

FORAGING ECOLOGY OF PARROTFISHES IN THE GREATER CARIBBEAN:
IMPACTS OF SPECIALIZATION AND DIETARY PREFERENCES
ON MARINE BENTHIC COMMUNITIES

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by
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TITLE: Foraging Ecology of Parrotfishes in the Greater
Caribbean: Impacts of Specialization and Dietary
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ABSTRACT

Foraging Ecology of Parrotfishes in the Greater Caribbean: Impacts of Specialization and Dietary Preferences on Marine Benthic Communities

Madelyn Virginia Roycroft

Coral reefs are one of the world's most diverse yet heavily impacted marine ecosystems. As a result of many direct and indirect stressors, coral reefs have experienced major degradation over the last several decades. Declines in coral reefs in the Caribbean have been particularly acute and generally associated with the loss of key herbivores and an increase in algae. Herbivorous fishes such as parrotfishes can positively impact coral reefs by removing algae that compete with corals for light and space. However, many parrotfishes are also important coral predators. Predation on corals, known as corallivory, can adversely affect coral growth, reproduction and survivorship. In this time of changing environments and coral reef decline, understanding the context-dependent nature of parrotfish foraging behavior is of critical importance to scientists and managers. Knowledge of the responses of parrotfishes across a range of resource abundance will help scientists and managers better predict the impacts that these herbivores have on benthic communities as both herbivores and corallivores.

In Chapter 1, we examined how six different species of coral reef herbivores (i.e. parrotfishes), all of which belong to a single feeding guild but represent a range of dietary specialization, respond to changes in the abundance of preferred food items. We conducted behavioral observations of parrotfishes in two regions of the Greater Caribbean, and compared consumption rates, diet preferences, and foraging territory size in relation to natural variation across sites in preferred resource abundance. We found that the more-specialized parrotfishes increased their dietary specialization, had smaller foraging territories, and increased their feeding

rate with increased preferred resource abundance. In contrast, less-specialized species exhibited constant foraging traits regardless of the abundance of their preferred resources. This study suggests that differences in dietary preference, specialization, and subsequent nutritional demand may drive a differential response in foraging behavior by generalists and specialist herbivores to changes in resource abundance. Recognizing that generalists and specialists differ in the degree to which their foraging behaviors are context-dependent can allow researchers to better predict how herbivores shape the structure and function of marine and terrestrial ecosystems.

In Chapter 2, we determined if and how corallivory rates and intensity by parrotfishes differ between two regions of the Greater Caribbean that vary in coral and parrotfish community composition and abundance. We found that more species of parrotfishes than previous studies suggest contribute to corallivory. However, corallivory rates and selectivity for coral species by parrotfishes were largely context-dependent, particularly with regards to the relative abundance of preferred corals and diversity of corallivores at a given site. Although we found that corallivory rates decrease with coral cover, it appears that areas of low coral cover may have high corallivory intensity and coral tissue loss, in part due to the relatively high abundance of corallivores in these areas. The impact of high corallivory intensity and tissue loss requires further knowledge regarding the fate of bite scars on corals. This information will help predict the positive and negative consequences of parrotfishes on coral persistence in the Caribbean.

Evidence provided in this thesis furthers our understanding of the dual role of parrotfishes as herbivores and corallivores. Additionally, it highlights the implications of changing coral reefs on parrotfish behavior and subsequent coral reef health and resilience.

Keywords: Herbivory, Corallivory, Coral reef, Feeding Selectivity, Generalists, Specialists, Foraging theory, Grazing, Resilience, Resource abundance

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1. RESOURCE ABUNDANCE INTERACTS WITH DIETARY SPECIALIZATION TO SHAPE FORAGING BEHAVIOR IN CARIBBEAN PARROTFISHES

1.1 INTRODUCTION

Herbivory is an important ecological process that can shape the structure and function of marine and terrestrial ecosystems (Lubchenco and Gaines 1981; Hawkins and Hartnoll 1983; Huntly 1991; Schmitz 2008). Herbivores can shape the community composition of primary producers (Augustine and McNaughton 1998; Hester et al. 2006), alter rates of primary production (McNaughton 1979; Carpenter 1986), and cause or prevent shifts in ecosystem state (Estes et al. 2011). A key mechanism by which herbivores can impact the composition of terrestrial plant and marine benthic algal communities is through selective feeding (Suding et al. 2004; Miller et al. 2011). For example, when herbivores specialize on competitively dominant species they can indirectly facilitate subordinate competitors through competitive release, thereby enhancing overall diversity in primary producers (Lubchenco and Gaines 1981; Augustine and McNaughton 1998; Crawley 2015). Likewise, less-specialized, generalist herbivores can facilitate coexistence in plant and benthic communities by foraging on common and accessible plant species, thereby reducing competition of common species with rarer species, which may help maintain biodiversity (Choat 1982; Gaines and Lubchenco 1982; Feng et al. 2009). Thus, both the relative abundance of generalist and specialist herbivores, and the diversity in specialization amongst individuals and species within each group can influence the net impact that herbivores have on plant and benthic communities.

Herbivore diversity influences ecological processes in a variety of systems. For example, herbivores with different diet preferences can more effectively control a wide variety of plant species (Deraison et al. 2015; Lefcheck and Duffy 2015). On coral reefs, different herbivore

species often have complementary diets and foraging modes. Therefore, diversity in herbivore diet can be critical for suppressing different species of algae that can be detrimental to coral growth and recruitment (Burkepile and Hay 2008, 2011, Rasher et al. 2013). Additionally, variation in how herbivores forage in space can alter effective intensity of herbivory and subsequent competitive outcomes in benthic communities (Sandin and McNamara 2012). However, the importance of herbivore diversity is not equal across every system. For example, a single species can drive patterns of bioerosion across the Great Barrier Reef (Hoey and Bellwood 2008) and can be responsible for reversing experimentally induced macroalgae phase shifts (Bellwood et al. 2006). Thus, the ecological impacts of a species assemblage may largely depend on the specific traits of certain species in the assemblage.

Furthermore, species traits such as foraging behavior can vary with environmental context. For example, generalists and specialists often respond differently to changes in resource abundance (Cleary and Genner 2004; Munday 2004). Specifically, as resource abundance increases, dietary specialists have been shown to increase specialization (Afeworki et al. 2011; Pérez-Matus et al. 2012; Lawton et al. 2012a), decrease foraging territory size (Jones and Norman 1986; Tricas 1989; Berumen 2001; Chandler et al. 2016), and increase feeding rate (Schoener 1971; Belovsky 1978; Pyke 1984). In contrast, generalist species are less likely to change their foraging behavior with fluctuations in the abundance of individual resources (Schoener 1971; Belovsky 1978; Dill 1983; Cleary and Genner 2004; Munday 2004). These findings generally support optimal foraging theory, which predicts that specialists consume the most profitable food when it is sufficiently available to maximize energy return, but that specialists are more sensitive to changes in preferred resources (Chesson 1983; Pyke 1984). Shifts in the behavior of species within a guild can influence the balance and composition of

functional traits and subsequently alter how the guild partitions available resources and affects community structure and function. However, few studies have examined these mechanisms within a single ecological guild (but see Cadotte et al. 2011; Rasher et al. 2013; Adam et al. 2015a). Therefore, investigating the differential impact of changes in resource abundance on generalists and specialists within an ecological guild could reveal if and how such responses can alter the ecological functions of the entire assemblage. Such knowledge can be used to better predict the net impacts of foraging on the community structure and function of primary producers.

On Caribbean coral reefs, the parrotfish assemblage contains both generalist and specialist herbivores that indirectly facilitate corals by controlling algae that compete with corals for space (Williams et al. 2001; Hughes et al. 2007; Mumby 2009b; Adam et al. 2015a). The presence of both types of foragers within this ecological guild makes it an attractive model for comparing the response of foraging behavior to changes in resource abundance — primarily algae, in the case of herbivorous parrotfishes. Algal abundance and community composition on coral reefs can vary spatially and temporally and may be impacted by a variety of drivers such as disturbance events and anthropogenic stressors (Pandolfi et al. 2003, 2011; Hughes et al. 2017). In extreme cases, changes in benthic communities can be severe and may represent a transition from a coral- to macroalgal-dominated reef (Hughes 1994; Gardner et al. 2003; Bruno and Selig 2007). Variation in algal abundance and community composition can alter the absolute and relative abundance of preferred food items for herbivorous fishes (Done 1992; Hughes 1994; Doropoulos et al. 2017). Therefore, understanding the responses of specialists and generalists across a range of resource abundance levels will help us better predict the impacts that these herbivores have on benthic communities, including potential indirect positive impacts on corals.

In this study, we examined how different species of generalist and specialist parrotfishes responded to changes in the abundance of preferred food items by comparing consumption rates, diet preferences, and foraging territory size along a natural gradient in abundance of their preferred resources. We hypothesized that the relationship between resource abundance and parrotfish foraging behavior would differ between species in relation to their level of resource specialization. Based on optimal foraging theory (reviewed by Pyke 1984), we predicted that as the abundance of preferred resources increase, more-specialized species will increase dietary specialization and feeding rate, and decrease their foraging distance, while less-specialized species will display no significant change in these foraging behaviors. Understanding these processes will help us better predict how different species of parrotfishes modify algal assemblages, which can ultimately impact corals and the future of Caribbean reefs.

1.2 MATERIALS AND METHODS

1.2.1 Study sites

We conducted fish surveys, behavioral observations, and benthic surveys at three sites in the Florida Keys National Marine Sanctuary (FKNMS) off of Key Largo, FL, USA: Carysfort Reef, Elbow Reef, and Molasses Reef in summer 2013 (Adam et al. 2015b) and three sites in St. Croix, US Virgin Islands, USA: Buck Island South Fore Reef, Cane Bay, and Long Reef in summer 2015 (Table S1). All sites were characterized by shallow, high-relief reefs that provide habitat for the common reef-associated parrotfish species in the region (McAfee and Morgan 1996; Bonaldo et al. 2014).

In the FKNMS, parrotfishes are considered marine ornamentals and both spearfishing and hook-and-line fishing of parrotfishes is prohibited (Bohnsack et al. 1994; Florida Fish and

Wildlife Conservation Commission 2013a, b). All species of Caribbean parrotfishes commonly associated with shallow high-relief coral reefs are present and abundant at Carysfort Reef, Elbow Reef and Molasses Reef (Adam et al. 2015b). On St. Croix, the south forereef surrounding Buck Island is a National Monument and has been protected from fishing since 1961, and the parrotfish populations have similar biomass to protected sites in the FKNMS (Pittman et al. 2008; Stoffle et al. 2009). Long Reef and Cane Bay are fished sites in St. Croix. Three key Caribbean parrotfish species (*Sc. coeruleus*, *Sc. coelestinus*, and *Sc. guacamaia*) that were once present on both FKNMS and St. Croix reefs are now absent from all St. Croix study sites. As a result, there are six species of parrotfishes commonly associated with shallow, high-relief reefs in St. Croix, and nine in FKNMS. Therefore, we only investigated the foraging behavior of the six parrotfish species present in both regions.

1.2.2 Study organisms

We investigated the foraging ecology of the most common reef-associated parrotfishes found at our study sites from the *Scarus* (*Sc.*) and *Sparisoma* (*Sp.*) genera: *Scarus taeniopterus* (princess parrotfish), *Scarus vetula* (queen parrotfish), *Sparisoma aurofrenatum* (redband parrotfish), *Sparisoma chrysopteron* (redtail parrotfish), *Sparisoma rubripinne* (yellowtail parrotfish), and *Sparisoma viride* (stoplight parrotfish). Recent studies have placed parrotfishes into distinct functional groups based on morphological or behavioral characteristics such as diet and foraging impact, collectively referred to as foraging traits (Bellwood et al. 2004; Adam et al. 2015b, 2018). Based on this work, researchers placed parrotfishes in FKNMS into four key functional groups: browsers, croppers, excavators and scrapers (Adam et al. 2018). Following these groupings, *Sp. aurofrenatum*, *Sp. chrysopteron* and *Sp. rubripinne* are browsers, *Sp. viride* is an excavator, and *Sc. vetula* and *Sc. taeniopterus* are scrapers (Adam et al. 2018). Scrapers and

excavators, which contact the reef substrate while foraging, can remove algal turfs and endolithic algae on dead coral substrate. Browsing species, which target fleshy macroalgae, often without contacting the substrate, can prevent established macroalgae from overgrowing substrates such as corals (Burkepile and Hay 2010). The suite of unique behavioral traits for each parrotfish species in combination defines the ecosystem function of their respective functional group. However, these functional groups and species-specific foraging behaviors observed in FKNMS may differ for conspecifics observed in other regions in the Caribbean. Therefore, we investigated whether the behavioral foraging trait characteristics such as feeding preferences and foraging rates observed in FKNMS are consistent for the species present in St. Croix prior to our main analyses (see next section).

1.2.3 Characterization of the benthos and parrotfish assemblage

We conducted benthic surveys at each study site so that we could quantify food preference and the site-level abundance for each of the preferred food items. At each study site, we photographed a quadrat every 1.5 m along 30 m transects ($n = \sim 6$ transects per site) and recorded whether the substrate was dead coral, pavement, boulder, rubble, ledge or sand. Dead coral included both convex and concave surfaces on the vertical and horizontal planes of three-dimensional coral skeletons that were attached to reef substrate. Coral pavement was carbonate reef with little topographic complexity (i.e., flat limestone pavement). Boulder was large remnants of dead mounding corals not clearly attached to the bottom and often partially buried in sand. Coral rubble consisted of small dead coral fragments (generally <10 cm in any dimension) that could be moved with minimal force. Ledges consisted entirely of the undercut sides of large spurs in spur and groove habitat. Sand was an accumulation of sediment >15 cm deep. In addition to recording foraging behavior, we also recorded other activities such as aggressive

interactions with other fish. We divided each quadrat into 16, 12 x 12 cm sections and photographed each section individually to provide a high-resolution image for benthic analysis. We estimated the percent cover of each benthic organism from 9 randomly stratified points per 12 cm x 12 cm section ($n = 144$ points per section). We identified macroalgae and coral to genus or species and other organisms to functional group (e.g., sponges, gorgonians, turf algae, crustose coralline algae). We calculated site-level average percent cover of the four main food groups on each of the main substrate types. To compare parrotfish food preference across regions, we calculated the site-level mean percent cover for four combined categories that made up the majority of parrotfish bites: (1) mixed algal turfs and crustose coralline algae (CCA), (2) foliose algae (e.g. *Lobophora*), (3) calcified alga (e.g. the green alga *Halimeda*) and (4) live coral.

To assess the relative abundance and biomass of each parrotfish species, we conducted fish surveys using a roving diver method. At each site we conducted 20 to 30 min timed swims on SCUBA while towing a GPS receiver (Garmin GPS 72) on a float (Adam et al. 2015b). The observer counted and estimated size to the nearest cm of all parrotfishes ≥ 15 cm in length encountered in a 5 m-wide swath (2.5 m on either side of the diver). We used published length-weight relationships to calculate the biomass of each species (Bohnsack and Harper 1988). Using this information and the area covered per transect, we calculated species-specific and total parrotfish densities per site. We accounted for unequal fish survey transect areas by weighting each transect replicate biomass estimate by the area surveyed in the transect relative to the total area surveyed at the site. The FKNMS data from 2013 used in this study was collected using identical methodology (Adam et al. 2015b). We tested for site and region effects on parrotfish densities using ANOVA and post-hoc TukeyHSD pairwise comparisons.

1.2.4 Behavioral observations to determine foraging traits

To obtain species-specific foraging traits, we conducted behavioral observations at each of our study sites on the most abundant six species of *Scarus* and *Sparisoma* parrotfishes: *Sc. taeniopterus*, *Sc. vetula*, *Sp. aurofrenatum*, *Sp. chrysopterus*, *Sp. rubripinne*, and *Sp. viride*. Observations were evenly distributed across each site (Table A1). We conducted our observations on or near high-relief habitat and targeted initial phase (IP) individuals >10 cm total length. We haphazardly selected focal individuals using criteria that ensured 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 and recorded (a) the number of bites taken on any food item and substrate, and (b) identified each targeted food item to the lowest taxonomic level or functional group possible (Table A2; see Adam et al. 2015b for detailed methods description and selection criteria). We used this information to estimate bite rates (bites min⁻¹) and the bite frequency on each food item (n bites on food item a / total bites, %) (Table A3a). To track the foraging territory of each individual, the diver towed a GPS unit on a surface float, which recorded a position every 15 s. From the GPS data, we estimated the maximum linear distance the fish traveled during the 20-min observation (Table A3b), which we used as a proxy for foraging territory size. The FKNMS data from 2013 used in this study was collected using identical methodology (Adam et al. 2015b).

1.2.5 Quantifying species-specific foraging behavior

We used Manly's α electivity index to quantify species-specific food preferences using the behavioral observation data (Chesson 1983):

$$\alpha_r = \frac{\frac{f_r}{g_r}}{\sum_{j=1}^{n_R} \frac{f_j}{g_j}},$$

where α_r = electivity for food item r , and f_r is the bite frequency for food items r , where $r \in 1, \dots, n_R$, and n_R is the number unique food item types available at each site. g_r is the abundance of that food item r at the site, where $r \in 1, \dots, n_R$. This allowed us to identify whether an individual targeted a food item more or less often than expected based on their relative availability at a study site. We calculated the food item abundance, g_r , for each individual fish by weighting the percent cover of food item r on a single substrate type by the proportion of bites the individual took from that substrate relative to the other substrate types. We performed this calculation for each substrate type (boulder, coral, dead coral, ledge, pavement, rubble, and sand) and then added the seven weighted proportions together to generate the individual-based food item abundance, g_r . If $\alpha_r = 1/n_R$, selective feeding did not occur and each resource was targeted in proportion to its availability. If $\alpha_r > 1/n_R$, then food item r was preferentially consumed. Conversely, if $\alpha_r < (1/n_R)$, then food item r was avoided (Table A3c).

For each site, we calculated species-specific diet specialization as the mean variance (σ^2) in preference (α) for all eight food items: turf algae and CCA, foliose algae, calcareous green algae, gorgonians, live coral, red calcareous algae, red non-coralline encrusting algae, and sponges. High diet variance across all food items (σ^2) indicates that, on average, a species has a high preference for a select few food items (i.e. specialized foraging), while low diet variance (σ^2) indicates that a species has moderate preference for many food items (i.e. generalized foraging). Lastly, for each site, we calculated the species-specific resource abundance by

calculating the sum the individual-based resource abundance g_r weighted by the electivity (α) value of the food item r for all preferred food items ($\alpha_r > 1/n_R$) (Table A3d). Doing so yields a metric of resource abundance that is more representative of the abundance of food items from the perspective of each individual fish rather than the absolute percent cover of potential food items in the habitat. For the remainder of the paper we will use diet variance (σ^2) as a metric for diet specialization.

