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BEHAVIORAL ECOLOGY – ORIGINAL RESEARCH

Application of diet theory reveals context-dependent foraging preferences in an herbivorous coral reef fish

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Abstract Dietary preferences of grazers can drive spatial variability in top-down control of autotroph communities, because diet composition may depend on the relative availability of autotroph species. On Caribbean coral reefs, parrotfish grazing is important in limiting macroalgae, but parrotfish dietary preferences are poorly understood. We applied diet-switching analysis to quantify the foraging preferences of the redband parrotfish (*Sparisoma aurofrenatum*). At 12 Caribbean reefs, we observed 293 redband parrotfish in 5-min feeding bouts and quantified relative benthic algal cover using quadrats. The primary diet items were macroalgal turfs, *Halimeda* spp., and foliose macroalgae (primarily *Dictyota* spp. and *Lobophora* spp.). When each resource was evaluated independently, there were only weak relationships between resource cover and foraging effort (number of bites taken). Electivity for each resource also showed no pattern, varying from positive (preference for the resource) to negative (avoidance) across sites. However, a diet-switching analysis consisting of pairwise comparisons of relative cover and relative foraging effort revealed clearer patterns: parrotfish (a) preferred *Halimeda* and macroalgal turfs equally, and those two resources were highly substitutable; (b) preferred *Halimeda* to foliose macroalgae, but those two resources were complementary; and (c) also preferred turf to foliose macroalgae, and those resources were also complementary. Thus parrotfish grazing rates depend on relative, not absolute, abundance of macroalgal types, due to differences in substitutability among resources. Application of similar analyses may help predict potential changes in foraging effort of benthic grazers over spatial gradients that could inform expectations for reef recovery following the protection of herbivore populations.

Keywords Diet choice · Diet switching · Resource complementarity · Foraging theory · *Sparisoma aurofrenatum*

Introduction

Grazing herbivores are important to the structure and dynamics of many high-productivity ecosystems (Byrnes et al. 2006; Olff and Ritchie 1998). This is particularly true on Caribbean coral reefs, where there is a trend towards dominance by macroalgae (Burkepile and Hay 2011; Mumby 2009; Norström et al. 2009; Rotjan and Dimond 2010). The decline in corals and rise in macroalgae has been linked to declines in the diversity of reef herbivores, particularly parrotfish (Scaridae) due to overharvesting (Burkepile and Hay 2009; Cheal et al. 2010; Hughes et al. 2003; but see Loh et al. 2015). Parrotfish and other herbivorous reef fishes can limit macroalgal growth and promote reef resilience (Bellwood et al. 2004; Hughes et al. 2007; Burkepile and Hay 2010; Cheal et al. 2010). However, the broad-brush focus on 'grazers' and 'macroalgae' as monolithic functional groups can obscure subtle but potentially important details of trophic interactions on coral reefs and

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other high-productivity ecosystems (Burkepile and Hay 2010; Pawlik et al. 2016).

Diet choice by grazers can influence their impact on the ecosystem (Miller et al. 2011; Suding et al. 2004). For example, size- and species-specific foraging preferences of grazing zooplankton can produce orders-of-magnitude variation in primary productivity among freshwater lakes with similar nutrient loading (Carpenter and Kitchell 1984). In both forest and grassland ecosystems, selective grazing by ungulates typically shift plant communities towards dominance by unpalatable species, unless herding or migratory behavior by the ungulates constrains their ability to forage selectively (reviewed by Augustin and McNaughton 1998). On coral reefs, macroalgal selectivity by herbivorous fishes can switch from positive to negative between reefs, and diet composition is not easily predicted by the absolute abundance of a resource (Bruggemann et al. 1994a; Francini-Filho et al. 2010). As a result we cannot reliably predict the expected diet of grazing reef fish on a particular reef, nor how the grazing community will respond to increased macroalgal abundances on degraded reefs (e.g., Burkepile and Hay 2010, 2011).

A key aspect of diet breadth (i.e., how many prey items are included in the diet) and diet choice (i.e., the relative foraging effort for each item) is the nutritional similarity between resources (Oaten and Murdoch 1975; Raubenheimer and Simpson 2003; Simpson and Raubenheimer 2001; van Leeuwen et al. 2013; Visser and Fiksen 2013). One formulation of diet theory, the 'geometric framework', predicts that the stoichiometric needs of grazers determine how they select among available resources (Raubenheimer and Simpson 2003). Animals should allocate foraging effort among resources to regulate their relative intake of specific nutritional components such as proteins, carbohydrates, and lipids, and micronutrients such as vitamins and minerals, to achieve a specific nutritional goal (Simpson et al. 2004). However, the predictions of the geometric framework have not been applied to studies of herbivorous coral reef fish diets (Clements et al. 2009).

Coral reefs support a wide diversity of macroalgae species that vary in nutritional value and micronutrient composition (Bruggemann et al. 1994b). When the relative abundance of different macroalgae changes, the nutritional and micronutrient seascape inhabited by grazing fishes also changes. These changes affect what grazing fish choose to eat (Abrams and Matsuda 2003; van Leeuwen et al. 2013), although other factors such as physical and chemical defenses can also influence foraging decisions (Hay et al. 1994; Loh and Pawlik 2014). If grazing reef fish forage according to the geometric framework (a nutritional approach), we can make predictions about the substitutability of different food resources based on the relationship between diet and the abundance of all available food resources. In general, two resources that are nutritionally similar (i.e., substitutable) should be consumed at rates proportional to their relative abundances, whereas two nutritionally dissimilar (i.e., complementary) resources should be consumed at rates based on the current nutritional requirements of the grazer, independent of the relative abundance of the resources (Raubenheimer and Simpson 2003). In other words, as two resources become nutritionally complementary it becomes more necessary for a specified grazer to keep both resources in their diets regardless of resource scarcity.

