Influences of ontogenetic phase and resource availability on parrotfish foraging preferences in the Florida Keys, FL (USA)

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ABSTRACT: Over the previous 35 yr, Caribbean coral reefs have experienced decreases in coral cover and increases in algal cover, leading to calls for increased protection of reef herbivores such as parrotfish. Previous studies have classified parrotfish into functional foraging groups based on beak morphology, gut content analyses, isotopic composition, and direct observations of foraging behaviors. However, few studies have examined how parrotfish foraging behaviors change with ontogenetic phase, substrate composition, and parrotfish biomass. In this study, we determined the foraging preferences of 10 parrotfish species and examined how these preferences varied with ontogeny, algal composition, and parrotfish biomass. We observed foraging behaviors of 3 phases (juvenile, intermediate, terminal) of 10 parrotfish species on 34 reefs in the middle Florida Keys (USA) that varied in coral and algal composition. Cluster analysis of Manly's alpha electivity indices revealed 3 functional feeding groups that differed in their selectivity of turf, calcareous, and fleshy algal communities as preferred foraging habitats. Juvenile parrotfishes of different foraging groups had similar foraging preferences that diverged with maturation. Preferences for turf algal communities increased with increasing turf algal cover but were not influenced by parrotfish biomass. In contrast, preferences for fleshy algal communities decreased with increasing parrotfish biomass. These results suggest that parrotfish species have different foraging preferences, which may vary with ontogeny, algal abundance, and parrotfish biomass. Thus, efforts to increase parrotfish biomass may not always lead to a predictable decrease in algal abundance.

KEY WORDS: Diet selectivity · Diet electivity · Herbivory · Coral reefs · Parrotfish

INTRODUCTION

Herbivory is an important ecosystem function that can structure marine communities such as kelp forests (Estes et al. 1978), seagrass flats (Mortimer 1981), and coral reefs (Carpenter 1986). Reef herbivores play a crucial role in promoting healthy coral ecosystems by limiting the abundance of algae that compete with coral (Ogden & Lobel 1978, Mumby & Steneck 2008). Parrotfishes are morphologically specialized herbivores that scrape or browse on a variety of surfaces (Lewis & Wainwright 1985, Williams & Polunin 2001, Bonaldo et al. 2014). Despite fishing impacts, they are among the most abundant piscine herbivores left in

Caribbean coral reef communities (Smith 2015, Pinheiro et al. 2016, Shulzitski et al. 2018). Throughout the Caribbean, macroalgae have replaced coral cover in the past several decades (Gardner et al. 2003, Pandolfi et al. 2003, Schutte et al. 2010). Numerous algae compete with coral for settlement space, and directly impair corals through shading, the producion of allelochemicals that suppress coral growth, and disease transmission (Lirman 2001, Nugues et al. 2004, Nugues & Bak 2006, Box & Mumby 2007, Rasher & Hay 2010; but see also Vu et al. 2009, McClanahan et al. 2011a). This increased competition between coral and algal species may have been intensified by one or more of an increase in nutrients (Burkepile et al.

2013), mass mortality of herbivorous long-spined sea urchins *Diadema antillarum* (Carpenter 1988), or overfishing of parrotfishes (Newman et al. 2006). However, protected reefs may not have cascading positive effects on parrotfish abundance, nor alter the composition of the benthos (McClanahan et al. 2011b, Cox et al. 2017, Tewfik et al. 2017); as a result, the role of parrotfish herbivory in coral reef communities has been debated (e.g. Russ et al. 2015).

Ecologists have attempted to classify parrotfish into functional foraging groups based on their jaw morphology, gut contents, isotopic composition, and feeding observations (Choat et al. 2004, Cardoso et al. 2009, Bonaldo et al. 2014, Jouffray et al. 2015). These functional groups have been described as excavators, browsers, scrapers, and grazers based primarily on the type of algae grazed and the degree to which substrate is removed in the process (Bellwood & Choat 1990, Streelman et al. 2002). However, parrotfish often display a high degree of variation in their dietary preferences, and forage on a wide range of macroalgal, sponge, and coral species, blurring the distinction between these functional groups (Bruggemann et al. 1994a, Price et al. 2010, Burkepile 2012, Pawlik et al. 2013). A recent study suggests that parrotfish may not be herbivores at all, but instead target specific species or substrates for their protein-rich epiphyte and endophyte microorganisms, which may explain some of the previously observed variation in parrotfish grazing behaviors (Clements et al. 2016). Others have suggested that ecological factors, such as herbivore diversity (Burkepile & Hay 2008, Hamilton et al. 2014), interspecific competitive interactions (Muñoz et al. 2000, Catano et al. 2014), predator presence (Catano et al. 2016), reef structure (Brandl et al. 2015, Catano et al. 2015), substrate type (Brandl & Bellwood 2014, Adam et al. 2015b), and ontogenetic phase (Robertson & Warner 1978, Feitosa & Ferreira 2015) influence parrotfish foraging preferences. For example, parrotfish may respond to increased competition by either varying their diet or their habitat associations (Bruggemann et al. 1994b, Burkepile & Hay 2011, Bonaldo et al. 2014, Adam et al. 2015b). Thus, inconsistency in dietary preferences across environmental gradients complicate traditional methods of assigning species to functional foraging groups and quantifying redundancy in trophic guilds (Adam et al. 2015a, Dromard et al. 2015).

The Florida Keys, like elsewhere in the Caribbean, have experienced a rapid decline in live coral cover and a corresponding increase in macroalgae (Alevizon & Porter 2015). However, unlike other regions of the Caribbean, parrotfishes in the Florida Keys are protected from fishing and have higher than average biomass (10–45 g m^{-2} in the middle Florida Keys; Smith 2015). Consequently, the variation in algal cover, parrotfish biomass, and species richness allows for estimation of parrotfish foraging preferences across a broad range of ecological conditions without strong fishing impacts (Kramer & Heck 2007, Adam et al. 2015a, Kenkel et al. 2015, Manzello et al. 2015, Smith 2015). Changes in dietary preferences of parrotfishes across ontogeny and environmental conditions could improve our understanding of parrotfish–algae interactions.

