discernable interval between successive bites. Note that the x-axis was truncated at 30 for clarity, but a small percentage of bites by *Sc. vetula* (4%), *Sc. taeniopterus* (1%), and *Sc. coelestinus* (1%) were taken in forays of > 30 bites

Table 2. Proposed functional group classification of 9 species of Caribbean parrotfishes based on field observations of foraging behavior, diet, and bite mechanics. Browsers feed on significant amounts of macroalgae as well as filamentous turfs. In contrast to scrapers and excavators, browsers tend to feed on longer filamentous turfs which they tear from the reef. Unlike browsers, scrapers and excavators forage on short, sparse filamentous turfs and endolithic algae and crustose coralline algae (CCA), which they scrape or excavate from the reef framework. M: macroalgae; LT: long turf algae; E endolithic algae; ST: short turf algae; S: sand; I: intermediate

	Primary bite type	Grazing scars ^a	Diet	Bite rate (bites min ⁻¹)	Foray size (bites)
Browsers					
<i>Sparisoma aurofrenatum</i>	Tearing	Occasional	M, LT	Low (<10)	Median = 1, mean = 1.5
<i>Sparisoma chrysopterum</i>	Tearing	Occasional	M, LT	Low (<10)	Median = 1, mean = 1.4
<i>Sparisoma rubripinne</i>	Tearing	Occasional	M, LT	Low (<10)	Median = 1, mean = 1.3
Excavators					
<i>Sparisoma viride</i>	Scraping/excavating	Usual	E, CCA, ST	Low (<10)	Median = 1, mean = 1.9
<i>Scarus guacamaia</i>	Scraping/excavating	Usual	E, CCA, ST	I (10–20)	Median = 2, mean = 2.7
<i>Scarus coelestinus</i>	Scraping/excavating	Usual	E, CCA, ST	I (10–20)	Median = 2, mean = 3.6
Scrapers					
<i>Scarus vetula</i>	Scraping/excavating	Often	E, CCA, ST	High (>20)	Median = 4, mean = 5.8
<i>Scarus taeniopterus</i>	Scraping/excavating	Often	E, CCA, ST	High (>20)	Median = 4, mean = 5.4
Croppers					
<i>Scarus coeruleus</i>	Cropping	Rare	LT, S	I (10–20)	Median = 2, mean = 3.1

