



Few Herbivore Species Consume Dominant Macroalgae on a Caribbean Coral Reef

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Coral reefs have changed radically in the last few decades with reefs in the Caribbean now averaging 13% coral cover and 40% macroalgal cover (mostly *Dictyota* and *Lobophora*). So, it is time we re-evaluate which species are key to the process of herbivory in these new conditions. The role herbivorous fishes play in controlling macroalgae is often considered by managers and researchers at a guild or family level, but greater resolution is needed to understand the impact of herbivores more fully. We performed feeding assays and behavioral observations of fish feeding to quantify the removal of the most common macroalgae by different herbivorous fish species. In total, we ran 34 h-long trials using *Dictyota* and *Lobophora* across two sites and conducted over 34 h of observation of 105 fish from eight species in the Cayman Islands, Caribbean. We show that many nominal herbivores did not consume macroalgae but instead targeted the epibionts on macroalgae and other substrates. In fact, only three fish taxa consumed macroalgae as a significant proportion of their feeding: one species of surgeonfish (*Acanthurus coeruleus*), one species of parrotfish (*Sparisoma aurofrenatum*), and the third, the chubs (*Kyphosus* spp.), is a group of species which is not consistently considered as part of the herbivore community in the Caribbean. From our observations, an individual *A. coeruleus* can consume ~44 g of *Dictyota* per day, while *S. aurofrenatum* can consume ~50 g and *Kyphosus* spp. can consume ~100 g. These values are significantly more than all other herbivorous fish species and suggest these three taxa are key macroalgal consumers in the Caribbean. These results highlight that disentangling the role of individual herbivore species is necessary for critical species to be identified and protected. Furthermore, as reef conditions change, we need to re-evaluate the key functions and species to be more effective at protecting and managing these important ecosystems. With far higher macroalgal coverage than in the past, the few browsing species that remove macroalgae may be increasingly important in promoting reef health.

Keywords: herbivory, macroalgae, *Kyphosus*, *Sparisoma*, *Acanthurus*, browser, *Dictyota*, *Lobophora*

INTRODUCTION

In the Caribbean, coral cover has declined to a regional average of 13%, while macroalgal cover is now ~ 40% of the forereef (between 28 and 45% by ecoregion, AGRRA, 2018). This region-wide decline in reef health has been observed since the 1970s and is likely a result of a combination of factors including hurricanes, coral disease, temperature stress, over-fishing of herbivorous fishes and the die-off of the algal-grazing urchin, *Diadema antillarum* (Gardner et al., 2003; Jackson et al., 2014). Of the ~40% macroalgal cover, *Dictyota* and *Lobophora* are often the most abundant genera (Cardoso et al., 2009; Diaz-Pulido et al., 2011; Suchley and Alvarez-Filip, 2017). This increase in macroalgae can cause problems for corals and hence the resilience of the reef system by reducing their growth (Tanner, 1995; Box and Mumby, 2007) and fecundity (Kuffner et al., 2006), increasing the prevalence of disease (Birrell et al., 2008) and pre-empting space and inhibiting coral recruitment (McCook et al., 2001; Birrell et al., 2008; Venera-Ponton et al., 2011). Given these negative effects of macroalgae and their increasing abundance, the herbivore species that remove them are key to promoting reef health (Burkepile and Hay, 2008; Adam et al., 2015).

Since the mass mortality of the urchin *Diadema antillarum* in 1983 and subsequent lack of recovery of urchin populations to previous densities (Lessios, 1988; Lessios, 2005), fishes are the most abundant herbivores on Caribbean coral reefs. Studies to date suggest that the herbivore guild in the Caribbean is composed almost exclusively of parrotfish (*Scarus* and *Sparisoma*) and surgeonfish (*Acanthurus*; Mumby, 2006; Burkepile and Hay, 2008; Kramer et al., 2017; Longo et al., 2019). Although chubs (*Kyphosus*), unicornfish (*Naso*), and rabbitfish (*Siganus*) are also recognized as important herbivores in the Indo-Pacific (Cheal et al., 2010; Rasher et al., 2013; Knudsen and Clements, 2016; Steneck et al., 2017), they are either absent (unicornfish and rabbitfish) in the Caribbean or not studied in the same intensity as other members of the Caribbean herbivore guild (chubs, see Mumby, 2006; Burkepile et al., 2013; Kramer et al., 2017; Suchley and Alvarez-Filip, 2017 as examples of *Kyphosus* not being considered). Indeed, research on herbivory in the Caribbean has been heavily focused on parrotfish while other taxa have received far less attention (Duran et al., 2019). This disregard of *Acanthurus* and *Kyphosus* is curious because these genera can be abundant in the Caribbean (each genus can form 25% of the herbivorous fish biomass on Caribbean coral reefs, Paddack et al., 2006; Hernández-Landa et al., 2015) and because they are recognized as important herbivores in the Indo-Pacific (for example see Clements and Choat, 1997; Green and Bellwood, 2009; Marshall and Mumby, 2015; Knudsen and Clements, 2016). One potential ramification of this focus is that browsing species (those that consume established macroalgae) may have been understudied and underappreciated in the Caribbean. With macroalgae now covering almost half of the reef, more attention should be paid to the species that consume these algae.

Herbivores are often assessed at the community or family level (for example, see Paddack et al., 2006; Suchley et al., 2016; Steneck et al., 2017), rather than emphasizing the role of individual species or taxa. When distinctions are made, herbivores are typically categorized as a “browser,” “scrape,” or “excavator” (scrapper and excavator both remove the epilithic algal matrix, EAM, from the reef; Bellwood and Choat, 1990; Bellwood et al., 2004; Adam et al., 2018). The drawbacks with this generalized approach are that critical species will not be identified and so could be overlooked in management strategies. Without a more detailed understanding of the impact individual species within the guild have on the reef, conservation and management efforts may be misguided. Indeed, recent work investigating herbivore feeding at the species level has found differences within genera that emphasize the species-specific nature of herbivores’ roles and effects (Longo et al., 2019). For example, Ruttenberg et al. (2019) found species identity a critical feature in estimating how much of the reef area is grazed: while *Scarus guacamaia* was responsible for a considerable proportion of areal grazing in the Florida Keys, *Scarus iserti* and *Scarus taeniopterus* had negligible impact in all reef habitats. Likewise, Duran et al. (2019) reported that congeners *Acanthurus tractus* and *Acanthurus coeruleus*, targeted significantly different proportions of food items. Similarly, in the Indo-Pacific, *Sargassum* was removed almost exclusively by *Naso unicornis* (Hoey and Bellwood, 2009) and the batfish (*Platax pinnatus*) was unexpectedly found to be a key herbivore on some reefs (Bellwood et al., 2006). Thus, greater resolution is required to understand herbivory more fully and to understand the impact each species, particularly the browsers, have on Caribbean reefs (Adam et al., 2015). Additionally, since macroalgal cover has increased on Caribbean reefs, we may currently be underappreciating the role browsers play in consuming these macroalgae and thereby promoting reef health and resilience.

Furthermore, Clements et al. (2017) intimated that many nominal herbivores are not targeting macroalgae and are in fact consuming other food sources including epilithic/endolithic cyanobacteria, microbes, and detritus. This would mean that the number of species actively targeting and consuming macroalgae is much smaller than appears from observation and that this role may be performed by fewer species than currently appreciated. Therefore, understanding which herbivorous fishes are targeting the dominant macroalgae in the Caribbean requires information on feeding behavior and food targets at the species level. Consequently, we closely observed the feeding of fish and made a distinction between bites taken from the surface of macroalgae and actual consumption of macroalgal tissue. In addition, we also cleaned two of the most prevalent macroalgae, *Dictyota* spp. and *Lobophora variegata*, of particulates and epibionts and presented them in feeding assays so that we could measure consumption of these algae without any confounding food items. We found that only three fish taxa consumed these dominant macroalgae and that many other nominal herbivores were actually feeding on epibionts on the macroalgal surface, rather than the macroalgae themselves.

MATERIALS AND METHODS

All experiments were conducted with permission from the Cayman Islands Department of Environment (permits awarded 21 May, 2016, 12 June and 23 August, 2017).