The goals of this study were to evaluate the foraging preferences of parrotfish species in the middle Florida Keys National Marine Sanctuary (FKNMS) and to determine how feeding preferences change with ontogenetic phases, substrate cover, and parrotfish biomass. First, we examined the foraging preferences of individual parrotfishes and compared them to the local availability of relative substrate cover. Second, we analyzed by species which substrates were preferred and avoided. Third, we used a cluster analysis to determine similarities among species in their foraging preferences, to assign them to distinct functional foraging groups. Finally, we evaluated how the substrate electivity of each functional group varied with ontogenetic phase (juvenile, adult, terminal), reef type (nearshore vs. offshore), algal abundance, and parrotfish biomass. We hypothesized that (1) species will differ in their foraging preferences, (2) juveniles will share more similarities between species than adults, (3) electivity will be proportional to the abundance of the preferred algal substrates, and (4) parrotfish biomass will influence electivity for preferred algal substrates.

MATERIALS AND METHODS

Study sites

The reef tract of the middle Florida Keys stretches along the Atlantic Ocean from Islamorada to Marathon, parallel to the island chain. These reefs are located inside the FKNMS, and include shallow (2–5 m), highly complex reefs close to shore (<5 km from shore) and deeper (4–8 m), low relief reefs on the outer edges of the shallow limestone shelf (>5 km from shore). Ten species of parrotfish from 2 genera (*Scarus* and *Sparisoma*) are commonly found on the reefs of the Florida Keys, and are protected from spearfishing. We established 17 study locations spanning the middle Florida Keys reef tract near Layton,

FL, USA (Fig. 1). Each location consisted of 2 reefs of continuous hard substrate (minimum size: 50 m long by 20 m wide) that were separated by sand/seagrass substrate (minimum distance apart: 150 m). Data were collected from June 2013 to June 2015.

Estimating substrate composition

To estimate the percent cover of each substrate category, we haphazardly placed a 50 m transect parallel with the long axis of the reef. Divers took paired (left and right side of the transect) photo quadrants (0.25 m^2) of the substrate every 10 m along the transect. Photographs were taken from a distance of 0.75 m with a Canon PowerShot A710IS. These photographs were analyzed for percent cover using Coral Point Count V4.1 (Kohler & Gill 2006). Twenty-five points were randomly placed on each photo and classified into 7 general substrate categories including live hard coral, turf algae, fleshy algae, calcareous algae, gorgonians, sponges, and other (for more details about substrate type classification, see the Supplement at www.int-res.com/articles/suppl/m603 p175_supp.pdf). Points that were placed over temporary objects (camera frame, transect tape, etc.) were excluded. Substrate cover for the site was calculated by averaging the percent cover estimated from photographs taken along the entire transect (300 points

site^{-1}). Substrate surveys were conducted for each of the time periods mentioned above. Average values of substrate composition (% cover of each algal type) by reef location can be found in Table S2 in the Supplement.

Estimating parrotfish density and biomass

Parrotfish density was estimated using diver visual surveys (50 × 10 m) along the same transect where the substrate cover was measured. Two divers swam along either side of the transect simultaneously while counting the number of all parrotfish species observed within 5 m of the transect tape (Kramer & Heck 2007). Parrotfish species were further classified based on their ontogenetic phase (juvenile, intermediate, terminal) using size, coloration, and morphology (Schultz 1969). For parrotfish species with no change in color between juvenile and intermediate phases, individuals <50% of the terminal phase length were classified as juveniles and individuals >50% of the terminal phase length were classified as intermediate phase. Terminal phases were distinguished from intermediate phases either by distinctive color pattern or morphological traits such as an enlarged forehead and extensions of the first and last caudal fin rays. Parrotfish biomass on each site was then estimated by multiplication of the species/phase-specific counts by previously published length–weight relationships of the average-sized phase for each species (Bohnsack et al. 1988). Total parrotfish biomass (g m^{-2}) was estimated for each reef and census period.

Fig. 1. Study sites (n = 17) located in the middle Florida Keys, USA. Our 34 reefs (2 reefs site^{-1}) are located inside the Florida Keys National Marine Sanctuary in the Atlantic Ocean. Sites were sampled from June 2012 to June 2015. Light gray depth contours are at 2 m depth intervals

Estimating parrotfish foraging preferences

We observed the foraging behavior of 2009 individual parrotfish across the 10 species. The feeding behavior of individual parrotfish were estimated by focal animal continuous sampling. Each diver haphazardly selected a parrotfish, noted its species and developmental phase, and followed the fish for 3 to 5 min (mean = 3.1 min) at a distance of 5 m. All observations were made between 10:00 and 15:00 h. Although the parrotfish did
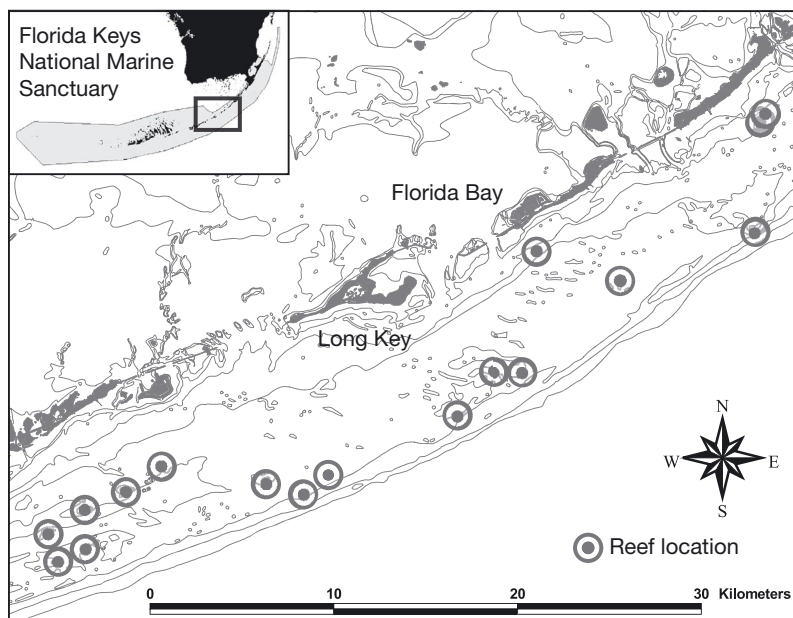
notice the presence of the divers, their behaviors did
not seem to be strongly impacted by diver presence,
and their foraging rates were similar to those re-
corded by fixed-station video cameras (K. Smith pers.
obs.). While following the fish, the diver would note
the number of bites each individual fish took on each
of the 7 substrate types. To minimize the potential of
observing the same individual twice, divers would
only watch 1 individual of a specific species/phase
per reef. Only observations where parrotfish took at
least 5 bites on the substrate during the observation
period were used, to exclude individuals that might
have been disturbed by the presence of a diver and
to obtain the highest resolution for an individual's
preferences (as a result, n = 1801). The median bite
number for our focal animal observations was 17
bites (first quartile = 11, third quartile = 27). Sample
sizes of parrotfish foraging observations by species
and ontogenetic phase including average electivity
indices are available in Table S1.

