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COMMUNITY ECOLOGY – ORIGINAL RESEARCH

Investigating functional redundancy versus complementarity in Hawaiian herbivorous coral reef fishes

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Abstract Patterns of species resource use provide insight into the functional roles of species and thus their ecological significance within a community. The functional role of herbivorous fishes on coral reefs has been defined through a variety of methods, but from a grazing perspective, less is known about the species-specific preferences of herbivores on different groups of reef algae and the extent of dietary overlap across an herbivore community. Here, we quantified patterns of redundancy and complementarity in a highly diverse community of herbivores at a reef on Maui, Hawaii, USA. First, we tracked fish foraging behavior in situ to record bite rate and type of substrate bitten. Second, we examined gut contents of select herbivorous fishes to determine consumption at a finer scale. Finally, we placed foraging behavior in the context of resource availability to determine how fish selected substrate type. All species predominantly (73–100 %) foraged on turf algae, though there were differences among the types of macroalgae and other substrates bitten. Increased resolution via gut content analysis showed the composition of turf algae consumed by fishes differed across herbivore species. Consideration of foraging behavior by substrate availability revealed 50 % of herbivores selected for turf as opposed to other substrate types, but overall, there were variable foraging portfolios across all species. Through these three methods of investigation, we found higher complementarity among herbivorous fishes than would be revealed using a single metric. These results suggest differences across species in the herbivore “rain of bites” that graze and shape benthic community composition.

Keywords Herbivore · Functional redundancy · Complementarity · Functional guild · Selectivity

Introduction

Species with different functional roles within an ecosystem comprise a variety of guilds, in which the species of a single guild use similar resources often through similar means (Root 1967; Steneck 1988; Simberloff and Dayan 1991). While these similarities are used to identify a feeding guild, the species within the guild may be considered to be functionally redundant, occupying the same ecological niche, or functionally complementary, in which niches amongst species do not overlap. Theoretically, there may be a large degree of functional redundancy among individuals in a guild within an ecosystem, but competition and/or limited availability of the resource will result in niche partitioning and an apparent functional complementarity among consumers (Hutchinson 1959; Chase and Leibold 2003). Studies across terrestrial, marine, and aquatic systems of

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seedling diversity in old fields (Ostfeld et al. 1997), macroalgal consumption on tropical reefs (Burkepile and Hay 2011), and insect larvae in streams (Rudolf et al. 2014) suggest that functional complementarity among consumers results in a wider breadth of resources being consumed and a greater efficiency in energy transfer to higher trophic levels. There is still debate as to the true ecological feasibility of functional redundancy within or among ecosystems (Loreau 2004).

On coral reefs, complementarity versus redundancy within herbivorous fish communities is important for understanding how the herbivore community influences the composition, biomass, and productivity of benthic algal assemblages. The complexity and high species diversity within coral reef food webs (Odum and Odum 1955; Polovina 1984), including unrelated organisms feeding on the same food source (Hay and Taylor 1985), suggest that there could be high levels of functional redundancy across trophic levels within the reefscape. Grazing of algae by the herbivore guild is believed to be particularly important on coral reefs for promoting coral dominance by reducing algal standing stock and cover, thus minimizing coral–algal competition (Ogden and Lobel 1978; McCook et al. 2001) and promoting crustose coralline algae (Smith et al. 2010), an important reef builder and preferred substrate for coral settlement. However, coral reef herbivorous fish biomass and diversity are known to be widely impacted by fishing, with some species more impacted than others (Edwards et al. 2014). Thus, there is a need to consider the role of individual species in reef dynamics. Given widespread concerns about the decline in the abundance of reef corals and the rise in the abundance of fleshy algae (Pandolfi et al. 2005), there has been growing interest in the use of herbivore restoration or enhancement as a tool for reef management (Jackson et al. 2014; Mumby 2014). For this approach to be effective, we need to better understand the roles of individual herbivore species, including the degree of redundancy versus complementarity in their consumption of benthic algal assemblages.

Benthic reef algae have evolved numerous adaptations and defenses to herbivory including physical protection of the thallus (calcium carbonate, leathery thalli, etc.), chemical defenses (secondary metabolites), cryptic growth forms, and rapid growth rates to cope with frequent grazing (Steneck Steneck and Dethier 1994; Hay et al. 1987; Williams and Carpenter 1990, respectively). Thus, not all algae are equally palatable to herbivores and likewise, not all herbivores are capable of extracting nutrients from all types of algae (Choat et al. 2004). In addition, field examination of algae can be challenging. While macroalgae are usually identifiable to at least genus level, turf algae are generally too diminutive for identification by eye in the field. Turf algal assemblages can also contain hundreds of species (Adey and Steneck 1985) and be highly spatially variable even at scales of less than a meter (Harris et al. 2015). Turf assemblages are often the most common competitors for space with corals (as reviewed in McCook et al. 2001; Barott et al. 2009; Haas et al. 2010), and there is evidence that turf algae are more abundant on reefs with localized human impacts (Jouffray et al. 2015). Thus, there is a need to better quantify the frequency and intensity of grazing by herbivorous fishes on turf algae to provide a greater understanding of benthic community dynamics.

The functional niches of herbivorous fish may be defined based on their feeding behavior (Bruggemann et al. 1994b), mouth morphology (Bellwood and Choat 1990), phylogeny (Bellwood 1994; Choat et al. 2002), and/or assimilation rate (Ogden and Lobel 1978). More recently, differences in feeding substrate and habitat selection have added to these characterizations (Brandl and Bellwood 2014; Adam et al. 2015). Several of these traits as well as the impact of a fish on the benthos have helped to delineate herbivore guilds (Steneck 1988; Green and Bellwood 2009), although none of these classifications fully explain the within-guild variation in species' functional roles, thus precluding a sound judgment of the extent of functional redundancy among herbivorous fishes. Therefore, investigation into herbivore gut contents (Choat et al. 2004) and in situ observational bite rate data (Hamilton et al. 2014) can provide insight into the nutritional ecology of fishes with regard to growth, maturation, and reproduction (Clements et al. 2009) as well as the ecological impact of fishes on the reef benthos (Burkepile and Hay 2010). Field studies of herbivore preferences and feeding rates typically focus on grazing on macroalgae (Mantyka and Bellwood 2007; Burkepile and Hay 2008) or use grazing assays of one or a few, often highly palatable, macroalgal or seagrass species as a proxy for overall grazing rates on reefs (Hoey and Bellwood 2009; Chong-Seng et al. 2014). Fewer studies have considered bite rates on turf algae (but see Brandl and Bellwood 2014; Hamilton et al. 2014; Adam et al. 2015), although turf can exceed 50 % cover on some reefs (Smith et al. 2016).