Site Description

Our experiments and observations were conducted at three sites in the fringing reef of the Cayman Islands, an island nation situated in the central Caribbean, ~240 km south of Cuba and ~220 km north-west of Jamaica (**Supplementary Figure S1**). The three Cayman Islands are surrounded by a narrow fringing foreereef that begins at about 8 m depth and extends for about 400 m to the wall at 25 to 30 m depth. Photographs of the benthos from May 2017 indicated that the foreereefs were representative of the Caribbean with coral cover between 9 and 12% and macroalgal cover between 40 and 53% across the three islands. *Dictyota* and *Lobophora* in particular dominate the benthos of the Cayman Islands and together comprise ~38% of the foreereef (**Supplementary Figure S2**). Observations of fish feeding were conducted over a 1.5 km stretch (~700 m wide) of continuous foreereef that was representative of local reefs, on the north side of Little Cayman at 15 m depth. Feeding assays were conducted at two foreereef sites at 8 m depth, one on the north side of Little Cayman and one on the north side of Grand Cayman (**Supplementary Figure S1**). These two sites were selected because they had the lowest macroalgal cover and so were appropriate sites to run feeding assays.

Observations of Fish Feeding

To quantify feeding behavior of common herbivorous fishes, in May 2017 three observers followed between nine and 12 adults across all sizes of the following taxa and phases: *Acanthurus coeruleus* (blue tang), *Acanthurus tractus* (ocean surgeonfish), *Scarus iserti* (striped parrotfish initial phase), *Scarus taeniopterus* (princess parrotfish initial phase), *Scarus vetula* (queen parrotfish initial phase), *Sparisoma aurofrenatum* (redband parrotfish initial phase and terminal phase), *Sparisoma viride* (stoplight parrotfish initial phase and terminal phase) and *Kyphosus* spp. (chub). Observations were conducted for 20 min per fish maintaining a distance of about 5 m so that our presence would not affect fish feeding behavior. We haphazardly selected each fish for observation and, before commencing data collection, followed the fish for three minutes so that it could become accustomed to our presence. After this time, we recorded depth, estimated fish standard length to the nearest whole centimeter, then counted the number of bites each fish took off the benthos and identified food items bitten (e.g., algae, sponge, coral, etc.). We focused particularly on consumption of macroalgae (>1 cm thallus length as per Steneck and Dethier, 1994), which we identified to the lowest taxonomic resolution possible in the field, versus the EAM growing on the reef substrate (EAM, the filamentous turf assemblage <1 cm as per Steneck and Dethier, 1994). No distinction was made between scraping and excavating functions in consumption of EAM. Several fish species were observed feeding off algae, gorgonians, and sponges, but on closer inspection no tissue had been removed and there was no evidence

of bite marks or damage/striations on the surface. So, these bites were recorded as bites of epibionts on the surface of these larger organisms. Thus, our dataset yielded three major food types: macroalgae, EAM, and epibionts. We did not count bites taken from food items floating in the water column.

To reduce the likelihood of resampling the same individual, upon completion of the first 20-min observation, we immediately switched from the first targeted fish to another of the same species in the immediate vicinity. We then moved to a new location ~700 m away to repeat this process and observe subsequent fish. All observations commenced after 1000 h and were concluded before 1,600 h. Observations of each species were conducted on the same day or on consecutive days within a 1.5 km stretch of continuous foreereef and all observations were concluded within 3 weeks.

Differences in proportion of bites taken between initial and terminal phase parrotfish were analyzed statistically by Pearson Chi Squared test of Homogeneity using SPSS version 22. Differences between species in bite rate and percent consumption of different food items were analyzed by Permutations ANOVA using the package “Imperm” (Wheeler, 2010) in the software R (R Core Team, 2019) because data were non-normal even after transformation.

Feeding Assays With Common Macroalgae

To determine which fish species grazed the most common macroalgae without the confounding presence of epibionts, we ran feeding assays in September 2017 with algal thalli that had been thoroughly cleaned of epibionts and we video the trials so that diver presence would not influence fish behavior. Furthermore, to assess as many different herbivore species as possible, the experiment was conducted at two different sites of equivalent depth but with different species of herbivorous fish present.

In order to acclimatize the fish to the experimental set up, feeding assay equipment was installed on the reef 2 weeks prior to collecting data. A mixture of the macroalgae found in the area were fixed in 50 cm long, three-strand ropes that were deployed on the reef and replaced daily. This was done to attract as many different species as possible to the ropes and so ensure that the resident fish community was familiar with and comfortable with the apparatus. The days prior to running the *Dictyota* and *Lobophora* assays, we trialed the experimental set-up with *Sargassum fluitans* and *Laurencia gemmifera* which are known to be palatable to herbivores (Littler and Littler, 2000). These assays acted as a control because they were visited by several fish species that did not appear in the *Dictyota* and *Lobophora* assays. As a result, we knew the feeding behavior of the fish in the subsequent feeding assays was due to algal species in the trial and not influenced by fear of unfamiliar equipment.

For the videoed feeding trials, *Dictyota* and *Lobophora* were collected in shallow areas (1–2 m depth) near the sites where the feeding assays were conducted. All algae were cleaned by shaking in seawater to remove particulates, then by brushing gently with a toothbrush to remove epibionts and picking off

any remaining with fine pointed tweezers. This was done in the lab using natural seawater and ensured that any bites would be of the macroalgae and not of associated flora or fauna. Pieces of *Dictyota* or *Lobophora* (1.5–2 g *Lobophora* or 4 g *Dictyota*) were fastened within the strands of the 50 cm long, three-strand feeding rope and a tripod-mounted GoPro (Hero 4, San Mateo, CA, United States) was secured ~0.5 m away so that the alga was within the frame the entire trial. Five such assays were installed a minimum of 5 m apart on the forereef at two sites 8 m deep and ran for 1 h between 0700 and 0800 and again between 1200 and 1300, although at site two only the midday trial was possible for *Dictyota*. This yielded $n = 10$ for *Dictyota* and *Lobophora* at site one, $n = 5$ for *Dictyota* at site two and $n = 9$ for *Lobophora* at site two because one camera failed. We sampled these two periods because food selectivity is reported to decrease over the course of the day and so sampling earlier and later in the day was expected to cover both high and low food selectivity (Khait et al., 2013). During each of these sessions a snorkeler recorded which fish species >5 cm in length were present in the area for the majority of the hour-long trial period, and also noted whether any large schools visited the area during the trial. The two algal species were run on separate days within the same week. The number of bites taken per hour by each fish species was then counted from each video and averaged across all videos from the day to give a mean number of bites per hour for each species at each site. Because our goal was to measure consumption of algae, bites that were spat out were not included in the count.

These assays provided information on which species consumed the macroalgae, but we then ran a subsequent, separate trial to calculate the wet weight in grams consumed per bite for each fish species. For this trial, a piece of either *Sargassum fluitans*, *Lobophora variegata*, or *Laurencia gemmifera* ~1 g in size was weighed to within 0.1 g and secured within the three strands of a rope. One snorkeler deposited the rope on the reef while the second snorkeler observed the rope continuously counting the bites taken of the alga and identifying the fish consumer to species. Once a fish had been able to bite the alga a few times, the first snorkeler immediately removed the rope so that only one fish species consumed the alga on each rope. The alga was then re-weighed and the difference in weight divided by the number of bites that had been observed from that rope. We used *Sargassum* in place of *Dictyota* because consumption of *Dictyota* was too low to obtain sufficient bites from only one fish species per trial. We were only able to obtain data for *A. coeruleus* using *Laurencia*, because the other fish always consumed *Sargassum* or *Lobophora* before *A. coeruleus* could.

In total, we obtained data for *A. coeruleus* from nine pieces of *Laurencia*, for *Kyphosus* spp. from 10 pieces of *Lobophora* and 10 of *Sargassum*, and for *S. aurofrenatum* from 13 pieces of *Sargassum* and 11 of *Lobophora*. We then calculated an average weight (g) of algae removed per bite for each fish species and multiplied this by the number of bites counted in each video to calculate the grams consumed by each fish species on each algal species. Data were highly non-normal and could not be successfully transformed, so analysis of differences in grams consumed by fish species was performed in SPSS version 22

using the Kruskal–Wallis test for site one and Mann Whitney-*U* test for site two.

Fish Density Surveys at Feeding Assay Sites

To quantify the abundance and diversity of the fish community in the vicinity of the feeding assays, we conducted visual transect surveys immediately following the final feeding assay and recorded the species of each fish >5 cm in length both on the reef and in the water column above. Each transect was 2 m wide, 23 to 30 m in length and were a minimum of 4 m apart ($n = 3$ at site one, $n = 4$ at site two). These surveys provided average species density per 100 m².