Statistical analyses

In order to distinguish the foraging preferences
of the parrotfish, we used 2 different metrics: (1)
Strauss' linear resource selection index (L) and (2)
Manly's alpha electivity index (α, referred to as the
electivity index). Strauss' linear resource index (re-
ferred to as the selectivity index) allows for assessment
of individual items in the diet, and whether they are
significantly preferred or avoided based on their fre-
quency. This index is calculated using the formula:

$$L = r_i - p_i \tag{1}$$

where i is the focal substrate type, r_i is the proportion
of the number of bites taken on that substrate type
and p_i is the proportion of the substrate type in the
environment (Strauss 1979). Significant selectivity
indices (positive or negative) were indicated by an
average selection index (L) whose 95% confidence
interval did not overlap 0. We used this selectivity
index to examine which substrate communities were
preferred (positive) or avoided (negative) for each
fish. These indices were then averaged for each of
the 10 species of parrotfish.

Strauss' linear resource selection index is ideal for
identifying feeding preferences of individual dietary
items or substrate communities. However, because
they are compared to local abundances of only 1 sub-
strate category, they are not influenced by changes
in the abundance of the other substrate categories.
Therefore, we chose the electivity index to represent

a proportional foraging preference given the entire
diet. α was calculated using the formula:

$$\alpha_i = \frac{r_i}{n_i} \frac{1}{\sum (r_j/n_j)} \tag{2}$$

where α_i is Manly's alpha for substrate type i, r is the
proportion of prey type i bitten, and n is the propor-
tion of substrate type i on the reef (Manly et al. 1972,
Chesson 1978, 1983, Brooker et al. 2013). Manly's
alpha for each substrate type was calculated in refer-
ence to the summation of the proportion of all sub-
strate types ($i - j$) in the diet to the proportion of all
substrate types ($i - j$) in the environment. This for-
mula for α assumes that food resources are not being
depleted during the time of observation and empha-
sizes the most abundant substrate types.

To classify the 10 species of parrotfishes into func-
tional feeding groups, we performed a cluster analy-
sis using the species-specific averages of the 7 sub-
strate electivity indices and the average body mass.
We included average body mass as proxy for jaw
size, which strongly influences the amount of sub-
strate removed by each bite. We used a K-means
method of identifying the optimal number of clusters.
Our cluster analysis identified 3 functional feeding
groups that differed primarily by the number of pre-
ferred algal substrates, i.e. either 1, 2, or 3. All subse-
quent analyses of factors that potentially influence
foraging preferences were analyzed for each forag-
ing group separately.

To examine how foraging preferences change with
ontogenetic phase, substrate composition, and par-
rotfish biomass, we also used Manly's alpha electivity
index because it better meets the assumptions of
normality and homogeneity of variances. We used
general linear models (GLMs) with a binomial distri-
bution to determine the effects of reef habitat and on-
togenetic phase on the electivity indices for each of
the 3 functional groups and each of the 3 algal com-
munities. We also used GLMs to examine how % sub-
strate cover and biomass (log total parrotfish biomass)
impact electivity indices for each of the 3 functional
groups and each of the 3 algal types. All statistical
tests were performed using JMP 13.0 (SAS Institute).

RESULTS

Dietary selectivity by species

Strauss' linear resource indices indicated that all
parrotfishes, of both genera *Scarus* and *Sparisoma*,
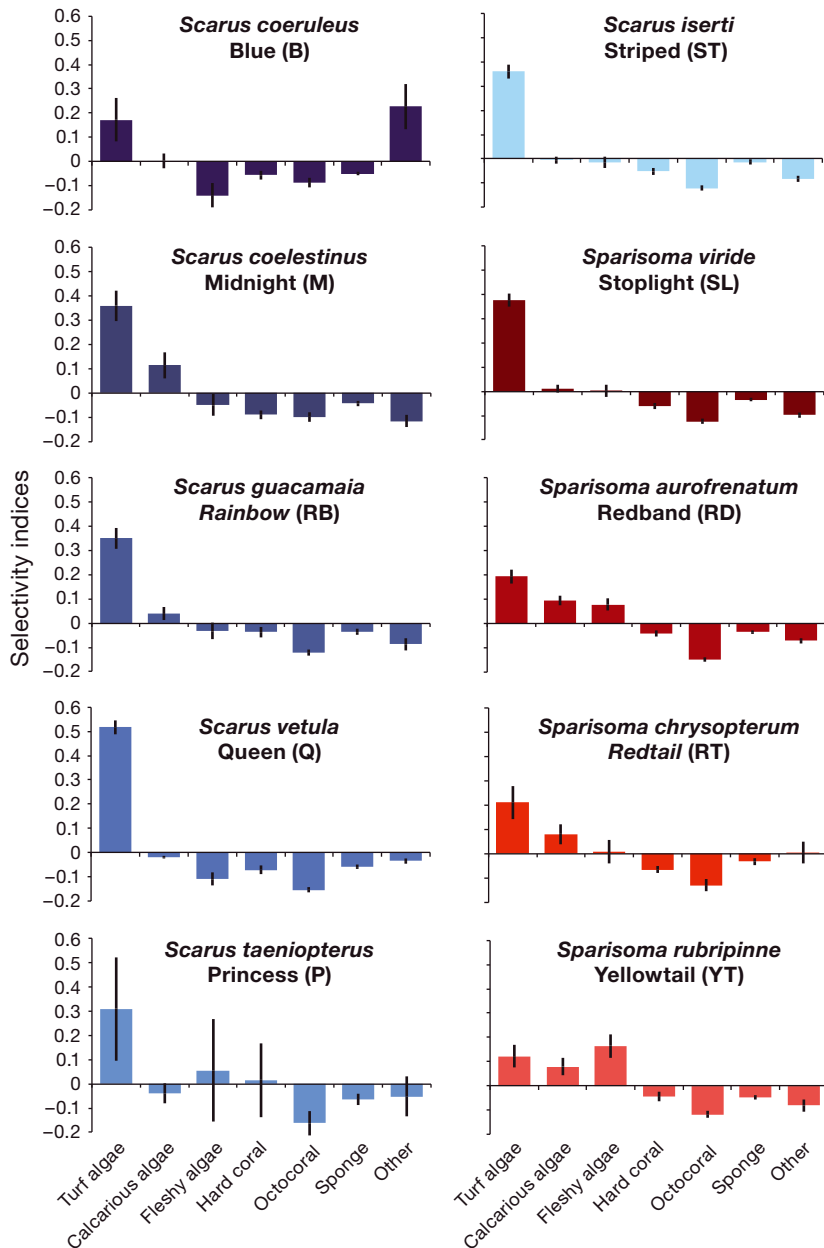showed foraging preferences towards 1 or more of the