We can evaluate the relative substitutability vs. complementarity of diet items in a quantitatively rigorous fashion by applying models from prey switching theory (Murdoch 1969; Oaten and Murdoch 1975; Abrams 1990; Abrams and Matsuda 2003; Van Leeuwen et al. 2013). The range of possible foraging patterns on a pair of resources is best illustrated by plotting the log ratio of relative consumption of the two resources vs. the log ratio of their relative abundances (Fig. 1; using the logarithm linearizes the relationship between the two ratios across multiple orders of magnitude). Purely substitutable (i.e., nutritionally equivalent) resources will be consumed in proportion to their relative abundance because there is no advantage to choosing one substitutable resource over another (Raubenheimer and Simpson 2003; van Leeuwen et al. 2013). This will produce a curve with slope $= 1$ on the consumption–abundance plot (Fig. 1a). Additionally, among two perfectly substitutable resources one of the two may be preferred (and experience proportionately higher grazing) if, for example, it has higher nutritional content per unit mass. This would be reflected by an intercept $\neq 0$ on the vertical axis; if the first resource is preferred when the two are at equal abundance, then the intercept would be >0.

In some cases, as one resource becomes more abundant relative to substitutable alternatives it is favorable for the grazer to focus effort on that resource at a greater-than-proportional rate; i.e., switching to the more abundant resource at the expense of less-abundant resources (Murdoch 1969). This leads to a curve with slope >1 on the consumption–abundance plot (Fig. 1b; van Leeuwen et al. 2013). Note that at the extremes of the plot, when one resource is vastly more abundant than the other, it is sometimes not practical for the forager to maintain a correspondingly high preference ratio and the slope of the curve flattens; as a result, this curve sometimes takes on an S-shape.

Finally, non-substitutable complementary resources are not consumed based on their relative abundance because the physiological stoichiometry of the grazer requires a consistent ratio of the two diet items (Abrams 1990; Raubenheimer and Simpson 2003; Behmer and Joern 2008). Therefore, relative foraging effort for one

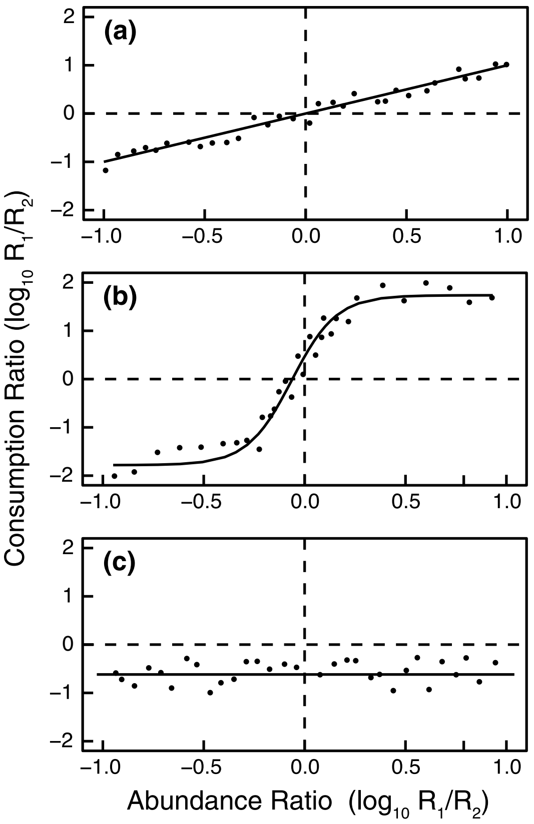

Fig. 1 Dietary response to food resources varying in similarity. The *vertical axis* represents the log ratio of consumption between two food items, R_1 and R_2. The *horizontal axis* represents the log ratio of abundance between the two food items. **a** Two resources with similar nutritional profiles (i.e., substitutable). Each resource is consumed as it is discovered in the environment, resulting in a slope of 1. **b** Two substitutable resources with similar nutritional profiles, but the forager switches to focus on the more abundant of the two resources, producing a slope >1. At the extremes of the abundance ratio the slope curves back towards a 1:1 relationship due to diminished switching when one resource is extremely rare. Note the vertical axis intercept is >0, indicating a preference for R_1 when both resources are in equal abundance. **c** Two complementary resources that provide unique benefits to the grazer. Here the slope is 0 and intercept is <0, indicating that there is no similarity between R_1 and R_2 but R_2 is preferred when the two are in equal abundance. As either resource becomes rare the grazer must expend energy to locate and consume that rare resource, because it provides necessary nutrients not available via the more abundant resource

resource should actually increase as it becomes more rare (Fig. 1c; Raubenheimer and Simpson 2003). This would produce a curve with slope <1. The slope would depend on the degree of nutritional difference between the resources; completely complementary resources would have a slope of 0 (Abrams 1993; Rindorf et al. 2006; van Leeuwen et al. 2013). By examining the relative foraging effort on alternative prey items across a wide range of relative abundances, it is possible to deduce the degree of their substitutability (or complementarity), potentially explaining otherwise obscure patterns of preference for individual resources and allowing predictions for grazing patterns on altered landscapes.