To compare with regional reports of fish density (and benthic cover) we accessed the Atlantic and Gulf Rapid Reef Assessment (AGRRA) database 20180310 and averaged the values reported for forereefs for each ecoregion. This yielded results for parrotfish, surgeonfish, and chub families (as well as scaled percent macroalgal cover, scaled percent turf cover and scaled percent live coral cover) from the Bahamian, Eastern Caribbean, Greater Antilles, Southwestern Caribbean and Western Caribbean ecoregions.

Consumption of *Dictyota* and *Lobophora* by the Herbivore Community per 100 m²

To estimate the quantity of *Dictyota* and *Lobophora* consumed by the herbivore community, we integrated data from our observational fish follows, feeding assays, and fish density surveys. For each of the three species (*A. coeruleus*, *Kyphosus* spp., and *S. aurofrenatum*) that commonly fed on *Dictyota* and *Lobophora*, we multiplied the bites taken per hour of each alga from our observations by the mass of alga removed per bite as determined from our assays. We then scaled this consumption per hour by the density estimates from our transect surveys at sites one and two. This calculation allowed us to estimate the quantity of algae removed by each herbivore species per hour per 100 m² of reef.

RESULTS

Observations of Fish Feeding

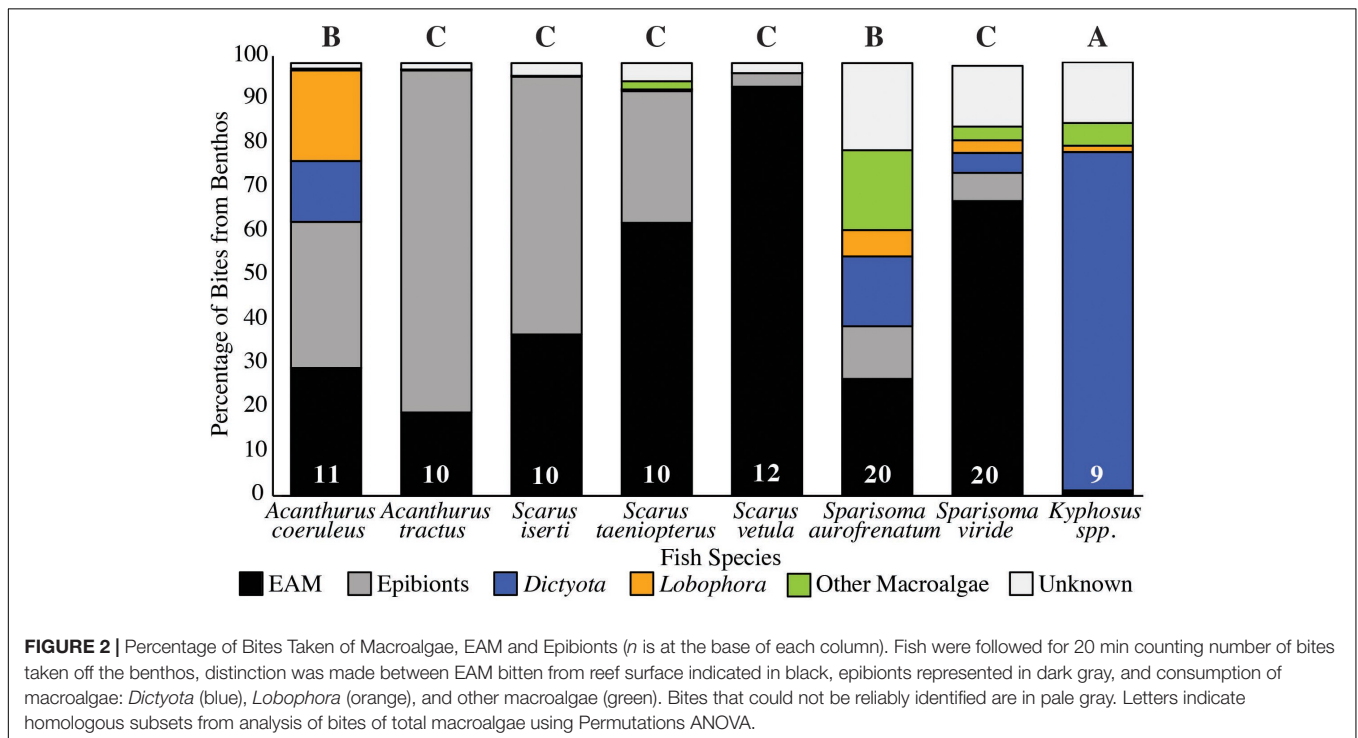
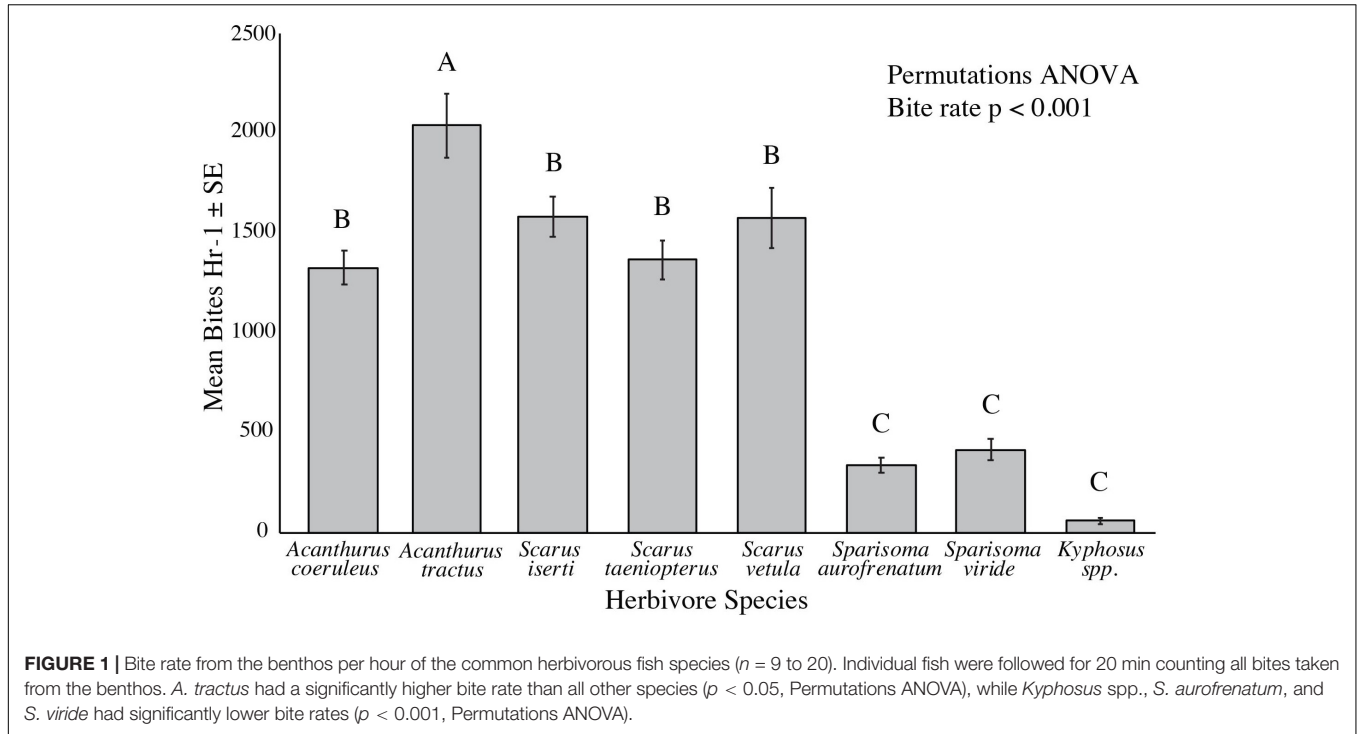
In total, we conducted over 34 h of observation of 105 fish from eight species counting the bites from the benthos. All individuals we observed fed from the benthos during these observations except for three *Kyphosus* spp. which remained in the water column during the observation period. There were no significant differences in proportions of bites between phases for either *S. aurofrenatum* or *S. viride* ($p = 0.672$; $p = 0.100$, respectively; Pearson Chi Square test for Homogeneity) so these were combined for subsequent analyses giving $n = 20$ for these two species.

Mean bite rate from the benthos varied significantly among species, ranging from 80 per hour for *Kyphosus* spp. to 2,036 per hour for *A. tractus* ($p < 0.001$, Permutations ANOVA). *Kyphosus* spp., *S. aurofrenatum*, and *S. viride* had significantly lower bite

rates than all other species we observed ($p < 0.001$, Permutations ANOVA, **Figure 1**), while *A. tractus* took significantly more bites from the benthos per hour than all other species ($p < 0.05$, Permutations ANOVA, **Figure 1**).