Fig. 2. Strauss' selectivity indices for individual parrotfish species on the 6 substrate categories. Parrotfish are divided by genus (blue: *Scarus*; red: *Sparisoma*). Confidence intervals (95%) above (below) the horizontal axis indicate a dietary preference (avoidance). Confidence intervals that cross the horizontal axis indicate neither a preference nor avoidance

natum, S. rubripinne), 1 species preferring turf and calcareous algal communities (*S. chrysopterum*), and 1 species preferring only turf algal communities (*S. viride*).

Functional foraging groups

Using the species-specific average values of the electivity index for 7 substrates and biomass, we found that parrotfish clustered into 3 distinct foraging functional groups based on the number of algal communities preferred (Fig. 3). The dietary preferences of these functional groups were significantly different (Wilks' λ = 0.873, $F_{10,3410}$ = 23.901, p < 0.0001), and post hoc comparisons revealed significant differences between each of the groups. Functional group I preferred turf algal communities and included the 3 small-bodied *Scarus* species (*S. vetula, S. taeniopterus*, and *S. iserti*) and 1 *Sparisoma* species (*S. viride*). Functional group II included the 3 larger-bodied *Scarus* parrotfishes (*S. coeruleus, S. coelestinus*, and *S. guacamaia*) and showed preferences for both turf and calcareous algal communities. The exception to this pattern was *S. coeruleus*, which neither preferred nor avoided calcareous algal communities but instead took many bites in open sand (other). Functional group III followed a generalist feeding behavior by grazing on all 3 algal communities and included the remaining *Sparisoma* species (*S. aurofrenatum, S. chrysopterum*, and *S. rubripinne*). The average electivity index for each species and developmental phase is given in Table S1.

3 algal communities, and significantly avoided taking bites on sponges, hard corals, and soft corals (Fig. 2). Large-bodied *Scarus* species (*S. coeruleus, S. coelestinus, S. guacamaia*) preferred to forage in turf and calcareous algal communities, whereas small-bodied *Scarus* species (*S. vetula, S. taeniopterus, S. iserti*) preferred only turf algal communities. *Sparisoma* species showed more variation, with 2 species preferring turf, calcareous, and fleshy algal communities (*S. aurofre-*

Ontogenetic phase and foraging preferences

We found that ontogenetic phases influenced dietary behaviors with preferences for turf algae being highest for group I, intermediate for group II, and lowest for group III (Fig. 4A), while preference for fleshy algae showed the reverse pattern (Fig. 4C). Ontogenetic phases significantly influenced electivity for turf algal community for both group I (χ^2 = 6.303,
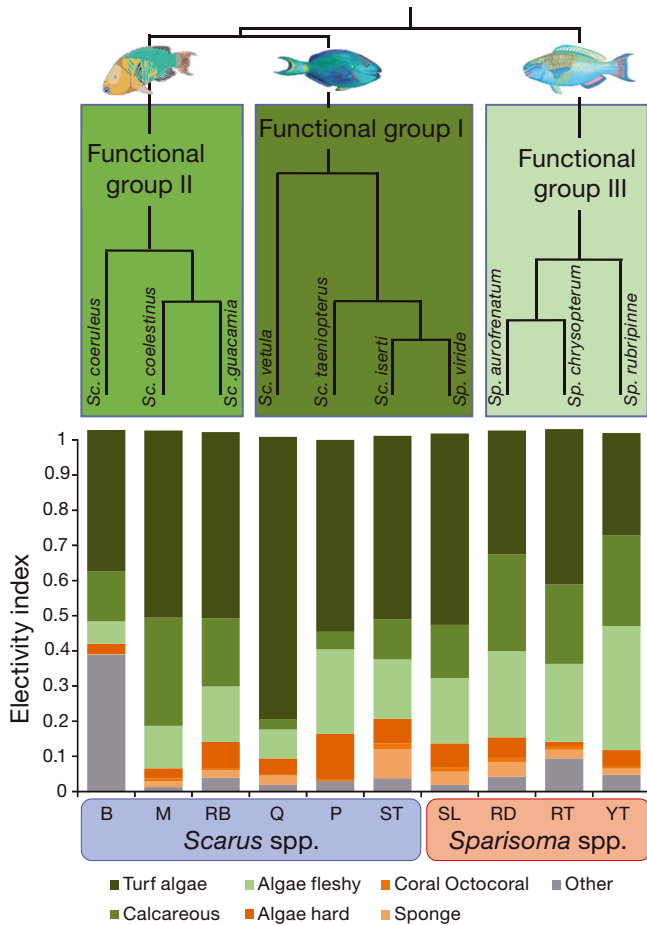
Fig. 3. Electivity indices showing the dietary preferences of the 10 species of parrotfish towards the 7 substrate categories. Species dendrogram was created using the species average electivity indices and biomass. Cluster analysis of these factors identified 3 functional groups (FGs). FG I feeds on turf algal communities, FG II feeds on turf and calcareous algal communities, and FG III feeds on communities associated with turf, calcareous, and fleshy algae. Species abbreviations refer to common names presented in Fig. 2

p = 0.043) and group II ($\chi^2 = 6.119$, p = 0.047), but was not significant for group III ($\chi^2 = 5.575$, p = 0.068) (Table 1). Parrotfishes in groups I and II increased the proportion of turf in their diet as adults, while parrotfishes in group III decreased the proportion of turf in their diet as adults (Fig. 4A). Ontogenetic phases did not affect electivity indices towards either calcareous (Fig. 4B) or fleshy algae communities (Fig. 4C).