The goals of this study were to identify the individual roles of herbivorous reef fish species and to quantify the extent of functional complementarity and redundancy of herbivores on the island of Maui, Hawaii using several different approaches. First, we used in situ behavioral observations to quantify the grazing intensity (bite rates) and grazing preferences (consumption relative to availability) of the 15 most abundant herbivorous fish species on the reef, which comprise 90.5 % of the reef's total herbivore biomass. Second, we examined gut contents of a subset of herbivore taxa to examine finer scale detail of the diets of these fishes. Comparing data across these two methods of inquiry and scales of observation provides insight into the functional role of herbivorous fish in the Hawaiian Islands.

Methods

This study was conducted on the leeward side of the island of Maui, Hawaiian Islands, USA. The observational component was conducted at the Kahekili Herbivore Fisheries Management Area (KHFMA), established in 2009 as a 2 km^2 no-take area for herbivorous fish and sea urchins. Destructive sampling of fish guts was conducted north of KHFMA at Kapalua Bay and south of KHFMA at Olowalu mile marker 14. All data were collected in the shallow (less than 10 m) inshore reef. Further characterization of the reef benthos is given in the results section.

Behavioral observations

To determine the ecological impact of herbivorous fishes and their pattern of algal consumption on the reef, grazing rates for all abundant herbivorous fish species were determined using timed foraging observations. Divers followed individuals of the families Labridae (Scarinae; parrotfish) and Acanthuridae (surgeonfish) between 10 a.m. and 4 p.m. (e.g., Bruggemann et al. 1994a) to record bite rates and type of substrate consumed by fish during 3–5 min timed swims. This time period allowed for multiple forays (grazing episodes) and has been successfully implemented in other studies (Bellwood and Choat 1990; Hamilton et al. 2014). If fish behavior appeared to be altered by diver presence, observation of that fish was terminated and the data excluded from analysis. Between 10 and 48, observations were made for each of the 15 most common species of herbivorous fishes in Maui (Figure S1). Observational data for other, more rare species are included here, but sample size is limited for some of those taxa. All observational data were taken between 2 and 10 m depth at Kahekili Herbivore Fisheries Management Area between 2009 and 2013.

During each behavioral observation, divers recorded the herbivore species, total length (to the nearest cm), number of bites, and type of benthic substrate that was consumed per bite. Substrate type was recorded to the finest taxonomic classification possible through field identification. Macroalgae were identified to genus, while turf algae, crustose coralline algae, and other benthic groups were identified as functional groups. Turf algae were defined as a mixed assemblage of algae that are 2 cm or less in height (Adey and Steneck 1985). In cases where turf algae were growing as epiphytes on macroalgae, the bite was considered a bite on turf algae unless tissue from macroalgae was clearly removed. Species grazing on turf algae were recorded as grazing on “turf” despite the heterogeneous nature of the turf community, because turf algae cannot be identified at a finer scale in situ. Differentiation in these bites among turf algae was done through gut content analysis described below.

To describe the distribution of the observed bites by herbivores on different benthic taxa, the bites per minute on each benthic group for each herbivore species were averaged, and data were transformed using log $(x + 1)$ to account for the large number of zeros in the dataset (Anderson et al. 2008). Bray Curtis similarity (BCS) distances (BCS = 1 − Bray Curtis dissimilarity distance) were then calculated for transformed data (Clarke et al. 2006). Nonmetric multidimensional scaling (nMDS) plots were used to visualize the BCS values among the different herbivore species’ bite data on different benthic categories. To account for differences among species in feeding rates, in addition to absolute bite rates, the proportion of bites for each herbivore taken on different substrate types was also calculated and averaged for each herbivore species. These data were then transformed using log $(x + 1)$ and BCS calculated for each pair. nMDS plots were used to visualize the ranked BCS among the different herbivore species’ proportional bite data on different benthic categories.

To determine whether foraging behaviors within herbivore species were more similar to each other than foraging behaviors among species, we used a single-factor permutation-based multivariate analysis of variance (PERMANOVA; Anderson et al. 2008), in which fish species was the fixed factor and pseudo-F was calculated using 9999 unrestricted permutations of data. Post hoc pairwise comparisons were used to test for significant differences in bite rates and bite proportions on particular algal species. We acknowledge the possibility of a Type I Error in using multiple pairwise comparisons, but for consistency in evaluating the evidence of differences, we did not calculate an adjusted p value (Hurlbert and Lombardi 2009, 2012).

We further examined the variability of individual fishes in their proportional bite data. nMDS plots were used to visualize the ranked BCS among the different herbivore species’ proportional bite data on different benthic categories. Furthermore, we used the data to calculate the dispersion of data as deviations from the centroid (PERMDISP; Anderson et al. 2008).

We investigated whether foraging behavior of herbivores within feeding guild was more similar to each other than to species in other guilds. We categorized each species in this study according to feeding guild (Steneck 1988; Green and Bellwood 2009) as follows: scraper/small excavator (all *Scarus* and *Chlorurus* <35 cm), browser (all *Naso* and *Calatomus*), grazer/detritivore (all *Acanthurus* aside from planktivores and *Ctenochaetus*) (Table 1). We compared the mean proportion of total bites for each species on each benthic category to compare foraging composition as opposed to bite rate across species. These data were then transformed using log $(x + 1)$ and BCS calculated for each pair. nMDS plots were again used to visualize the ranked BCS and further overlaid with a cluster analysis of the BCS data