^aUsual > often > occasional > rare

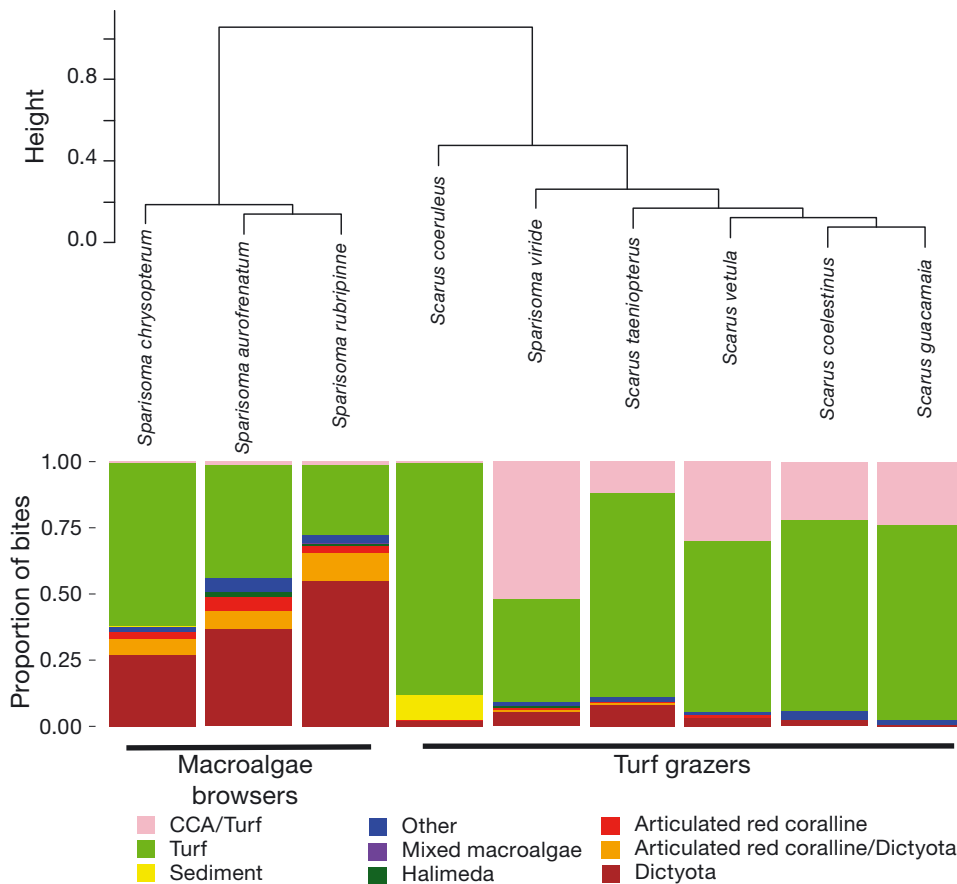


Fig. 2. Dendrogram showing that parrotfishes cluster into 2 groups based on diet; those that largely browse on macroalgae (*Sparisoma aurofrenatum*, *Sp. chrysopterum*, and *Sp. rubripinne*), and those that scrape, excavate, and/or crop turf algae and associated detritus, microbes, crustose coralline algae (CCA), and endolithic algae from carbonate surfaces (*Sp. viride*, *Scarus coelestinus*, *Sc. guacamaia*, *Sc. coeruleus*, *Sc. taeniopterus*, and *Sc. vetula*) (n = 153–313 bites species⁻¹; see Table 1 for exact sample sizes)

primarily on abundant *Dictyota* spp. as well as other macroalgae associated with *Dictyota*, especially articulated red coralline algae such as *Amphiroa* spp., *Galaxaura* spp., and *Jania* spp. The probability of feeding on macroalgae increased with fish length for all 3 of the macroalgae-browsing species (logistic regression, $p < 0.01$ for each species; see Fig. S8 in the Supplement). *Sp. viride*, *Sc. coelestinus*, *Sc. guacamaia*, *Sc. taeniopterus*, and *Sc. vetula* all fed primarily on EAM and CCA. *Sc. coeruleus* fed primarily on EAM but was also frequently observed ingesting sediment.

Bite types

Observations of individual bites revealed that different species consistently used different bite types. *Sparisoma* species exhibited more tearing bites while *Scarus* species scraped, excavated, or cropped algae (Fig. 3). Cluster analysis revealed 3 distinct groups of species based on different bite types. The first in-

cluded 3 of the 4 species of *Sparisoma* (*Sp. aurofrenatum*, *Sp. chrysopterum*, and *Sp. rubripinne*), which fed primarily by tearing algae from the reef. The second group included *Sp. viride* and the 2 largest species of *Scarus* parrotfishes (*Sc. coelestinus* and *Sc. guacamaia*), which fed primarily by scraping and excavating EAM, endolithic algae, and CCA from reef surfaces (Fig. 3). The final group included *Sc. coeruleus*, *Sc. taeniopterus*, and *Sc. vetula*, and varied in the extent that they scraped versus cropped algae. *Sc. vetula* primarily scraped algae, *Sc. coeruleus* primarily cropped algae, and *Sc. taeniopterus* scraped and cropped to a similar degree (Fig. 3).

Bite type was strongly associated with diet (Mantel test, $r = 0.78$, $p < 0.001$), with the 3 macroalgae-browsing species predominantly using a tearing bite. In contrast, the species that fed mainly on EAM tended to use scraping and excavating bites and thus were likely targeting the underlying CCA and endolithic algae in addition to epilithic algae. The exception was *Sc. coeruleus*, which almost exclusively cropped filamentous algae.