Reef habitat and foraging preferences

Reefs nearshore (<5 km from shore) and offshore (>5 km from shore) in the middle Florida Keys differed in number of important features. First, nearshore reefs were shallower (4.1 vs. 5.7 m) and more structurally complex than offshore reefs due to more dead mound corals. Second, nearshore reefs had more live hard corals (13.0 vs. 5.8%), fewer soft corals (10.5 vs. 18.6%), and fewer sponges (4.5 vs. 5.9%) than offshore reefs. Third, nearshore reefs had more calcareous algae (*Halimedia* spp.) (9.1 vs. 3.7%) and fewer fleshy algae (primarily *Dictyota* spp) (10.9 vs. 17.3%) than offshore reefs (Table S2). We found no significant effect of reef habitat on electivity indices for either turf (Fig. 5A) or fleshy algae communities (Fig. 5C) with the exception of a significant increase in turf algae electivity for group II parrotfishes on offshore reefs ($\chi^2 = 6.271$, p = 0.012) (Table 1). However, foraging preferences on calcareous algal communities for group II ($\chi^2 = 4.476$, p = 0.034) and group III parrotfishes ($\chi^2 = 5.958$, p = 0.015) were significantly lower offshore (Fig. 5B) and lower (but not significantly) for group I parrotfishes ($\chi^2 = 2.877$, p = 0.090) (Table 1).
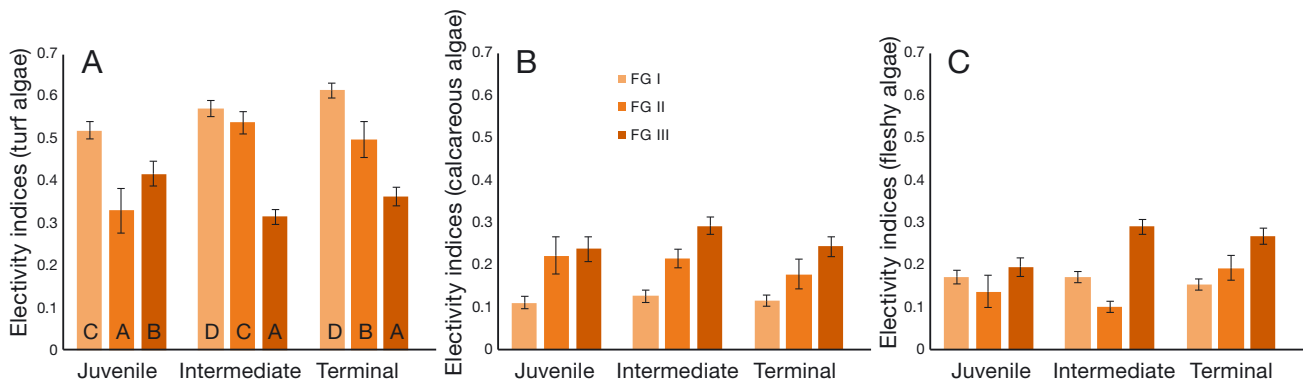

Fig. 4. Electivity indices for the 3 developmental phases of parrotfish for (A) turf, (B) calcareous, and (C) fleshy algae (mean ± SE). The 3 functional foraging groups (FG I–III) are groups of parrotfish species as defined in Fig. 3. Unshared letters on different bars indicate significant pairwise differences among ontogenetic phases

Table 1. Generalized linear model of electivity indices (Manly's alpha) for 3 substrate communities and 3 parrotfish functional feeding groups (FGs) as a function of reef habitat (nearshore vs. offshore) and ontogenetic phase (juvenile, intermediate, adult). Parrotfish FG composition is based on substrate preferences (I = turf, II = turf + calcareous, III = turf + calcareous + fleshy algae) from Fig. 3. Values in **bold** indicate significance (p < 0.05)

Substrate	FG	—	Phase	—	—	Reef habitat	—
		df	χ^2	p	df	χ^2	p
Turf	I	**2**	**6.303**	**0.0428**	1	0.378	0.5385
Turf	II	**2**	**6.119**	**0.0469**	**1**	**6.271**	**0.0123**
Turf	III	2	5.392	0.0675	1	0.080	0.7761
Calcareous	I	2	1.046	0.5926	1	2.877	0.0898
Calcareous	II	2	0.216	0.8972	**1**	**4.476**	**0.0344**
Calcareous	III	2	1.575	0.4549	**1**	**5.958**	**0.0146**
Fleshy	I	2	0.271	0.8732	1	0.005	0.9418
Fleshy	II	2	3.699	0.1573	1	0.230	0.6314
Fleshy	III	2	3.879	0.1438	1	2.122	0.1452