We applied diet theory to understand the foraging decisions of a common grazing parrotfish on Caribbean coral reefs. We took an observational approach, recording foraging behavior on multiple reefs that varied widely in relative abundance of potential macroalgal resources. By examining relative consumption across spatial gradients in resources, we were able to discern the relative value of resources to grazers and predict how fluctuations in resource abundance would affect diets, ultimately shaping coral reef community dynamics. Our study represents a case study in the application of dietary switching theory, because we were able to make observations across a wide range of resource abundances.

Materials and methods

Study organism

Parrotfishes (family Scaridae) are generalist grazers that are abundant on coral reefs across the Caribbean. They possess a number of specialized adaptations for grazing on macroalgae that are defended by secondary compounds (e.g., phlorotannins) or inclusion of calcium carbonate, including fused front teeth for scraping, grinding pharyngeal jaws, and a basic gut pH (Crossman et al. 2005; Mumby 2009; Targett and Arnold 1998). These adaptations help parrotfishes access a variety of foods, ranging from relatively protein-rich and undefended macroalgal turfs and associated detrital matter (Bruggemann et al. 1994a; Crossman et al. 2005; Targett and Targett 1990) to more carbohydrate-rich, chemically defended macroalgae including *Dictyota* spp., *Lobophora* spp., and *Halimeda* spp. (Burkepile and Hay 2010; Catano et al. 2015). In general, parrotfishes are more efficient at assimilating proteins and lipids (>90% assimilation efficiency) than carbohydrates (<70% assimilation efficiency; Crossman et al. 2005). As a result, parrotfishes can be expected to focus foraging effort on protein-rich resources, including macroalgal turfs. Parrotfishes will opportunistically consume other resources when they become available, such as palatable, undefended marine sponges (Dunlap and Pawlik 1996); however, such resources are sufficiently rare (Loh and Pawlik 2014) that analyzing foraging preferences for them is impractical.

Redband parrotfish (*S. aurofrenatum*) are a particularly appropriate organism in which to test diet-switching theory because they have a broad dietary range and are abundant across the Caribbean on reefs that vary widely in macroalgal composition (Loh and Pawlik 2014). Adult redband parrotfish occupy feeding territories approximately 100 m^2 in size (Catano et al. 2015). In general, smaller territory sizes are linked to greater resource quality; territories expand as resource quality declines (Mumby and Wabnitz 2002; Catano et al. 2015). These territories generally encompass a large enough patch of reef to minimize any variability in the cover of potential food resources at a given locality (Harris et al. 2015).

Like other parrotfishes, redband parrotfish are protogynous hermaphrodites; they begin their life in the initial phase (most if not all initial-phase fish are female) and older, larger individuals change sex to become terminal phase males. Initial and terminal phases are readily distinguished by coloration.

Study sites

During 2012–2013, we observed redband parrotfish feeding at 13 reef sites spread across the Eastern Yucatan peninsula (7 sites, May 2012: Cancun (Isla Mujeres), Cozumel (Paraiso Bajo), South Cozumel, Akumal, North Banco Chinchorro, Mid Banco Chinchorro, and South Banco Chinchorro), and the Southern Bahamas (6 sites, July 2013: Danger Reef (Exumas), Little Inagua, Great Inagua (Charmicle Bay), Aklins Island, Mayaguana, and Concepcion). The study sites consisted of either spur and groove reefs or patch reefs; map and site details are given in Online Resources 1 and 2.

Field foraging observations

Across all study sites, we followed a total of 293 redband parrotfish for 5-min intervals between 9 A.M. and 4 P.M. using SCUBA at depths ranging from 4.5 to 21 m. The number of fish per site ranged from 15 to 68 individuals depending on fish density and number of dives (Online Resource 2). During each 5-min interval, we recorded the sexual phase, visually estimated the total length of each focal fish to the nearest cm (length ranged from 8 to 25 cm) and recorded the number of bites taken on each type of food resource. Bites taken by redband parrotfish were used as a proxy for resource consumption because a bite represents a unit of foraging effort.

For foraging observations, we used food resource categories similar to those used by Burkepile and Hay (2011), which were in turn based on the functional groupings developed by Steneck and Dethier (1994). The food categories included macroalgal 'turf', defined as filamentous or articulated coralline algae <3 cm in length, including any other macroalgae, detrital matter, or crustose coralline algae associated with the turf. Clearly distinguishable bites on crustose coralline algae alone were counted separately. 'Foliose' macroalgae was defined as non-filamentous, non-calcareous macroalgae >3 cm in length; in our observations this category almost exclusively consisted of *Dictyota* spp. and *Lobophora* spp. The other major macroalgal category was *Halimeda* spp., which was both common and distinctive enough to be a separate category (hereafter referred to simply as *Halimeda*). We also enumerated bites on 'other' diet items, including bites taken in the water column, sponges, corals, fecal matter, gorgonians and sand, but these represented <2% of the total.

Resource cover was recorded at each study site using a point-intercept method. We used a 1 × 1 m quadrat frame containing an equally spaced 5 × 5 string grid forming 25 individual intersection points; in each quadrat we recorded the identity of organisms underneath each intersection point, using the same categories as in the foraging observations. Each study site was sampled between 7 and 25 times (number of quadrats), depending on the number of dives available at each site.

The majority of all observed bites were on items in the turf, foliose, or *Halimeda* categories (see "Results"), so our analysis focused exclusively on those three diet categories.