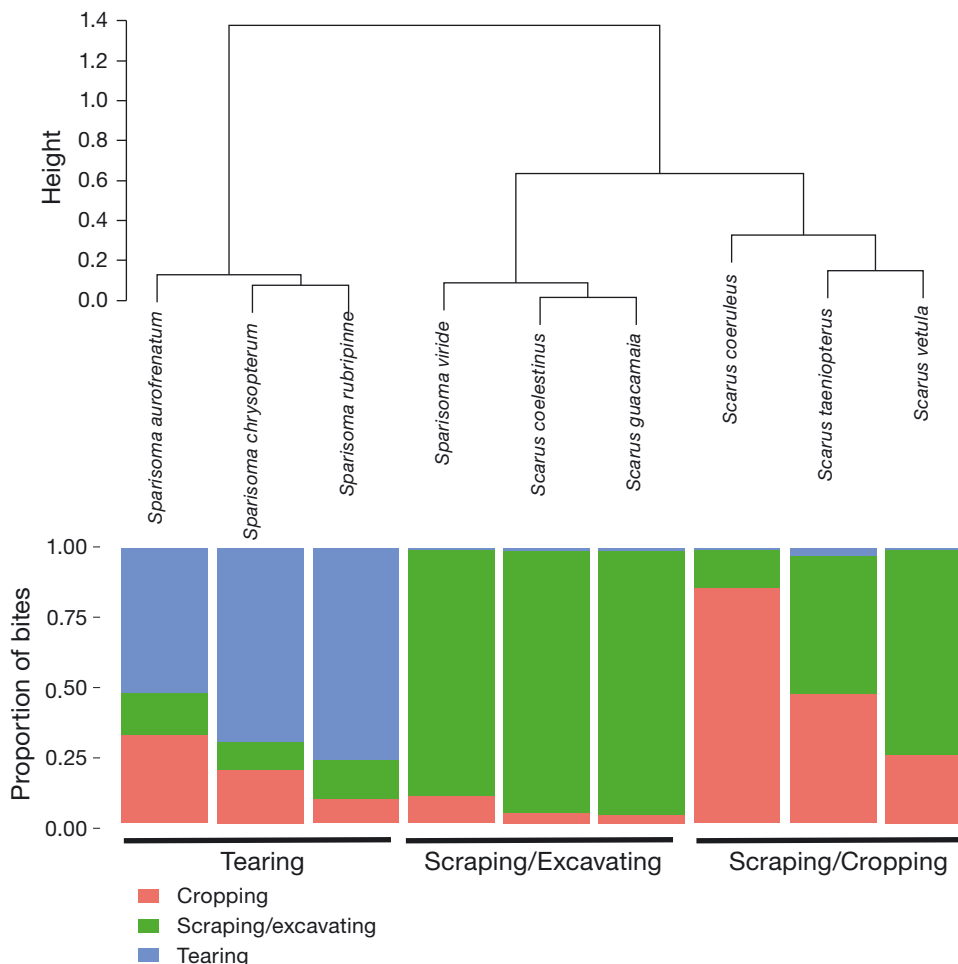


Fig. 3. Dendrogram showing that parrotfishes cluster into 3 groups based on bite types. *Sparisoma aurofrenatum*, *Sp. chrysopterum*, and *Sp. rubripinne* primarily tear algae from the reef; *Sp. viride*, *Scarus coelestinus*, and *Sc. guacamaia* scrape and excavate algae; and *Sc. coeruleus*, *Sc. taeniopterus*, and *Sc. vetula* primarily scrape and/or crop algae from the reef ($n = 153\text{--}313$ bites species⁻¹; see Table 1 for exact sample sizes). Note that species that use similar bite types tend to have similar diets (Mantel test, $r = 0.78$, $p < 0.001$)

Turf assemblages

EAM made up a large fraction of the diets of all species, including those that fed on significant amounts of macroalgae. However, close inspection of the bites on EAM revealed that different species targeted turf assemblages of different heights (ANOVA, $F_{8,1173} = 24.9$, $p < 0.0001$; Fig. 4a) and sediment depths (ANOVA, $F_{8,1533} = 70.0$, $p < 0.0001$; Fig. 4b). The 3 macroalgae-browsing species (*Sp. aurofrenata*-