1.2.6 Statistical analysis

1.2.6.1 Testing whether functional groups are consistent among regions

The first objective of this study was to determine if there were similarities in the species composition of each functional group across our two sampling regions. First, we determined whether conspecifics in FKNMS and St. Croix can be placed in the same functional groups based on food preference. We used hierarchical cluster analysis with Ward's linkage on Bray-Curtis distance matrices from square root transformed data to identify how species cluster based on the food preference data for both FKNMS and St. Croix. For this analysis, we modified the preference data by removing the data for food items that are rarely targeted by parrotfishes and aggregated the remaining data into four main food groups: (1) turf algae and CCA, (2) calcified algae, (3) foliose algae (i.e. *Dictyota* and *Lobophora* spp.), and (3) live coral.

To test whether clustering based on food preference was congruent for our two regions we conducted a Mantel test on two distance matrices containing the site- and species-specific mean electivity for the four main food groups. A positive correlation between the two matrices would indicate that parrotfishes in the two regions, FKNMS and St. Croix, cluster similarly based on their food preference.

We used nonmetric multidimensional scaling (nMDS) on multiple feeding behavior variables to evaluate similarities in functional group clustering across our two regions, which provide graphical information about how species' functional roles are conserved across regions. We used a random starting configuration and Sorensen (Bray-Curtis) method to generate an nMDS input distance matrix across four feeding behavior variables: foraging distance and bite rate (each square root transformed), and two diet preference variables for each individual observation. We calculated each diet preference variable by reducing the individual-based preference (electivity, α) variables for each main food group using a Principal Components Analysis (PCA) into two diet preference variables (Feeding_PC1, Feeding_PC2) that accounted for 90% of variation in the data (Table A4). We also evaluated the nMDS stress value to determine the fit: a value below 0.1 is an indication of an acceptable fit and equal to or below 0.05 is an indication of good fit (Clarke and Warwick 1994). We subjected the distance matrix to multiple runs of an NMDS algorithm to determine the necessary dimensions for the nMDS plot. For the nMDS ordination plot, we grouped the individual observation data based on region (St. Croix or FKNMS) and functional group (macroalgae browser or turf grazer) to which the individual belonged. From these groupings, we created ellipses using 95% confidence intervals, which represent the pairwise dissimilarity between the region-specific functional groups in two-dimensional space. All statistics were conducted in R programming language (R Development Core Team 2011) using the 'vegan' package (Oksanen et al. 2017).

1.2.6.2 Specialization categorization

We used hierarchical cluster analysis with Ward's linkage Bray-Curtis distance matrices from square root transformed data to identify how species cluster based on diet specialization (σ^2) for both FKNMS and St. Croix data. We then generated a box and whisker plot of diet

variance means grouped by each species cluster generated from the dendrogram. Based on the results from the box and whisker plot (i.e. relatively low or high diet variance), we categorized each group of species as either generalists or specialists.

1.2.6.3 Feeding behavior, resource abundance and diet specialization

Our goal was to determine how resource abundance affects three key foraging trait variables (diet specialization, foraging distance, and feeding rate) and whether these patterns are the same for specialist and generalist parrotfish species. For each specialization group, we ran a linear model with categorical and numeric predictors that tested the interaction of species and the covariate, resource abundance, on the following response variables: diet specialization (diet variance, σ^2), foraging distance (maximum linear distance, m) and feeding rate (bite rate, bites min^{-1}). We tested for main effects and interactions using type II sums of squares as calculated by the ‘car’ package in R (Fox and Weisberg 2011). Finally, we used model selection criteria (log likelihood ratio test) using the “lmtest” package in R (Zeileis and Hothorn 2002) to determine the final model complexity for each of the three analyses and whether to drop species interaction term or species from each model.

1.3 RESULTS

1.3.1 Characterization of the parrotfish assemblage and benthos

Total parrotfish biomass differed between sites in St. Croix and FKNMS (ANOVA $F_{5,26} = 5.51$, $P = 0.001$; Figure 1). Post-hoc pairwise comparisons using the Tukey HSD test indicated that the mean total parrotfish biomass (g m^{-2}) for Buck South Forereef, Elbow Reef, Carysfort Reef and Molasses Reef were significantly greater than the mean total parrotfish biomass at

Long Reef and Cane Bay. Existing benthic cover varied among study sites and on the three main substrates: (1) high-relief, (2) boulder, rubble, sand, and (3) pavement. Across nearly all substrate categories and sites, turf algae and CCA made up the greatest percentage of benthos. The other dominant benthos included cyanobacteria and foliose algae (Figure 2).

1.3.2 Detecting regional similarities in functional roles

Hierarchical cluster analysis of species-averaged food electivity (α) values for the four main food groups revealed that the six parrotfish species in both FKNMS and St. Croix clustered into the same two main groups based on their food preference (Figure 3). The first group comprised of *Sp. aurofrenatum* and *Sp. rubripinne*, and *Sp. chrysopterum* which had relatively little preference for turf algae and crustose coralline algae (CCA) and a large preference for foliose macroalgae and other mixed food items such as calcified algae. The two *Scarus* species and *Sp. viride* clustered together based on their large preference for turf algae and CCA. Lastly, the results from the Mantel test further confirm this similarity in group separation and found a strong, positive relationship between the FKNMS and St. Croix food preference distance matrices (Mantel Test, $r = 0.869$, $P = 0.002$).

Nonmetric multidimensional scaling using individual foraging traits (bite rate, foraging distance and food preference) grouped by region and functional group resulted in a two-dimensional ordination (stress = 0.065). From the species and site-specific foraging traits for each individual we generated 95% confidence interval ellipses for each functional group. Individuals from both FKNMS and St. Croix separated along Axis 1 and Axis 2 into the same functional groups, as evidenced by both the overlapping ellipses for the same functional groups and nonoverlapping ellipses for different functional groups (Figure A1).

1.3.3 Specialization categorization

The dendrogram based on diet variance placed the two *Scarus* spp. and *Sp. chrysopterus* into one group, which we classified as “more-specialized”, and the three remaining *Sparisoma* spp. into a second group, which we classified as “less-specialized”, based on the analysis that follows (Figure A2a). Using the results from the cluster analysis, we generated a box and whisker plot (Figure A2b) of diet variance means for each group. We categorized the group with significantly lower diet variance (mean $\sigma^2 = 0.054 \pm 0.0049$, $n = 18$) as “less-specialized” and the group with significantly higher diet variance as “more-specialized” (mean $\sigma^2 = 0.097 \pm 0.0057$, $n = 18$).

1.3.4 Feeding behavior, resource abundance, and diet specialization

For more-specialized species, the models that included species as a term but not the interaction between species and the numeric predictors provided a significantly better fit than those without (likelihood ratio test (LRT), Table A5; diet specialization: $X^2 = 8.2$, $df = 5$, $P = 0.02$; foraging distance: $X^2 = 14.4$, $df = 5$, $P < 0.0001$; bite rate: $X^2 = 34.3$, $df = 5$, $P < 0.0001$). All models for less-specialized species were nonsignificant. The linear regression analyses for more-specialized species revealed a positive relationship between diet variance and resource abundance ($R^2=0.63$, $P = 0.05$; Figure 4a; Table 1a), a negative relationship between foraging distance and resource abundance ($R^2=0.77$, $P < 0.05$; Figure 4b; Table 1b), and a positive relationship between bite rate and resource abundance ($R^2=0.91$, $P < 0.05$; Figure 4c; Table 1c). Thus, for more-specialized species, as preferred resource abundance increased, diet specialization increased, foraging distance decreased and bite rate increased, but each species had varying levels (i.e. different intercepts) of each response variable. For less-specialized

species there was no significant relationship between resource abundance and diet variance ($R^2=0.09$, $P = 0.46$; Figure 4a; Table 1a), foraging distance ($R^2=0.15$, $P = 0.58$; Figure 4b; Table 1b), or bite rate ($R^2=0.42$, $P = 0.41$; Figure 4c; Table 1c).

We note that there is a smaller range in abundance of preferred resources for the generalist species than specialist species, which likely results in part from their lack of a strong preference for any given food item. Since a small range in the predictor variables may influence the strength of an observed relationship, we reran the analyses restricting the data to have the same range in predictors for the two groups. . Even with this more limited dataset, resource abundance is still a better predictor of foraging behavior for the specialist species (Table A6), indicating that our results are robust.

1.4 DISCUSSION

In this study, we found that different species of parrotfishes within a single ecological guild, including those in the same genus, responded differently to changes in resource abundance depending on their degree of dietary specialization. Specifically, the more-specialized parrotfish species exhibited: (1) increased dietary specialization (2) smaller foraging territory, and (3) increased feeding rate with increased abundance of preferred resources. In contrast, the foraging traits of less-specialized species did not vary with the abundance of preferred resources. Thus, while each species within the Caribbean parrotfish assemblage has unique foraging traits (Adam et al. 2015b), species with similar levels of diet specialization respond similarly to changing resource abundance. These results suggest that generalist and specialist herbivores respond to changes in resource abundance in very different ways, which may have profound impacts on their foraging ecology, functional roles, and their ultimate net ecological impacts on reefs.

1.4.1 Dietary specialization

Previous studies of fishes in marine systems have shown a positive relationship between dietary specialization and resource abundance (Afeworki et al. 2011; Pérez-Matus et al. 2012; Lawton et al. 2012a). This study indicates that only the more-specialized parrotfishes, *Sc. vetula*, *Sc. taeniopterus* and *Sp. chrysopterus*, follow this relationship; they had clear dietary preferences for a select few groups (e.g. turf algae and crustose coralline algae by *Scarus* spp.), but greater dietary variability in areas where preferred food items were scarce. Such opportunistic exploitation has also been seen in other marine organisms, such as coral reef butterflyfishes (Chandler et al. 2016), kelp forest-associated fishes (Pérez-Matus et al. 2012), and glaucous-winged gulls in rocky intertidal communities (Irons et al. 2009). Our results suggest that the more-specialized parrotfishes increased their dietary specialization when preferred resources were abundant by eliminating non-preferred resources from their diets and targeting the preferred resources with high value (Chesson 1983; Sih and Christensen 2001). Non-preferred resources are likely of lower value, which may depend on energy density (Tullock and Murdoch 1970; Schoener 1971), content of rare, limiting nutrients (Simpson et al. 2004), as well as palatability (e.g. chemical or physical defenses) (Hay et al. 1994; Loh and Pawlik 2014). In contrast, it may have been more favorable for the less-specialized species to shift their diet and target nearby food items, such that their relative foraging effort for each item, or degree of specialization, did not change (Lawton et al. 2012b). Thus, our data suggest that generalist and specialist species respond differently in their foraging to variation in the availability of preferred resources.

1.4.2 Consumption rates

Optimal foraging theory predicts that grazers will consume resources at a rate proportional to their abundance and relative nutritional qualities (Schoener 1971; Stephens and Krebs, J. R. 1986; Sih and Christensen 2001). Following this theory, the more-specialized species in our study exhibited a functional response, where bite rate increased linearly with an increase in preferred resource abundance. Evidence suggests that the more-specialized species foraged at a higher rate on preferred resources as these resources increased in abundance, likely because doing so maximized their nutritional benefit with minimal energy expenditure (Tullock and Murdoch 1970). In contrast, the less-specialized species did not increase their foraging rate when preferred resources were more abundant. This result suggests that their preferred food items may yield similar nutritional benefits at the same energetic cost as the other available, nutritionally similar (i.e. substitutable) resources. Therefore, less-specialized species may have a constant feeding rate regardless of resource abundance because their preferences are weaker, such that the value of one resource over another is much less pronounced (Raubenheimer 2003). Likewise, recent work on generalist parrotfishes found that absolute resource abundance did not predict foraging rates, likely due to differences in substitutability among resources (Hanmer et al. 2017; see also Bruggemann, Van Oppen, et al. 1994, Francini-Filho et al. 2010). Overall, these findings suggest that the differences in dietary preference, specialization, and subsequent nutritional demand of more- and less-specialized parrotfishes may drive differential functional responses to changes in resource abundance.

1.4.3 Foraging territory size

Many studies that have applied optimal foraging theory to herbivore foraging behavior have shown that foraging territory size and search effort often increase as resource abundance

decreases (Clarke 1970; Hixon 1980; Schoener 1983). Our results support this theory for specialist parrotfishes, whose foraging territory increases as preferred resource abundance decreases. Interestingly, this pattern does not hold true for generalist species, who maintain their territory size and forage on resources available in their immediate environment, independent of food item availability. Such behavior is characteristic of generalist species, who often have low search effort and fixed foraging territory size (Belovsky 1978). However, optimal foraging theory also predicts that the size of a defended territory or foraging range can increase as competition decreases (Schoener 1971; Hixon 1980). While this pattern has been shown in empirical studies on various coral reef fishes (Robertson and Gaines 1986; White and Warner 2007; Mumby et al. 2014), we did not find a significant relationship between foraging distance and competitor density for either group (Figure A3). Therefore, our data suggest that the territory expansion by more-specialized parrotfishes was a response to reduced abundance of preferred food items rather than competitor densities. While further work is needed to extricate the effects of these potentially confounding variables, these findings highlight the complexities of foraging ecology and reveals the applicability of optimal foraging theory to multiple systems and species assemblages.

1.4.4 Broader implications

Our results suggest that the relative abundance of benthic organisms such as macroalgae and coral in resource-limited environments could determine the degree to which shifts in foraging intensity by more-specialized parrotfishes impact coral health and recovery. We found that more-specialized species foraged across larger spatial scales with a reduced bite rate in resource-limited environments. This suggests that on a reef with abundant macroalgae and limited preferred resources such as turf algae and CCA, foraging intensity by more-specialized

parrotfishes may significantly decrease. The positive impacts of parrotfish grazing on macroalgae-dominated coral reefs can be greatly diminished if foraging intensity decreases (Williams & Polunin 2001, Mumby 2006, Adam, Burkepile, et al. 2015, Adam et al., *in press*). For example, herbivory over larger spatial scales has been shown to be less effective than spatially constrained herbivory for opening up space for coral settlement and recruitment (Sandin and McNamara 2012). In addition, macroalgae can directly inhibit settlement of coral larvae (Beatty et al. 2018) and reduce postsettlement survival of larvae (Kuffner et al. 2006; Hughes et al. 2007; Dixon et al. 2014; Webster et al. 2015). Thus, macroalgae can negatively impact corals directly through competition and indirectly by reducing parrotfish grazing intensity. This idea may provide an additional explanation for a finding by a previous study that herbivores are unable to effectively control algal growth at sites with low coral cover and high macroalgae cover (Williams et al. 2001; see also Francini-Filho et al. 2010). Future work could further examine this idea by comparing parrotfish foraging behavior across a gradient of macroalgae cover relative to abundance of food items that specialists prefer. Such information could highlight the potential disproportionate effect that the duality in the parrotfish assemblage response to resource abundance may have on coral reef community structure and function.

1.5 CONCLUSION

We found that a dichotomy exists within a common coral reef herbivore assemblage, where more-specialized parrotfishes exhibit a clear response to changes in preferred resource abundance and less-specialized parrotfishes do not. In addition, within this parrotfish assemblage characterized by unique species-specific foraging traits, the species that belong to the same dietary specialization group responded similarly to resource abundance. We suggest that the differential response in generalist and specialist parrotfishes to change in resource abundance can

alter the assemblage-wide functional impact on the coral reef community. Therefore, predictions for how herbivores shape the structure and function of marine and terrestrial ecosystems should consider that generalist and specialist herbivores may differ in the degree to which they do so in response to alterations in environmental conditions.

2. CORAL AND PARROTFISH COMMUNITY COMPOSITION AND ABUNDANCE INFLUENCE CORALLIVORY RATES AND INTENSITY ON CARIBBEAN REEFS

2.1 INTRODUCTION

Coral reefs are one of the world's most diverse yet heavily impacted marine ecosystems that face threats from both direct and indirect stressors such as rising sea surface temperatures, coastal development, overfishing and nutrient pollution (Reaka-Kudla 1997; Hughes et al. 2003; Halpern et al. 2008). As a result, coral reefs have experienced major degradation over the last several decades, particularly in the Caribbean (Gardner et al. 2003; Schutte et al. 2010; Jackson et al. 2014). While the drivers of coral decline are complex and vary among locations, an increase in algae resulting from the loss of key herbivores via overfishing is a significant factor (Jackson et al. 2014; Adam et al. 2015a; Steneck et al. 2018).

Herbivorous fishes such as parrotfishes can positively impact coral reefs and increase coral survivorship and recruitment by removing algae that compete with corals for light and space (Mumby et al. 2006; Burkepile and Hay 2008; Steneck et al. 2014). However, some parrotfishes are also regular corallivores, or consumers of live coral tissue, that can cause significant coral tissue loss and bioerosion of the coral skeleton (Rotjan & Lewis 2008, Bonaldo et al. 2014). In addition to causing whole and partial coral mortality, recovering from corallivory is energetically costly and can increase the coral's susceptibility to other chronic stressors such as nutrient pollution, temperature stress, and disease (Rotjan et al. 2006; Zaneveld et al. 2016). As coral cover decreases, corallivory may intensify on the remaining corals, creating a positive feedback that could prevent coral recovery once corals reach low densities (Burkepile 2012). Thus, the adverse effects of corallivory in comparison to the beneficial effects of herbivory by

parrotfishes may also depend on local factors such as coral abundance. Understanding the net ecological impact of parrotfish corallivory relative to herbivory, in addition to the context-dependent nature of corallivory, is therefore a high priority for coral reef conservation and management efforts.

Identifying which parrotfish species are significant corallivores is crucial for understanding the net impact of parrotfishes on coral reefs. However, no studies to date have quantified the relative contribution of different parrotfish species to the total level of corallivory occurring on Caribbean reefs. Previous research suggests that *Sparisoma viride*, *Sparisoma aurofrenatum*, and *Scarus vetula* are regular corallivores on Caribbean reefs, with *Sparisoma viride* having markedly higher rates of coral predation (Bruggemann et al. 1996; Bruckner and Bruckner 1998; Miller and Hay 1998; Bruckner et al. 2000; Rotjan et al. 2006; Rotjan and Lewis 2008). In addition, some studies have quantified corallivory rates for *Sp. viride* and some large *Scarus* species (Bruggemann et al. 1994a, c; McAfee and Morgan 1996), however there is need for a more comprehensive assessment of corallivory rates for all species in the Caribbean parrotfish assemblage (Bonaldo et al. 2014). Because a current management goal in the U.S. Caribbean is to increase the abundance of reef fishes such as parrotfishes (Rothenberger et al. 2008), knowledge of species-specific corallivory rates and impact will be crucial information to make proper management decisions (Adam et al. in press, 2015b, a; Mumby 2009a).