Data analysis

We first examined diet choice using Vanderploeg and Scavia's Relativized Electivity Index (Vanderploeg and Scavia 1979; Lechowicz 1982). This index is calculated by first finding the selectivity coefficient for diet item i, W_i:

$$W_i = \frac{r_i/p_i}{\sum r_i/p_i},$$

where r_i is the proportion of bites taken in each category i and p_i is the proportional cover of each category i. The index W_i ranges from 0 (total avoidance) to 1 (total preference). The relativized index is then

$$E_i = \frac{W_i - 1/n}{W_i + 1/n},$$

where n represents the number of diet categories available (in our case $n = 3$). The values of E_i range from −1 (total avoidance) to 1 (total preference).

Next we tested for a direct effect of resource abundance (proportional cover of each food resource group) on bite rate using a generalized linear mixed model (GLMM; logit link, Poisson error distribution). We used site as a random effect to account for potential variation in foraging effort due to site-specific factors (e.g., depth, swell, light conditions).

We also tested for the effects of relative resource cover on relative consumption, using the diet-switching framework (Fig. 1; van Leeuwen et al. 2013). We took a pairwise approach to this analysis for each of the three major resource types; therefore, the categories for relative resource cover and relative foraging effort were (1) turf/*Halimeda*, (2) *Halimeda*/foliose, and (3) turf/foliose. The relationship between relative resource cover and relative foraging effort was estimated using a linear mixed-model (LMM) regression with site as a random effect. The resulting slope and intercept were used to characterize resource similarity (slope) and resource preference (intercept), respectively. A slope ≥1 indicates substitutable resources, with switching occurring if slope >1 (Fig. 1a, b). A slope <1 indicates complementary resources; theoretically a slope approaching 0 would indicate no nutritional substitutability between two resources (Fig. 1c). Because we were primarily interested in deviations from perfect substitutability, our null hypothesis was slope = 1, and we report p values that test that null hypothesis (note the difference from typical linear regressions that test differences from a slope of zero). The intercept of the line reveals resource preference: intercept = 0 indicates neutral preference for the two resources, while intercept >0 indicates preference for the resource in the numerator (and vice versa); therefore, we tested the null hypothesis that the intercept = 0. Data from Cozumel (Paraiso Bajo) were removed from these analyses because the ratio of macroalgal turf cover to *Halimeda* spp. cover was much greater (295:1) than any other study site, making it a high-leverage and potentially misleading outlier.

Finally, we used one additional analysis to quantify the substitutability between each pair of the three resources. If resources are fully substitutable, then a scatterplot of the pairwise consumption rates should form a triangular distribution, with the outer edge of the triangle representing the maximal consumption rate of both resources (Fig. 2a). The triangular shape represents the substitution of one resource for the other. Alternatively, complementary, non-substitutable resources should produce a rectangular distribution, with consumption rates that do not depend on the other resource (Fig. 2b). We used a quantile regression (Scharf et al. 1998) to quantify the shape (triangle vs. rectangle) of the pairwise consumption relationship between each pair of the three resources. Quantile regression results may be sensitive to which quantile is used, so we performed the regression on the 90th, 75th and 60th quantile of the bite data to capture the range of outcomes. Multiple quantiles were represented in the analysis to illustrate uncertainty in substitutability between each resource combination. A bootstrap resampling procedure (10,000 replications) was used to calculate the standard errors of quantile regression coefficients (Scharf et al. 1998).

Our initial analyses showed that there was no effect of size or sexual phase on foraging preferences, so our reported results include all individuals pooled together. All analyses were performed in R 3.0.1 (R Core Team 2016). Mixed-model analyses (GLMM and LMM) were performed using the lme4 package (Bates et al. 2015). For GLMMs and LMMs we calculated the amount of variance explained by the fixed effects (marginal r^2) following Nakagawa and Schielzeth (2013) using the sem.model.fits function in the piecewiseSEM package (Lefcheck 2015).

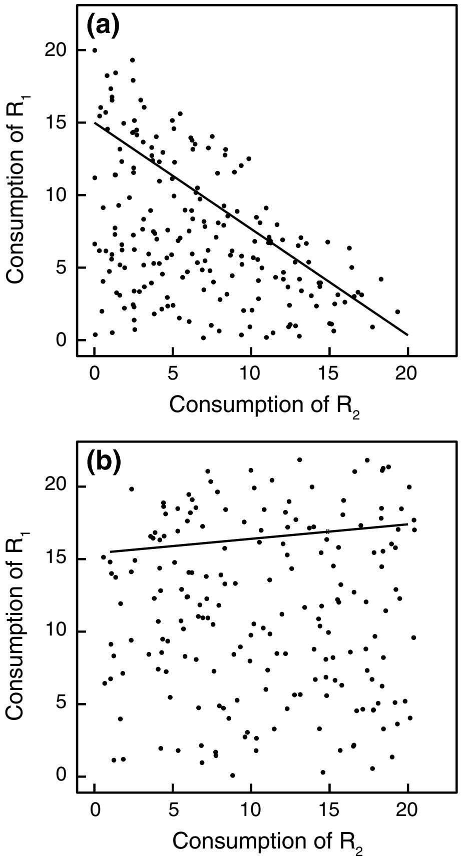

Fig. 2 Schematic illustrating substitution vs. complementarity. **a** Consumption (e.g., number of bites taken) of two substitutable resources. As the consumption of resource R_2 increases consumption of resource R_1 decreases. This results in a triangular distribution of the data and a negative slope at the maximal rate of consumption. **b** Consumption between two complementary resources. Increased consumption of resource R_2 does not affect consumption of resource R_1, resulting in a rectangular distribution of the data

Results

Macroalgal turf and foliose macroalgae dominated the benthic cover at all study sites (Online Resource 3). The absolute cover of macroalgal turf ranged from 15.4% (Great Inagua, Carmichael Bay) to 47% (Cozumel). Fleshy brown algae ranged from 3% (Cozumel) to 56% (Akumal); and *Halimeda* spp. ranged from 0.1% (Cozumel) to 21% (Middle Banco Chinchorro; Online Resource 3).