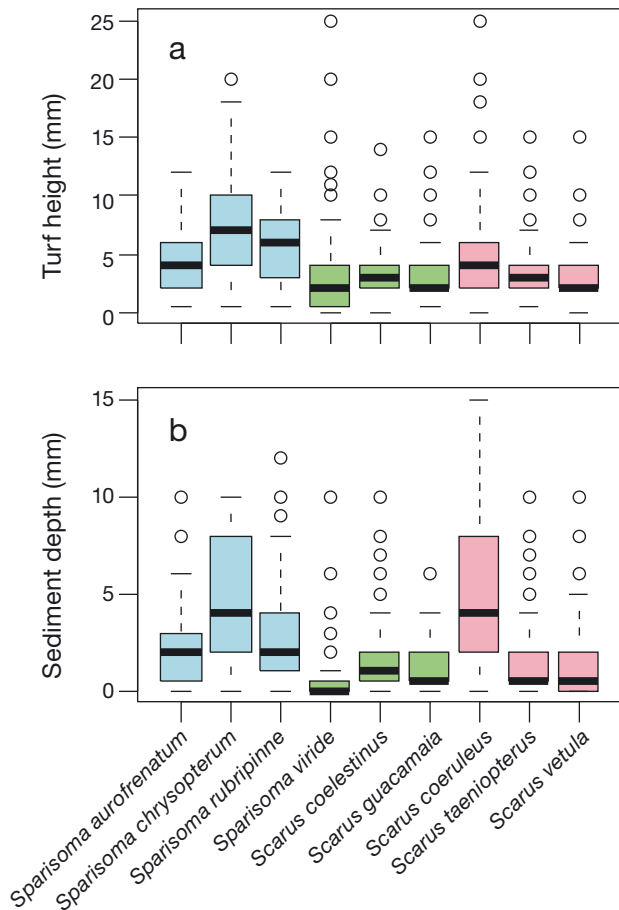


Fig. 4. (a) Height of turf algae targeted and (b) sediment depth for parrotfishes that tear algae (shown in blue: *Sparisoma aurofrenatum*, $n = 93$; *Sp. chrysopterum*, $n = 90$; and *Sp. rubripinne*, $n = 54$), scrape and excavate algae (shown in green: *Sp. viride*, $n = 205$; *Scarus coelestinus*, $n = 201$; and *Sc. guacamaia*, $n = 180$), and scrape and crop algae (shown in pink: *Sc. coeruleus*, $n = 133$, *Sc. taeniopterus*, $n = 106$, and *Scarus vetula*, $n = 173$). Boxes: medians with the 1st and 3rd quantile; whiskers: $\pm 1.58 \times$ interquartile range (IQR)/ \sqrt{n} ; dots: data points that fall beyond this range (we observed several bites by *Sc. coeruleus* and *Sp. chrysopterum* in sediment up to 12 cm deep that are not shown for clarity). Note that species that tear algae target longer turfs growing in deeper sediments compared to species that scrape and excavate algae. Also note that *Sc. coeruleus* was unique among the *Scarus* parrotfishes in targeting algae growing on and within deeper sediments

tum, and especially *Sp. chrysopterum* and *Sp. rubripinne*) consistently targeted longer turfs (Figs. 4a & S9, Table S1 in the Supplement) with deeper sediments (Figs. 4b & S10, Table S2) than the species that scraped/excavated EAM. *Sc. coeruleus*, which primarily cropped algae, also fed on long turfs with deep sediments (Figs. 4, S9 & S10). In contrast, *Sp. viride*, an excavator, targeted turfs with fewer sediments than all other species (Tukey's HSD, $p < 0.05$ for all comparisons; Figs. 4b & S10, Table S2). Among the 3 macroalgae-browsing species, *Sp. chrysopterum* targeted longer turf algae with deeper sediments than *Sp. aurofrenatum* and *Sp. rubripinne* (Figs. 4a,b, S9 & S10). Within species, fishes of different lengths tended to target similar turf assemblages (Figs. S11 & S12). The major exception to this pattern was *Sp. viride*. Larger *Sp. viride* consistently targeted shorter turf assemblages than smaller conspecifics (ANOVA, $F_{1,189} = 25.0$, $p < 0.0001$; Fig. S11).

Grazing scars

Species varied widely in the proportion of bites that left a grazing scar on the reef. Most bites (74%) by medium to large sized *Sp. viride* (ind. ≥ 20 cm TL) resulted in a grazing scar. Yet less than 10% of the bites of similarly sized individuals from the other 3 *Sparisoma* species (*Sp. aurofrenatum*, *Sp. chrysopterum*, and *Sp. rubripinne*) left a scar (Fig. 5). In contrast, *Scarus* species were highly variable in their tendency to leave a grazing scar. *Sc. coelestinus* and *Sc. guacamaia* usually left a grazing scar (60 and 67% of bites, respectively). *Sc. vetula* and *Sc. taeniopterus* often left grazing scars (46 and 27% of bites, respectively). *Sc. coeruleus* rarely left a grazing scar (<2% of bites). The probability of a bite leaving a scar was positively correlated with TL for *Sc. guacamaia*, *Sc. coelestinus*, and *Sp. viride* (logistic regression, $p < 0.01$ for each species). *Sc. taeniopterus* and *Sc. vetula* exhibited the same trend, although the relationships were not statistically significant for either species (logistic regression, $p = 0.21$ and 0.13 , respectively; Fig. 5).