Table 1 Species observed at Kahekili as categorized by family and feeding guild

Family	Feeding guild	Species	Avg total bite rate (±SE)	# Fish observed	Substrate richness	Average # substrates bitten (±SE)
Labridae [Scarinae]	Scraper/small excavator	*Scarus psittacus*	20.4 (±1.6)	26	5	1.2 (±0.4)
		Scarus rubroviolaceus	14.7 (±1.5)	15	4	1.3 (±0.6)
		Chlorurus perspicillatus	20.1 (±4.5)	5	1	1.0 (±0.0)
		Chlorurus spilurus	16.2 (±1.7)	10	3	1.1 (±0.3)
Acanthuridae	Browser	*Naso lituratus*	12.3 (±1.2)	16	6	1.5 (±0.9)
		Naso unicornis	9.4 (±0.7)	22	8	2.0 (±0.9)
		Naso brevirostris	6.4 (±0.9)	27	7	1.5 (±0.7)
		Calotomus carolinus	6.0 (±0.8)	18	5	1.8 (±0.9)
	Grazer/detritivore	*Acanthurus triostegus*	51.4 (±5.6)	6	2	1.2 (±0.4)
		Acanthurus olivaceus	37.3 (±3.9)	27	4	1.6 (±0.6)
		Acanthurus nigrofuscus	36.7 (±1.8)	48	10	1.5 (±0.7)
		Acanthurus leucopareius	33.9 (±4.1)	11	3	1.2 (±0.7)
		Acanthurus blochii	21.7 (±5.3)	7	3	1.4 (±0.8)
		Ctenochaetus strigosus	21.7 (±1.9)	37	6	1.4 (±0.5)
		Zebrasoma flavescens	20.2 (±5.0)	13	4	1.2 (±0.4)

Average total bite rate is the average bite rate of each species on all substrate types combined (±standard error). Total number of fish observed per species is noted. Substrate richness is the total number of substrate types each herbivore species was observed biting and average substrate richness is the average number of substrates bitten by an individual in a given observation (±standard error)

to show similarity contours among species. To determine whether foraging behavior within herbivore guilds were more similar within-guild than between guilds, we used a two-factor permutation-based multivariate analysis of variance (PERMANOVA; Anderson et al. 2008), in which species was a fixed factor nested in guild, a fixed factor, and pseudo-F was calculated using 9999 unrestricted permutations of data.

The nMDS and PERMANOVA analyses were performed using PRIMER v6.1.11 ® (Clarke and Gorley 2006) with PERMANOVA + 1.0.1. add-on package (Anderson et al. 2008).

Gut contents

To examine the fine-scale composition of herbivorous fish diets, gut contents were analyzed from six species of acanthurids (*Acanthurus leucopareius*, *Acanthurus nigrofuscus*, *Acanthurus nigroris*, *Acanthurus olivaceus*, *Acanthurus triostegus*, and *Ctenochaetus strigosus*) collected in 2011 and 2012. Gut content specimens were taken at different reefs than behavioral observation data due to herbivore management, but gut contents of fishes were compared across the same reefs. Individuals of each of these species were speared by snorkelers and stored on ice immediately upon return to shore. Collected fish were dissected within 2 h of being caught or frozen immediately for later dissection. Stomachs were removed, slit along the side to open, and stomach tissue and contents were stored in glass vials in 10 % formalin in seawater.

In the lab, stomachs were removed from formalin and were emptied by flushing with seawater to isolate all contents into a dish. Contents in seawater were transferred into a 50-mL Falcon tube, shaken to break up clumps, and poured back into a plastic gridded petri dish where they were spread evenly. At twenty randomly chosen points on the gridded dish, contents were examined using a dissecting microscope at 40× magnification. Gut contents were identified to morphological group according to functional form groups adopted from Steneck and Dethier (1994) as follows: (1) filamentous, (2) foliose, (3) complex cylinder, (4) net-like, (5) coenocytic, (6) jointed calcareous, (7) encrusting, (8) calcified crust, and (9) thick and leathery (Table S2). It was possible to identify seaweeds to this level of functional form despite their typically small size or partially digested nature. Functional forms are known to reflect algal traits, including the degree of grazing palatability (Padilla and Allen 2000). Cyanobacteria, detritus, sand, and invertebrates were also identified. Contents were quantified using the proportion of algal functional groups at each point to eliminate variance due to volume of gut contents per sample (Choat et al. 2002).

We examined differences within the turf algal functional group across herbivorous fish gut contents to assess whether there was evidence for selectivity at a finer scale. While turf algae are typically defined as a mixed assemblage of algae that are 2 cm or less in height (Adey and Steneck 1985), "turf" can incorporate many of the functional forms of algae described in Steneck and Dethier (1994). Here, we defined turf algae functional forms in gut contents based on turf algae surveys in Hawaii (Stuercke and McDermid 2004) to include the cyanobacteria, filamentous, foliose, complex cylinder, and net-like forms.

Total gut content data and turf functional form gut content data are expressed as the mean proportion of gut contents by herbivore species with standard error. Potential differences in similarity of gut contents across herbivore species were evaluated using PERMANOVA, and post hoc pairwise comparisons were used to determine differences among species gut contents (Anderson et al. 2008) as in the analysis of observational data.

These data were then transformed using log $(x + 1)$ and BCS calculated for each pair. nMDS plots were again used to visualize the ranked BCS data for all turf functional forms as well as only those associated with turf algae. These plots were further overlaid with a cluster analysis of the BCS data to show similarity contours among species.

Feeding selectivity

To determine the degree to which fish bites on different benthic groups were a reflection of the availability of those groups on the benthos versus the degree to which fish preferentially selected certain species or functional groups of algae, a selectivity analysis was conducted on bite rate data following Chesson (1978, 1983). Per Chesson (1978), selectivity is defined as:

$$\hat{\alpha}_i = \frac{{}^{r_i}\!/_{n_i}}{\sum_{j=1}^{m} {}^{r_j}\!/_{n_j}}, \qquad i = 1, \ldots, m,$$

where α is the selectivity index between 0 and 1, r is the bite rate on a given benthic group, and n is the percent cover of that benthic group on the reef. α was calculated for all algae consumed by each fish species, from 1 to m. The null selectivity (α_{null}), for the herbivore community is defined as $1/m$, where m is the total number of benthic groups available to herbivores on the reef and bitten by any of the herbivores observed. Benthic groups were assessed at the genus level for macroalgae and at the functional group level for everything else (turf algae, crustose coralline algae (CCA), cyanobacteria, coral, and sand). If the calculated α equals α_{null}, then a benthic group was bitten at a rate predicted from its availability on the reef, whereas an α below α_{null} indicates that the benthic group was chosen less than its availability would predict and an α above α_{null} indicates that the benthic group was chosen more than its availability would predict.

Benthic cover was determined from surveys conducted twice a year from 2009 to 2013 by the Hawaii Division of Aquatic Resources and NOAA's Coral Reef Ecosystem Division at KHFMA. During each survey, ~80–100 transects were surveyed in stratified random sampling pattern according to reef habitat types, and 1 m^2 photoquadrats were taken every 1 m along 25-m belt transects. Photographs were analyzed using the image analysis program PhotoGrid 1.0 in which 15–100 stratified random points per photo were identified to genus level for corals and algae or functional group for turf algae, crustose coralline algae, and cyanobacteria.