Accurately quantifying the net impact of parrotfishes on corals also requires knowledge of species-specific selection for different coral species. Caribbean parrotfishes prey on many species of corals but preferentially target different corals to varying degrees (Bythell et al. 1993; Rotjan and Lewis 2006; Burkepile 2012). Such selectivity is also characteristic of parrotfish foraging on other food items such as algae (Roycroft et al. in prep. Mantyka and Bellwood 2007

Burkepile and Hay 2008, 2011; Adam et al. 2015b). Coral species that parrotfishes frequently target include *Porites porites*, *Porites astreoides* and *Orbicella* species (Frydl 1979; Bythell et al. 1993). Of particular concern are the potential impacts of corallivory on *Orbicella annularis*, a dominant reef-building coral in the Caribbean that was recently listed as threatened under the US Endangered Species Act (NMFS and NOAA 2014). Large coral colonies of *O. annularis* are subject to chronic corallivory by parrotfishes, which field-parameterized demographic models suggest could contribute significantly to their population declines (Hughes and Tanner 2000; Edmunds 2007). Although grazing scars on corals provide insight into overall grazing intensity on specific coral colonies and species, such data are limited in that they represent single snapshots in time and are not based on focal observations of parrotfish corallivory (Roff et al. 2011). Observing parrotfish corallivory behavior can allow scientists to quantify parrotfish preferences for specific coral species and corallivory rates. This specific information can improve predictions of corallivory intensity on reefs and provide further insight into the context-dependent nature and temporal component of parrotfish grazing.

In this study, we use a combination of focal behavioral observations, detailed coral predation scar data, and analysis of remote underwater video of focal coral colonies to comprehensively document corallivory events of Caribbean parrotfishes. Our first objective was to improve our overall understanding of corallivory on coral reefs by addressing the following research questions: (1) *Which coral species are preyed on by parrotfishes?* (2) *Which parrotfish species are corallivores (i.e. target live coral)?* (3) *Are different species of corals fed on by different species of parrotfishes?* (4) *What are the impacts of corallivory on coral reefs?* and (5) *Is there a relationship between corallivory rates and coral abundance?* Our second objective was to examine how the response to these research questions differ for coral reefs from two

regions in the Greater Caribbean: the Florida Keys, USA (FKNMS) and St. Croix, US Virgin Islands.

We chose to investigate corallivory by parrotfishes in FKNMS and St. Croix because these two regions differ in parrotfish abundance, parrotfish species richness, and coral cover. Insights gained from this study can focus future research towards understanding the driving factors behind selectivity for specific corals across reefs of varying coral cover in the Caribbean. This information can help managers understand the net ecological impact of different parrotfish species as both corallivores and herbivores and allow us to better predict how changes in fisheries regulations aimed at increasing herbivory may directly impact ESA-listed corals.

2.2 MATERIALS AND METHODS

2.2.1 Study sites and organisms

We conducted fish surveys, behavioral observations, and benthic surveys at three sites in St. Croix, US Virgin Islands, USA: Buck Island South Fore Reef, Cane Bay, and Long Reef in summer 2015 and 2016. All of these sites are shallow, high-relief reefs that provide habitat for the common reef-associated parrotfish species in the region (Bruggemann et al. 1994b; McAfee and Morgan 1996; Green and Bellwood 2009; Bonaldo et al. 2014). We compared data from our three study sites in St. Croix to similar data collected in summers of 2010, 2012, 2013, and 2014 at three sites in the Florida Keys National Marine Sanctuary (FKNMS) off of Key Largo, FL, USA: Carysfort Reef, French Reef, and Molasses Reef (Table A7). Large-scale weather and temperature patterns were not fundamentally different across years as to confound our comparisons between study sites and years in FKNMS and St. Croix.

In FKNMS, parrotfishes are considered marine ornamentals and are protected from both spearfishing and hook-and-line fishing (Bohnsack et al. 1994; Florida Fish and Wildlife Conservation Commission 2013b). All species of reef-associated parrotfishes in the Caribbean relevant to this study are present and abundant at Carysfort Reef, French Reef and Molasses Reef (Burkepile 2012; Adam et al. 2015b). On St. Croix, the south forereef surrounding Buck Island is a National Monument and has been protected from fishing since 1961, and the parrotfish populations have similar biomass to protected sites in the FKNMS (Pittman et al. 2008; Stoffle et al. 2009). Long Reef and Cane Bay on St. Croix are fished sites. The three largest Caribbean parrotfish species (*Sc. coeruleus*, *Sc. coelestinus*, and *Sc. guacamaia*) that were once present on both FKNMS and St. Croix reefs, are now absent from all St. Croix study sites. As a result, there are six species of larger reef-associated parrotfishes in St. Croix, and nine in FKNMS. We considered our site at Buck Island (Buck South Forereef) as a separate region from the other St. Croix sites for all analyses since the parrotfish densities and biomass were different at this site than the other two sites in St. Croix, likely because of its protected status. Corallivory rates were also different at Buck Island on a population basis.

We investigated the corallivorous foraging behavior of the most common reef-associated parrotfishes found at our study sites from the *Scarus* (*Sc.*) and *Sparisoma* (*Sp.*) genera: *Scarus taeniopterus* (princess parrotfish), *Scarus vetula* (queen parrotfish), *Sparisoma aurofrenatum* (redband parrotfish), *Sparisoma chrysopteron* (redtail parrotfish), *Sparisoma rubripinne* (yellowtail parrotfish), and *Sparisoma viride* (stoplight parrotfish). We also collected behavioral data from *Sc. coelestinus* (midnight parrotfish), *Sc. coeruleus* (blue parrotfish), and *Sc. guacamaia* (rainbow parrotfish) from FKNMS. Both *Sparisoma* and *Scarus* species forage on

high-relief spur and groove habitat on coral reefs throughout the Caribbean and previous studies have documented corallivorous foraging behavior by species in both genera (Table 2).

2.2.2 Characterization of the parrotfish assemblage

To assess the relative abundance and biomass of each parrotfish species, we conducted fish surveys using a roving diver method. At each site we conducted 20 to 30 min timed swims on SCUBA while towing a GPS receiver (Garmin GPS 72) on a float (Adam et al. 2015b). The observer counted and estimated size to the nearest cm of all parrotfishes ≥ 15 cm in length encountered in a 5 m-wide swath (2.5 m on either side of the diver). Using this information and the area covered per transect, we calculated species-specific and total parrotfish densities per site. We accounted for unequal fish survey transect areas by weighting each transect replicate density and biomass estimate by the area surveyed in the transect relative to the total area surveyed at the site. We calculated the weighted mean parrotfish density and biomass for each parrotfish and the total parrotfish density and biomass for all six study sites. To determine whether there were differences in parrotfish abundance across regions and study sites, we tested for an effect of study site on weighted parrotfish density (fish/100 m²) and parrotfish biomass (g/100 m²). If the ANOVA revealed significant site effect, we conducted post-hoc pairwise comparisons adjusted for multiple comparisons using the Holm's method to identify the specific sources of variation (Holm 1979).

2.2.3 Identification of corals preyed on by parrotfishes

2.2.3.1 Benthic Surveys

In assessing coral species abundance across study sites, we focused on ten scleractinian coral species or species complexes that are commonly preyed on by parrotfishes in the Caribbean: *A. palmata*, *Agaricia* spp., *Colpophyllia natans*, *Diploria strigosa*, *Montastrea*

cavernosa, *M. mirabilis*, *Orbicella* spp., *Porites porites* species complex (SC), *Porites astreoides* and *Siderastrea siderea*. At each study site, we conducted benthic surveys where we photographed a quadrat every 1.5 m along 30 m transects ($n = \sim 8$ transects per site; Table A7) and recorded the substrate type (e.g. boulder, dead coral, sand) which we grouped into “high relief” and “low relief” categories. We divided each quadrat into 16, 12 x 12 cm sections and photographed each section individually to provide a high-resolution image for benthic analysis. We estimated the percent cover of each coral species from nine randomly stratified points per 12 cm section ($n = 144$ points per quadrat). We used data from the quadrats placed on high-relief substrates (i.e. coral and dead coral substrates) to calculate the mean percent cover of each of the ten coral species and total coral cover for each region, with each site as a replicate. We calculated percent cover only from quadrats placed on high-relief substrates to ensure that our estimates of coral cover were representative of the corals we encountered during coral surveys, which we ran along high-relief reef spurs. In FKNMS, we calculated the percent cover of each coral species directly from the coral predation scar surveys (see next section) due to data limitations. We used either ANOVA or the nonparametric equivalent of Kruskal-Wallis rank test (when data were not normal or variance was unequal as tested for with Shapiro–Wilk test and Cochran’s test, respectively). To test for differences between St. Croix and FKNMS in coral cover for individual coral species we used either two-sample t-tests or the nonparametric equivalent of Wilcoxon rank-sum test (when data were not normal or variance was unequal as tested for with Shapiro–Wilk test and Cochran’s test, respectively) adjusted for multiple comparisons.

2.2.3.2 Coral and predation scar surveys

To determine which coral species are preyed on by corallivores, we conducted predation

scar surveys on corals at each study site. We haphazardly chose transect starting positions but laid them out on the reef parallel to the main reef structure (e.g., parallel to the main spur or ledge structure). Within each 30 m x 1m belt transect, we recorded every coral by size class in bins of: 5-10 cm, 10-20 cm, 20-40 cm, 40-80 cm, >> 80 cm. We also included corals that were only partially within the belt, but we only counted the colony area inside the belt (e.g. a colony that is 50% inside would be included, but estimated at half the actual size). For every colony with a predation scar, we measured colony max length and max width and counted the number of both fresh and recovering grazing scars. We were usually able to identify parrotfish grazing scars specifically, since parrotfishes make distinctive paired grazing scars on coral skeletons where marks from the upper and lower jaws are clearly visible (Bruckner et al. 2000; Rotjan et al. 2006); Figure A4). If some scars had upper and lower jaw marks visible but were separated by live coral tissue, we counted them as two separate grazing scars.

We used the bite scar data and coral abundance data to calculate the (1) relative scar frequency (n colonies of coral species i with scars/ n colonies with scars, %) for each region, and (2) mean scar density on live coral (n predation scars per unit live coral area) for each coral species and each region. Therefore, to test for an effect of region on scar density and scar frequency across coral species we used either ANOVA or the nonparametric equivalent Kruskal-Wallis rank (when data were not normal or variance was unequal as tested for with Shapiro-Wilk test and Cochran's test, respectively). If the test revealed a significant effect, we conducted post-hoc pairwise comparisons adjusted for multiple comparisons using the Holm's method using either TukeyHSD or Dunn's multiple comparisons depending on whether the test was an ANOVA or the non-parametric equivalent, respectively, to identify the specific sources of variation (Holm 1979).

2.2.3.3 Coral selectivity

We used Strauss's linear resource selection index (L) (Strauss 1979) to calculate a metric of selectivity to determine whether parrotfishes preferentially preyed on certain species of corals based on predation scar frequency. We calculated colony-based selectivity using the equation $L = r_i - p_i$ where r_i is the proportion of all parrotfish bites that were taken on the i th coral species and p_i is the proportion of the i th coral species in the community based on colony abundance (i.e., proportion of total coral colonies made up of the i th coral species). We calculated area-based selectivity using the same equation where r_i is the proportion of all parrotfish bites that were taken on the i th coral species and p_i is the proportion of the i th coral species in the community based on coral area. Confidence intervals (95%) that did not include zero indicate that parrotfishes either preferred or avoided that coral species. For all the statistical analysis, we considered site as the level of replication and calculated a single value for each site as either the average or sum depending on the variable. In addition, for all statistical analyses, we excluded species for which we recorded no predation scars, or those that were only present at a single site, even if we observed scars on them outside of our surveys. These corals include *A. palmata* ($n = 1$ scar), *C. natans* ($n = 2$ observations), *D. strigosa* ($n = 1$ observation), and *M. mirabilis* ($n = 4$ scars, 1 site). Corallivory is likely not a concern for these species given the near-absence of scars.

2.2.4 Behavioral observations to identify corallivorous parrotfishes

2.2.4.1 Remote video observations

We filmed focal coral colonies using remote underwater video cameras (GoPros) to document corallivory by parrotfishes. We videoed colonies of the corals *Diploria clivosa*,

Orbicella annularis, *Orbicella faveolata*, *Colpophyllia natans*, *Porites porites*, *Porites astreoides*, and *Siderastrea siderea* across each of our six study sites in FKNMS and St. Croix (see Table 2 for total hours of footage on each coral). To maximize the chance of observing corallivory, we preferentially filmed coral colonies with a high density of fresh parrotfish bites. We filmed each coral for ~ 4 hours and then scored the videos in the lab. When corallivory was observed, we recorded the species of parrotfish, phase (initial phase or terminal phase), estimated size of the individual, and counted the number of bites taken on live coral. We only used data from fishes with a fork length >10 cm for analyses because the foraging behavior of fishes below this size was often difficult to observe and thus the quality of such data was questionable. Excluding these fishes from analyses likely had minimal impact on our data, since studies suggest that parrotfishes < 10 cm are not capable of removing a significant amount of coral tissue (Bruggemann et al. 1996, Ruttenberg et al. *unpublished data*).

2.2.4.2 Focal behavioral observations

In addition to remote observations, we also conducted focal behavioral observations of the most common shallow reef-associated parrotfishes found at our study sites from the *Scarus* (*Sc.*) and *Sparisoma* (*Sp.*) genera: *Sc. coelestinus*, *Sc. coeruleus*, *Sc. guacamaia*, *Sc. taeniopterus*, *Sc. vetula*, *Sp. aurofrenatum*, *Sp. chrysopterus*, *Sp. rubripinna*, and *Sp. viride*. We did not collect behavioral data for *Sc. coelestinus*, *Sc. coeruleus*, and *Sc. guacamaia* in St. Croix, as they are absent from these reefs. Divers haphazardly selected approximately six individuals of each species for focal observations, with observations evenly distributed across each site (Table A7). We conducted our observations on or near high-relief habitat and targeted initial phase (IP) individuals >10 cm total length. In addition, we followed terminal phase *Sp. viride* and *Sc. vetula* in St. Croix after we noticed that they had notably different foraging behavior based on personal

observations and video data. However, we did not combine this data with initial phase data for analyses, as these data suggest that phase may influence corallivory rates and we did not collect such data in FKNMS.

During the 20-min focal follows, the divers followed the fish from a close distance (~2 m), and recorded (a) the number of bites, and (b) identified each targeted food item to the lowest taxonomic level or functional group possible (see Chapter 1 and Adam et al. 2015 for detailed methods description and selection criteria). For example, if a parrotfish took a bite on live coral, we marked the coral species or species complex that it targeted. We used this information to estimate site and species-specific (1) corallivory rates (bites hr^{-1}), and (2) corallivory frequency (bites on live coral/total bites, %) for initial phase parrotfishes. We used ANOVA to test for differences between St. Croix and FKNMS in species-specific corallivory rates and corallivory frequency. If the ANOVA revealed significant region or species effect, we conducted post-hoc pairwise comparisons adjusted for multiple comparisons using the Holm's method to identify the specific sources of variation (Holm 1979).

2.2.5 Corallivory events by parrotfishes on specific coral species

We combined the total corallivory events (one foraging bout by a unique individual) by each parrotfish species on specific coral species from focal observations, remote footage and opportunistic *in situ* observations of corallivory across all years of observations in both regions to determine whether different species of corals are fed on by different species of parrotfishes (Table 2).

2.2.6 Corallivory impacts on coral reefs

2.2.6.1 Corallivory intensity

We combined data from focal observations with parrotfish density estimates and bite scar size estimates (Ruttenberg et al., *unpublished data*) to calculate predictions for the (1) mean corallivory intensity on live coral per coral area (bites on live coral m⁻² day⁻¹), and (2) the percent of live coral area grazed per year by all initial phase parrotfishes in FKNMS, St. Croix and Buck Island South Forereef (Buck SoFR). We calculated corallivory intensity as the mean species-specific bite rate (converted to bites day⁻¹) multiplied by the mean number fish of that parrotfish species at the given site per m² live coral. We derived live coral area estimates from the total percent cover of coral as estimated from benthic surveys in St. Croix and coral surveys in FKNMS. We calculated the percent of live coral area grazed per year by accounting for the area of a single bite taken by an individual of a given species and length.

To test for an effect of region on corallivory intensity and percent of coral area grazed per day across regions we used either ANOVA or the nonparametric equivalent Kruskal-Wallis rank (when data were not normal or variance was unequal as tested for with Shapiro–Wilk test and Cochran’s test, respectively). If the test revealed a significant effect, we conducted post-hoc pairwise comparisons adjusted for multiple comparisons using the Holm’s method using either TukeyHSD or Dunn’s multiple comparisons depending on whether the test was an ANOVA or the non-parametric equivalent, respectively, to identify the specific sources of variation (Holm 1979).

2.2.6.2 Corallivory rates and coral cover

To test if there is a correlation between the corallivory frequency (n bites on live coral/total bites, %) by initial phase *Sp. viride* and absolute coral abundance (% cover) at each

site we combined our FKNMS and St. Croix behavioral observation data with that from Bonaire on three reef types (shallow reef, gorgonian zone, and drop off slope) collected in 1989-1990 (Bruggemann et al. 1994c). We selected *Sp. viride* for this analysis because it is the most abundant and dominant corallivore in the Caribbean based on this study and previous studies (see Bonaldo et al. 2014). We ran a single-term linear regression model with corallivory frequency versus the percent cover of coral species commonly preyed upon by corallivorous parrotfishes, where study site ($n=9$) was the level of replication.

2.3 RESULTS

2.3.1 Parrotfish density and coral abundance

Parrotfish density ranged between 1.96 ± 0.22 and 5.09 ± 1.28 fish/100m² and parrotfish biomass ranged between 641 ± 91 and 3065 ± 750 g/100 m². There was a significant effect of site on parrotfish density (ANOVA $F_{5,25}= 2.87$, $P = 0.035$; Figure 5a) and parrotfish biomass (ANOVA $F_{5,25}= 3.85$, $P = 0.01$; Figure 5b). Post-hoc pairwise comparisons indicated that the mean total parrotfish density (data presented as mean \pm SE fish 100 m⁻²) for Cane Bay (1.96 ± 0.22) was significantly lower than Molasses reef (5.16 ± 0.57) (Table A8a). Post-hoc comparisons did not reveal any significant differences in total parrotfish biomass between sites; however, Cane Bay and Long Reef were lower than Buck SoFR, French Reef and Molasses based on significant, non-adjusted p-values (Table A8b).

Benthic and coral surveys in St. Croix and FKNMS, respectively, show that total coral cover for coral species commonly found with grazing scars (see next section) varied among regions (St. Croix: $7.1 \pm 0.4\%$, Buck SoFR: 12.0 ($n = 1$), FKNMS: $3.6 \pm 1.70\%$, respectively), but there was no effect of region on total coral cover ($X^2=3.7$, $df=2$, $P = 0.16$; Wilcoxon signed-

rank test; Figure 6). Coral cover for all individual coral species except *Agaricia* spp., *A. palmata*, and *S. siderea* was higher on St. Croix reefs than FKNMS reefs (Table A9a) but these trends were non-significant (Wilcoxon, $P_{\text{adj}} > 0.05$; Figure 6; Table A9b). *Orbicella* species dominated the coral cover on all reefs (Buck SoFR: 11.44 %, St. Croix: $2.12 \pm 0.07\%$) and FKNMS reefs ($1.57 \pm 1.09\%$).