Bite area was linearly related to TL^2 for both *Sc. guacamaia* and *Sc. coelestinus* (ANOVA, $F_{1,51} = 15.48$, $p < 0.0001$, slope = 0.000579 , intercept not significantly different than 0) with no evidence that the relationship differed between the 2 species (ANOVA main effect species: $F_{1,51} = 0.24$, $p = 0.62$; species $\times TL^2$: $F_{1,51} = 0.0$, $p = 0.97$). Bites by *Sc. guacamaia* and *Sc. coelestinus* were larger than bites by equivalently sized *Sc. vetula* in Bonaire (Bruggemann et al. 1994b). Among the

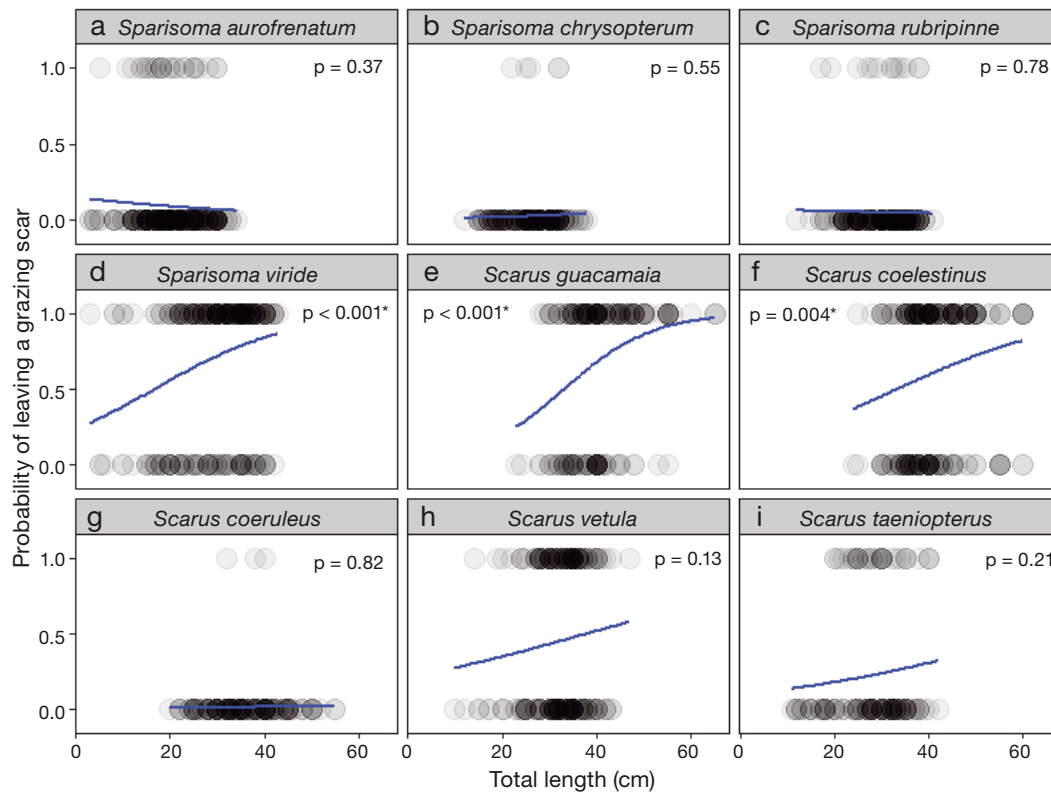


Fig. 5. Relationships between fish size and the probability that a bite would leave a grazing scar on the substrate for (a) *Sparisoma aurofrenatum* (n = 312), (b) *Sp. chrysopterus* (n = 214), (c) *Sp. rubripinne* (n = 279), (d) *Sp. viride* (n = 304), (e) *Scarus guacamaia* (n = 206), (f) *Sc. coelestinus* (n = 240), (g) *Sc. coeruleus* (n = 182), (h) *Sc. vetula* (n = 251), and (i) *Sc. taeniopterus* (n = 153). Curves are predicted probabilities from logistic regression model (p-values indicate significance of model)