Due to logistical constraints, it was not possible to instantaneously quantify benthic community composition directly at the points of substrate where an herbivore was grazing at the time of each bite. Therefore, α was calculated using a resampled bootstrapped distribution of benthic cover from all samples (2009–2013) of the habitat in which bite data were collected. This benthic distribution was then used in the calculation of α for each bite observation, and the mean and standard deviation were calculated.

Results

Behavioral observations

The overall foraging behavior of herbivorous fish based on absolute bite rate per substrate type was significantly different among species (PERMANOVA Pseudo-F = 9.162, $p = 0.0001$; Fig. 1a). However, all herbivorous fishes in this study were observed predominantly biting on turf algae. The species with the greatest bite rates on turf algae were *Acanthurus triostegus* (51.4 bites min^{-1}), *A. olivaceus* (37.3 bites min^{-1}), *A. nigrofuscus* (36.7 bites min^{-1}), *A. leucopareius* (33.9 bites min^{-1}), and *Scarus psittacus* (20.4 bites min^{-1}). In addition to bites taken on turf algae, most fish also took a small proportion of their bites on different genera of macroalgae. Pairwise comparisons show that the foraging behavior of over half of the herbivore species were between 80 and 100 % similar (Figure S2a). Despite these high levels of similarity, there are differences among

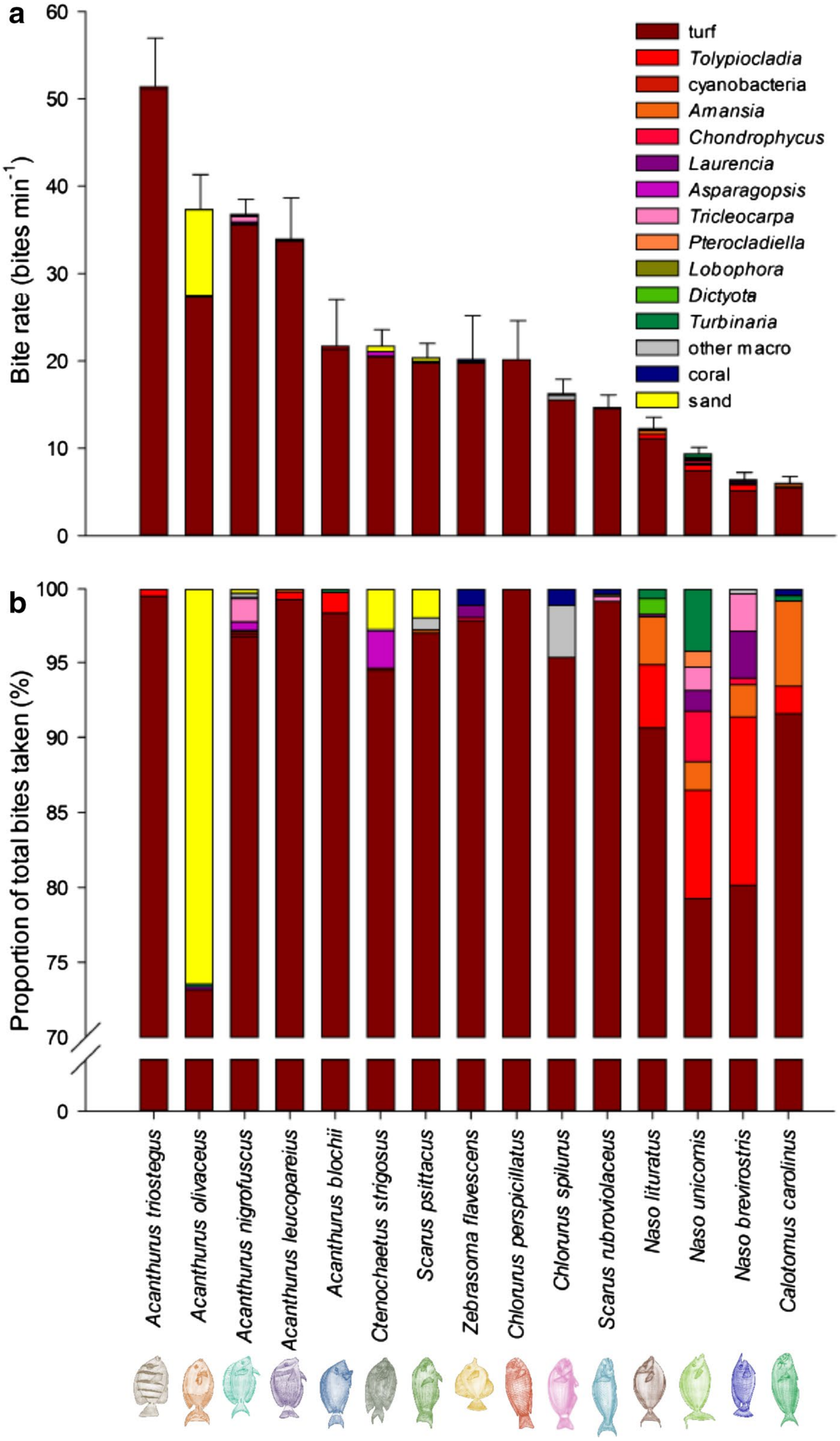


Fig. 1 **a** Bite rates and substrates bitten by herbivorous fish species at Kahekili. **b** Proportional bite data with bites on turf at least 70 % of total bites for all species of herbivores on the reef

several species particularly driven by *A. olivaceus* and *C. carolinus* and to a lesser extent *N. brevirostris*, *N. lituratus*, and *N. unicornis* (Figure S2a).