Redband parrotfish focused most of their foraging effort on turf, *Halimeda*, and foliose macroalgae; together these categories made up on average >97% of observed bites. However, both absolute and relative bite rates varied considerably among sites (Online Resource 4).

Resource selection, measured by the Vanderploeg and Scavia Relativized Index, showed that redband parrotfish selected against foliose macroalgae at all sites ($E_i < 0$; Fig. 3). Electivity was neutral to positive ($E_i \geq 0$) for macroalgal turf at all study sites except South Banco Chinchorro, where electivity was negative. Selectivity for *Halimeda* was highly variable, both among and within study sites. At South Cozumel, North Banco Chinchorro, and Mayaguana, electivity for *Halimeda* ranged from nearly −1 to 1 for fish within the same site. At Cancun there was highly negative electivity for *Halimeda*, while electivity was neutral or positive at the remaining sites (Fig. 3).

The effect of resource abundance cover on diet choice varied among diet items, but generally relative benthic cover of a resource was not strongly related to the bite rate on that resource (Fig. 4). The percent cover of turf had a significant positive relationship with bite rate (Poisson GLMM; $df = 281$, $p = 0.014$; Fig. 4a, Online Resource 5), but explained relatively little variation in the data (marginal $r^2 = 0.25$). The percent cover of *Halimeda* (Poisson GLMM; $df = 281$, $p = 0.067$, marginal $r^2 = 0.14$; Fig. 4b, Online Resource 5) and fleshy algae (Poisson GLMM; $df = 281$, $p = 0.46$, marginal $r^2 = 0.03$; Fig. 4c, Online Resource 5) did not have any relationships with the number of bites on those respective resources.

The relationship between foraging effort and the relative cover of each pair of resources afforded a clearer view of redband parrotfish diet choices than the analyses that focused on each individual resource (Fig. 5). Redband parrotfish did not exhibit a foraging preference for either *Halimeda* or turf when the two resources had equal cover, as indicated by a regression intercept not statistically different from zero (linear mixed model [LMM]; intercept = 0.53 ± 0.06; $p = 0.07$). Relative foraging effort on *Halimeda* increased proportionally when *Halimeda* cover increased relative to turf cover, and vice versa, as indicated by a regression slope not statistically different from 1 (LMM; slope = 0.91 ± 0.21; $r^2 = 0.41$; $p = 0.34$ for null hypothesis of slope = 1; Fig. 5a). The random effect of site explained 20% of the variance in that regression, and the marginal $r^2 = 0.30$.

Redband parrotfish consumed proportionally more *Halimeda* than foliose macroalgae when the two resources had equal cover (LMM; intercept = 0.77 ± 0.34; $p = 0.01$). However, relative foraging effort on *Halimeda* did not increase as the abundance of *Halimeda* increased relative to foliose macroalgae (LMM; slope = 0.26 ± 0.21; $p = 0.1$ for null hypothesis of slope = 0; $p = 3\times10^{-4}$ for null hypothesis of slope = 1; Fig. 5b). The statistically flat slope indicates complementarity between these resources, suggesting each resource provides a different nutritional benefit to redband parrotfish. The random effect of site explained 30% of the variance in that regression, and the marginal $r^2 = 0.09$.

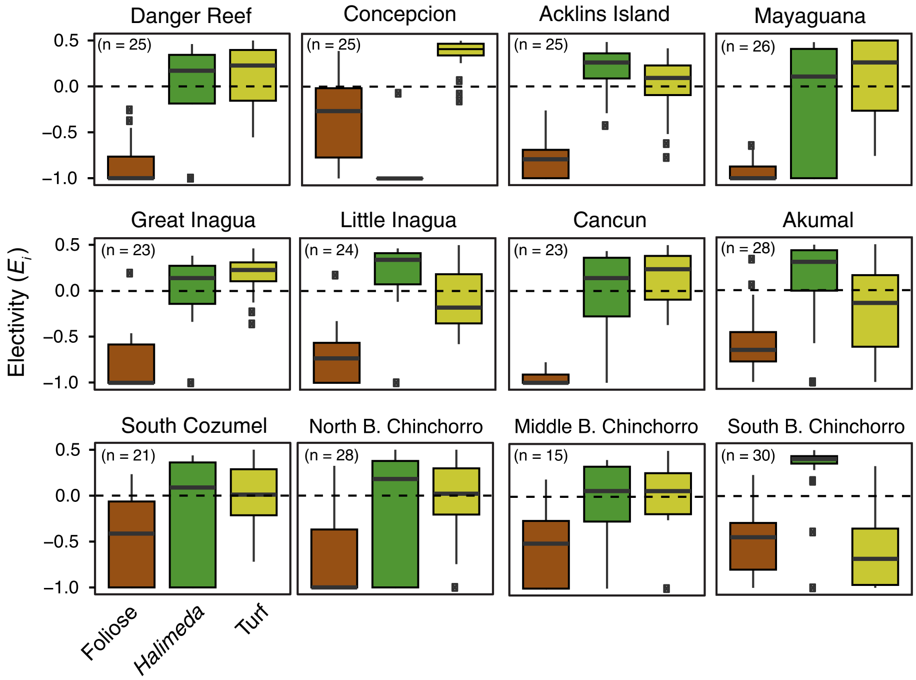

Fig. 3 Boxplots showing redband parrotfish resource electivity (Vanderploeg and Scavia's relativized index, E_i) by study site for the three main diet items: foliose macroalgae (*left bars* brown), *Halimeda* (*center bars* dark green), and turf macroalgae (*right bars* light green). Electivity is represented on the *vertical axis*: values >0 represent active selection disproportionate to abundance, values <0 represent resource avoidance. *Box* indicates interquartile range; *horizontal line* indicates median; *vertical lines* indicate 95% quantile range; *points* represent observations outside the 95% quantile range. Sample size for each site indicated in the corresponding panel