2.3.2 Identification of corals preyed on by parrotfishes

Predation scar surveys revealed that seven total coral species were preyed on by parrotfishes in FKNMS and St. Croix (Table 3; Figure 7). Across all reefs, *Porites porites* SC and *Orbicella* spp. had the highest incidences of corallivory, with 21 and 10% of colonies showing predation scars, respectively (Table 3). However, the frequency of scars on specific coral species (n colonies of coral species i with scars/total n colonies with scars, %) differed with both region and coral species (ANOVA, $F_{30,143} = 5.82$, $P < 0.0001$). For example, we found predation scars on *Agaricia* spp., *M. cavernosa*, and *S. siderea* colonies on FKNMS reefs but no scars on these coral species on St. Croix reefs. There was no difference in relative scar frequency on *P. astreoides*, *Porites porites* SC and *Orbicella* spp. colonies on FKNMS reefs and St. Croix reefs (Tukey post hoc, $P_{\text{adj}} > 0.05$; Figure 7a). In addition, the density of predation scars per unit area live coral also differed with coral species (ANOVA, $F_{30,143} = 5.82$, $P < 0.0001$) but not across regions (ANOVA, $F_{2,143} = 0.83$, $P = 0.44$) (Figure 7b). Specifically, across all regions there was a greater density of predation scars on *P. astreoides* and *Porites porites* SC than any other coral species (Tukey post hoc, $P_{\text{adj}} > 0.05$). *S. siderea* colonies had a greater density of predation scars (67.1 ± 12.2 scars m^{-2} ; Tukey post hoc, $P_{\text{adj}} < 0.05$) and relative scar frequency ($22.8 \pm 1.47\%$; Tukey post hoc, $P_{\text{adj}} < 0.01$) on FKNMS reefs than St. Croix and Buck SoFR reefs, which did not have any scars on this species.

The two selectivity metrics (colony-based and area-based) consistently showed that parrotfishes on both St. Croix and FKNMS reefs selected *Porites porites* SC corals (Figure 8). However, several corals showed contrasting patterns of selectivity based on the two metrics. For example, the colony-based metric showed that *Agaricia* spp. and *P. astreoides* in FKNMS were selected against and in proportion to their abundance, respectively. Yet, the area-based metric showed that parrotfishes in FKNMS significantly preferred *Agaricia* spp. and *P. astreoides*. Based on both metrics, parrotfishes preferred *S. siderea* in FKNMS, but selected against this species in St. Croix.

2.3.3 Behavioral observations to identify corallivorous parrotfishes

Focal observations, remote footage, and opportunistic observations of parrotfishes revealed that multiple parrotfish species in both regions contributed to corallivory events; however, these events were very rare (~250 events in nearly 450 hours of observations; Table 2). During our focal fish follows, we observed corallivory by *Sc. guacamaia*, *Sc. taeniopterus*, *Sc. vetula*, *Sp. aurofrenatum*, *Sp. rubripinne* and *Sp. viride* in FKNMS, and by *Sc. taeniopterus* and *Sp. viride* in St. Croix (Figure 9). There was a significant effect of species on corallivory rate (ANOVA, $F_{8,36} = 4.10$, $P < 0.01$) and corallivory frequency (ANOVA, $F_{8,36} = 5.23$, $P < 0.001$) but no interactive effect of region and species on either variable (rate: ANOVA, $F_{8,36} = 0.82$, $P = 0.62$; frequency: $F_{8,36} = 0.76$, $P = 0.66$). *Scarus guacamaia* had a higher corallivory rate and corallivory frequency than all other parrotfish species except *Sp. viride* and *Sc. taeniopterus* (post hoc Tukey tests, $P < 0.01$ for all comparisons). While *Sp. viride* had a greater corallivory rate and corallivory frequency (%) on live coral in St. Croix than FKNMS, these trends were non-significant (post hoc Tukey tests, $P > 0.05$). Based on corallivory rates and bite frequency on

live coral, the main corallivores in St. Croix were *Sp. viride* and to a lesser extent *Sc. taeniopterus*, and in FKNMS *Sp. viride* and *Sc. guacamaia*, and to a lesser extent *Sc. taeniopterus* and *Sc. vetula*.

2.3.4 Corallivory events by parrotfishes on specific coral species

During focal, remote and opportunistic observations of parrotfishes, we observed corallivory events on nine total coral species in FKNMS (Figure 10a) and three in St. Croix (Figure 10b). Three parrotfish species (*Sp. viride*, *Sc. taeniopterus*, *Sc. vetula*) targeted three coral species or species complexes (*Orbicella* spp., *P. astreoides*, *Porites porites* SC) in St. Croix. However, a greater diversity of parrotfish species targeted a larger variety of corals in FKNMS. In FKNMS, *S. siderea* was preyed on by all corallivorous species in ($n = 27$), and was preyed on most by *Sc. coelestinus* ($n = 7$, 26%) and *Sp. viride* ($n = 6$, 22%; Table 2). In St. Croix, *Orbicella* spp. was targeted mostly by *Sp. viride* ($n = 101$, 87%) but mostly by *Sc. vetula* in FKNMS ($n = 3$, 60%). All corallivorous parrotfishes targeted *P. astreoides* in both St. Croix and FKNMS. Most of the foraging bouts on *Porites porites* SC in both regions were by *Sp. viride* (FKNMS: $n = 74$, 85%, St. Croix: $n = 18$, 95%). See Table 2 and Figure 10 for additional comparisons.

2.3.5 Corallivory impacts on coral reefs

Different species of parrotfishes contributed differently to total corallivory intensity across our study regions (bites on live coral $\text{m}^{-2} \text{day}^{-1}$; Kruskal-Wallis, $X^2 = 20.7$, $P < 0.01$), but corallivory intensity did not differ among regions (Kruskal-Wallis, $X^2 = 0.02$, $P = 0.99$). Specifically, corallivory intensity by parrotfishes, as derived from focal observation and parrotfish abundance data (presented as mean bites on live coral $\text{m}^{-2} \text{day}^{-1} \pm \text{SE}$), was $48.5 \pm$

14.2 in FKNMS, 28.2 ± 6.5 in St. Croix, and 33.7 ($n = 1$) at Buck SoFR (Figure 11a). In addition, corallivorous parrotfishes grazed $0.12 \pm 0.05\%$ and $0.19\% \pm 0.05$ of live coral area per day in St. Croix and FKNMS, respectively, and 0.16% of live coral per day at Buck SoFR ($n = 1$). While the total percent of live coral tissue grazed per day by parrotfishes did not vary across regions (Kruskal-Wallis, $X^2 = 1.24$, $P = 0.3$; Figure 11b), parrotfish species differed in their contribution to the total percent of coral area grazed per day (Kruskal-Wallis, $X^2 = 29.8$, $P < 0.001$). The two corallivores absent from St. Croix but present in FKNMS (*Sc. coelestinus* and *Sc. guacamaia*) contributed to 7% of the total corallivory intensity in FKNMS and 13% of the total coral area grazed per day. Lastly, there was a significant positive relationship between site-specific corallivory frequency of initial phase *Sp. viride* (n bites on live coral/total bites, %) and site-specific percent cover of live coral ($R^2 = 0.78$; $p < 0.001$; Figure 12).

2.4 DISCUSSION

Our results show that the foraging patterns of parrotfishes on corals are dynamic and appear to vary with local factors such as coral and parrotfish community composition. While a diversity of parrotfishes targeted live coral at varying degrees within and among regions, our findings support previous work and suggest that *Sparisoma viride* may be one of the most significant corallivores on Caribbean reefs (reviewed by Bonaldo et al. 2014; see also Bruckner and Bruckner 2015). In addition, we provide evidence of species-specific patterns of corallivory by the suite of Caribbean parrotfishes on specific coral species, specifically the ESA-listed *Orbicella annularis* species complex, *Porites astreoides* and the *Porites porites* species complex. Furthermore, our estimates of coral tissue removal rates, although conservative, indicate that although coral and parrotfish abundance and community composition differ across our study

regions, in general, coral reefs in these regions are subjected to relatively similar degrees of corallivory intensity. Lastly, we found that corallivory frequency by an abundant and significant corallivore, *Sparisoma viride*, decreases with low coral cover. While this result suggests that reefs with low coral cover may have lower incidences of corallivory, it is unclear whether the intensity of grazing on a single coral colony increases with a decrease in coral cover across these sites (but see Burkepile 2012). Overall, our findings support previous literature that indicate that corallivory intensity may be restricted to particular coral species and within specific reef habitats (Littler et al. 1989; Rotjan and Lewis 2005; Mumby 2009a; Bonaldo and Bellwood 2011). Such context-dependency of corallivory rates and preferences for specific coral species indicates that site-specific information on these factors will be needed to predict the impact of corallivory in other locations.

Evidence that patterns of parrotfish foraging can be context-dependent (Rotjan and Lewis 2005; Adam et al. 2015a) suggests that the incidence and intensity of parrotfish corallivory could be influenced by local factors such as coral abundance (see Mumby 2009a). To date, few studies have tested how the rate of coral predation scales with coral cover and coral density (e.g. Burkepile and Hay 2010; Roff et al. 2011), and of the studies that have, few have investigated this relationship across a large range in coral cover. Our investigation of corallivory rates over a moderate range in coral cover in St. Croix, Bonaire and FKNMS revealed that corallivory frequency (% of bites on live coral) for *Sp. viride* increases as coral abundance increases (Figure 12). However, we also found that, in general, corallivory intensity was greater on reefs with low coral abundance yet high parrotfish abundance (e.g. FKNMS reefs). While parrotfishes may take fewer bites on live coral as coral abundance decreases, corallivory intensity may remain high if there is a high abundance of corallivores on reefs with low coral cover. Under this scenario,

corallivory may be relatively intensive on each coral colony. Such high-intensity grazing on coral tissue can cause whole-colony mortality and thereby have a disproportionate impact on the few remaining corals on the reef (Rotjan and Lewis 2005; Rotjan et al. 2006). Further research on the dynamic between coral abundance, corallivory rates, and the impact of corallivory on coral health and survivorship is essential to accurately predict the impact of parrotfishes on corals in Caribbean, especially in areas with high corallivore abundance and low coral cover (Hughes and Tanner 2000).

While studies have predicted the net algae or carbon removal by herbivores across coral reefs using herbivory rates and estimated grazing parameters (Carpenter 1988; Hamilton et al. 2014; Bozec et al. 2016), to our knowledge this is the first study to generate estimates for coral tissue loss using corallivory rates from behavioral observations in the Caribbean (but see Hoey and Bellwood 2008; Bellwood et al. 2012). We estimated that parrotfishes across our study sites in St. Croix and FKNMS can remove up to 0.20% of live coral tissue per day. However, these estimates are conservative because we applied initial phase corallivory rates to terminal phase individuals. In doing so, we accounted for the abundance of terminal phase parrotfishes in the calculations for corallivory intensity, with the caveat being that the corallivory rates were likely underestimated, since some terminal phase parrotfish species (e.g. *Sp. viride*) may contribute disproportionately to corallivory (Table 2) (Bythell et al. 1993; Bruggemann et al. 1994c, a, 1996; Bruckner and Bruckner 1998; Van Rooij et al. 1998; Bruckner et al. 2000; Rotjan and Lewis 2008; Mumby 2009a). Nonetheless, there was a weak trend in higher coral tissue removal rates by parrotfishes in regions with the greatest density of parrotfishes (i.e. FKNMS and Buck Island). While further studies are needed to determine whether the non-significant difference in corallivory intensity across regions is an artifact of small sample sizes, it appears that the absence

of two important corallivores, *Sc. coelestinus* and *Sc. guacamaia*, from St. Croix reefs contributes to the difference in corallivory rates between regions. In addition, although *Sp. viride* had nearly 3 times higher corallivory rates in St. Croix than FKNMS, the relatively low abundance of *Sp. viride* across St. Croix reefs reduced their total corallivory impact. These findings indicate that site-specific variables such as parrotfish abundance, assemblage composition, and corallivory rates may have a significant effect on the predictions of the total impact of parrotfishes on coral reefs and thus warrant further investigation. In addition, future observations of terminal phase parrotfishes, particularly *Sp. viride* and *Sc. vetula*, are needed to determine whether it is necessary to account for the phase of each parrotfish when predicting the total corallivory intensity and coral tissue removal on coral reefs.

In addition to corallivory rates and intensity, we also found that the coral species targeted by corallivorous parrotfishes varied across regions. Specifically, more parrotfish species targeted a greater diversity of corals in FKNMS than in St. Croix. Whether the diversity in coral species targeted by parrotfishes is a function of corallivore species richness rather than other local factors such as abundance of preferred corals remains unclear. When preferred food items are scarce, some Caribbean parrotfishes with high dietary specialization may have broader diets (Chapter 1). Likewise, the rarity of *O. annularis* in FKNMS and St. Croix (<2% cover in FKNMS and St. Croix, but 11% cover in Buck SoFR), a preferred coral by parrotfishes (Bythell et al. 1993; Bruckner et al. 2000; Rotjan and Lewis 2006), may cause parrotfishes to expand their diet breadth and increase predation on other coral species. While we see evidence that parrotfishes target a larger diversity of coral species in FKNMS (i.e. *Agaricia* spp., *M. cavernosa*, *S. siderea*), as seen in previous studies (see Rotjan and Lewis 2006; Burkepile 2012), this does not appear to be the case on St. Croix reefs which have lower corallivore species richness. Although additional

studies are needed to validate this finding that coral community composition may influence coral selectivity, our findings suggest that the high predation intensity found in FKNMS on a greater diversity of coral species may be explained by both the low abundance of preferred coral species and the higher corallivore species richness and abundance as compared to St. Croix reefs.

Similar to the variability we found in corallivory on specific coral species, our two selectivity metrics (area-based and colony-based electivity) show that the preferences by parrotfishes for specific coral species were relatively inconsistent across all reefs. Based on both selectivity metrics, parrotfishes preferentially targeted *Porites porites* SC coral colonies. However, the two metrics did not always show the same patterns; for example, the area-based electivity suggested that parrotfishes in FKNMS prefer *Agaricia* spp. and *P. astreoides*, while the colony-based electivity showed no preference or avoidance for these corals (i.e. parrotfishes targeted them in proportion to colony abundance). The colony-based metric likely underestimates the true abundance of coral tissue available for parrotfishes to prey upon by counting small and large corals equally and likely underestimates the selectivity for small, but abundant coral colonies. Therefore, the discrepancy we found for *Agaricia* spp. and *P. astreoides* selectivity was likely driven by their high density yet low colony area (i.e. relatively large numbers of small colonies, such that area of live coral tissue available for the parrotfishes to bite is low)—traits that are common for these two coral species (Smith et al. 2011). Accounting for this limitation in colony-based electivity, we conclude that parrotfishes preferentially targeted *P. astreoides*, in addition to *Porites porites* SC corals across all reefs. This finding is generally consistent with previous literature (Roff et al. 2011; Burkepile 2012; Bonaldo et al. 2014). It also appears that *Orbicella* species colonies are disproportionately targeted by parrotfishes at Buck SoFR; however, additional data from Buck Island are needed to validate this claim. These

findings further highlight the need to focus corallivory research towards understanding the drivers of corallivory and scar healing rates on these three coral species, especially on Buck Island because *Orbicella annularis* is listed as threatened under the US Endangered Species Act (NMFS and NOAA 2014).

There are also noteworthy differences in parrotfish species preferences for corals in St. Croix versus FKNMS. Specifically, we observed many incidences of corallivory on *S. siderea* in FKNMS during behavioral observations ($n = 9$ events from focal follows) but we did not witness any in St. Croix. Likewise, coral surveys revealed that parrotfishes selected against *S. siderea* in St. Croix but they preferentially targeted this species in FKNMS. Two corallivorous parrotfishes, *Sc. coelestinus* and *Sc. guacamaia*, that were present in FKNMS but absent from St. Croix, contributed to approximately half of these events on *S. siderea*. Although we cannot conclude from behavioral observations that these parrotfishes prefer *S. siderea* (i.e. target this species at a proportion greater than its abundance), our selectivity measures from bite scar data in combination with the behavioral data suggest that *Sc. coelestinus* and *Sc. guacamaia* may be the major species that target *S. siderea*. If so, this may indicate that the absence of *Sc. coelestinus* and *Sc. guacamaia* from St. Croix could release certain corals from predation pressure. However, it will be necessary for future studies to account for differences in coral cover in the interpretation of behavioral observations to validate this claim. Such information will be valuable to elucidate the influence of parrotfish assemblage composition on coral selectivity irrespective of coral cover.

2.4.1 Future Directions and Implications

A limitation of many previous studies that have investigated corallivory rates from predation scar data is that the standing stock of bite scars (i.e. what we observe on corals) is a function of both corallivory rate and scar healing time. Thus, scar densities may inaccurately

represent the true intensity rates by parrotfishes depending on the regeneration rate of that specific coral species. For example, the abundance of grazing scars on *P. porites* may underestimate the intensity of parrotfish corallivory, as growth rates of *P. porites* are up to 5-fold that of *O. annularis* (Davies 1990). The data generated in this study, with the addition of more sampling, can provide a more accurate representation of the corallivory intensity by parrotfishes on specific coral species. For example, not only did we find a relatively high density of scars on *P. porites*, but even more so in FKNMS where parrotfishes appear to have relatively high corallivory intensity and abundance of *Sp. viride*, a predator of *P. porites* (Figure 10). Future studies can use these data to generate estimates of healing rates on specific coral species by accounting for the relationship between corallivory by an individual parrotfish and the standing stock of grazing scars on a given coral colony. Understanding the equilibrial dynamic between injury and recovery will help scientists determine the relative impact of predation events that vary in frequency and the amount of tissue removed.

In addition, high corallivory intensity by parrotfishes may significantly increase the area of total coral tissue loss relative to live coral tissue. While some studies have emphasized the importance of understanding the impact of grazing scar size on coral tissue regeneration rates (Meesters et al. 1994, 1997; Bruckner and Bruckner 1998; Bruckner et al. 2000; Mumby and Steneck 2011), the factors driving the fate of bite scars remain poorly understood. There is need for future studies to determine the threshold at which the total scar size significantly decreases the coral's ability to recover from a predation event. This information can reveal insight into the importance of high intensity grazing relative to the total area of live coral removed by parrotfishes on coral survivorship and health, particularly if such metrics are context-dependent. This can improve our understanding of the complex and dynamic relationship between

corallivory frequency, physical damage to the coral colony by predation scars and healing rates of coral tissue after predation events.

2.5 CONCLUSION

In this study, we improved our understanding of the dynamic relationship between corallivores and corals by incorporating data from both coral predation scars and behavioral observations of parrotfishes. While we estimate that parrotfishes can consume up to 5% of coral tissue on an annual basis, understanding the factors that impact coral healing rates such as bite scar size and density will be critical to understand the full impact of corallivory on reefs. In addition, our results provide further evidence that corallivory rates and selectivity of certain coral species by parrotfishes are context-dependent, which indicates that accurately predicting corallivory intensity may require detailed site-specific data. Lastly, we provide strong evidence that corallivory rates and intensity are related to coral abundance and community composition. Understanding the factors that influence the incidence and intensity of corallivory, in addition to the long-term fate of parrotfish bite scars on corals, will help us better predict the net ecological impact of parrotfish grazing and corallivory on corals.