Non-metric multidimensional scaling (nMDS, 2D, stress = 0.05) using BCS distance with log $(x + 1)$ transformation (Fig. 2a) shows herbivore species arranged following an increasing gradient of bite rate intensity from right to left. *Acanthurus olivaceus*, which had the second fastest bite rate of all species and took >25 % bites on sand, is separated from all other species of herbivores. Those

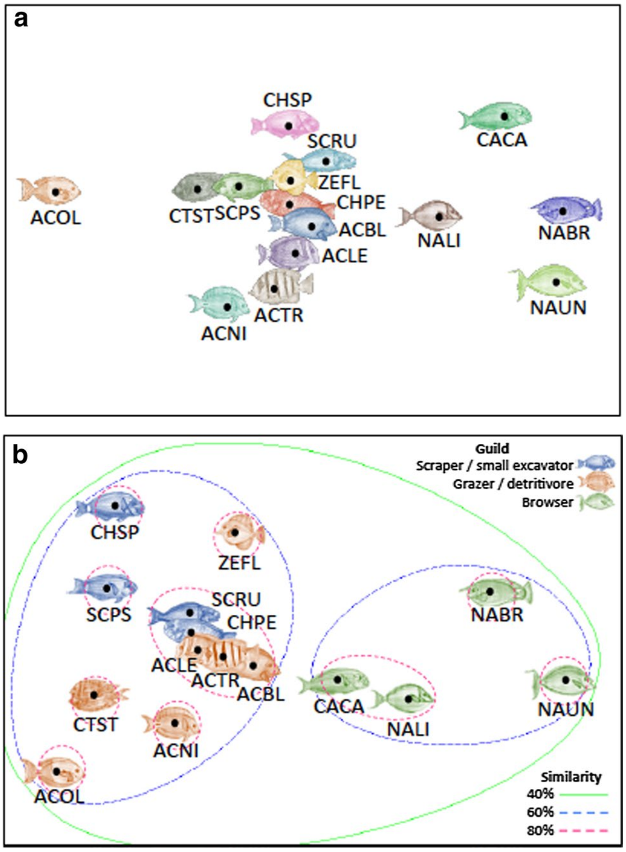


Fig. 2 nMDS of average Bray Curtis similarity (BCS) distances of log ($x + 1$) transformed fish **a** bite rates and **b** proportional bite data by herbivore guild with similarity contours. Similarity contours are the percent similarity among species using a cluster analysis overlay

herbivores with moderate bite rates are still clustered in the bottom middle of the plot. Finally, herbivores with lower bite rates and the highest substrate type diversity within their bites (*Naso lituratus*, *Naso unicornis*, *Naso brevirostris*, and *Calotomus carolinus*) are all on the right-hand side of the nMDS plot.

The proportion of bites taken on all substrate types also differed among herbivorous fish species (PERMANOVA Pseudo-F = 5.392, $p = 0.0001$). The average relative abundance of bites on turf algae ranged from 73 to 100 % across all species (Fig. 1b). *Naso unicornis*, *Naso brevirostris,* and *Naso lituratus* had the greatest diversity of substrate types consumed (9, 7, and 6, respectively) and also the greatest dispersion of bites across individuals (Table S1; Figure S3). *Acanthurus olivaceus* had the highest proportion of bites on something other than turf algae (sand = 27 %). Pairwise comparisons revealed similar patterns as the bite rate and composition data (Figure S2b), although foraging behavior of *N. brevirostris* and *A. nigrofuscus* was less similar. While *C. carolinus* and *C. strigosus* were still different, they were more similar to one another than when considering absolute bite rate data.

The nMDS plot of foraging behavior based on BCS distance with a log ($x + 1$) transformation of the proportion of bites (Fig. 2b; 2D, stress = 0.09) data shows greater spread of species. The greater spread in these data likely reflects the similarities among the proportion of bites taken on turf by most of the herbivore species studied here. Cluster analysis of the proportional bite rate data for species organized by feeding guild showed that the browsers are most similar to one another (60 % similarity), while the foraging behavior of the species in the other two guilds was less well delineated (Fig. 2b; see also Table 1). In this case, the foraging behavior based on proportional data for the scrapers *S. rubroviolaceus* and *C. perspicillatus* and the grazers *A. triostegus*, *A. leucopareius*, and *A. blochii* was all 80 % similar while less similar to others in their guilds (60 % or less). Individual differences in foraging behavior within species varied from one species to another (Table S1; Figure S3).

The proportion of bites taken on all substrate types also differed among herbivore guilds (PERMANOVA Guild Pseudo-F = 8.049, $p = 0.001$; Species(Guild) Pseudo-$F = 3.7327$, $p = 0.001$). In pairwise comparisons, browsers were significantly different than both grazer/detritivores ($t = 3.3493$, P(perm) = 0.001) and scraper/small excavators ($t = 2.5825$, P(perm) = 0.001), while the grazer/detritivores and scraper/small excavators guilds were not significantly different from one another ($t = 1.4394$, P(perm) = 0.102).

Gut contents

The composition of algae found in the guts of the herbivores studied here was significantly different among species (PERMANOVA Pseudo-F = 13.071, $p = 0.0001$; Fig. 3a). When looking just at the functional forms classified as turf algae, the composition of these forms also differed significantly among herbivore species (PERMANOVA Pseudo-F = 2.9759, $p = 0.0265$; Fig. 3b). Pairwise comparisons reveal several significant differences (Fig. 4). In particular, *A. olivaceus* and *C. strigosus* were both different from all other species (P(perm) <0.05). Composition of turf algae in the guts for *A. nigrofuscus* and *A. triostegus* was also different from one another (P(perm) <0.05). For *A. olivaceus* and *C. strigosus*, feeding observations showed high consumption on turf algae, but gut contents included considerable detritus and sand that feeding fishes of those species likely combed out of turf algal assemblages they appeared to be feeding on. The nMDS plot of gut content data for transformed BCS distances of all algal functional forms shows *C. strigosus* and *A. olivaceus* most similar (60 %) to one another, while all other herbivores were 60 % most similar to one another (Figure S4a, 2D, stress = 0). *Acanthurus nigrofuscus* and *A. nigroris* were 80 % similar to one