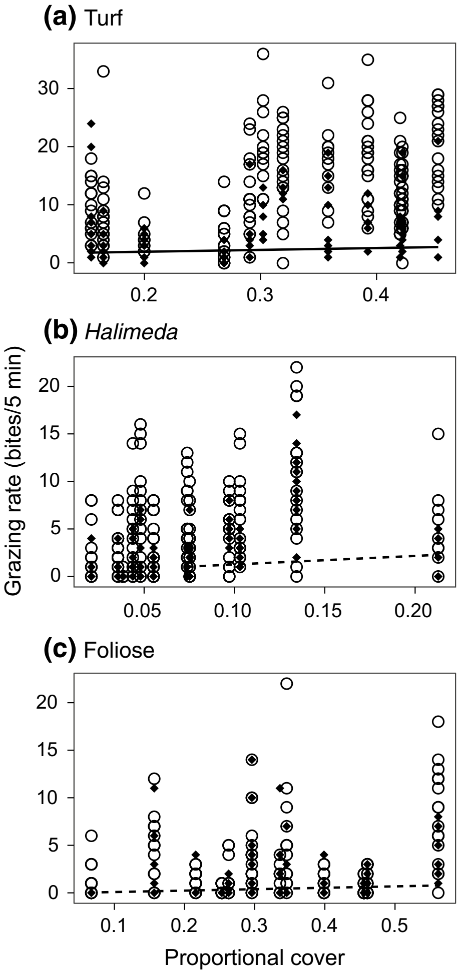

Fig. 4 Foraging response (number of bites taken in 5 min) of redband parrotfish as a function of resource cover for **a** macroalgal turf, **b** *Halimeda*, and **c** foliose macroalgae. Resource cover is expressed as a proportion of the total benthic cover. *Curves* are fits of a Poisson GLMM (*n* 293); *solid lines* indicate a relationship with a slope significantly different from zero ($p < 0.05$), and a *dashed curve* indicates slopes not significantly different from zero. *Marker shape* indicates the sexual phase of the parrotfish: initial phase (*open circle*) or terminal phase (*filled diamond*)

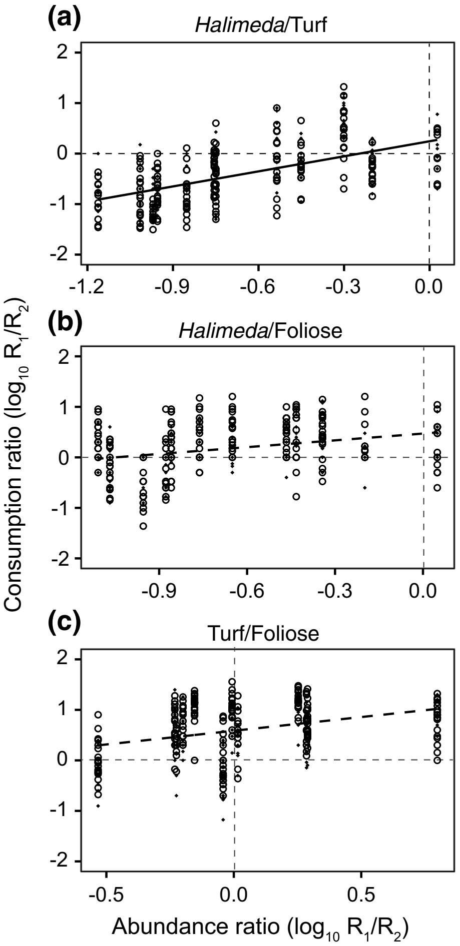

Fig. 5 Relative foraging effort of redband parrotfish in response to relative resource cover. The *horizontal axis* represents the $\log_{10}$ ratio of the proportional benthic cover of the two resources being compared. The *vertical axis* represents the $\log_{10}(x + 1)$ ratio of bites taken by parrotfish on the two resources over a 5-min period. Each pair of resources was compared: **a** *Halimeda* and macroalgal turf, **b** *Halimeda* and foliose macroalgae, and **c** turf and foliose macroalgae. *Curves* are fits of a linear mixed model ($n = 293$); *solid lines* indicate a relationship with a slope significantly different from zero ($p < 0.05$), and a *dashed curve* indicates slopes not significantly different from zero

Similarly, redband parrotfish consumed proportionally more macroalgal turf than foliose macroalgae at equal cover (LMM; intercept = 1.33 ± 0.29; $p = 2 \times 10^{-6}$), but increased their relative foraging on turf at a less-than-proportional rate when the abundance of turf relative to foliose macroalgae increased (LMM; slope = 0.57 ± 0.37; $p = 0.06$ for null hypothesis of slope = 0; $p = 0.13$ for null hypothesis of slope = 1; Fig. 5c). Note that the slope was not statistically different from either 0 or 1 at the 0.05 level, but the evidence points to a value that is closer to 1 than 0, suggesting some degree of substitutability between these two resources. The random effect of site explained 48% of the variance in that regression, and the marginal $r^2 = 0.11$.