For each species we divided the proportion of these bites from the benthos into bites of *Dictyota*, *Lobophora*, other macroalgae,

bites of EAM off the reef substrate and bites of epibionts on other substrates (sand, sponge, gorgonian, and macroalgae; **Figure 2**). *Kyphosus* spp. consumed a significantly higher proportion of total macroalgae (85%, $p < 0.001$, Permutations ANOVA; **Figure 2**), followed by *A. coeruleus* and *S. aurofrenatum* (35 and 41%, respectively, $p < 0.001$, Permutations ANOVA; **Figure 2**) than all



other species we observed. For the other species, macroalgae was less than 11% of the bites consumed ($p < 0.001$, Permutations ANOVA; **Figure 2**).

Of this macroalgae, *Kyphosus* spp. consumed the most *Dictyota* (78% of total bites from the benthos, $p < 0.001$, Permutations ANOVA; **Figure 2**), followed by *A. coeruleus* and *S. aurofrenatum* (14 and 16% of the total bites of the benthos, respectively, $p < 0.01$, Permutations ANOVA; **Figure 2**). *A. coeruleus* consumed significantly more *Lobophora* than any other species (21% of total bites of the benthos, $p < 0.001$, Permutations ANOVA; **Figure 2**), while *Lobophora* constituted less than 6% of the bites for the other species. Other macroalgae (predominantly *Halimeda* but occasionally also *Sargassum*) comprised 18% of the bites for *S. aurofrenatum*, significantly more than all other species ($p < 0.001$, Permutations ANOVA). Other macroalgae were less than 5% of the bites of other species (**Figure 2**).

Epilithic algal matrix formed a noticeable proportion of the bites of all species except for *Kyphosus* spp. (1% of total bites). Of the remaining species, bites of EAM ranged from 19% of total bites for *A. tractus* up to 94% for *S. vetula* (which consumed significantly more EAM than any other species, $p < 0.001$, Permutations ANOVA; **Figure 2**). *A. tractus* and *S. iserti* were the only two species whose feeding was primarily of epibionts: *A. tractus* consumed significantly more than all other species (79%, $p < 0.01$, Permutations ANOVA; **Figure 2**), followed by *S. iserti* (59%, $p < 0.01$, Permutations ANOVA; **Figure 2**).

In all these observations only one individual (*S. viride* initial phase) out of the 105 we followed was observed taking bites of a sponge (one event of four bites which was 3% of the total bites observed), so this food item is omitted from further analyses. All parrotfishes were observed occasionally consuming coral, however, at most this food item constituted <1% of the total bites (*S. viride* initial phase) so is also excluded from further analysis.

Feeding Assays

In total, we ran 34 h-long trials using *Dictyota* ($n = 15$) and *Lobophora* ($n = 19$) across two sites and two feeding periods (morning and midday) from which only three fish taxa were observed feeding from the ropes with any regularity: *A. coeruleus*, *Kyphosus* spp., and *S. aurofrenatum* (**Figure 3**). This pattern was despite seven to 10 herbivore species being present during the trials, including *A. tractus*, *S. iserti*, *S. taeniopterus*, *S. vetula*, and *S. viride* at both sites. Moreover, our trials with *S. fluitans* and *L. gemmifera* were also consumed by *Melichthys niger* (black surgeon), *Scarus iserti* (striped parrotfish), *Sparisoma rubripinne* (yellowtail parrotfish), and *Sparisoma viride* (stoplight parrotfish, in addition to *A. coeruleus*, *Kyphosus* spp., and *S. aurofrenatum*), indicating that the experimental set-up did not deter these other species from feeding.

To estimate the quantity of algae consumed by each species we calculated the grams consumed per bite for the three main consumers (from our second set of feeding assays; **Figure 4**). For *A. coeruleus*, we determined a mean of 0.02 g per bite from

Laurencia ($n = 9$). *Kyphosus* spp. consumed a mean of 0.16 and 0.18 g per bite of *Sargassum* and *Lobophora*, respectively ($n = 10$), and *S. aurofrenatum* consumed a mean of 0.09 and 0.03 g per bite of *Sargassum* ($n = 13$) and *Lobophora* ($n = 11$), respectively.

After multiplying the mean weight (g) of algae removed per bite (**Figure 4**) by the number of bites counted in each video (**Figure 3**, upper two panels), we found no significant differences in grams consumed by the three main herbivore species at either site (Site One *Dictyota*: $n = 10$, $p = 0.553$, Kruskal–Wallis; Site One *Lobophora*: $n = 10$, $p = 0.111$, Kruskal–Wallis; Site Two *Dictyota*: $n = 5$, $p = 0.095$, Mann–Whitney *U*; Site Two *Lobophora*: $n = 9$, $p = 0.546$, Mann–Whitney *U*; **Figure 3**, middle two panels).

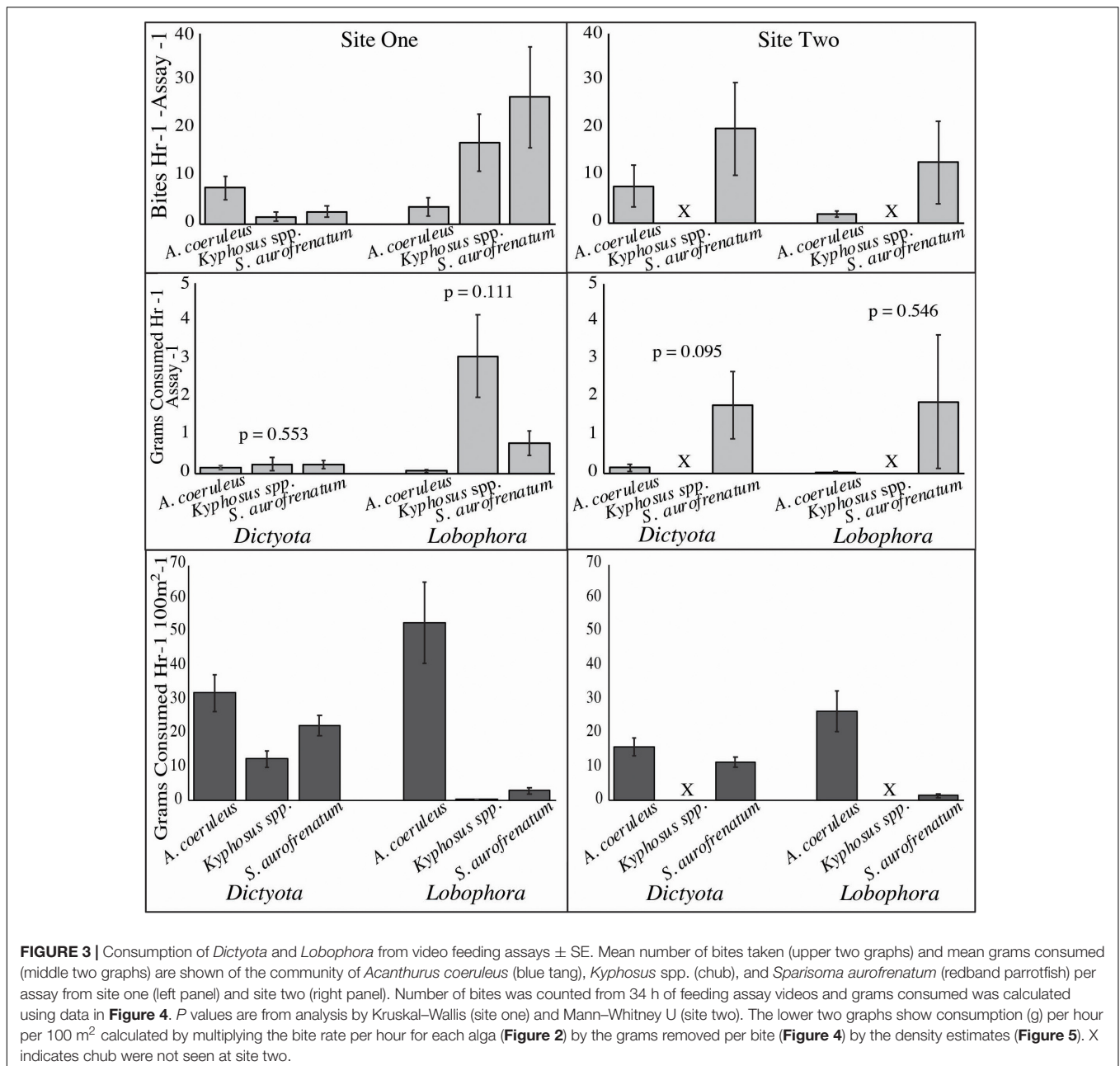
Herbivorous Fish Density at Feeding Assay Sites

Density of herbivorous fishes at site one was 36.2/100 m² and at site two was 24.6/100 m².