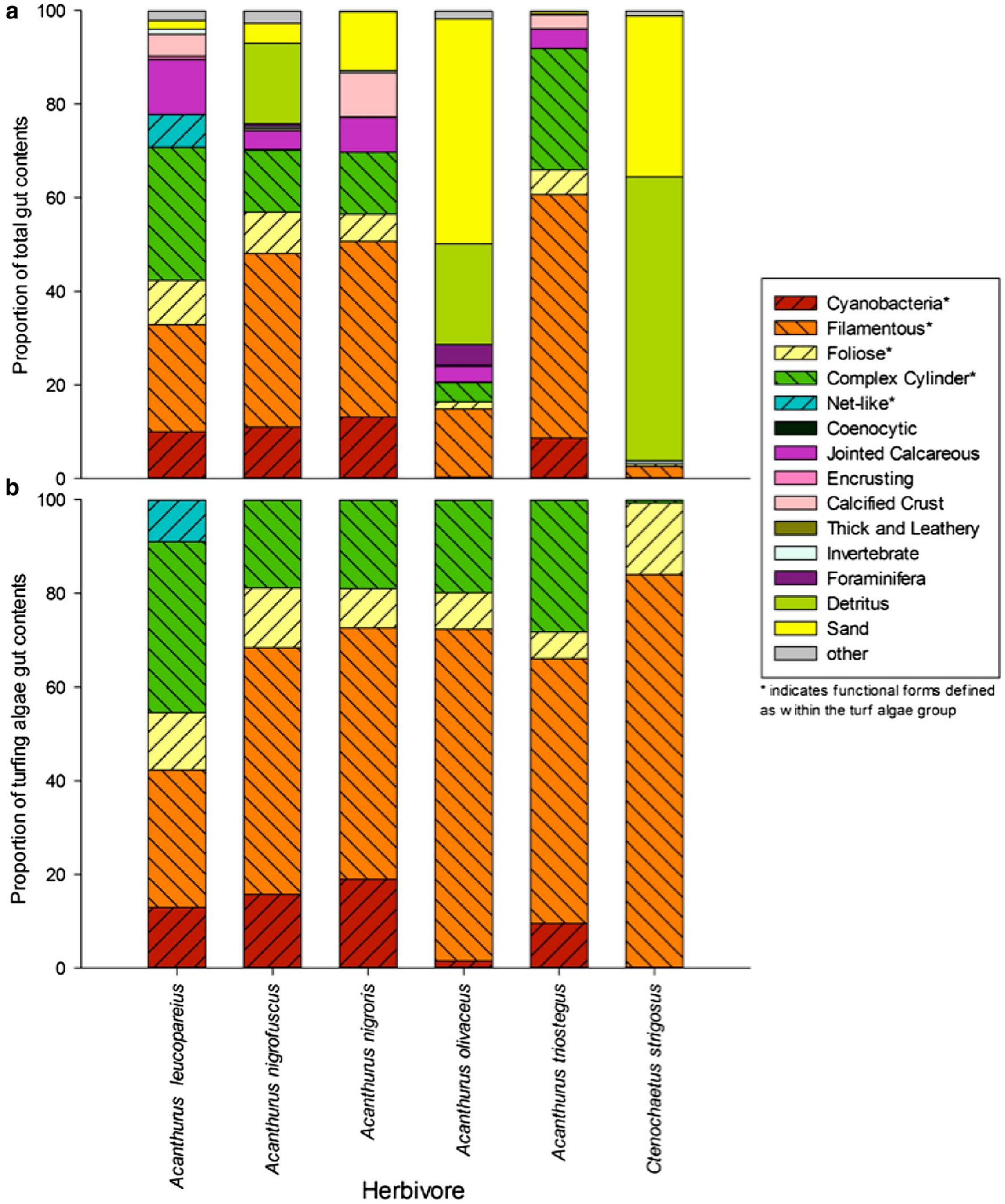
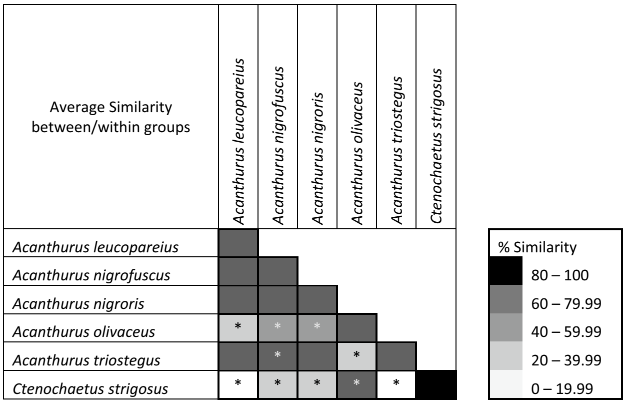


Fig. 3 Gut content analysis as the **a** proportion of different functional forms of algae in herbivore guts. **b** Of those functional forms that are typically found within the turf algae group (hashed bars and marked with *asterisk* in legend), composition of the types of turf algae that are consumed differs between herbivore species. (*A. leucopareius* $n = 2$, *A. nigrofuscus* $n = 17$, *A. nigroris* $n = 2$, *A. olivaceus* $n = 10$, *A. triostegus* $n = 6$, *C. strigosus* $n = 6$)

another. The nMDS of the transformed BCS distances of turf algal functional forms, a subset of the overall gut content data, showed all herbivores at least 60 % similar to one another, with all but *C. strigosus* 80 % similar to one another (Figure S4b, 2D, stress = 0.01).

Feeding selectivity

Average benthic cover between 2009 and 2013 across the reef at KHFMA was 34.6 % (±0.6) coral (*Porites lobata* = 19.1 % (±0.5), *Porites compressa* = 7.2 %



Average Similarity between/within groups	*Acanthurus leucopareius*	*Acanthurus nigrofuscus*	*Acanthurus nigroris*	*Acanthurus olivaceus*	*Acanthurus triostegus*	*Ctenochaetus strigosus*
Acanthurus leucopareius	▓					
Acanthurus nigrofuscus	▓	▓				
Acanthurus nigroris	▓	▓	▓			
Acanthurus olivaceus	░ *	▒ *	▒ *	▓		
Acanthurus triostegus	▓	▓ *	▓	░ *	▓	
Ctenochaetus strigosus	□ *	░ *	░ *	▓ *	□ *	■

% Similarity	
■	80 – 100
▓	60 – 79.99
▒	40 – 59.99
░	20 – 39.99
□	0 – 19.99

Fig. 4 Percent similarity of gut contents between and within herbivorous fish species. *Asterisk* indicates pairwise comparison in which P(perm) <0.05

(±0.3), *Montipora capitata* = 5.6 % (±0.3), etc.), 47.7 % (±0.7) turf algae, 6.9 % (±0.3) crustose coralline algae, and 2.7 % (±0.1) macroalgae (all species representing less than 1 % each).