Algal cover and foraging preferences

Our expectation was that foraging preferences for the preferred algal community would increase in proportion to its abundance and thus show no significant increases or decreases in relation to cover. Instead, we found that for certain functional groups, foraging preferences did significantly change with changes in the proportion of algal communities available (Fig. 6). Preferences for turf algal communities increased significantly with increases in % turf algae (Fig. 6A) for group I ($\chi^2 = 16.64$, p = 0.001) and group II ($\chi^2 = 7.504$, p = 0.006), but not for group III ($\chi^2 = 0.334$, p = 0.569) (Table 2). Preferences for fleshy algal communities decreased significantly with increases in % fleshy algae (Fig. 6C) for group I
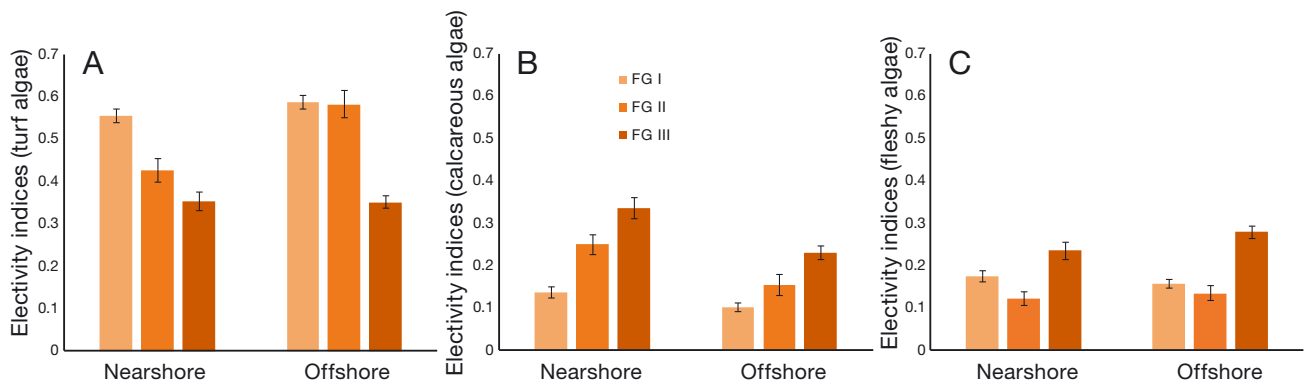

Fig. 5. Electivity indices of parrotfish observed on nearshore and offshore reefs for (A) turf, (B) calcareous, and (C) fleshy algae (mean ± SE). The 3 functional foraging groups (FG I–III) are groups of parrotfish species as defined in Fig. 3
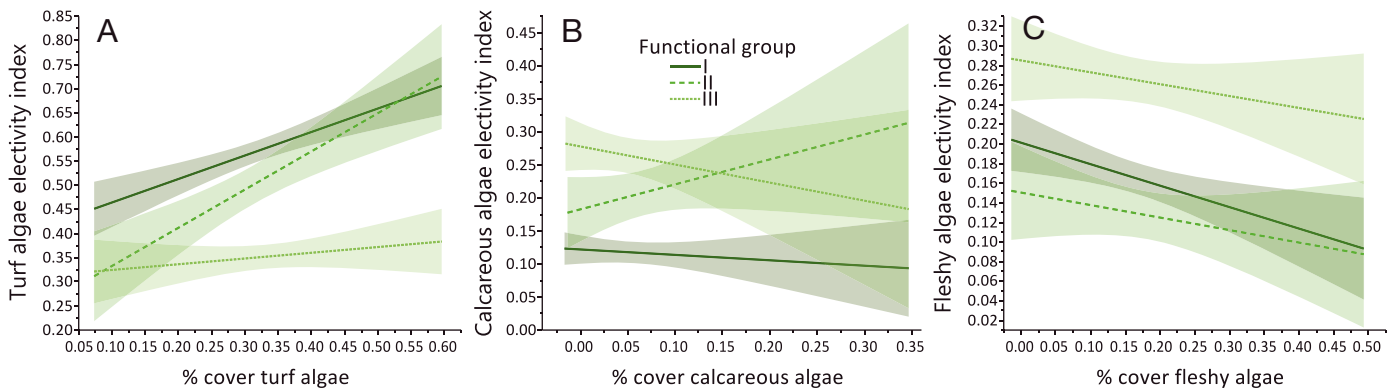

Fig. 6. Electivity indices for each algal type change with varying abundance of that algal type for each functional group on nearshore and offshore sites. (A) Turf, (B) calcareous, and (C) fleshy algae. Shaded regions indicate 95% confidence intervals. The 3 functional foraging groups (FG I–III) are groups of parrotfish species as defined in Fig. 3. See Table 2 for general linear model results

Table 2. Generalized linear model of electivity indices (Manly's alpha) for 3 substrate communities and 3 parrotfish functional feeding groups (FGs) as a function of % substrate cover (turf, calcareous, or fleshy algae) and total parrotfish biomass (log g m^{-2}). Parrotfish FG composition is based on significant preferences for substrates (I = turf, II = turf + calcareous, III = turf + calcareous + fleshy algae) from Fig. 3. Values in **bold** and *italic* indicate significant positive and negative relationships (p < 0.05), respectively

Substrate	FG	—— Algal cover ——			Parrotfish biomass		
		df	χ^2	p	df	χ^2	p
Turf	I	**1**	**5.921**	**0.0150**	**1**	**4.330**	**0.0374**
Turf	II	**1**	**7.504**	**0.0062**	1	0.044	0.8333
Turf	III	1	0.324	0.5687	1	0.353	0.5519
Calcareous	I	1	0.005	0.9419	**1**	**4.877**	**0.0272**
Calcareous	II	1	0.378	0.5382	1	2.429	0.1191
Calcareous	III	1	2.848	0.0915	**1**	**6.109**	**0.0134**
Fleshy	I	*1*	*4.203*	*0.0403*	**1**	**4.581**	**0.0323**
Fleshy	II	1	1.975	0.1599	*1*	*6.942*	*0.0084*
Fleshy	III	1	1.604	0.2053	1	2.082	0.1490

(χ^2 = 4.203, p = 0.040) and showed non-significant decreases for group II (χ^2 = 1.975, p = 0.160) and group III (χ^2 = 1.604, p = 0.205) (Table 2). Foraging preferences showed little change in response to changes in calcareous algae cover (Fig. 6B).