Acanthurus coeruleus, *Acanthurus tractus*, *Scarus iserti*, *Scarus taeniopterus*, *Scarus vetula*, *Sparisoma aurofrenatum*, and *Sparisoma viride* were recorded at both sites and *S. iserti* and *A. coeruleus* had the highest densities at both sites (*S. iserti* was 9.6/100 m² and 8.3/100 m² at sites one and two, respectively; *A. coeruleus* was 9.2/100 m² and 4.6/100 m² at sites one and two, respectively; **Figure 5**). On the contrary, *Kyphosus* spp. was only seen at site one (1.4/100 m²), while *Scarus guacamaia* (rainbow parrotfish) and *Sparisoma rubripinne* (yellowtail parrotfish) were only recorded at site two (0.4/100 m² and 1.25/100 m², respectively; **Figure 5**). Density of *S. aurofrenatum* was 4.9/100 m² and 2.5/100 m² at sites one and two, respectively. Densities of these families are in keeping with regional values: we recorded 21.2/100 m², 7.9/100 m², and 0.6/100 m² for parrotfish, surgeonfish and chub respectively, while densities from AGRRA (2018) were 24.3/100 m², 11.9/100 m², and 0.6/100 m² for parrotfish, surgeonfish, and chub, respectively. No *Acanthurus chirurgus* (doctorfish) were seen at either site and no anomalous large schools of herbivorous fish visited the feedings ropes during any trial.

Consumption of *Dictyota* and *Lobophora* by the Herbivore Community per 100 m²

Consumption of *Dictyota* and *Lobophora* from our observations was scaled to consumption per hour per 100 m² by multiplying the bite rate per hour for each alga (**Figure 2**) by the grams removed per bite (**Figure 4**) by the density estimates from site one and site two (**Figure 5**). At site one this gave 32.1, 12.4, and 22.5 g/h/100m² of *Dictyota* consumed by *A. coeruleus*, *Kyphosus* spp. and *S. aurofrenatum*, respectively, and 52.8, 0.3g/h/100m², and 3.0 g/h/100 m² of *Lobophora* consumed by *A. coeruleus*, *Kyphosus* spp. and *S. aurofrenatum*, respectively (**Figure 3**, lower two graphs). At site two this gave 16.0 and 11.5 g/h/100 m² of *Dictyota* consumed by *A. coeruleus* and *S. aurofrenatum*, respectively, and 26.4 and 1.5 g/h/100 m² of *Lobophora* consumed by *A. coeruleus* and *S. aurofrenatum*, respectively (**Figure 3**, lower two graphs). No *Kyphosus* spp. were seen at site two.



DISCUSSION

Modern Caribbean reefs are covered by \sim 40% macroalgae (AGRRA, 2018), often *Dictyota* and *Lobophora* (Diaz-Pulido et al., 2011; Suchley and Alvarez-Filip, 2017), yet in our study only three fish taxa consume these macroalgae as a substantial proportion of their feeding: *Acanthurus coeruleus* (blue tang surgeonfish), *Kyphosus* spp. (chub), and *Sparisoma aurofrenatum* (redband parrotfish; **Figures 2, 3**). As macroalgal cover has increased on Caribbean reefs it is important to determine which are the browsers that can control it.

We found our observations of fish feeding agreed with our results from the feeding assays. The three taxa we observed

feeding most frequently on macroalgae during our observations (*A. coeruleus*, *Kyphosus* spp., and *S. aurofrenatum*) were also the most frequent visitors to our ropes (**Figures 2, 3**). Similarly, those species which fed predominantly on EAM or epibionts (the other six species we followed) were never seen eating *Dictyota* or *Lobophora* from the ropes. However, there is a discrepancy in observations of *Kyphosus* spp. between our two experiments. *Kyphosus* that were present at site one were frequent visitors to the *Lobophora* assay and took 17 bites per hour of this alga. Conversely, of the individuals we followed on the reef only 1% of their bites were of *Lobophora* (less than one bite per hour). This discrepancy may be because *Lobophora* growing on the reef was often found in more cryptic habitats than when it was presented

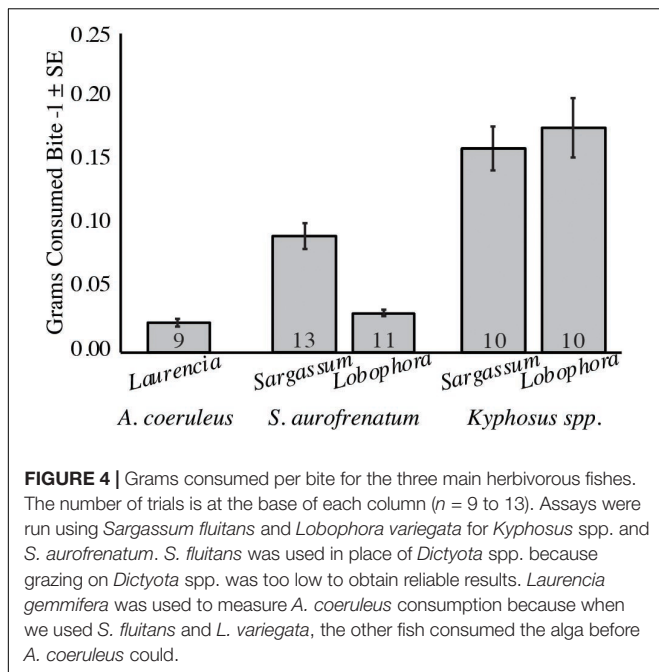


FIGURE 4 | Grams consumed per bite for the three main herbivorous fishes. The number of trials is at the base of each column ($n = 9$ to 13). Assays were run using *Sargassum fluitans* and *Lobophora variegata* for *Kyphosus* spp. and *S. aurofrenatum*. *S. fluitans* was used in place of *Dictyota* spp. because grazing on *Dictyota* spp. was too low to obtain reliable results. *Laurencia gemmifera* was used to measure *A. coeruleus* consumption because when we used *S. fluitans* and *L. variegata*, the other fish consumed the algae before *A. coeruleus* could.

in the feeding ropes. The relatively large *Kyphosus* (adult length ~30 to 75 cm; Humann and DeLoach, 2002) may not have been able to access naturally occurring *Lobophora* as easily as the smaller and more agile *A. coeruleus* and *S. aurofrenatum* (~13 to 25 cm and ~15 to 30 cm, respectively; Humann and DeLoach, 2002) and so, the feeding assay could have made *Lobophora* more accessible to the chub than under natural conditions. It follows then that removal of *Lobophora* from the reef by *Kyphosus* spp. is likely to be closer to the values from our observations

than from the feeding assays. However, during outbreaks or after dislodgement of *Lobophora* by storms, *Kyphosus* spp. may be one of the key consumers. The assay probably would not have affected access to the more conspicuous, upright *Dictyota*. Consumption of *Dictyota* and *Lobophora* from our feeding assays was lower than that calculated from our observations. This discrepancy may be due to difference in experimental design and the less “natural” presentation of algae in the feeding assays, or may suggest that epibionts encourage feeding. However, this needs to be investigated further.

Regardless, both experiments highlight the taxa that are “browsers” and consume established macroalgae as a substantial component of their diet at our sites. While this finding is limited to these sites in the boreal summer, it is important to note that the browsing function is performed by relatively few taxa. Since the browsers are the subset of herbivores that are more likely to reverse macroalgal dominance, their importance on the reef is growing as macroalgal cover rises on reefs (Cheal et al., 2010). It should be determined whether this critical browsing function is performed by other species elsewhere in the region so that herbivory can be more thoroughly understood and effective management strategies can be implemented.