Analysis of pairwise consumption rates revealed similar patterns in the degree to which the three resources were substitutable. Foraging effort between turf and *Halimeda* displayed a statistically significant inverse relationship (Fig. 6a; Online Resource 6). The negative slopes indicate a triangular distribution in feeding patterns, which suggests that redband parrotfish substituted between the two resources. The degree of substitutability between *Halimeda* and foliose macroalgae was quite opposite. The 90th quantile regression was positive, indicating that as parrotfish increased foraging effort on *Halimeda* they also increased foraging on foliose macroalgae. The lower quantiles had slopes not statistically

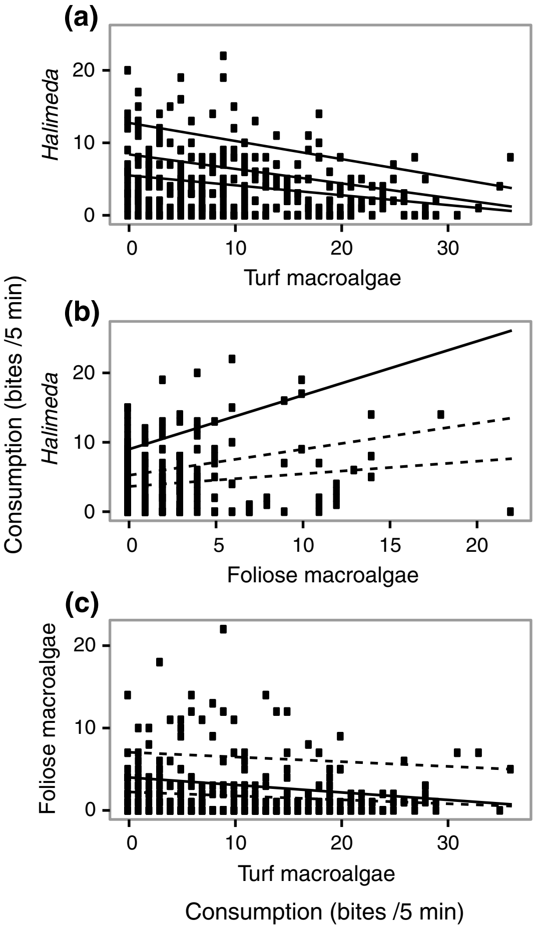

Fig. 6 Quantile regression to evaluate substitutability of resources. *Horizontal* and *vertical axes* indicate number of redband parrotfish bites per 5 min. Quantile regression reveals the shape of the outer edge of the distribution, indicating either a *triangle* (negative slope; substitutable resource) or *rectangle* (flat or positive slope; complimentary resources). We regressed the 60th (*lower curve*), 75th (*middle curve*) and 90th (*upper curve*) quantiles of each dataset in order to illustrate the degree of consistency in the shape of the distribution, and thus our confidence in the underlying substitutability patterns. *Solid lines* indicate a relationship with a slope significantly different from zero ($p < 0.05$), and a *dashed curve* indicates slopes not significantly different from zero ($n = 293$). **a** Macroalgal turf and *Halimeda*; **b** *Halimeda* and foliose macroalgae; **c** foliose macroalgae and macroalgal turf

different from zero, indicating a rectangular distribution of foraging effort between the two resources. Together these patterns suggest that the two resources are complementary (Fig. 6b; Online Resource 6). For the relationship between turf and foliose algae, the 90th and 60th quantile regressions had slopes not statistically different from zero, and the 75th quantile regression was significantly negative but very shallow. These patterns are indicative of a rectangular, complementary relationship with a weak indication of some degree of substitutability (Fig. 6c, Online Resource 6).

Discussion

Our results demonstrate that the dietary preferences of a reef herbivore, the redband parrotfish, depend on the relative cover of all available food resources. Foraging preferences of redband parrotfish did not correlate with the cover of each individual algal resource. Moreover, feeding electivity varied widely across study sites, with parrotfish exhibiting both positive and negative electivity for the same resource. Clearer patterns of resource use emerged only when we examined parrotfish foraging in the context of the relative abundances of all major diet items, as predicted by the theoretical framework developed by van Leeuwen et al. (2013).

By comparing relative foraging rates as a function of relative resource cover, we detected clear patterns of overall resource preference that were consistent across space: redband parrotfish preferred *Halimeda* spp. and macroalgal turfs equally, and preferred both of those diet items over foliose macroalgae. Additionally, by considering pairwise relative consumption, we deduced that turf macroalgae and *Halimeda* were substitutable resources, and redband parrotfish foraged on those two resource in proportion to their relative abundance at a given site. Conversely, foraging on *Halimeda* and foliose macroalgae exhibited a pattern typical of complementary resources: although redband parrotfish preferred *Halimeda*, they always consumed a consistent ratio of the two resources regardless of their relative abundance. The pattern of foraging on turf and foliose macroalgae was similar: a preference for turf, but foraging at a consistent ratio regardless of relative abundance. There was weak evidence for some degree of substitutability between turf and foliose macroalgae (e.g., the slope of the consumption–abundance plot was nearly different from zero, with $p = 0.06$; Fig. 5a), but in general the foraging patterns on those two resources were not statistically distinguishable from complementarity.

Predictions of the geometric framework

There is substantial evidence that animals will regulate their intake of different resources to achieve the desired balance of nutrition or nutrients (Raubenheimer and Simpson 2003, Simpson et al. 2004). This suggests that differences in the nutritional makeup of turf, foliose macroalgae, and *Halimeda* are an important factor determining grazer preferences for them (Abrams and Matsuda 2003; Raubenheimer and Simpson 2003). Prior work suggests that parrotfishes prefer protein-rich resources (Targett and Targett 1990; Crossman et al.