Parrotfish biomass and foraging preferences

Tests for whether foraging preferences for preferred algal communities decrease with increasing parrotfish competition (biomass) found that most parrotfishes decreased foraging in turf and fleshy algae communities as a function of parrotfish biomass while increasing foraging in calcareous algal communities (Fig. 7). Group I parrotfishes maintained a significantly positive relationship between foraging preference and parrotfish biomass (χ^2 = 4.330, p = 0.037; Table 2), while group II and group III showed no such relationship (Fig. 7A). All 3 functional groups showed an increase in foraging preferences for calcareous algal communities with increasing parrotfish biomass (Fig. 7B), including statistically significant increases for group I (χ^2 = 4.877, p = 0.027) and group III (χ^2 = 6.109, p = 0.013) (Table 2). However, for fleshy algal communities (Fig. 7C), group I (χ^2 = 4.581, p = 0.032) and group II (χ^2 = 6.942, p = 0.008) showed decreasing feeding preferences with increasing biomass while group III (χ^2 = 2.082, p = 0.149) showed no relationship (Table 2).

DISCUSSION

Our study corroborates the findings of previous studies that Caribbean parrotfishes forage primarily on algal communities, with all parrotfish species showing preferences towards substrates with one or more algal types (Cardoso et al. 2009, Adam et al. 2015b, Dromard et al. 2015). We found a continuum of foraging preferences that ranged from *Scarus vetula*, which fed preferentially on turf algal communities while actively avoiding calcareous and fleshy algal species, to *Sparisoma aurofrenatum*, which preferred all 3 algal communities with the strongest preference for substrates covered in fleshy algae.
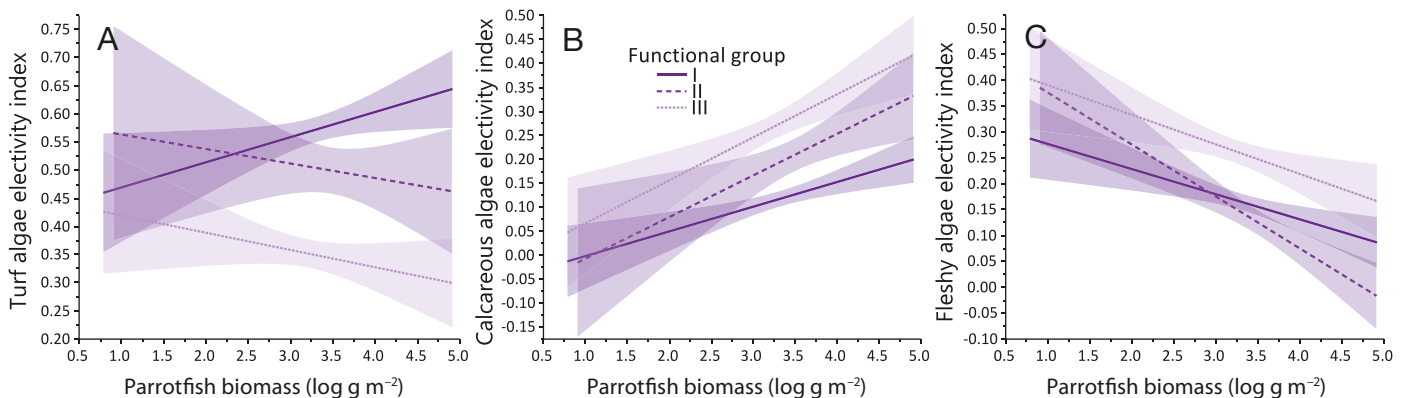

Fig. 7. Electivity indices for each algal type change with increasing biomass of total parrotfish for each functional group on nearshore and offshore sites. (A) Turf, (B) calcareous, and (C) fleshy algae. Shaded regions indicate 95% confidence intervals. The 3 functional foraging groups (FG I–III) are groups of parrotfish species as defined in Fig. 3. See Table 2 for general linear model results

Our cluster analysis of species-specific foraging preferences identified 3 distinct functional feeding groups and corroborate the findings of Adam et al. (2015b), who identified the same algal generalist *Sparisoma* species (macroalgal browsers), and the turf-grazing scrapers including all *Scarus* species and *Sparisoma viride*. The differences in our functional group designations were likely due to our inclusion of juvenile phases and inshore reefs with high calcareous algae cover allowing us to further subdivide the turf-grazing scrapers into 2 distinct functional groups based primarily on whether they preferentially foraged in calcareous algal communities or not.

This study and those that came before suggest that parrotfish do not strictly follow genus-specific diets predicted by specializations in their jaw morphology (Streelman et al. 2002, Burkepile & Hay 2008, Cardoso et al. 2009). Stoplight parrotfish *Sparisoma viride* have a diet more similar to the *Scarus* species that focus grazing on turf algal communities than to the *Sparisoma* species that graze in all 3 algal communities (Adam et al. 2015b). This is consistent with previous macroevolutionary models which suggested that diet variation is higher in the *Sparisoma* clade than in the *Hipposcarus–Scarus–Chlorurus* clade (Price et al. 2010, Brandl et al. 2015). Furthermore, a recent study by Clements et al. (2016) suggested that parrotfish are not targeting the algae, but are instead selectively grazing on the epiphytes and endophytes associated with different algal, seagrass, and invertebrate communities. While our observations do not allow us to identify the specific dietary items consumed by our parrotfishes, we can identify which substrate communities were visited and which were not. For example, our results showed that none of the parrotfish species in the middle Florida Keys preferentially fed on hard corals, gorgonians, or sponges. In fact, all species took far fewer bites of these substrates than expected given their proportional abundance on the substrate. Since the abundance of reef-building corals has declined drastically over the past 35 yr (Alevizon & Porter 2015), it not surprising that corallivory was observed less frequently than previously reported (Rotjan & Lewis 2006, Burkepile 2012). The abundance of coral species with the highest rates of predation in these studies (*Montastrea* spp. and *Porites porites*) have low abundances on the reefs of the middle Florida Keys. Furthermore, observations of coral biting by parrotfish may serve an alternative function such as territorial marking (Bruggemann et al. 1994a, van Rooij et al. 1995) or may be incidental while grazing on turf algal com-

munities (Carlson et al. 2017). Our results also indicate a clear hierarchy of preference for algal communities with turf > calcareous > fleshy. This is evident by preference for turf algal communities in all 3 functional groups, preference for calcareous algal communities in 2 of 3 functional groups, and preference for fleshy algal communities in 1 of 3 functional groups. Further evidence for this hierarchical ranking comes from the strength of preference, inferred from the slope of the electivity index versus the % cover of algal substrate, which is mostly positive for turf algae, neutral for calcareous algae, and negative for fleshy algae.