3. TABLES

Table 1: Linear model output for tests of the effect of resource abundance (% cover preferred food) and species on (a) diet specialization, (b) foraging distance and (c) bite rate. LS=less specialized, MS= more specialized.

Variable	Specialization	R^2 *	Term	Sum-sq	df	F	P		
(a) Diet specialization	LS	0.151	% cover	2.31E-04	1	0.58	4.61E-01		
			pref. food						
			species	3.01E-04	2	0.38	6.94E-01		
			Residuals	5.61E-03	14				
			MS	0.626	% cover	7.03E-04	1	4.26	5.81E-02
					pref. food				
species	1.34E-03	2			4.06	4.08E-02			
(b) Foraging distance	LS	0.421	Residuals	2.31E-03	14				
			% cover	6.45E-01	1	0.33	5.78E-01		
			pref. food						
			species	3.24E+00	2	0.82	4.62E-01		
			Residuals	2.78E+01	14				
			MS	0.771	% cover	1.36E+02	1	15.30	1.57E-03
pref. food									
species	7.13E+02	2			40.17	1.59E-06			
(c) Bite rate	LS	-0.088	Residuals	1.24E+02	14				
			% cover	1.40E+02	1	0.70	4.18E-01		
			pref. food						
			species	3.08E+03	2	7.67	5.62E-03		
			Residuals	2.81E+03	14				
			MS	0.906	% cover	7.89E+02	1	7.35	1.69E-02
pref. food									
species	1.85E+03	2			8.61	3.65E-03			
		Residuals	1.50E+03	14					

*Adjusted R^2 values

Table 2: Summary table of the total hours of observation for remote footage and focal behavioral observations for each parrotfish species and the associated total number of corallivory events (bouts) at both FKNMS (FL) and St. Croix (STX) study sites. Table shows whether corallivory by each species has been documented in previous literature and whether this study documented any new target coral species. These data also include observations from Elbow Reef in FKNMS (2013) and opportunistic observations from 2014.

Species	Region	Hours Remote Footage	Hours Focal Obs.	Total Events: Remote (R), Focal (F), Opportunistic (O)	Target Corals: Remote	Target Corals: Focal Obs.	Obs. in prev. studies ?	Corals Targeted (prev. lit)	New coral spp. doc.?
<i>Sc. coelestinus</i>	FL	168	7.9	2R, 2F, 3O	<i>S. siderea</i>	<i>P. astreoides</i> (n=1)	Y; Randall 1967, 1974	UK	Y, 2
<i>Sc. coeruleus</i>	FL	168	8.5	—	—	—	N	—	—
<i>Sc. guacamaia</i>	FL	168	7.3	31F, 1R, 2O	<i>C. natans</i> (n=1)	<i>P. astreoides</i> <i>P. porites</i> <i>S. siderea</i> (n=2), <i>Millepora</i> spp. (encrusting), <i>M. mirabilis</i> (n=3)	Y; Glynn 1997	UK	Y, 8
<i>Sc. taeniopterus</i>	FL	168	8.3	3R, 7F	<i>P. porites</i> , <i>S. siderea</i>	<i>Agaricia</i> spp., <i>P. astreoides</i> , <i>S. siderea</i> , <i>P. porites</i> , <i>Millepora</i> spp., <i>P. astreoides</i> (n=1), <i>P. porites</i> (n=1), <i>O. annularis</i>	N	—	Y, 6
	STX	177	5.0	8R, 8F	<i>O. annularis</i>				
<i>Sc. vetula</i>	FL	168	6.6	5R, 5F, 1O	<i>Orbicella</i> spp., <i>P. porites</i> , <i>S. siderea</i>	<i>P. astreoides</i> (n=1), <i>S. siderea</i>	N	—	Y, 2
	STX	177	6.3	1 F (TP)	<i>P. astreoides</i>	<i>P. astreoides</i> (n=1, TP)			
<i>Sp. aurofrenatum</i>	FL	168	8.0	7R	<i>P. porites</i> , <i>S. siderea</i> , <i>Orbicella</i> spp.	<i>Millepora</i> spp. (encrusting) (n=1)	Y; Miller & Hay 1998	<i>P. divaricata</i>	Y, 3
	STX	177	6.3	—	—	—			
<i>Sp. chrysopterus</i>	FL	168	6.8	1R	<i>P. porites</i> (n=1)	—	N	—	Y, 1
	STX	177	6.3	—	—	—			

Note: UK=unknown, TP=terminal phase; no phase indicated means all events by initial phases.

Table 2 Cont'd

Species	Region	Hours Remote Footage	Hours Focal Obs.	Total Events: Remote (R), Focal (F), Opportunistic (O)	Target Corals: Remote	Target Corals: Focal Obs.	Obs. in prev. studies ?	Corals Targeted (prev. lit)	New coral spp. doc.?
<i>Sp. rubripinne</i>	FL	168	8.1	1F	—	<i>S. siderea</i>	N	—	Y, 1
	STX	177	5.6	—	—	—			
<i>Sp. viride</i>	FL	168	8.2	52R, 5F, 1O 27R (TP), 1O (TP)	<i>C. natans</i> , <i>P. porites</i> , <i>S. siderea</i> , <i>P. porites</i>	<i>Agaricia</i> spp., <i>O. faveolata</i> , <i>P. astreoides</i> , <i>Millepora</i> spp. (plating), <i>P. astreoides</i> , <i>P. porites</i> ,	Y	see Bonaldo 2014	Y, 1
	STX	177	6.7	21R, 12F 35R (TP), 35F (TP) 13O (UK)	<i>O. annularis</i> , <i>P. astreoides</i>	<i>O. annularis</i> , <i>O. faveolata</i> , <i>O. franksi</i>			

Note: Obs = observation; UK=unknown; TP=terminal phase; no phase indication means initial phase.

Table 3: Incidences of parrotfish predation on coral species summed across all reefs at St. Croix, Buck Island and FKNMS

Coral Species	Total Colonies	Colonies Preyed On	Percent Preyed On
<i>Porites porites</i> SC	1076	228	21.19
<i>Orbicella</i> spp.	1178	114	9.68
<i>S. siderea</i>	843	58	7.00
<i>P. astreoides</i>	2512	166	6.61
<i>M. mirabilis</i>	144	5	3.47
<i>Agaricia</i> spp.	1264	26	2.06
<i>M. cavernosa</i>	212	2	0.94
<i>C. natans</i>	57	0	0
<i>D. clivosa</i>	59	0	0
<i>D. labyrinthiformis</i>	57	0	0
<i>D. strigosa</i>	547	0	0
<i>M. meandrides</i>	35	0	0
<i>Millepora</i> spp.	628	0	0
<i>S. intersepta</i>	115	0	0
<i>S. radians</i>	67	0	0

Species are ordered in decreasing frequency of predation. Corals with <25 colonies were not included

4. FIGURES

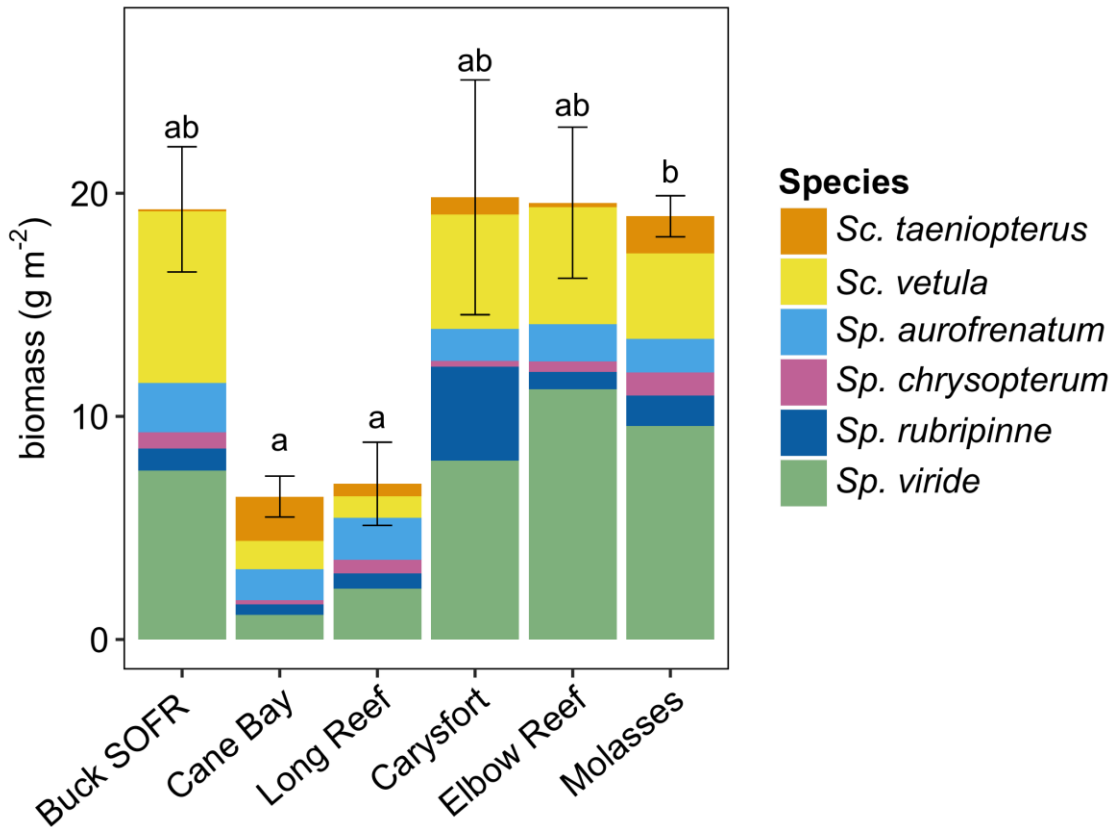


Figure 1: Mean parrotfish biomass estimates by species for each study site. Error bars represent standard error (SE). We calculated means and standard error using biomass estimates for each fish survey transect replicate weighted by the area surveyed in the transect relative to the total area surveyed at the site. St. Croix sites include Buck SOFR, Cane Bay, and Long Reef. FKNMS sites include Carysfort Reef, Elbow Reef and Molasses Reef. Letters above bars represent differences among groups based on TukeyHSD post-hoc analysis.

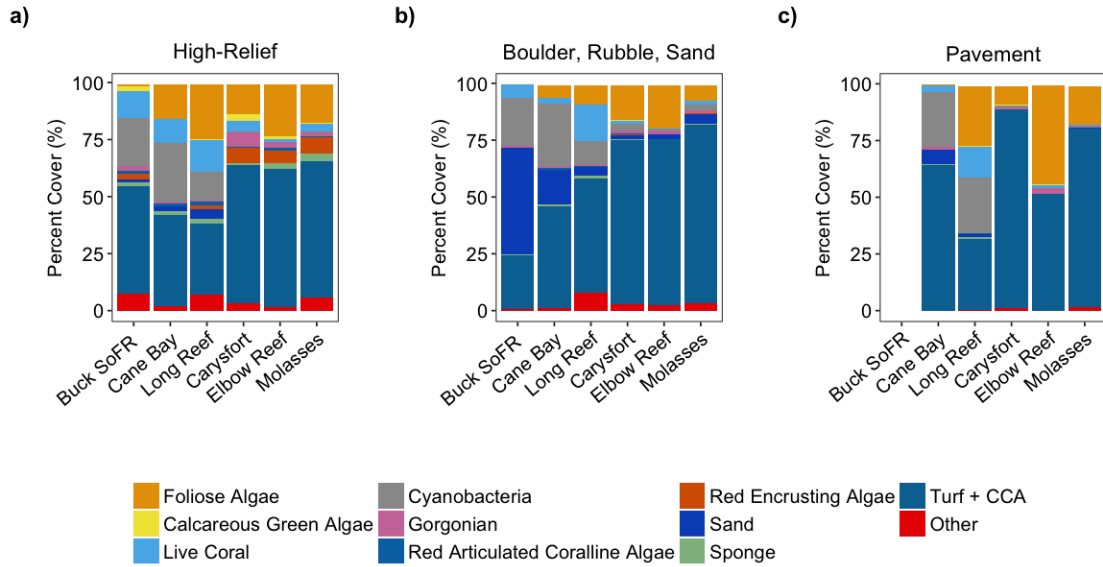


Figure 2: Benthic cover for the main food items targeted by parrotfishes at FKNMS and St. Croix sites across three different substrates: a) High-relief, b) boulder, rubble, sand, and c) pavement. Gorgonians, Sand, and Other are also included in figures to represent the entire benthos, but these are generally not targeted by parrotfishes. Note that there is no data for Buck SoFR on pavement substrate.

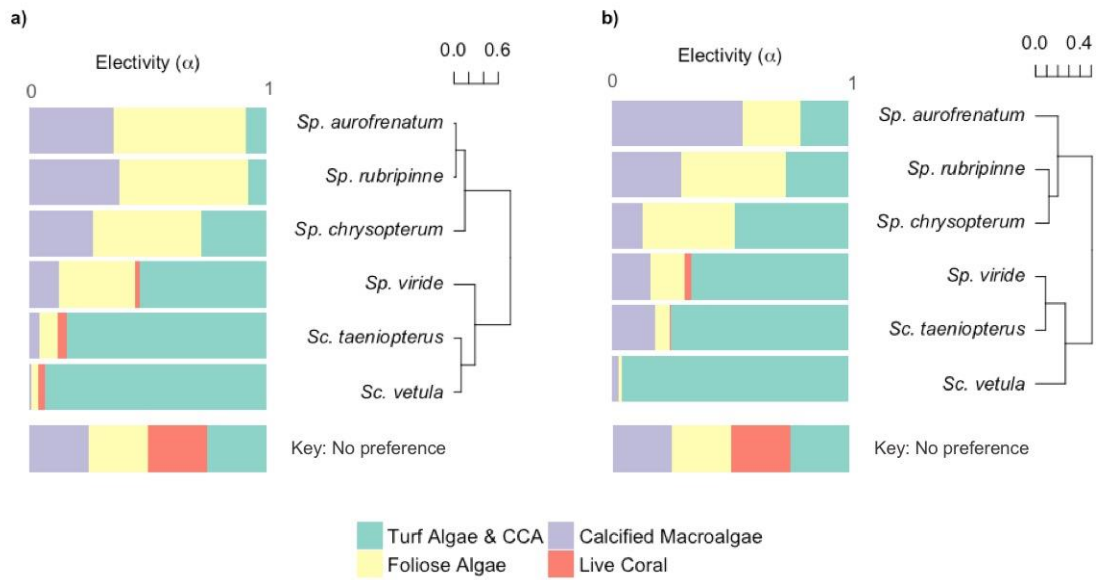


Figure 3: Species-averaged dendrograms using food preference data collected at a) FKNMS, and b) St. Croix. The bar labeled “Key: No preference” represents what the distribution would look like if a species were to exhibit no preference for a food item. Dendrograms for both FKNMS and St. Croix show that parrotfishes cluster into two groups based on their food preference. Bar charts show the mean electivity α , of each food group targeted ($N = \sim 18$ individuals per species; see Table A1 for exact sample sizes).

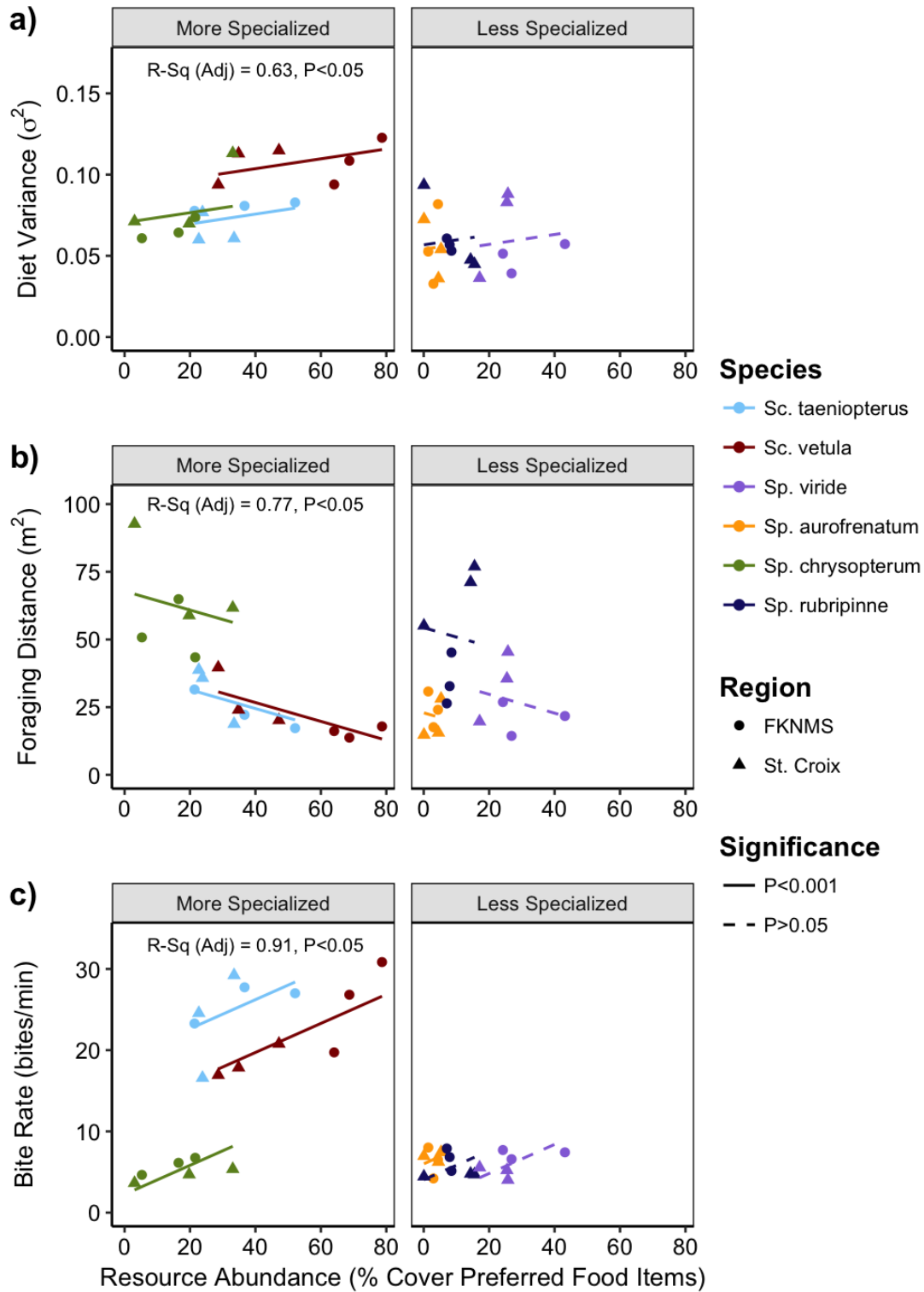


Figure 4: Resource abundance (weighted % cover preferred food items) and a) diet specialization, b) foraging distance, and c) bite rate for more specialized (left panels) and less specialized (right panels) species. Solid lines represent significant and marginally significant ($P = 0.05$) species-level fitted linear model regressions, dotted lines indicate non-significant species-level regressions. FKNMS sites are circles, St. Croix sites are triangles.