Our findings in this study agree with Dromard et al. (2015) who used stable isotope and stomach content analyses to show that *A. coeruleus* consumed a mixture of macroalgae, turf, and invertebrates. Similarly, they also found the proportions of food items in the *S. aurofrenatum* diet were more similar to the Acanthurids than other parrotfishes, which is very much in keeping with our results. Interestingly, they found a higher contribution of macroalgae than we did in the diets of all herbivore species. However, they suggest this could be from consumption of macroalgal propagules growing within the EAM which we could not have detected from our observations. Also

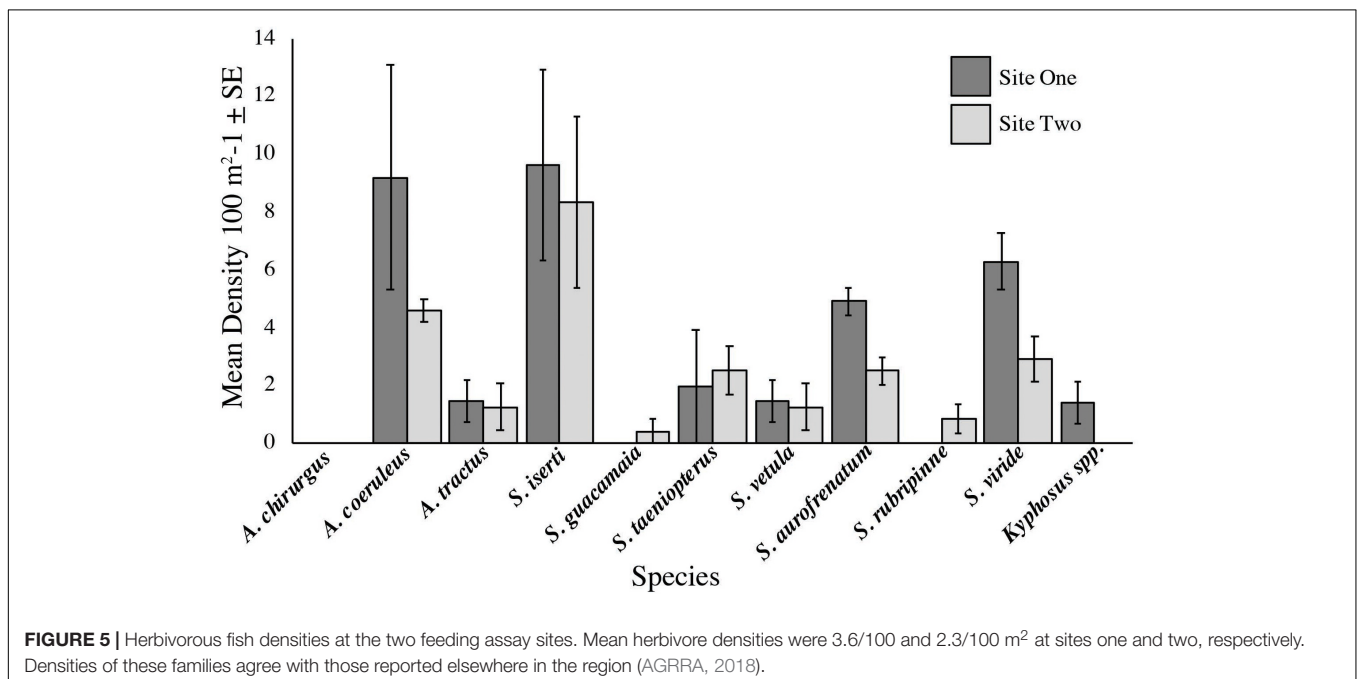


FIGURE 5 | Herbivorous fish densities at the two feeding assay sites. Mean herbivore densities were 3.6/100 and 2.3/100 m² at sites one and two, respectively. Densities of these families agree with those reported elsewhere in the region (AGRRA, 2018).

similar to our findings, Adam et al. (2018) and Ruttenberg et al. (2019) reported that all parrotfishes in their studies fed on EAM, but only *S. aurofrenatum*, *S. chrysopterum*, and *S. rubripinne* consumed macroalgae regularly. *S. chrysopterum* was absent from our study reefs and *S. rubripinne* was only seen at site two where we ran the feeding assays. However, this species did not feed from our *Dictyota* or *Lobophora* assays, perhaps because it was an infrequent visitor to the site and was not present in all our trials. Thus, the evidence from multiple sources indicates that *S. aurofrenatum* and *A. coeruleus* are key browsers in the Caribbean. It is worth noting that estimates of *Dictyota* consumption from our observations suggest an individual *A. coeruleus* could consume almost as much as one *S. aurofrenatum* per day, assuming they both feed from 0600 to 1600 h (44 g versus 50 g for *A. coeruleus* and *S. aurofrenatum*, respectively) although if this were scaled by density, *A. coeruleus* as a species could consume far more macroalgae at our sites. Thus, it appears that both *S. aurofrenatum* and *A. coeruleus* should be considered key browsers (Duran et al., 2019).

Contrary to our results, however, Cardoso et al. (2009) reported a high proportion of bites taken of macroalgae for the seven Caribbean species of parrotfish they observed. However, they made no distinction between bites taken of epibionts off the surface of macroalgae and actual removal of macroalgal tissue. This is a critical distinction to make because species such as *A. tractus* and *S. iserti* were observed feeding from the surface of macroalgae, but never once fed off *Dictyota* or *Lobophora* after they had been cleaned of epibionts in our assays. It is possible that the diet of these species varies across the region since Burkepile and Hay (2008) also found that *A. tractus* significantly reduced macroalgae in their experiments, including both *Dictyota* and *Lobophora*. Further, feeding assay results may also vary with factors that affect herbivore consumption (see below). It is also possible that a higher epibiont load on macroalgae in some locations allows some species to meet dietary requirements without consuming macroalgae itself. However, our results support those of Clements et al. (2017) who proposed that many nominal herbivores are not targeting macroalgae but instead consume other food items such as detritus, epilithic cyanobacteria, microalgae, or diatoms.

While parrotfish have received most attention in the literature, and surgeonfish to a lesser extent (Duran et al., 2019), the Kyphosidae are not consistently considered part of the herbivore guild in the Caribbean (for example, see Mumby, 2006; Burkepile et al., 2013; Kramer et al., 2017; Suchley and Alvarez-Filip, 2017 as examples of studies omitting Kyphosidae). Here we found that it was one of the top three consumers of macroalgae at one feeding assay site and that macroalgae formed a significantly higher proportion of its diet than any of the more familiar herbivores (Figures 2, 3). From our observations, an individual *Kyphosus* spp. can consume ~100 g of *Dictyota* per day (assuming they feed from 0600 to 1600 h), which is significantly more than all other herbivores in our study. (From our observations, in this time period *A. coeruleus* and *S. aurofrenatum* would consume 44 and 50 g of *Dictyota*, respectively). It should be noted that these calculations are “back-of-the-envelope” estimates from our observations. Consumption on different reefs will likely

vary from these values because consumption of algae by fishes is influenced by many factors including benthic community composition (Cvitanovic and Hoey, 2010), associational defenses (Littler et al., 1986), presence of epiphytes (Fong et al., 2006), season (Paddock et al., 2006) and reef structural complexity (Verges et al., 2011) among others. (The other “nominal herbivores” on these reefs consumed primarily either epibionts or EAM; Figure 2).

It should not be surprising that a species of *Kyphosus* was a frequent consumer of brown macroalgae. In 1967, Randall (1967) reported that the stomach contents of two species in the Caribbean were 100% brown macroalgae and 99.5% brown and red macroalgae ($n = 6$ and 19 , respectively). Further, the family Kyphosidae have long been recognized as important browsers in the Indo-Pacific (Clements and Choat, 1997; Green and Bellwood, 2009; Knudsen and Clements, 2016). This omission may be because traditional survey protocols miss many *Kyphosus* because of their distribution and behavior. At least on Cayman reefs we see solitary individuals in the shallows (5 to 8 m depth) and large schools of *Kyphosus* off the drop-off around 25 to 30 m depth. However, the AGRRA protocol for example stipulates fish transects be conducted between 1–5 m and 8–15 m (version 2.2). Similarly, survey protocols specify transects be conducted over the middle of the day (between 1000 and 1400 h in the AGRRA protocol version 2.2). The genus *Kyphosus* is known to use specific reef areas at specific times of day (Eristhee and Oxenford, 2001) so could often be missed in surveys that only occur in the middle of the day. Consequently, as “roving herbivores” they may be difficult to quantify during fish surveys with commonly used methods, but could still significantly impact algal communities. Thus, measurements of *Kyphosus* densities may be artificially low and hence their impact may have been underappreciated. While visual transect surveys may provide a reasonable estimation of species that exhibit site fidelity, we suspect that the number of *Kyphosus* impacting our sites is underestimated. Additionally, bite rates are not always proportional to abundance (Longo et al., 2014). For these reasons we advise caution when interpreting our estimates of consumption per 100 m². However, these calculations suggest that *A. coeruleus* may be the most important browser at this location, followed by *S. aurofrenatum* and *Kyphosus* spp. We anticipate this result will vary across the Caribbean, given that presence and density of *Kyphosus* and other herbivores are highly variable across the region (Floeter et al., 2005; Ruttenberg et al., 2019).