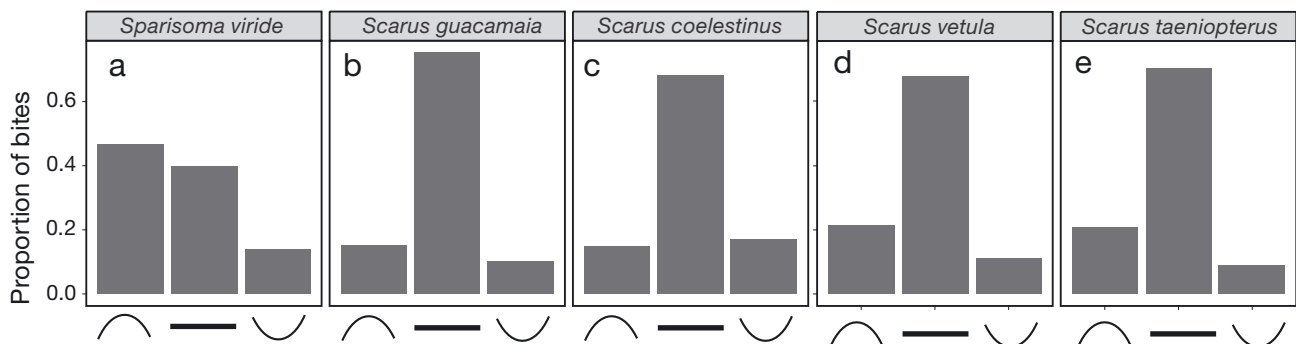


Fig. 6. Proportion of bites targeting epilithic algal matrix (EAM) (turf algae or turf algae on crustose coralline algae [CCA]) which were on convex, flat, and concave surfaces (see symbols) for scraping and excavating parrotfishes (a) *Sparisoma viride* (n = 275), (b) *Scarus guacamaia* (n = 201), (c) *Sc. coelestinus* (n = 236), (d) *Sc. vetula* (n = 239), and (e) *Sc. taeniopterus* (n = 139). All fishes targeted topographically similar substrates except the excavating species *Sp. viride*, which targeted convex surfaces a greater proportion of the time compared to other species ($\chi^2 = 110$, df = 8, $p < 0.0001$)

species that frequently left grazing scars while foraging, *Sp. viride* disproportionately targeted convex surfaces, while all other scraping and excavating species primarily targeted flat surfaces (chi-squared contingency test, comparisons between *Sp. viride* and all other species $p < 0.0001$; Fig. 6).

Bite speeds

Bite speeds varied greatly among species that fed by taking scraping/excavating bites (ANOVA, $F_{3,12} = 19.4$, $p < 0.0001$; Fig. 7). Bites by *Sp. viride* were longer in duration compared to the other 3 species

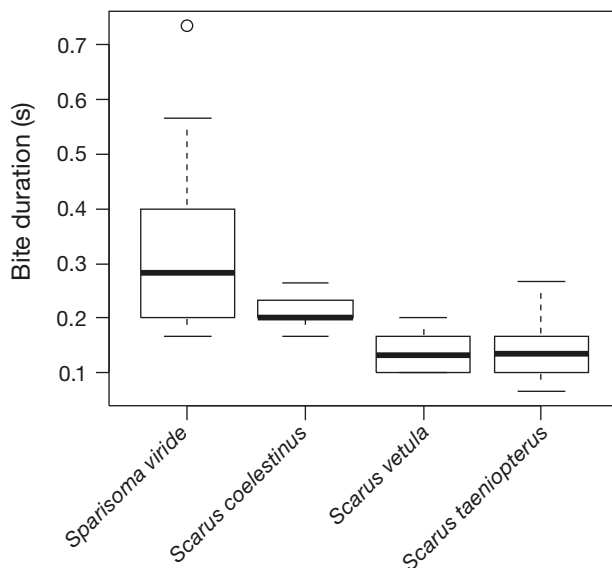


Fig. 7. Bite duration by species ($n = 22\text{--}28$ bites species⁻¹). Bite duration was recorded as the time between initial contact with the substrate and the time when an individual's jaws had completely closed and were no longer in contact with the substrate. Boxes: medians with the 1st and 3rd quantile, whiskers: $\pm 1.58 \times$ interquartile range (IQR)/ \sqrt{n} ; dots: data points that fall beyond this range. Note that *Sparisoma viride* tends to be in contact with the substrate for much longer than the other 3 species

(post hoc Tukey tests, $p < 0.01$ for all comparisons). In contrast, bite speeds by the 3 *Scarus* species were similar, despite a non-significant trend for *Sc. coelestinus* to take bites that were longer in duration than *Sc. vetula* and *Sc. taeniopterus* (post hoc Tukey tests, $p < 0.1$ for both comparisons). Similar to excavating species in the Pacific (see Bellwood & Choat 1990), bites by *Sp. viride* were frequently associated with a dorsal rotation of the body during the bite (see Video 2 in the Supplement). Scraping/excavating bites by other species did not show this behavior.