2005; Francini-Filho et al. 2010), so it is reasonable to presume that protein content is an important aspect of the resource preferences we observed. In general, macroalgal turfs have higher protein content than foliose macroalgae (Lourenço et al. 2002; McDermid and Stuercke 2003), which is consistent with the grazing preference observed in our study. We are not aware of any studies characterizing protein content of *Halimeda* relative to macroalgal turfs or foliose macroalgae, but our observational results predict it should be more similar to the former than the latter. It is clear, however, that protein content does not fully explain parrotfish foraging preferences; the complementarity between the two preferred resources and foliose macroalgae implies that the latter provides some additional important nutritional component. Additional research on the nutritional composition of algal resources would be required to determine the observed complementarity. One additional factor affecting resource preference could be that *Halimeda* spp. are calcareous, and foraging on them may provide redband parrotfish with abrasive substances that assist in the function of their pharyngeal mill. However, we are not aware of a specific experimental test of that hypothesis.

In addition to nutritional content of macroalgae, chemical or physical defenses play an important role in affecting dietary behavior. Both foliose macroalgae and *Halimeda* spp. are known to employ chemical defenses (Hay and Fenical 1987; Hay et al. 1994; Paul and van Alstyne 1988; Targett and Arnold 1998). However, in the context of our observations of this particular parrotfish species, it appears the effects of macroalgal defenses were minimal, or were not integral to the foraging responses of the fish. According to Targett and Arnold (1998), phlorotannins from brown algae (such as *Lobophora* spp. in our foliose category) would not be an effective deterrent for parrotfishes due to the basic pH of their guts. Under basic conditions, phlorotannins do not bond with the free amino groups of proteins, allowing protein assimilation by parrotfishes. Fishes with similar gut types have also been observed to consume phlorotannin-rich brown algae (Targett and Arnold 1998). Further, chemically defended *Halimeda* spp. were substitutable with undefended macroalgal turf, suggesting that the chemical defenses employed by *Halimeda* spp. (primarily the diterpenoids halimedatrial and halimedatetraacetate; Hay and Fenical 1987) were not a strong deterrent (Paul and van Alstyne 1988). Hay et al. (1994) also observed that calcium carbonate, a potential physical and chemical defense found in *Halimeda* spp., did not deter herbivory by parrotfishes.

Implications for coral reef ecology

Our observations of redband parrotfish diet preferences generally agree with previous studies of parrotfish species that reported foraging primarily on macroalgal turf and to some extent *Halimeda* spp. (Targett and Targett 1990; Bruggemann et al. 1994a; Francini-Filho et al. 2010). Redband parrotfish have also been observed to consume foliose macroalgae (including *Dictyota* and *Lobophora*) inside experimental enclosures in the Florida Keys, similar to our observations, though—similar to our results—it appears that category is not a preferred diet item (Burkepile and Hay 2008).

Across our study sites, redband parrotfish took far fewer bites from foliose macroalgae relative to its abundance when compared with other resources. Foliose algae such as *Dictyota* spp. and *Lobophora* spp. are among the most abundant macroalgae on Caribbean coral reefs and negatively affect the growth rates and fecundity of existing hard corals (Foster et al. 2008). It is widely accepted that reducing the cover of foliose macroalgae such as these is important for the resilience and recovery of Caribbean coral reefs, and grazing fishes are often prescribed as a solution for algal overgrowth (e.g., Bellwood et al. 2004, Hughes et al. 2007). However, caging experiments conducted by Burkepile and Hay (2010) showed that redband parrotfish were unable to prevent those foliose macroalgae from growing within their enclosures. Our data support the idea that redband parrotfish prefer other resources, such as macroalgal turfs, and should not be expected to significantly reduce the standing crop of foliose macroalgae, although other parrotfish species may prefer this particular resource. Nonetheless, redband parrotfish will continue to feed on foliose macroalgae as a complementary resource, despite the preference for turfs and *Halimeda*, and would be an important component of the overall grazing pressure on foliose macroalgae in a full community (as implied by the results of Burkepile and Hay 2010). This reinforces the lesson that the diet preferences of the individual species making up the grazing fish community must be taken into account in order to predict their combined influence on the benthic community (Adam et al. 2015). Our results support the findings of Burkepile and Hay (2010, 2011) and the recommendations of Adam et al. (2015) that a diverse assemblage of reef herbivores is essential to maintaining foraging pressure on the complete suite of reef macroalgae.

Conclusions

Raubenheimer et al. (2009) indicated that a priority goal of nutritional ecology is the application of organism-based models, such as the geometric framework, to specific studies in community ecology. We have taken a first step in that direction, using a quantitative accounting of relative resource cover to help explain the foraging patterns of a generalist grazer across a heterogeneous seascape. Our study provides testable predictions about resource preferences and nutritional relationships, as well as the expected grazing behavior of fish confronted with a mixture of algal resources. Viewing food resources as nutritional vectors can inform how an individual grazer will respond to changes in food resource abundance over spatial gradients. This approach could be applied to generalist grazers in any ecosystem, but in the context of coral reef ecology, the predictions that arise from the foregoing analysis could be used in resource and conservation management.

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Author contribution statement JH and JRP conceived and designed the study. JH collected the data. JH and JWW analyzed the data. JH, JWW, and JRP wrote the manuscript.

Compliance with ethical standards

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

Ethical approval All applicable institutional and national guidelines for the care and use of animals were followed.

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