Despite the high coverage of turf on the reef, about half of the herbivore species observed biting on turf were doing so at a rate in which $\alpha_{turf} > \alpha_{null}$, indicating that these fish were disproportionately selecting turf algae (Fig. 5; *Acanthurus blochii, Acanthurus leucopareius, Acanthurus nigrofuscus*, *Acanthurus triostegus, Chlorurus perspicillatus,* and *Scarus rubroviolaceus*). The scarid *C. perspicillatus* was only observed biting turf algae and nothing else ($\alpha_{turf} = 1$). This redundancy in consumption of and selection for turf algae across these herbivores is contrasted by other species that consumed turf algae as would be predicted by turf availability ($\alpha_{turf} = \alpha_{null}$; *Acanthurus olivaceus, Calotomus carolinus*, *Chlorurus spilurus*, *Ctenochaetus strigosus*, *Naso brevirostris*, *Naso lituratus, Scarus psittacus,* and *Zebrasoma flavescens*). These species were also seen biting on various species of macroalgae, coral biofilm, or sand. Because combined macroalgal cover on the reef was less than 3 % of total cover, even rare bites on macroalgae genera often result in selectivity exceeding α_{null}. *N. brevirostris*, for example, consumed turf, *Amansia*, *Tolypiocladia*, and other macroalgae as predicted by availability and strongly selected for *Laurencia*. Other species, like *N. unicornis*, strongly selected for *Turbinaria*, while avoiding turf algae ($\alpha_{turf} < \alpha_{null}$). All species were seen to select for at least one substrate type.

Discussion

The results of this study demonstrate that species within a diverse community exhibit a degree of feeding redundancy at a scale observable in situ (Fig. 1). However, when algae are examined at a finer taxonomic resolution, complementarity across herbivore species is revealed (Figs. 3, 4). Furthermore, despite the large degree of redundancy across observed bites by fishes, the selectivity for different algal genera by these fishes differs when foraging behavior is compared to substrate availability (Fig. 5). Thus, using three metrics of foraging behavior, we found higher complementarity among fishes than would be revealed through foraging behavior observations alone. Similar studies investigating herbivorous fish foraging behavior have also found high complementarity among fishes with additional ecologically relevant metrics (Adam et al. 2015; Brandl et al. 2015). This pattern of increasing functional diversity (and decreasing functional redundancy) is rooted in a reduction of functional overlap as more ecological dimensions are considered (Rosenfeld 2002). The critical contribution of increasing functional diversity for ecosystem functioning and stability has been demonstrated in various organismal assemblages ranging from beetles (Scheffer et al. 2015) to grasslands (Isbell et al. 2011) and suggests that redundancy patterns in herbivorous coral reef fishes ought to be interpreted with caution.

Still, herbivores studied here predominantly foraged on turf algae (Fig. 1) and half of the species selected turf algae more than expected based upon availability (Fig. 5). Heavy foraging by many species for turf algae is consistent with observations from elsewhere in the Pacific (Brandl and Bellwood 2014; Hamilton et al. 2014). We attribute this predominance of bites on turf algae in this and other studies to the morphology and nature of algal turfs. These often simple filamentous, palatable, and fast-growing species of algae can be readily digested as compared to more complex or defended macroalgae species. These characteristics of turf as well as its abundance on reefs may have resulted in herbivores focusing their diets toward higher proportions of turf consumption (Brandl et al. 2015). Other highly diverse systems also have large numbers of grazers that can take advantage of similar resources. In grasslands, for example, cohabitating species of ungulates have been known to reflect this similarity in dung and gut contents (Arsenault and Owen-Smith 2002).

While herbivores in this study took fewer overall bites on macroalgae, their consumption revealed complementarity (Figs. 1, 3). Complementarity in macroalgal consumption across herbivorous fishes has been highlighted in both the Caribbean (Burkepile and Hay 2008) and Pacific (Hoey and Bellwood 2009). Despite the low abundance of macroalgae on the benthos, fish still selected for individual algal taxa (Fig. 5), including both leathery (*Turbinaria*) and chemically defended species (*Asparagopsis*). Notably, however, these bites were dwarfed by the number of bites taken on turf algae.