DISCUSSION

Our behavioral observations and detailed descriptions of over 2000 individual bites indicate that *Sparisoma* species are major consumers of macroalgae while *Scarus* species feed at much higher rates on diminutive algal turfs. These observations are consistent with previous work (Bruggemann et al. 1994b, McAfee & Morgan 1996, Cardoso et al. 2009, Burkepile & Hay 2010, Adam et al. 2015b). Yet our study also revealed significant, but previously unknown differences in foraging behavior between the 2 genera. For example, parrotfishes in both genera

fed on EAM, but they foraged in fundamentally different ways (tearing versus scraping algae in *Sparisoma* vs. *Scarus*, respectively) and targeted very different kinds of turf assemblages. *Sparisoma* species tended to target longer, sediment-laden turfs, while most of the *Scarus* species, along with *Sp. viride*, targeted shorter, relatively sediment-free turfs (and/or the endolithic algae and CCA growing beneath those turfs).

In addition to these major differences between genera, we also found that different parrotfish species in the same genus often forage in distinct ways. Thus, closely related species in the same genus may have fundamentally different impacts on the benthos. For example, whereas *Sp. viride* functions as an excavator (Bruggemann et al. 1996), other *Sparisoma* parrotfishes largely feed by tearing macroalgae and long filamentous algae from the reef without scraping or excavating the reef framework (see also Bonaldo et al. 2014). Similarly, among the *Scarus* species, some species, such as *Sc. guacamaia* and *Sc. coelestinus*, scrape and excavate algae, while others, such as *Sc. coeruleus* and *Sc. taeniopterus*, frequently crop algae. As major drivers of bioerosion, scraping and excavating species can strongly impact reef carbonate dynamics, but species that primarily crop or tear algae are unlikely to have the same capacity for bioerosion (Bellwood & Choat 1990, Bruggemann et al. 1996, Bonaldo et al. 2014). Thus, our observations suggest that *Sp. viride* has a much greater capacity for bioerosion compared to other *Sparisoma* species. Our data also suggest that *Sc. guacamaia* and *Sc. coelestinus* take larger bites than equivalently sized *Sc. vetula*, and hence may be more important for bioerosion than existing data from *Sc. vetula* would suggest. In contrast, the other large-bodied parrotfish, *Sc. coeruleus*, was rarely observed scraping or excavating reef substrate, and thus is likely to be much less important for bioerosion than other large *Scarus* species. Carbonate budgets for Caribbean reefs have generally been parameterized assuming that parrotfish species in the same genus are functionally equivalent (e.g. Perry et al. 2013, 2014), but our study suggests that this approach may greatly over- or under-estimate carbonate losses from parrotfish grazing, depending on the species composition of the parrotfish assemblage.

The foraging ecology of each parrotfish species was size-dependent. For example, bites from larger individuals of the scraping and excavating species were more likely to leave a grazing scar than bites from smaller conspecifics. These observations are consistent with earlier observations of *Sp. viride* and *Sc. vetula* in Bonaire (Bruggemann et al. 1996) as well as observations of scraping and excavating par-

rotfishes on the Great Barrier Reef (Bonaldo & Bellwood 2008) and Hawaii (Ong & Holland 2010) and suggest that larger-bodied individuals of a few species will contribute disproportionately to bioerosion (Bellwood et al. 2012). This suggests that changes in the size-structure of parrotfish assemblages, in addition to changes in the total biomass or species composition, may alter reef carbonate dynamics (see also Lokrantz et al. 2008). In contrast to the scraping and excavating species, the 3 macroalgae-browsing *Sparisoma* species rarely scarred the substrate, regardless of their size. However, larger individuals of all 3 species were more likely to consume macroalgae than smaller individuals, suggesting that their functional roles also change with ontogeny. This suggests that alterations to the size structure of these populations via fishing could reduce levels of macroalgal browsing, even if there were minimal changes in fish biomass.

The extent that different parrotfish species and size classes feed on different types of algae will influence whether they play complementary versus redundant roles in the ecosystem (Burkepile & Hay 2011, Rasher et al. 2013). In agreement with previous work, our data revealed major differences in diet between *Sparisoma* and *Scarus* parrotfishes, with generally smaller differences within each genus. However, broad characterization of diet items as 'turf' or 'macroalgae' are likely to underestimate the degree of partitioning that occurs among different parrotfish species. Further, the algal assemblages fed on by parrotfishes harbor diverse microbial assemblages, including protein-rich cyanobacteria (Tribollet 2008, Barott et al. 2011), which are likely major targets of consumption (Clements et al. 2017). Thus, much of the diet partitioning that occurs among different species of parrotfishes probably involves selection for microscopic organisms that cannot be readily identified in the field.