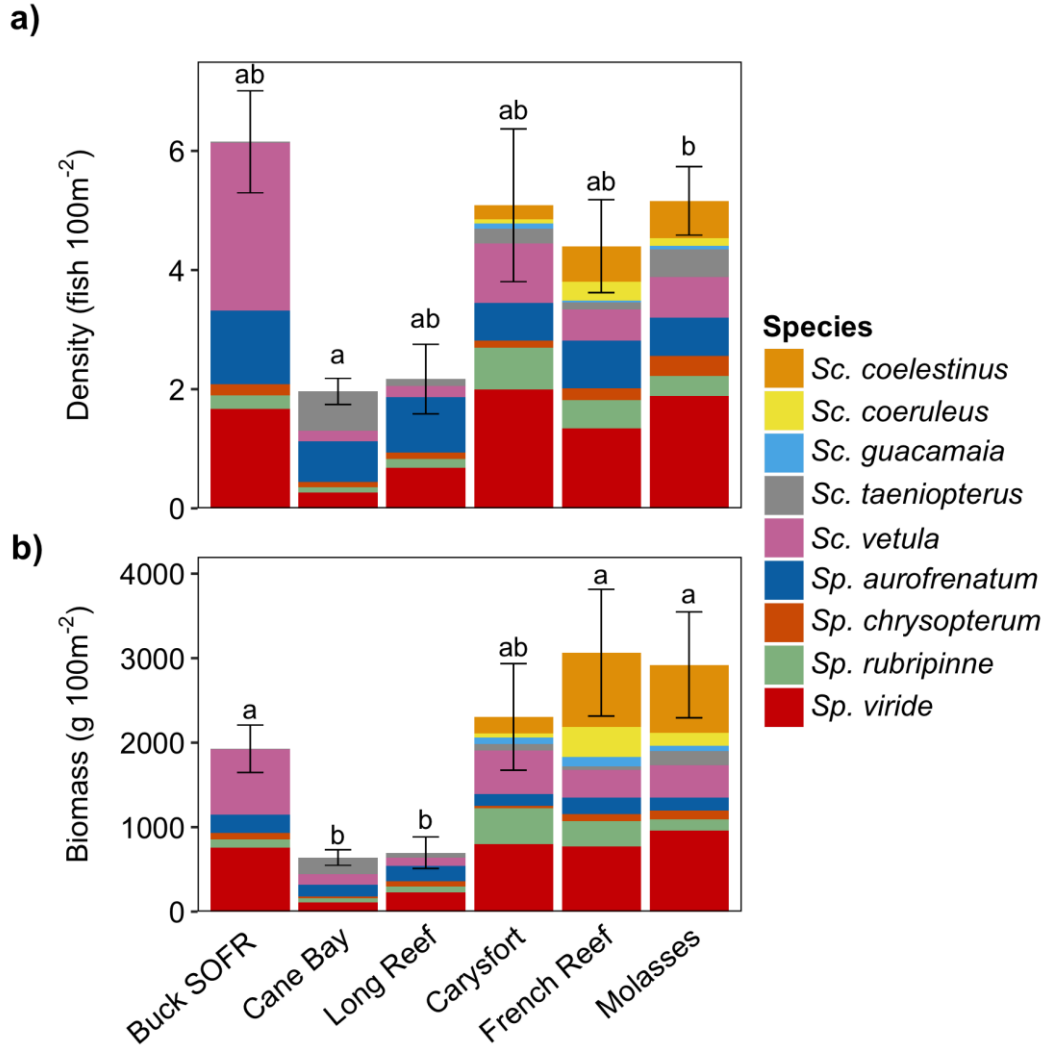


Figure 5: Stacked bar chart of (a) density (weighted mean $n\ 100\ m^{-2} \pm SE$) and (b) biomass (weighted mean $g\ 100\ m^{-2} \pm SE$) of parrotfishes at each study site. Letters represent significant differences between study sites according to pairwise comparisons using the Holms-Bonferroni correction for multiple comparisons. Letters above bars on (b) are based on non-adjusted p-values. St. Croix sites include Buck SoFR, Cane Bay, and Long Reef. FKNMS sites include Carysfort, French Reef and Molasses.

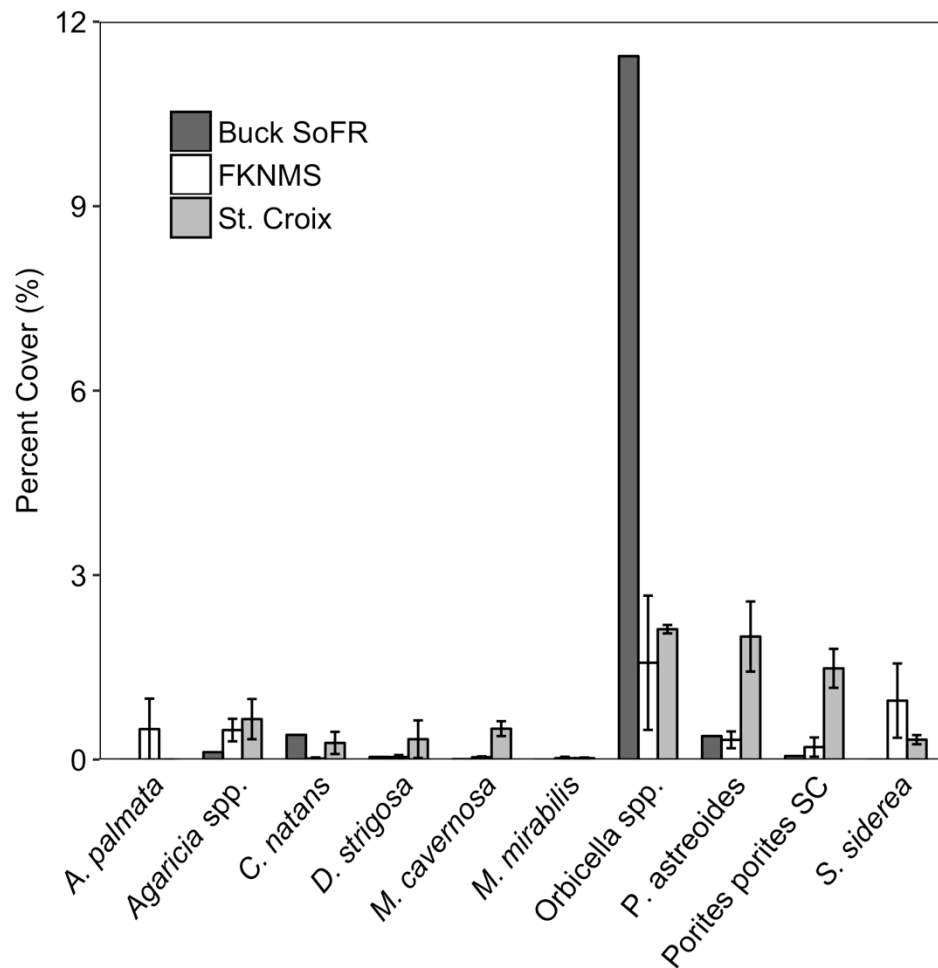


Figure 6: Absolute percent cover (mean \pm SE) of coral taxa preyed on by parrotfishes for each region on high-relief substrate. There was no effect of region on total coral cover and there were no significant differences in coral cover for any coral species between FKNMS and St. Croix. *Porites porites* SC represents the species complex composed of *Porites porites*, *Porites furcata*, *Porites divaricata*. FKNMS percent cover values calculated from coral surveys, while St. Croix and Buck SoFR percent cover values calculated from benthic surveys.

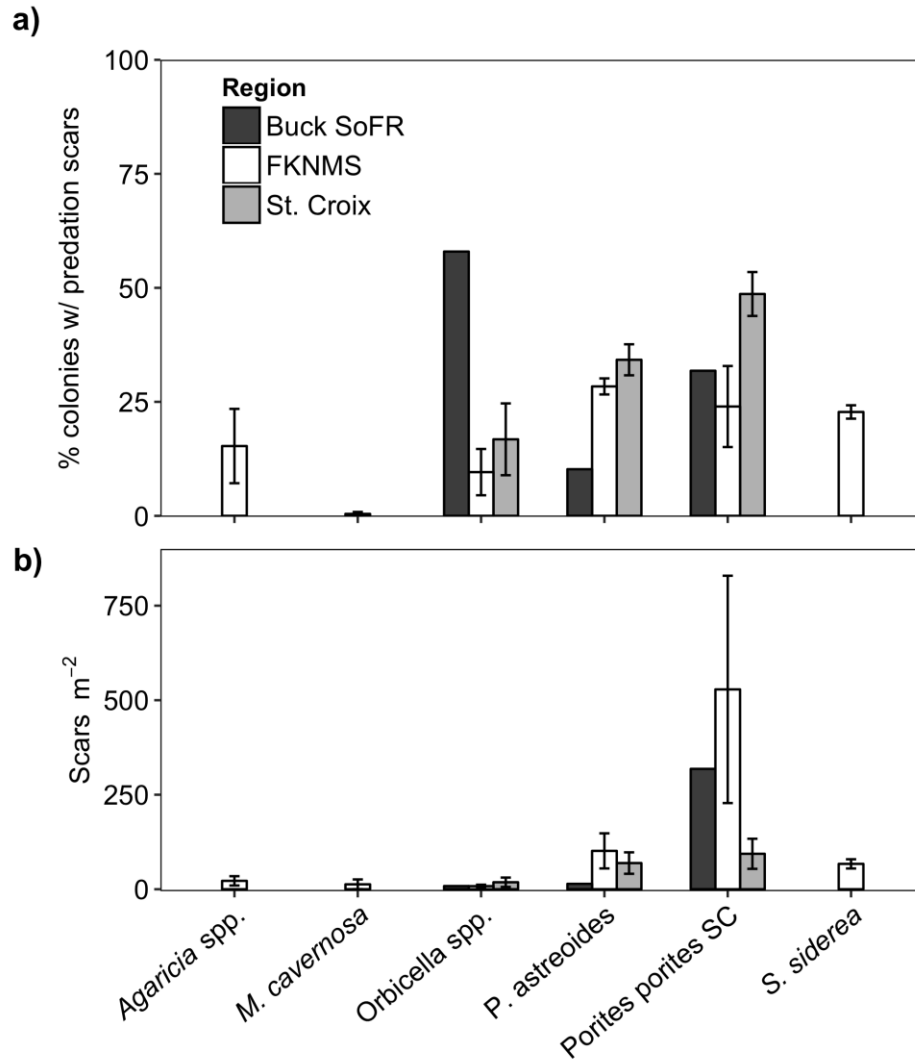


Figure 7: Bar charts showing the (a) percent of coral colonies with predation scars and (b) density of predation scars per area live coral for all regions (mean \pm SE). No bars represent 0 values.

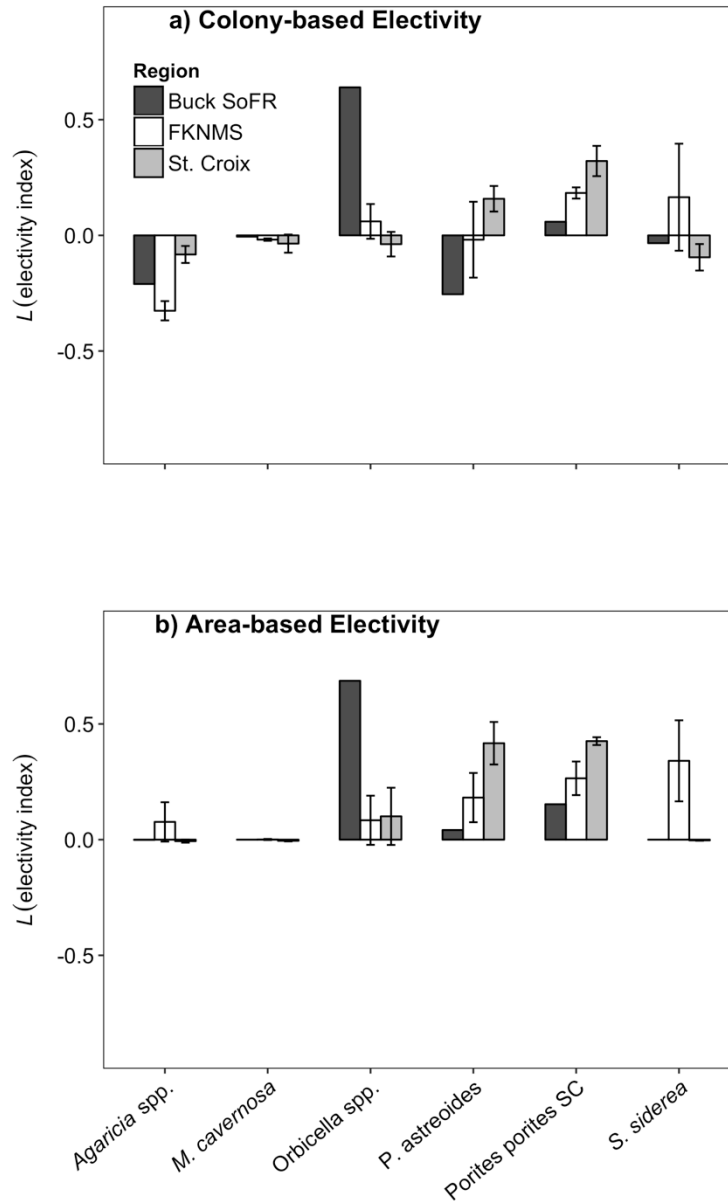


Figure 8: Feeding selectivity for (a) colony-based and (b) area-based electivity of grazing scars on common corals based on Strauss' electivity index (mean \pm 95% CI). Positive significant values indicate that the coral species was preferentially preyed on, while negative significant values indicate that the coral species was avoided.

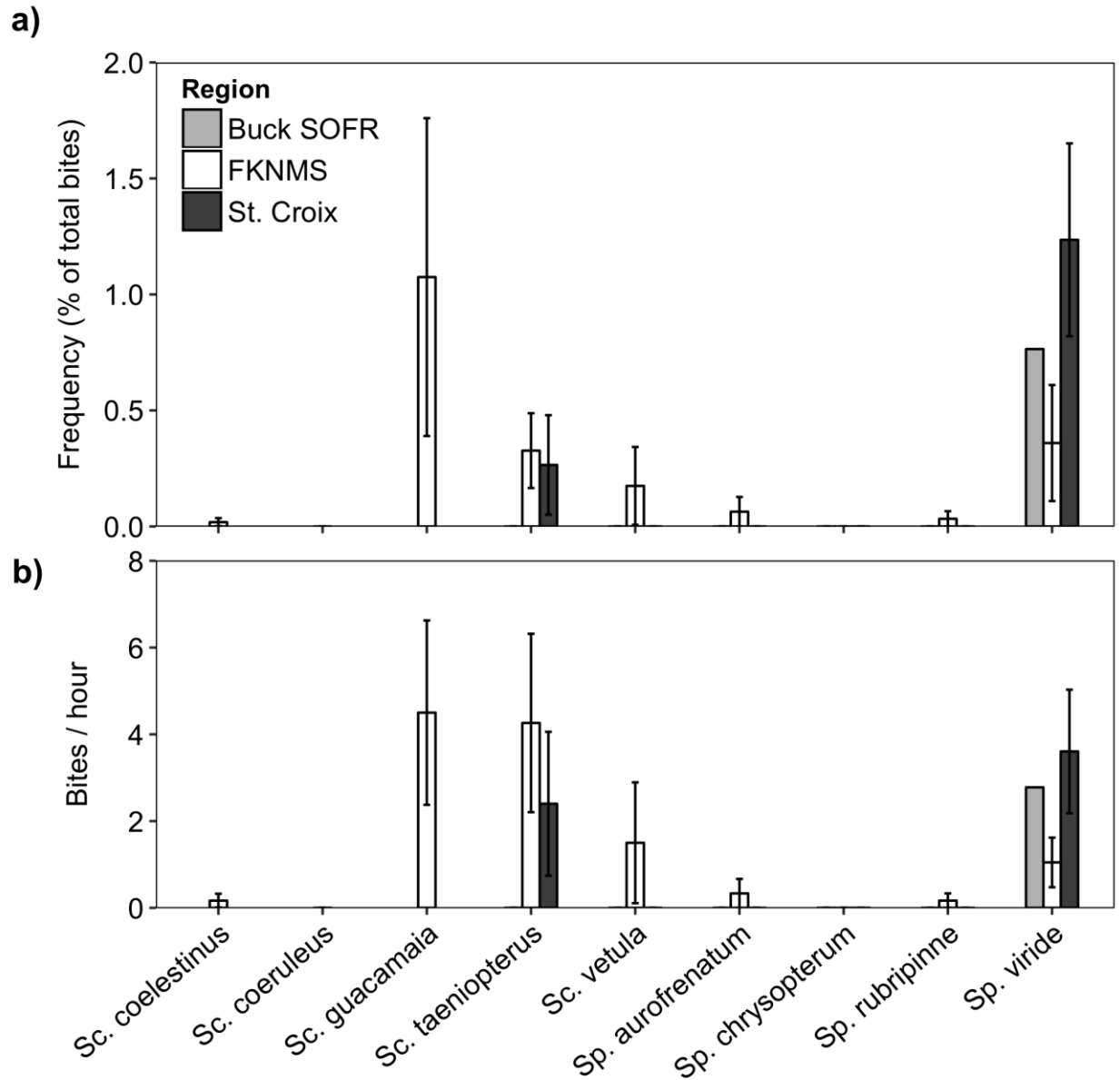


Figure 9: Bar charts showing the (a) frequency (% of bites taken on live coral) and (b) bites on live coral per hour observation for each parrotfish species in FKNMS and St. Croix (mean \pm SE) based on focal behavioral observations. Data for *Sc. coelestinus*, *Sc. coeruleus*, and *Sc. guacamaia* are NA for St. Croix and Buck SoFR, since these species are absent from these reefs. Data are from initial phase parrotfishes only.