The *Kyphosus* individuals we followed appeared to have divergent feeding strategies. Six of the 12 chub we followed took less than 12 bites/hour from the benthos (average 3 bites/hour) and stayed higher in the water column throughout the 20-min observation period. In contrast, the other six individuals took an average of 107 bites/hour from the benthos. This dichotomy in feeding may be an artifact of the relatively short duration of observation, however, it could also be because these were a different species of *Kyphosus*. There are four species of *Kyphosus* in the western Atlantic (*Kyphosus bigibbus*, *K. cinerascens*, *K. sectatrix*, and *K. vaigiensis*; Knudsen and Clements, 2016), some of which can be very difficult to

distinguish (Humann and DeLoach, 2002). So, it is possible that more than one species featured in our observations. Further research will be necessary to determine the identity of *Kyphosus* on these reefs and if their feeding behavior differs.

Traditionally, herbivores have been assigned to one of three functional groups: the “browsers,” “scrapers,” and “excavators” (Bellwood and Choat, 1990; Bellwood et al., 2004; Adam et al., 2018). Historically, parrotfish may have been key herbivores in the Caribbean because they remove turf and macroalgal propagules off the reef surface by scraping or excavating and this is critical in preventing a shift to macroalgal dominance (Mumby, 2006; Suchley and Alvarez-Filip, 2017). However, in many places macroalgae are now established as the dominant benthic community: indeed in 2018, macroalgae were 40% of Caribbean forereefs, whereas turf was only 15% (AGRRA, 2018). Since many parrotfish do not consume established macroalgae, parrotfish alone are unlikely to reverse a phase shift once it is proceeding (Cheal et al., 2010; Rasher et al., 2013). Thus, while herbivory is still a key process, we contend that the “browsers” rather than the “scrapers” are of increasing importance on modern reefs. From our observations and experiments, we found that the taxa responsible for consuming established macroalgae are *Acanthurus coeruleus* (blue tang), *Sparisoma aurofrenatum* (redband parrotfish), and *Kyphosus* spp. (chub). But, since species composition varies with habitat, it is likely that other species are performing this role on other reefs (Floeter et al., 2005; Ruttenberg et al., 2019). Hence, it will be imperative to determine which are the key browsers elsewhere in the region so that they can be monitored and protected. Governments around the region have implemented bans on fishing parrotfish and some countries, such as Belize, have also banned fishing of surgeonfish (Kramer et al., 2017). However, we encourage region-wide protection of all browsers. At a time when reefs around the world are undergoing rapid change and are at severe risk (Heron et al., 2017), it is vital to reevaluate the role species perform in the system and protect those that are key to promoting ecosystem health.

DATA AVAILABILITY STATEMENT

The datasets generated in this study can be found in Zenodo: <http://doi.org/10.5281/zenodo.3762238>.

REFERENCES

- Adam, T. C., Duran, A., Fuchs, C. E., Roycroft, M. V., Rojas, M. C., Ruttenberg, B. I., et al. (2018). Comparative analysis of foraging behavior and bite mechanics reveals complex functional diversity among Caribbean parrotfishes. *Mar. Ecol. Progr. Ser.* 597, 207–220. doi: 10.3354/meps12600
- Adam, T. C., Kelley, M., Ruttenberg, B. I., and Burkepile, D. E. (2015). Resource partitioning along multiple niche axes drives functional diversity in parrotfishes on Caribbean coral reefs. *Oecologia* 179, 1173–1185. doi: 10.1007/s00442-015-3406-3
- AGRRA (2018). *Atlantic and Gulf Rapid Reef Assessment (AGRRA): An Online Database of AGRRA coral reef survey data*. Available: <http://agrra.org>. (accessed March 10, 2018).

ETHICS STATEMENT

The animal study was reviewed and approved by the Cayman Islands Department of Environment.

AUTHOR CONTRIBUTIONS

CD and CM conceived of the study and designed the experiments. CD conducted all field work. CD, GL, and DB formed the concept of the manuscript. CD and GL performed the statistical analyses. CD took lead writing the manuscript with input from all authors and under the supervision of CM and DB. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2020.00676/full#supplementary-material>

- Bellwood, D. R., and Choat, J. H. (1990). A functional analysis of grazing in parrotfishes (family Scaridae): The ecological implications. *Environ. Biol. Fish.* 28, 189–214. doi: 10.1007/978-94-009-2065-1_11
- Bellwood, D. R., Hughes, T. P., Folke, C., and Nyström, M. (2004). Confronting the coral reef crisis. *Nature* 429, 827–833. doi: 10.1038/nature02691
- Bellwood, D. R., Hughes, T. P., and Hoey, A. S. (2006). Sleeping functional group drives coral-reef recovery. *Curr. Biol.* 16, 2434–2439. doi: 10.1016/j.cub.2006.10.030
- Birrell, C. L., McCook, L. J., Willis, B. L., and Diaz-Pulido, G. A. (2008). “Effects of benthic algae on the replenishment of corals and the implications for the resilience of coral reefs,” in *Oceanography and Marine Biology*, eds S. J. Hawkins, A. L. Allcock, A. E. Bates, L. B. Firth, I. P. Smith, S. E. Swearer, and P. A. Todd (Boca Raton, FL: CRC Press), 31–70.