When we looked at easily quantifiable aspects of the turf assemblages targeted by parrotfishes, such as turf height and sediment depth, we found that different species of parrotfishes targeted turfs with very different characteristics. For example, the excavating species *Sp. viride* targeted shorter turfs than other species, and this was particularly true for large individuals, likely because they were primarily targeting endolithic algae and CCA rather than epilithic turfs. Previous work suggests that the majority of algae consumed by the excavating species *Sp. viride* are endolithic, and that endolithic algae also make up a significant, though smaller, fraction of the diet of the scraping species *Sc. vetula* (Bruggemann et al. 1994a,b). In contrast, our data suggest that endolithic

algae and CCA make up a smaller fraction of the diets of other *Sparisoma* species, which primarily browse on macroalgae and tear filamentous algae from the reef without removing large amounts of reef carbonate. Thus, the different bite types employed by the different species likely result in even greater partitioning of trophic resources than what we have documented here.

Regardless of the actual targets of consumption (e.g. microbial assemblages vs. macroscopic algae), the differences in diet we observed among species are important for understanding how parrotfishes impact benthic communities. For example, experiments by Burkepile & Hay (2008, 2010) demonstrated that parrotfishes with complementary diets suppress algae more effectively together than any single species can alone. In particular, they found that *Sparisoma aurofrenatum* controlled the proliferation of macroalgae, but was unable to prevent the establishment of thick algal turfs in locations where macroalgae were absent. In the same experiments, the authors found that *Sc. taeniopterus* largely avoided feeding on macroalgae, but controlled algal turfs and prevented macroalgae from becoming established by rapidly grazing sparse algal turfs. Thus, when both species were present together they were more efficient at limiting algal abundance. Our results indicate similar levels of diet complementarity among most species of *Scarus* and *Sparisoma* parrotfishes, suggesting that a mix of species from each genus may be needed to simultaneously (1) prevent established macroalgae from becoming abundant and (2) prevent the establishment of macroalgae and development of thick algal turfs. Both of these processes may benefit adult corals, juvenile corals, and coral settlement given the negative effects of algae on corals at different life stages (Kuffner et al. 2006, Box & Mumby 2007, Rasher & Hay 2010, Dixson et al. 2014).

CONCLUSIONS AND IMPLICATIONS

By drawing attention to the ecological processes performed by different parrotfish species and size classes, functional groups can improve our understanding of herbivory on coral reefs, inform ecological models, and help guide management (Green & Bellwood 2009). Our results suggest that Caribbean parrotfish species belong in 1 of 4 functional groups (Table 2). In agreement with previous work, we found that *Sparisoma viride* is functionally similar to the excavating parrotfishes from the Pacific, whereas

Scarus vetula primarily functions as a scraper (Bruggemann et al. 1996). Unlike *Sp. viride*, the other *Sparisoma* species appear to be browsers that feed on macroalgae and long filamentous algae they tear from the reef (though all of these species sometimes scrape algae and occasionally leave grazing scars) (see also Cardoso et al. 2009, Bonaldo et al. 2014). Two of the large species of *Scarus* (*Sc. guacamaia* and *Sc. coelestinus*) had traits consistent with both scraping and excavating parrotfishes. For example, both species were more likely to leave a grazing scar than *Sc. vetula*, and their scars were larger, even for equivalently sized fish. But, similar to *Sc. vetula* and other scraping parrotfishes, *Sc. guacamaia* and *Sc. coelestinus* tended to forage on flat substrate rather than the convex substrates targeted by *Sp. viride*. Despite these differences, our data suggest that *Sc. guacamaia* and *Sc. coelestinus* are functional excavators based on the size of their bite scars and their capacity for bioerosion relative to the smaller scraping species, *Sc. vetula* and *Sc. taeniopterus* (see Table 2). Finally, our data suggest that *Sc. coeruleus* neither scrapes nor excavates algae, feeding primarily by cropping the tops of filamentous algae from heavily sedimented turfs, unlike other *Scarus* parrotfishes.

In many places in the Caribbean, parrotfishes are targeted in multi-species fisheries (Hawkins & Roberts 2004b). Managers throughout the region increasingly seek to reduce potential negative impacts of parrotfish fishing on reef ecosystems (Mumby 2016). Yet in many locations, parrotfishes are being managed as a single species-complex (i.e. a single combined harvest limit is set for the entire species group; NOAA NMFS 2011). Our work indicates that different species and size classes of parrotfishes often have unique feeding preferences and behaviors and likely play different, non-substitutable roles in the coral reef ecosystem. By recognizing distinct functional groups, managers can focus on the specific ecological processes carried out by different parrotfish species and use this information to help guide management.

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