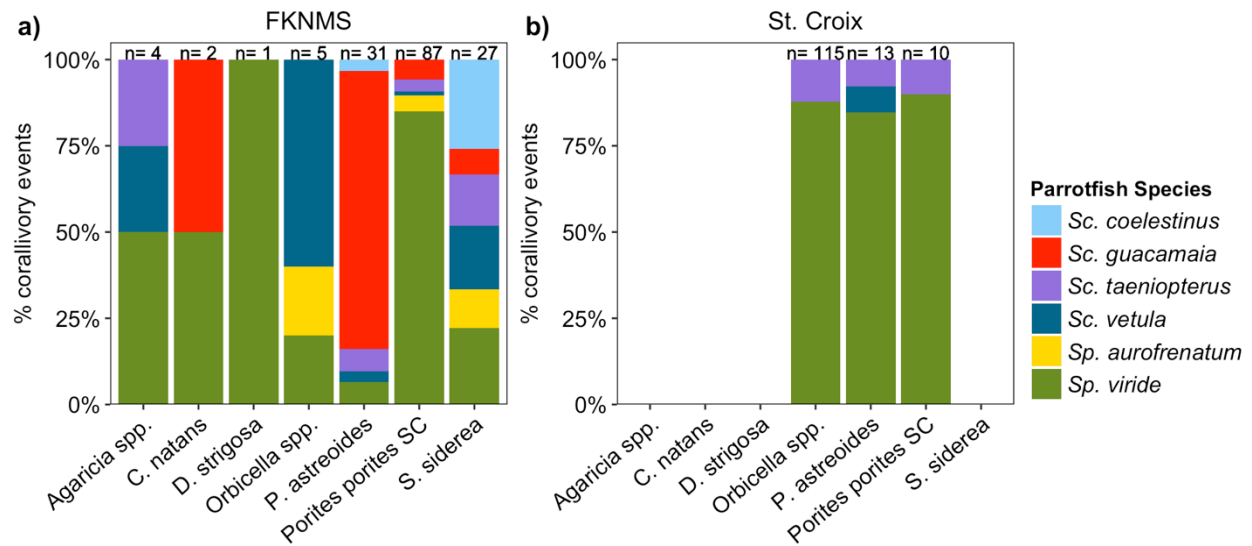


Figure 10: Percent of all foraging bouts on live coral (fish follows, opportunistic observations, and remote footage) by each parrotfish species on different coral species in FKNMS (a) and St. Croix (b). Blank bars represent no corallivory events witnessed on the given coral species. Total foraging bouts on the given coral are represented on the top of each bar.

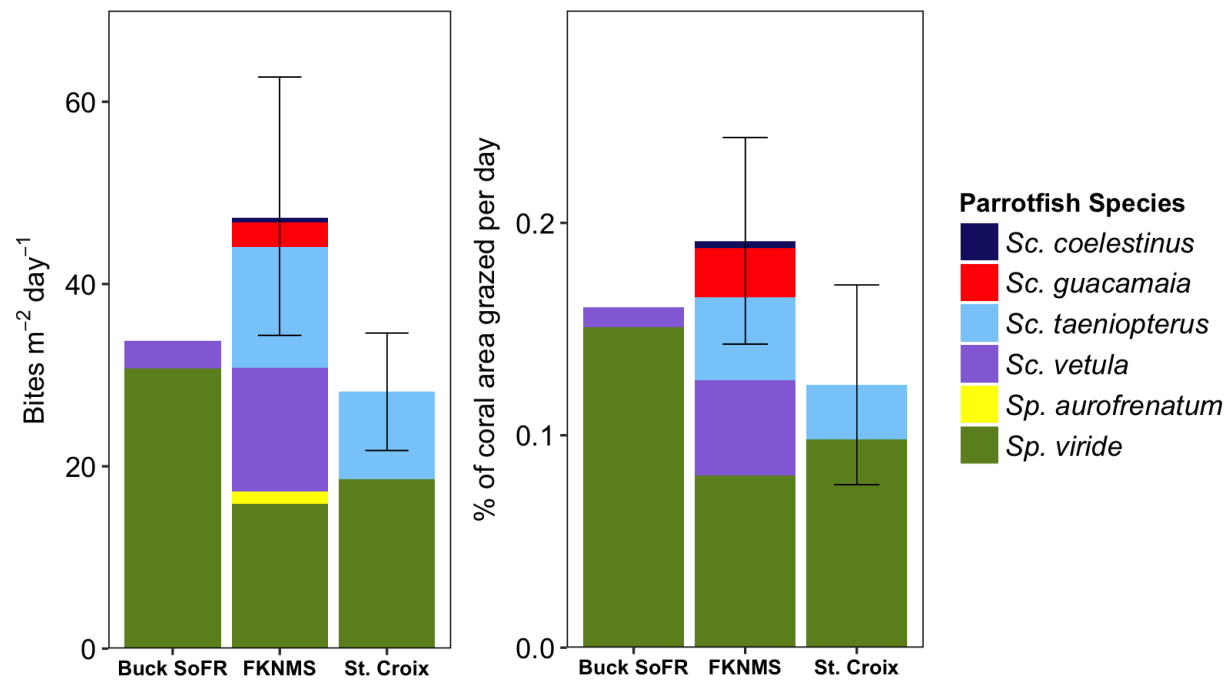


Figure 11: Bar charts representing the (a) mean total corallivory rate per area of live coral (bites $\text{m}^{-2} \text{day}^{-1} \pm \text{SE}$) and the (b) mean total area of live coral that is grazed per year (%) by all parrotfishes ≥ 15 cm in length. Corallivory rates for initial phase parrotfishes were used for terminal phase parrotfishes.

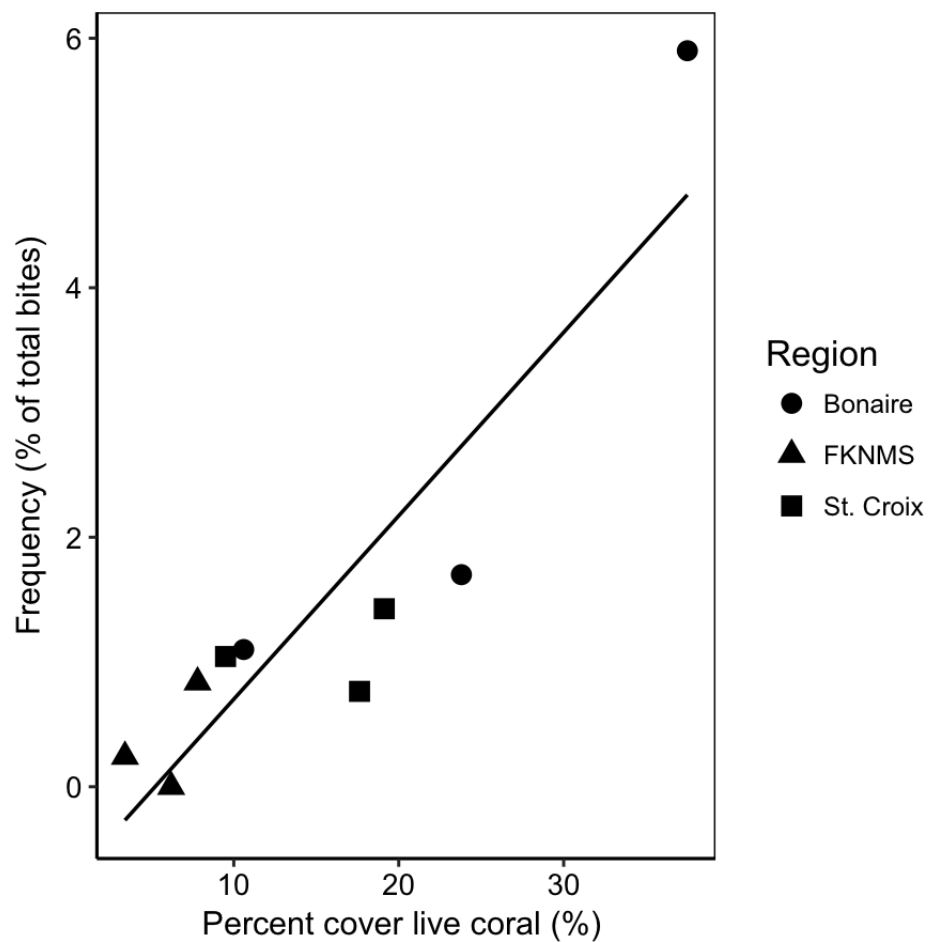


Figure 12: Corallivory frequency (n bites on live coral/total bites, %) as a function of the percent cover of live coral for *Sparisoma viride* (IP only). Corallivory frequency was correlated with percent cover of live coral ($R^2=0.78$; $P < 0.001$). Bonaire data are from Bruggemann et al 1994.

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APPENDIX
Supplementary Figures

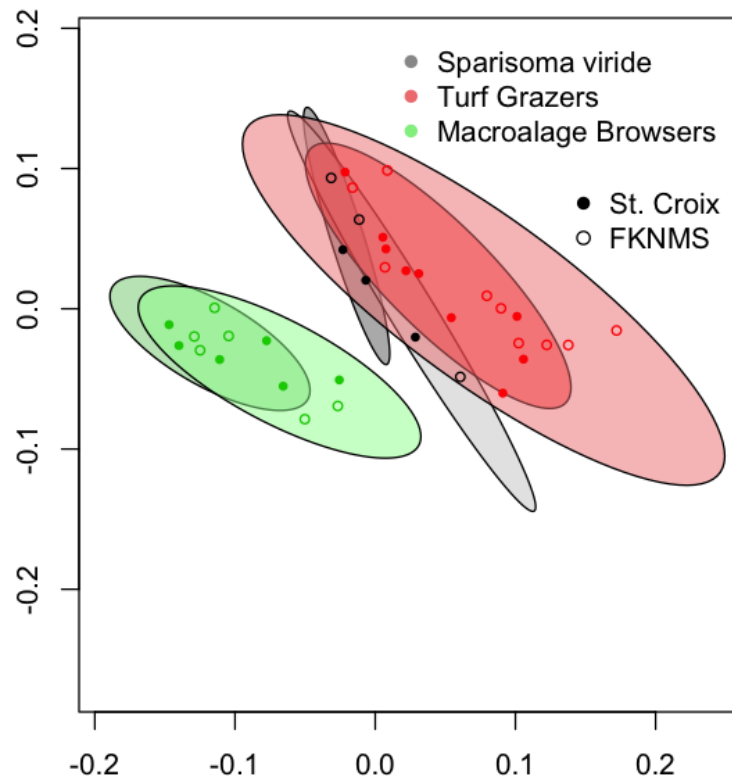


Figure A1: Nonmetric multidimensional scaling based on bite rate, foraging distance and food preference showing similarity of parrotfish feeding behavior from FKNMS and St. Croix when grouped by functional group. Ellipses are 95% confidence intervals and represent species distribution in axis space when grouped by functional group. Ellipse color represents the functional group and its respective region. Darker shade ellipses represent St. Croix functional groups, while lighter shade ellipses represent FKNMS functional groups.

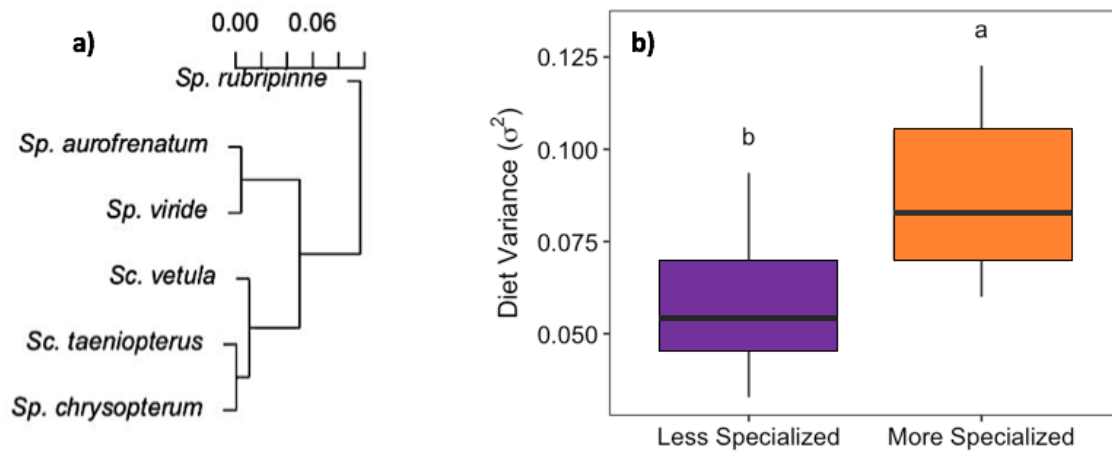


Figure A2: Parrotfish species specialization categorization using (a) a dendrogram generated from univariate hierarchical cluster analysis of diet variance data, and (b) box and whisker plot of mean diet variance per specialization group.

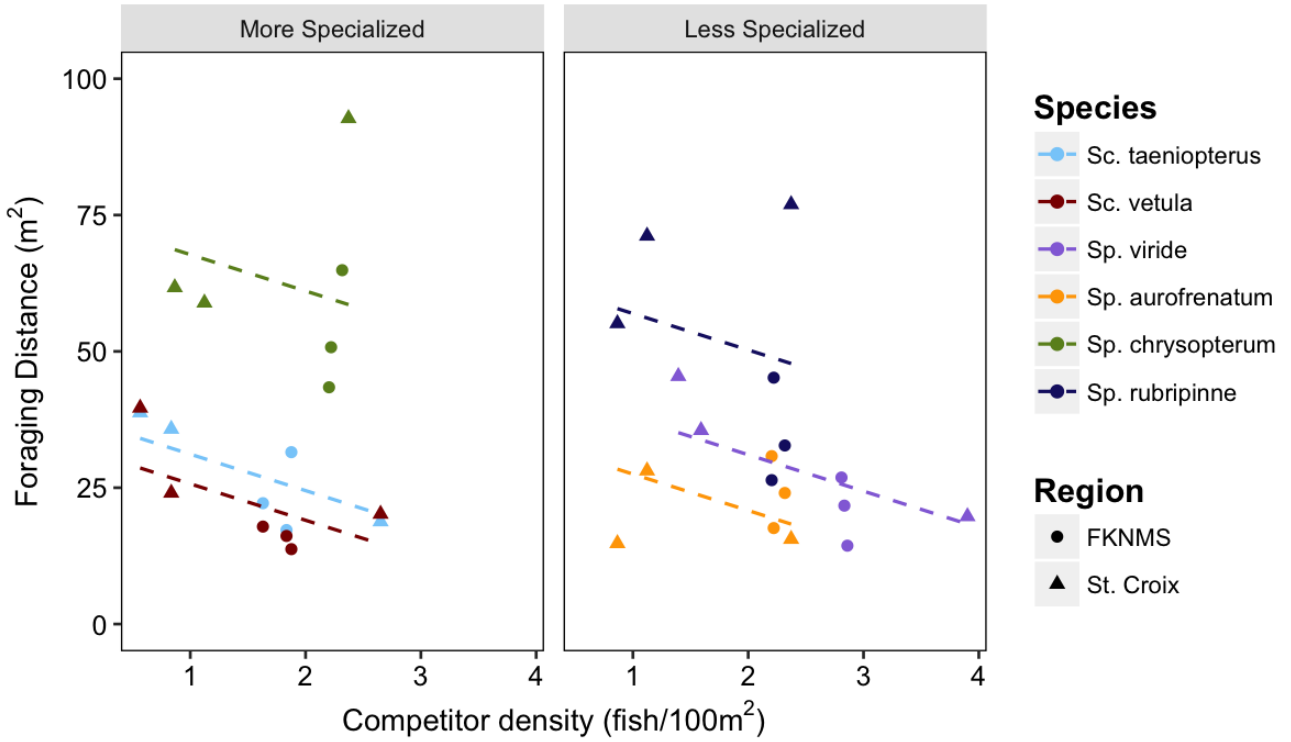


Figure A3: Scatter plot of foraging distance (m^2) versus competitor density (weighted, fish/ 100m^2) for more specialized (left panels) and less specialized (right panels) species. Dotted lines indicate non-significant species-level regressions. FKNMS sites are circles, St. Croix sites are triangles. There was no significant relationship between competitor density and foraging distance for more-specialized species ($R^2 = -0.06$, $P > 0.05$) or less-specialized species ($R^2 = 0.08$, $P > 0.05$).

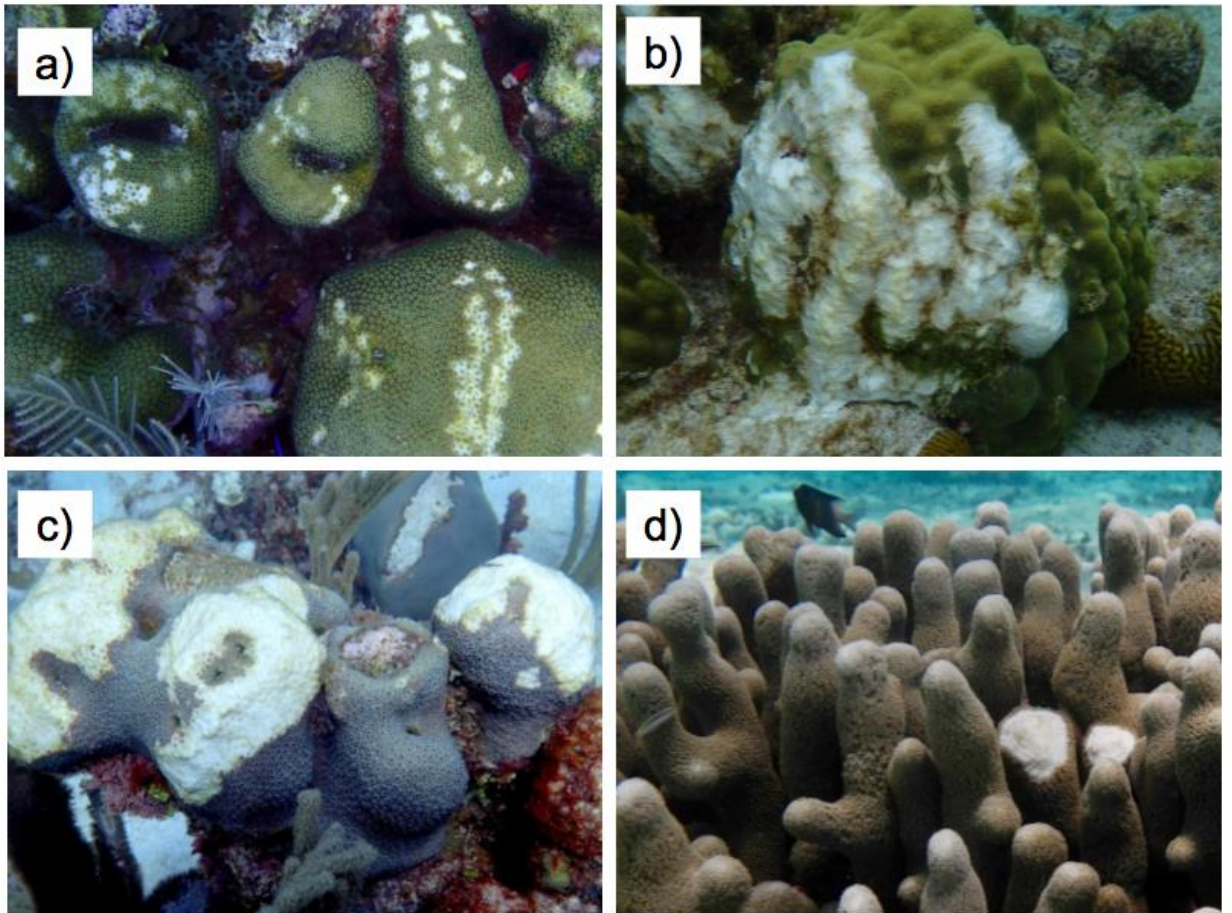


Figure A4: Predation scars from parrotfishes on three species of corals in St. Croix: *Orbicella annularis* (a, c) *Porites astreoides* (b) and *Porites porites* (d).

Table A1: Sample sizes for focal behavioral observations at (a) the three St. Croix study sites (2015) and (b) the three FKNMS sites (2013). N=~6 fish follows per species at each site. Observations of each species at each site were approximately evenly distributed between 1000 and 1600 hrs.