- Box, S. J., and Mumby, P. J. (2007). Effect of macroalgal competition on growth and survival of juvenile Caribbean corals. *Mar. Ecol. Progr. Ser.* 342, 139–149. doi: 10.3354/meps342139
- Burkepile, D. E., Allgeier, J. E., Shantz, A. A., Pritchard, C. E., Lemoine, N. P., Bhatti, L. H., et al. (2013). Nutrient supply from fishes facilitates macroalgae and suppresses corals in a Caribbean coral reef ecosystem. *Sci. Rep.* 3:1493.
- Burkepile, D. E., and Hay, M. E. (2008). Herbivore species richness and feeding complementarity affect community structure and function on a coral reef. *Proc. Natl. Acad. Sci.* 105, 16201–16206. doi: 10.1073/pnas.0801946105
- Cardoso, S. C., Soares, M. C., Oxenford, H. A., and Côté, I. M. (2009). Interspecific differences in foraging behaviour and functional role of Caribbean parrotfish. *Mar. Biodivers. Rec.* 2:e148.
- Cheal, A. J., MacNeil, M. A., Cripps, E., Emslie, M. J., Jonker, M., Schaffelke, B., et al. (2010). Coral–macroalgal phase shifts or reef resilience: links with diversity and functional roles of herbivorous fishes on the Great Barrier Reef. *Coral Reefs* 29, 1005–1015. doi: 10.1007/s00338-010-0661-y
- Clements, K. D., and Choat, J. H. (1997). Comparison of herbivory in the closely-related marine fish genera *Girella* and *Kyphosus*. *Mar. Biol.* 127, 579–586. doi: 10.1007/s002270050048
- Clements, K. D., German, D. P., Piché, J., Tribollet, A., and Choat, J. H. (2017). Integrating ecological roles and trophic diversification on coral reefs: multiple lines of evidence identify parrotfishes as microphages. *Biol. J. Linnean Soc.* 120, 729–751.
- Cvitanovic, C., and Hoey, A. S. (2010). Benthic community composition influences within-habitat variation in macroalgal browsing on the Great Barrier Reef. *Mar. Freshw. Res.* 61, 999–1005.
- Diaz-Pulido, G., Gouezo, M., Tilbrook, B., Dove, S., and Anthony, K. R. (2011). High CO₂ enhances the competitive strength of seaweeds over corals. *Ecol. Lett.* 14, 156–162. doi: 10.1111/j.1461-0248.2010.01565.x
- Dromard, C. R., Bouchon-Navaro, Y., Harmelin-Vivien, M., and Bouchon, C. (2015). Diversity of trophic niches among herbivorous fishes on a Caribbean reef (Guadeloupe, Lesser Antilles), evidenced by stable isotope and gut content analyses. *J. Sea Res.* 95, 124–131. doi: 10.1016/j.seares.2014.07.014
- Duran, A., Adam, T. C., Palma, L., Moreno, S., Collado-Vides, L., and Burkepile, D. E. (2019). Feeding behavior in Caribbean surgeonfishes varies across fish size, algal abundance, and habitat characteristics. *Mar. Ecol.* 40:e12561.
- Eristhee, N., and Oxenford, H. A. (2001). Home range size and use of space by Bermuda chub *Kyphosus sectatrix* (L.) in two marine reserves in the Soufriere Marine Management Area, St Lucia, West Indies. *J. Fish Biol.* 59, 129–151. doi: 10.1111/j.1095-8649.2001.tb01383.x
- Floeter, S. R., Behrens, M. D., Ferreira, C. E. L., Paddock, M. J., and Horn, M. H. (2005). Geographical gradients of marine herbivorous fishes: patterns and processes. *Mar. Biol.* 147, 1435–1447. doi: 10.1007/s00227-005-0027-0
- Fong, P., Smith, T. B., and Wartian, M. J. (2006). Epiphytic cyanobacteria maintain shifts to macroalgal dominance on coral reefs following ENSO disturbance. *Ecology* 87, 1162–1168. doi: 10.1890/0012-9658(2006)87[1162:ecmstm]2.0.co;2
- Gardner, T. A., Côté, I. M., Gill, J. A., Grant, A., and Watkinson, A. R. (2003). Long-term region-wide declines in Caribbean corals. *Science* 301, 958–960. doi: 10.1126/science.1086050
- Green, A. L., and Bellwood, D. R. (2009). “Monitoring functional groups of herbivorous reef fishes as indicators of coral reef resilience – A practical guide for coral reef managers in the Asia Pacific region,” in *IUCN working group on Climate Change and Coral Reefs* (Gland: IUCN), 70.
- Hernández-Landa, R. C., Acosta-González, G., Núñez-Lara, E., and Arias-González, J. E. (2015). Spatial distribution of surgeonfish and parrotfish in the north sector of the Mesoamerican Barrier Reef System. *Mar. Ecol.* 36, 432–446. doi: 10.1111/maec.12152
- Heron, S. F., Eakin, C. M., Douvère, F., Anderson, K. L., Day, J. C., Geiger, E., et al. (2017). *Impacts of climate change on World Heritage Coral Reefs: A First Global Scientific Assessment*. Paris: UNESCO.
- Hoey, A. S., and Bellwood, D. R. (2009). Limited functional redundancy in a high diversity system: single species dominates key ecological process on coral reefs. *Ecosystems* 12, 1316–1328. doi: 10.1007/s10021-009-9291-z
- Humann, P., and DeLoach, N. (2002). *Reef fish identification, Florida Caribbean Bahamas*, 3rd Edn. Florida: New World Publications Inc.
- Jackson, J. B. C., Donovan, M. K., Cramer, K. L., and Lam, V. V. (eds) (2014). *Status and Trends of Caribbean Coral Reefs: 1970-2012*. Gland: Global Coral Reef Monitoring Network, IUCN.
- Khait, R., Obolski, U., Hadany, L., and Genin, A. (2013). Food selectivity and diet switch can explain the slow feeding of herbivorous coral-reef fishes during the morning. *PLoS One* 8:e82391. doi: 10.1371/journal.pone.0082391
- Knudsen, S. W., and Clements, K. D. (2016). World-wide species distributions in the family Kyphosidae (Teleostei: Perciformes). *Mol. Phylogenet. Evol.* 101, 252–266. doi: 10.1016/j.ympev.2016.04.037
- Kramer, P., McField, M., Drysdale, I., Rueda, M., GirÅ, A., and Pott, R. (2017). *2015 Report card for the Mesoamerican reef*. Washington, DC: The Summit Foundation.
- Kuffner, I. B., Walters, L. J., Becerro, M. A., Paul, V. J., Ritson-Williams, R., and Beach, K. S. (2006). Inhibition of coral recruitment by macroalgae and cyanobacteria. *Mar. Ecol. Progr. Series* 323, 107–117. doi: 10.3354/meps323107
- Lessios, H. A. (1988). Mass mortality of *Diadema antillarum* in the Caribbean: what have we learned? *Ann. Rev. Ecol. Syst.* 19, 371–393. doi: 10.1146/annurev.es.19.110188.002103
- Lessios, H. A. (2005). *Diadema antillarum* populations in Panama twenty years following mass mortality. *Coral Reefs* 24, 125–127. doi: 10.1007/s00338-004-0443-5
- Littler, D. S., and Littler, M. M. (2000). *Caribbean Reef Plants*. Washington, DC: OffShore Graphics.
- Littler, M. M., Taylor, P. R., and Littler, D. S. (1986). Plant defense associations in the marine environment. *Coral Reefs* 5, 63–71. doi: 10.1007/bf00270354
- Longo, G. O., Ferreira, C. E. L., and Floeter, S. R. (2014). Herbivory drives large-scale spatial variation in reef fish trophic interactions. *Ecol. Evol.* 4, 4553–4566. doi: 10.1002/ece3.1310
- Longo, G. O., Hay, M. E., Ferreira, C. E., and Floeter, S. R. (2019). Trophic interactions across 61 degrees of latitude in the Western Atlantic. *Glob. Ecol. Biogeogr.* 28, 107–117. doi: 10.1111/geb.12806
- Marshall, A., and Mumby, P. J. (2015). The role of surgeonfish (Acanthuridae) in maintaining algal turf biomass on coral reefs. *J. Exp. Mar. Biol. Ecol.* 473, 152–160. doi: 10.1016/j.jembe.2015.09.002
- McCook, L., Jompa, J., and Diaz-Pulido, G. (2001). Competition between corals and algae on coral reefs: a review of evidence and mechanisms. *Coral Reefs* 19, 400–417. doi: 10.1007/s003380000129
- Mumby, P. J. (2006). The impact of exploiting grazers (Scaridae) on the dynamics of Caribbean coral reefs. *Ecol. Appl.* 16, 747–769. doi: 10.1890/1051-0761(2006)016[0747:tioegs]2.0.co;2
- Paddock, M. J., Cowen, R. K., and Sponaugle, S. (2006). Grazing pressure of herbivorous coral reef fishes on low coral-cover reefs. *Coral Reefs* 25, 461–472. doi: 10.1007/s00338-006-0112-y
- R Core Team (2019). *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing. Available online at: <https://www.R-project.org/>
- Randall, J. E. (1967). “Food habits of reef fishes of the west indies,” in *Proceedings of the International Conference on Tropical Oceanography*, Miami Beach.
- Rasher, D. B., Hoey, A. S., and Hay, M. E. (2013). Consumer diversity interacts with prey defenses to drive ecosystem function. *Ecology* 94, 1347–1358. doi: 10.1890/12-0389.1
- Ruttenberg, B. I., Adam, T. C., Duran, A., and Burkepile, D. E. (2019). Identity of coral reef herbivores drives variation in ecological processes over multiple spatial scales. *Ecol. Appl.* 29:e01893. doi: 10.1002/eap.1893
- Steneck, R. S., Bellwood, D. R., and Hay, M. E. (2017). Herbivory in the marine realm. *Curr. Biol.* 27, R484–R489.
- Steneck, R. S., and Dethier, M. N. (1994). A functional group approach to the structure of algal-dominated communities. *Oikos* 69, 476–498.
- Suchley, A., and Alvarez-Filip, L. (2017). Herbivory facilitates growth of a key reef-building Caribbean coral. *Ecol. Evol.* 7, 11246–11256. doi: 10.1002/ece3.3620
- Suchley, A., McField, M. D., and Alvarez-Filip, L. (2016). Rapidly increasing macroalgal cover not related to herbivorous fishes on Mesoamerican reefs. *PeerJ* 4:e2084. doi: 10.7717/peerj.2084
- Tanner, J. E. (1995). Competition between scleractinian corals and macroalgae: an experimental investigation of coral growth, survival and reproduction. *J. Exp. Mar. Biol. Ecol.* 190, 151–168. doi: 10.1016/0022-0981(95)00027-0

- Venera-Ponton, D. E., Diaz-Pulido, G., McCook, L. J., and Rangel-Campo, A. (2011). Macroalgae reduce growth of juvenile corals but protect them from parrotfish damage. *Mar. Ecol. Progr. Ser.* 421, 109–115. doi: 10.3354/meps08869
- Verges, A., Vanderklift, M. A., Doropoulos, C., and Hyndes, G. A. (2011). Spatial patterns in herbivory on a coral reef are influenced by structural complexity but not by algal traits. *PLoS One* 6:e17115. doi: 10.1371/journal.pone.0017115
- Wheeler, R. E. (2010). *Permutation tests for linear models in R*. Available online at: <http://cran.r-project.org/web/packages/lmPerm/vignettes/lmPerm> (accessed October 12, 2019). doi: 10.1371/journal.pone.0017115

Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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