Reef fishes often undergo ontogenetic changes in behavior, including shifts in habitat use (Dahlgren & Eggleston 2000), predator evasion (Fuiman & Magurran 1994), and foraging strategies (Schmitt & Holbrook 1984). To our knowledge, ontogenetic shifts in foraging preferences have never been previously described in Caribbean parrotfishes. We found that the foraging preferences of all 3 functional groups were more similar for juveniles and more dissimilar for adults. Feeding on turf communities increased from juvenile to intermediate phase in *Scarus* spp. and *Sparisoma viride* (functional groups I and II), but decreased in *Sparisoma* spp. (functional group III). Ontogenetic shifts in diet have long been thought to be a mechanism to reduce intraspecific competition for resources, and may also explain why the foraging preferences of adult parrotfishes have diverged. The complex social structure of parrotfish and the behaviors associated with these ontogenetic phases offer explanations for these dietary shifts with age (Bruggemann et al. 1994a). Juvenile parrotfish spend much of their time in schools composed of individuals from all 3 functional groups and graze together as a group (Overholtzer & Motta 2000). When they reach maturity, some species undergo a color transition and school more often with conspecifics (Robertson & Warner 1978). In these species, terminal-phase males defend harems of females, potentially restricting the entry of other parrotfish to their foraging areas (Muñoz et al. 2000, Mumby & Wabnitz 2002, Catano et al. 2015). Territorial behaviors have the potential to change algal community structure and resource availability at local scales (Catano et al. 2014) and suggest that the composition of parrotfishes inhabiting particular areas of the reef can have intense local effects on algal communities.

Variation in the species composition and abundance of algal types between different locations make it difficult to generalize about the foraging preferences of parrotfishes (Adam et al. 2015a). For

example, higher abundances of calcareous algae (*Halimeda* spp.) occurred on nearshore reefs compared to reefs located offshore (Smith 2015). Our results suggest that the decreased foraging in calcareous algal communities from inshore to offshore reefs is proportional to the decreased abundance of calcareous algae. However, there is a different pattern for fleshy algae, which were more abundant on offshore reefs but taken less often as their abundance increased. There is little doubt that the availability of food sources can alter the foraging behavior and location of organisms, including parrotfish (Carlson et al. 2017). When resources are more scarce, grazing areas become larger as the search for food continues. As fleshy algae became more abundant, foraging preferences decreased, suggesting that parrotfish are shifting preferences towards turf algal communities, which are abundant in all habitats. Other studies that have reduced the abundance of macroalgae observed increases in herbivorous fish abundance and grazing pressure, potentially due to changes in algal succession favoring turf algae (McClanahan et al. 2000, 2001). These changes in substrate composition can also increase the aggressiveness of interactions with other reef fish, such as damselfishes, adding a further deterrent for grazing parrotfish (Jones 1992). These grazing patterns across sites with varying algal composition can have major implications on algal abundances and coral recruitment (Arnold et al. 2010), suggesting that the density of fish belonging to each functional group can greatly alter the trajectory of coral reef recovery (Jouffray et al. 2015).

Intense resource competition and the availability of potential mates both increase with increasing conspecific density, making some locations more valuable than others (McAfee & Morgan 1996). In previous studies, food partitioning was not enough evidence to explain the coexistence of multiple parrotfishes belonging to the same functional foraging group (van Rooij et al. 1996). However, if parrotfish shift their foraging preferences to other algal communities, their coexistence is plausible. We found evidence of density-dependent shifts in foraging preferences that differed between our functional groups. Small-bodied *Scarus* spp. (functional group I) significantly increased their use of turf algal communities with increasing biomass, while large-bodied *Scarus* spp. (functional group II) and *Sparisoma* spp. (functional groups II and III) foraged more in calcareous algal communities. Interestingly, all parrotfishes (functional groups I, II, III) decreased foraging preferences in fleshy algal communities with increasing biomass. This density-dependent shift in diet can have important conse-

quences for the Florida Keys and may potentially explain why the marine protected areas of the Keys see increased adult parrotfish biomass, but not necessarily reduction in macroalgal abundance (Kramer & Heck 2007). While previous studies have found that fleshy algae do increase when herbivorous fishes are excluded at a localized scale (Lirman 2001), compensatory shifts in diet due to inter- and intraspecific competition likely prevent a strong negative association of herbivore biomass and fleshy algal cover (Burkepile & Hay 2008, Adam et al. 2015b). Damselfishes are abundant in the Florida Keys, and their farming behavior increases their site fidelity and territoriality (Ceccarelli et al. 2011). During this study, damselfish chases of focal parrotfish were commonly observed and could contribute to the avoidance of fleshy algal communities (K. Smith pers. obs.) Furthermore, the positive effects of increased local nutrients from high herbivore biomass may increase the abundance of fleshy algae, offsetting the regulatory effects due to herbivory (Burkepile et al. 2013). In addition to food, resource competition may also be driven by the need for shelter. While macroalgae can provide some degree of physical complexity, the refuge provided by algae may favor predators instead of herbivores (Hoey & Bellwood 2011). Strong competitive interactions on coral reefs may influence both the amount and type of algae remaining on reefs, as well as the potential for future reef recovery (Sandin & McNamara 2012).

In the Caribbean, there is some evidence that herbivores, such as parrotfish, regulate the abundance of macroalgae and may be a key to the recovery of degraded coral reefs (Newman et al. 2006, Jackson et al. 2014). However, recent studies have found that increases in macroalgal cover in Florida, Mexico, and Belize are unrelated to herbivore biomass in regions protected from overfishing (McClanahan et al. 2011b, Suchley et al. 2016, Cox et al. 2017). This may be due to parrotfish preferentially foraging in turf algal communities and minimizing foraging in fleshy algal communities, and calls into question the generality of top-down control of macroalgae in reef ecosystems (McClanahan et al. 2011b, Russ et al. 2015). Perhaps a better understanding of how parrotfish foraging preferences change in response to algal cover and parrotfish abundance are the keys to unlocking the true relationship between these important reef fishes and the coral reefs they occupy.

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