(a)

	Buck Island	Cane Bay	Long Reef	Total
<i>Sc. taeniopterus</i>	4	6	5	15
<i>Sc. vetula</i>	7	6	6	19
<i>Sp. aurofrenatum</i>	8	6	7	21
<i>Sp. chrysopteron</i>	6	6	6	18
<i>Sp. rubripinne</i>	5	6	7	18
<i>Sp. viride</i>	7	6	6	19

(b)

	Carysfort	Elbow	Molasses	Total
<i>Sc. taeniopterus</i>	6	6	7	19
<i>Sc. vetula</i>	6	6	5	17
<i>Sp. aurofrenatum</i>	6	6	6	18
<i>Sp. chrysopteron</i>	6	6	6	18
<i>Sp. rubripinne</i>	5	6	7	18
<i>Sp. viride</i>	6	6	6	19

Table A2: Breakdown of food categories for food preference data.

Food Category	Food item(s) targeted
Turf Algae + CCA	Various turf alga, turf associated sediment (TAS), Crustose Coralline Algae (CCA)
Foliose Algae	<i>Dictyota</i> spp.; <i>Sargassum</i> spp.; <i>Stypopodium</i> spp.; <i>Lobophora</i> spp.
Green Calcareous Algae	<i>Halimeda</i> spp.
Gorgonian	Various gorgonian spp.
Live Coral	<i>Porites porites</i> ; <i>Porites astreoides</i> ; <i>Orbicella annularis</i> ; <i>Siderastrea siderea</i> ; <i>Agaricia</i> spp., <i>Orbicella faveolata</i> , <i>Millepora</i> spp.
Red Calcareous Algae	Articulated red coralline; <i>Amphiroa</i> spp.; <i>Galaxaura</i> spp.
Red Non-Coralline Encrusting Algae	<i>Peysonnelia</i> spp.
Sponge	Various sponge spp.

Table A3: Feeding behavior variables averaged for each species at each study site: (a) bite rate, (b) foraging territory size, (c) diet variance, and (d) food preference/electivity.

			a) Bite rate	b) Foraging Territory Size	c) Diet Variance	d) Electivity values across all food items							
Region	Site	Species	Bites min ⁻¹	Distance m ²	σ^2	α TC	α foliose	α CGA	α RCA	α REA	α sponge	α gorg.	α coral
FL	Carysfort	SCTAE	27.53	19.17	0.083	0.695	0.022	0.060	0.040	0.000	0.000	0.183	0.000
FL	Carysfort	SCVET	19.99	16.67	0.094	0.851	0.050	0.000	0.000	0.000	0.000	0.007	0.092
FL	Carysfort	SPAURO	4.24	18.33	0.033	0.011	0.261	0.302	0.216	0.014	0.035	0.160	0.000
FL	Carysfort	SPCHRY	4.78	52.33	0.061	0.068	0.175	0.255	0.502	0.000	0.000	0.000	0.000
FL	Carysfort	SPRUB	5.34	50.00	0.053	0.051	0.520	0.270	0.088	0.003	0.000	0.067	0.000
FL	Carysfort	SPVIR	6.63	14.83	0.039	0.312	0.397	0.103	0.000	0.033	0.000	0.155	0.000
FL	Elbow	SCTAE	23.55	32.17	0.078	0.604	0.070	0.000	0.000	0.046	0.155	0.124	0.000
FL	Elbow	SCVET	27.21	14.00	0.109	0.935	0.023	0.000	0.000	0.024	0.000	0.018	0.000
FL	Elbow	SPAURO	6.58	30.83	0.082	0.062	0.264	0.288	0.303	0.032	0.000	0.052	0.000
FL	Elbow	SPCHRY	6.16	71.17	0.064	0.307	0.376	0.000	0.162	0.000	0.000	0.154	0.000
FL	Elbow	SPRUB	6.92	34.00	0.057	0.045	0.277	0.093	0.074	0.452	0.059	0.000	0.000
FL	Elbow	SPVIR	7.49	24.33	0.057	0.559	0.195	0.000	0.032	0.213	0.000	0.000	0.000
FL	Molasses	SCTAE	27.91	22.86	0.081	0.480	0.052	0.000	0.000	0.000	0.342	0.116	0.009
FL	Molasses	SCVET	31.17	18.00	0.123	0.992	0.008	0.000	0.000	0.000	0.000	0.000	0.000
FL	Molasses	SPAURO	8.08	41.17	0.053	0.035	0.214	0.294	0.088	0.000	0.249	0.119	0.000
FL	Molasses	SPCHRY	6.83	44.67	0.074	0.254	0.400	0.000	0.146	0.000	0.000	0.034	0.000
FL	Molasses	SPRUB	8.05	26.83	0.061	0.087	0.493	0.046	0.069	0.218	0.052	0.032	0.003
FL	Molasses	SPVIR	7.74	31.50	0.051	0.319	0.180	0.088	0.051	0.035	0.132	0.135	0.060
STX	BuckSoFR	SCTAE	29.35	20.27	0.061	0.671	0.041	0.099	0.000	0.120	0.000	0.069	0.000
STX	BuckSoFR	SCVET	21.44	23.74	0.115	0.960	0.000	0.014	0.000	0.026	0.000	0.000	0.000
STX	BuckSoFR	SPAURO	6.31	17.51	0.036	0.122	0.294	0.478	0.076	0.030	0.000	0.000	0.000
STX	BuckSoFR	SPCHRY	3.77	95.24	0.071	0.086	0.560	0.308	0.020	0.026	0.000	0.000	0.000
STX	BuckSoFR	SPRUB	4.78	84.33	0.045	0.297	0.472	0.098	0.000	0.133	0.000	0.000	0.000
STX	BuckSoFR	SPVIR	5.62	22.28	0.036	0.324	0.241	0.156	0.000	0.262	0.000	0.000	0.018
STX	Cane Bay	SCTAE	16.73	51.08	0.077	0.614	0.083	0.000	0.288	0.000	0.007	0.000	0.008
STX	Cane Bay	SCVET	18.17	26.47	0.113	0.954	0.031	0.000	0.015	0.000	0.000	0.000	0.000
STX	Cane Bay	SPAURO	7.01	14.89	0.073	0.013	0.022	0.613	0.069	0.276	0.007	0.000	0.000
STX	Cane Bay	SPCHRY	5.48	62.35	0.113	0.924	0.076	0.000	0.000	0.000	0.000	0.000	0.000
STX	Cane Bay	SPRUB	4.65	57.36	0.094	0.011	0.049	0.245	0.004	0.690	0.001	0.000	0.000
STX	Cane Bay	SPVIR	5.28	38.82	0.083	0.697	0.058	0.102	0.063	0.059	0.000	0.000	0.022

Note: **Regions:** STX=St. Croix, FL=FKNMS; **Food category:** TC=turf algae and CCA, foliose=foliose algae, CGA=calcareous green algae, RCA=red calcareous algae, REA=red encrusting algae, gorg=gorgonian; **Species:** SCTAE=*Scarus taeniopterus*,

SCVET=*Scarus vetula*, SPAURO=*Sparisoma aurofrenatum*, SPCHRY=*Sparisoma chrysopterum*, SPRUB=*Sparisoma rubripinne*, SPVIR=*Sparisoma viride*
 Table A3 Cont'd

Region	Site	Species	Bites min ⁻¹	Distance m ²	σ^2	α TC	α foliose	α CGA	α RCA	α REA	α sponge	α gorg.	α coral
STX	Long Reef	SCTAE	24.71	45.90	0.060	0.687	0.025	0.105	0.043	0.137	0.000	0.000	0.003
STX	Long Reef	SCVET	17.02	51.86	0.094	0.856	0.017	0.033	0.000	0.094	0.000	0.000	0.000
STX	Long Reef	SPAUR	7.53	36.86	0.054	0.202	0.037	0.351	0.211	0.196	0.003	0.000	0.000
STX	Long Reef	SPCHRY	4.78	60.30	0.070	0.392	0.365	0.000	0.201	0.000	0.042	0.000	0.000
STX	Long Reef	SPRUB	4.93	84.44	0.048	0.272	0.264	0.077	0.068	0.308	0.010	0.000	0.000
STX	Long Reef	SPVIR	4.22	46.61	0.088	0.744	0.030	0.000	0.000	0.167	0.000	0.026	0.034

Note: **Regions:** STX=St. Croix, FL=FKNMS; **Food category:** TC=turf algae and CCA, foliose=foliose algae, CGA=calcareous green algae, RCA=red calcareous algae, REA=red encrusting algae, gorg=gorgonian; **Species:** SCTAE=*Scarus taeniopterus*, SCVET=*Scarus vetula*, SPAURO=*Sparisoma aurofrenatum*, SPCHRY=*Sparisoma chrysopterum*, SPRUB=*Sparisoma rubripinne*, SPVIR=*Sparisoma viride*

Table A4: Loadings from PCA of food groups targeted with the total variance explained by each principal component. Variables are denoted in bold face.

	PC1	PC2	PC3	PC4
Turf + CCA	-0.649	0.03	-0.363	0.667
Foliose Algae	0.537	-0.686	-0.179	0.457
Calcified Algae	0.538	0.725	-0.215	0.373
Live Coral	-0.028	0.05	0.889	0.455
Standard deviation	0.465	0.275	0.159	0.09
Proportion of Variance	0.664	0.232	0.078	0.025
Cumulative Proportion	0.664	0.897	0.975	1

Table A5: Model selection results from log likelihood ratio tests. The most parsimonious model for each analysis is denoted in bold face. Models were generated using data for the more-specialized species group. Bold face indicates significant models.

(a) More-specialized Species Models		d.f.	LogLik	X^2	P
(1) Diet Specialization					
Model 1: Diet variance ~ % cover preferred food	3	51			
Model 2: Diet variance ~ species + % cover preferred food	5	55.1	8.23	0.016	*
Model 3: Diet variance ~ % cover preferred food *species	7	57.7	5.19	0.075	.
(2) Foraging Distance					
Model 1: Distance ~ % cover preferred food	3	-72.6			
Model 2: Distance ~ % cover preferred food + species	5	-65.4	14.43	7.3E-04	***
Model 3: Distance ~ % cover preferred food * species	7	-65	0.71	0.70068	
(3) Bite Rate					
Model 1: Bite rate ~ % cover preferred food	3	-60.1			
Model 2: Bite rate ~ % cover preferred food + species	5	-42.9	34.34	3.5E-08	***
Model 3: Bite rate ~ % cover preferred food * species	7	-41.7	2.53	0.28	

(b) Less-Specialized Species Models		d.f.	LogLik	X^2	P
(1) Diet Specialization					
Model 1: Diet variance ~ % cover preferred food	3	46.7			
Model 2: Diet variance ~ species + % cover preferred food	5	47.1	0.94	0.62	
Model 3: Diet variance ~ % cover preferred food *species	7	49.4	4.61	0.1	
(2) Foraging Distance					
Model 1: Distance ~ % cover preferred food	3	-77.7			
Model 2: Distance ~ % cover preferred food + species	5	-71	13.32	0.0013	
Model 3: Distance ~ % cover preferred food * species	7	-69.3	3.48	0.1756	
(3) Bite Rate					
Model 1: Bite rate ~ % cover preferred food	3	-30.4			
Model 2: Bite rate ~ % cover preferred food + species	5	-29.4	1.98	0.37	
Model 3: Bite rate ~ % cover preferred food * species	7	-28.9	1.06	0.59	

Table A6: Linear model output for tests of the effect of resource abundance (% cover preferred food) and species using range-limited data for the predictor (i.e. all data bounded from 0-44% cover resource abundance) on (a) diet specialization, (b) foraging distance and (c) bite rate. LS=less specialized, MS= more specialized.

Variable	Specialization	R^2 *	Term	Sum-sq.	df	F	P
(a) Diet specialization	LS	0.151	% cover	2.31E-04	1	0.58	0.46
			pref. food				
			species	3.01E-04	2	0.38	0.69
			Residuals	5.61E-03	14		
	MS	0.626	% cover	9.70E-04	1	4.26	0.04
			pref. food				
			species	1.30E-03	2	4.06	0.05
			Residuals	1.43E-03	14		
(b) Foraging distance	LS	0.421	% cover	6.45E-01	1	0.33	0.58
			pref. food				
			species	3.24E+00	2	0.82	0.46
			Residuals	2.78E+01	14		
	MS	0.771	% cover	2.14E+01	1	15.30	0.16
			pref. food				
			species	5.93E+02	2	40.17	7.59E-05
			Residuals	8.20E+01	14		
(c) Bite rate	LS	-0.088	% cover	1.40E+02	1	0.70	0.42
			pref. food				
			species	3.08E+03	2	7.67	0.01
			Residuals	2.81E+03	14		
	MS	0.906	% cover	5.19E+02	1	7.35	0.09
			pref. food				
			species	1.12E+03	2	8.61	0.06
			Residuals	1.33E+03	14		

Table A7: Sample sizes for (a) coral abundance and bite scar surveys, and (b) focal behavioral observations at three St. Croix study sites (2015, 2016) and three FKNMS study sites (2012, 2013).

(a) Coral abundance and bite scar surveys

Region	Site	Year(s)	n transects (benthic surveys) *	n transects (coral surveys)
St. Croix	Buck SoFR	2015, 2016	8, 9	3,8
St. Croix	Cane Bay	2015, 2016	10, 10	6,8
St. Croix	Long Reef	2015, 2016	8, 10	8, 8
FKNMS	Carysfort	2010	—	4
FKNMS	French Reef	2013	—	4
FKNMS	Molasses	2013	—	2

* Percent cover of coral was calculated using benthic surveys for St. Croix sites only

(b) Focal behavioral observations sampling effort

	FKNMS			St. Croix			Total
	Carysfort	French*	Molasses	BuckSoFR	Cane Bay	Long Reef	
<i>Sc. coelestinus</i>	6	7	6	—	—	—	19
<i>Sc. coeruleus</i>	6	7	6	—	—	—	19
<i>Sc. guacamaia</i>	6	6	6	—	—	—	18
<i>Sc. taeniopterus</i>	6	6	7	4	6	5	34
<i>Sc. vetula</i>	6	3	5	6 IP, 1 TP	6 IP, 2 TP	6 IP, 4 TP	39
<i>Sp. aurofrenatum</i>	6	6	6	6	6	7	37
<i>Sp. chrysopterum</i>	6	3	6	6	6	6	33
<i>Sp. rubripinne</i>	5	6	7	5	6	7	36
<i>Sp. viride</i>	6	7	6	6 IP, 7 TP	6 IP, 10 TP	6 IP, 7 TP	61

* French Reef focal fish follows are from 2012

Note: Number indicates the total number of unique individuals followed at a given site. IP=Initial Phase, TP=Terminal Phase. No phase indicates all IP follows. Line indicates species not present at study site.

Table A8: Pairwise comparisons of (a) total parrotfish density (fish 100 m⁻²) and (b) total parrotfish biomass (g 100 m⁻²) using Holm's method for multiple comparisons corrections. Bold face indicates $P < 0.05$.

(a)

Comparison	T statistic	<i>df</i>	P value	P _{adj}
Buck SoFR: Cane Bay	4.78	4.51	0.007	0.078
Buck SoFR: Long Reef	3.92	6.87	0.006	0.077
Buck SoFR: Carysfort	0.70	7.02	0.506	1.000
Buck SoFR: French	1.52	6.98	0.172	1.000
Buck SoFR: Molasses	0.97	7.22	0.364	1.000
Cane Bay: Long Reef	-0.35	5.19	0.740	1.000
Cane Bay: Carysfort	-2.45	4.23	0.067	0.605
Cane Bay: French	-3.03	3.46	0.047	0.517
Cane Bay: Molasses	-5.27	6.38	0.002	0.023
Long Reef: Carysfort	-2.12	5.49	0.082	0.659
Long Reef: French	-2.34	5.71	0.060	0.601
Long Reef: Molasses	-3.77	8.94	0.004	0.062
Carysfort: French	0.46	6.39	0.658	1.000
Carysfort: Molasses	-0.05	5.61	0.959	1.000
French: Molasses	-0.79	6.03	0.459	1.000

(b)

Comparison	T statistic	<i>df</i>	P value	P _{adj}
Buck SoFR: Cane Bay	4.40	4.83	0.008	0.114
Buck SoFR: Long Reef	3.73	6.77	0.008	0.114
Buck SoFR: Carysfort	-0.56	5.56	0.600	1.000
Buck SoFR: French	-1.43	3.84	0.230	1.000
Buck SoFR: Molasses	-1.46	6.88	0.188	1.000
Cane Bay: Long Reef	-0.29	6.01	0.783	1.000
Cane Bay: Carysfort	-2.66	4.17	0.054	0.513
Cane Bay: French	-3.22	3.09	0.047	0.513
Cane Bay: Molasses	-3.64	5.21	0.014	0.179
Long Reef: Carysfort	-2.50	4.65	0.058	0.513
Long Reef: French	-3.08	3.34	0.047	0.513
Long Reef: Molasses	-3.45	5.80	0.014	0.179
Carysfort: French	-0.78	6.30	0.462	1.000
Carysfort: Molasses	-0.70	8.89	0.500	1.000
French: Molasses	0.15	6.65	0.886	1.000

Table A9: Region wide coral cover of ten scleractinian corals or species complexes that are the commonly preyed on by parrotfishes in the Caribbean (a) and pairwise comparisons of mean coral cover between St. Croix and FKNMS regions (b).

(a)

Coral species	Buck SoFR	FKNMS	St. Croix
<i>A. palmata</i>	0.00	0.50 ± 0.50	0.00 ± 0.00
<i>Agaricia</i> spp.	0.12	0.48 ± 0.18	0.66 ± 0.33
<i>C. natans</i>	0.40	0.02 ± 0.02	0.27 ± 0.18
<i>D. strigosa</i>	0.04	0.04 ± 0.03	0.33 ± 0.31
<i>M. cavernosa</i>	0.01	0.04 ± 0.01	0.50 ± 0.12
<i>M. mirabilis</i>	0.00	0.02 ± 0.02	0.02 ± 0.01
<i>Orbicella</i> spp.	11.44	1.57 ± 1.09	2.12 ± 0.07
<i>P. astreoides</i>	0.38	0.32 ± 0.14	2.00 ± 0.57
<i>Porites porites</i> SC	0.06	0.20 ± 0.16	1.48 ± 0.32
<i>S. siderea</i>	0.00	0.96 ± 0.60	0.32 ± 0.08

(b)

Comparison	P value	P_{adj}
<i>A. palmata</i>	0.56	1.00
<i>Agaricia</i> spp.	1.00	1.00
<i>C. natans</i>	0.04	0.44
<i>D. strigosa</i>	0.21	1.00
<i>M. cavernosa</i>	0.40	1.00
<i>M. mirabilis</i>	0.70	1.00
<i>Orbicella</i> spp.	0.21	1.00
<i>P. astreoides</i>	0.23	1.00
<i>Porites porites</i> SC	0.23	1.00
<i>S. siderea</i>	0.28	1.00