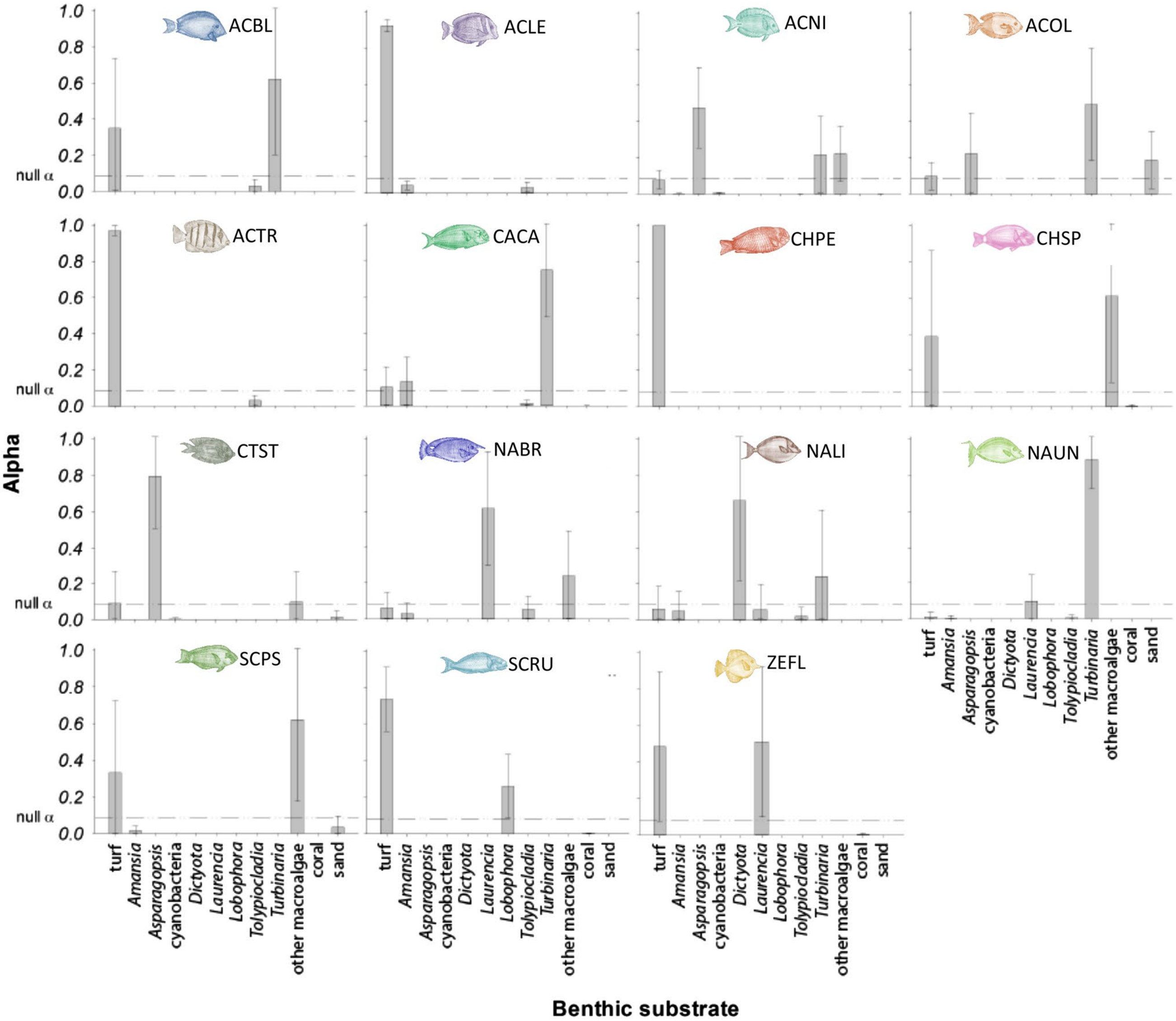


Fig. 5 Selectivity of herbivores for different types of substrate. *Error bars* are 95 % confidence intervals. Significant selectivity for or against a substrate type is indicated by 95 % CI fully above or below the null selectivity ($\alpha_{\text{null}} = 1/m$). Fish that only consumed turf algae (*Chlorurus perspicillatus*) lack 95 % CI, because all bites were taken on turf algae. ACBL, *Acanthurus blochii*; ACLE, *Acanthurus leucopareius*; ACNI, *Acanthurus nigrofuscus*; ACOL, *Acanthurus olivaceus*; ACTR, *Acanthurus triostegus*; CACA, *Calotomus carolinus*; CHPE, *Chlorurus perspicillatus*; CHSP, *Chlorurus spilurus*; CTST, *Ctenochaetus strigosus*; NABR, *Naso brevirostris*; NALI, *Naso lituratus*; NAUN, *Naso unicornis*; SCPS, *Scarus psittacus*; SCRU, *Scarus rubroviolaceus*; ZEFL, *Zebrasoma flavescens*

It is important to consider functional redundancy at different levels of scale and ecological impact. While our data are not hierarchical in nature, gut contents revealed that the composition of algae functional forms differed among the subset of herbivores dissected (Fig. 3a). In particular, functional forms of algae most commonly associated with turf algae differed (Fig. 3b; Table S2), although they still showed strong (60–80 %) similarity (Figure S4). Thus, we are able to see evidence of increasingly distinct functional resolution with taxonomic resolution of observation. Due to their diminutive nature and the impossibility of identification in the field, turf algae are often considered a single functional group in in situ analyses. Yet, our results indicate that herbivorous reef fish species do discriminate among different types of turf algae. Thus, finer scale consideration of turf communities would be necessary to truly evaluate functional redundancy of grazing on this group of algae. For example, we used gut contents to examine fine scale detail of consumption by *Acanthurus olivaceus* and *Ctenochaetus strigosus*, which both graze on patches of turf algae but are known to be ingesting detritus, sand, and other organic matter in addition to turf filaments (Choat et al. 2002). Despite behavioral observations indicating that these fishes were feeding on turfs, gut contents analysis showed that they consume organic material within turf assemblages but do not actually remove substantial filamentous turf biomass (Fig. 3a). These results corroborate work by Choat et al. (2004) in which turf-grazing acanthurids were found to be selective and have lower bite rates than detrital acanthurids (the analog in this study being *A. olivaceus* and *C. strigosus*) (Table 1; Fig. 1a). We can again draw upon analogous studies in grassland systems in which DNA metabarcoding reveals high complementarity in large African mammalian herbivores (Kartzinel et al. 2015). As in our study, using additional fine-scale tools provides additional insight into partitioning in herbivore communities.

Categorizing herbivorous fish into functional feeding guilds of scrapers/small excavators, grazers/detritivores, and browsers (Bellwood et al. 2004; Green and Bellwood 2009; Burkepile and Hay 2010) provides a framework for understanding how herbivore populations interact with the reef benthos (Edwards et al. 2014). Based upon feeding rate and type of substrate consumed, we found all three guilds at Kahekili to be at least 40 % similar to one another in grazing behavior. We further found the guild categorization for browsers to be robust at Kahekili, while scrapers/small excavators and grazers/detritivores showed overlapping foraging behavior (Fig. 2b). For all guilds, individual variability of fishes differed and was generally greatest amongst browsers (Table S1; Figure S3), reflecting their observable choices of different types of macroalgae (Fig. 1).

In addition, the impact of an herbivore on the reef is not only the type of algae an individual removes, but also the ecological fate of that bite, as in what happens to the substrate after the bite. While the majority of fish bite on turf algae in our study, the ecological impact of their bites differs due to differences in their feeding behavior and jaw morphology. In particular, such differences define the scraper and grazer/detritivore guilds (Steneck 1988; Green and Bellwood 2009). Grazing by some of the larger bodied scrapers such as *C. perspicillatus* results in bite scars about half of the time (Bellwood 1995; Ong and Holland 2010) where most or all of the turf biomass is removed and calcium carbonate is exposed. These bites will tend to promote CCA and coral cover by opening bare limestone substrate for new recruitment (Smith et al. 2010). Those excavating or gouging bites contribute to bioerosion by large parrotfishes (Bellwood and Choat 1990). Meanwhile, bites by grazer/detritivores such as *Z. flavescens* remove individual filaments with each bite leaving turf filaments cropped but capable of rapidly regrowing. The remnant turf prevents successful CCA recruitment and such cropping bites rather promote more rapid turf production through partial grazing (Carpenter 1986).

Feeding strategy is known to have variable impact in grassland ecosystems as well, in which the high density and diversity of grazers can impact grasses and shrubs differently based on feeding approach (Du Toit and Cumming 1999; Pringle et al. 2014). Some grazers are known to increase productivity in grasses through regularly cropping (McNaughton 1984; Frank et al. 1998), while others are known to open space (Andrew 1988), although the parallel feedback of colonizing habitat-forming organisms as on reefs may be lacking. Thus, the ecological fate of an herbivore bite provides a further metric for delineating the role of individual species herbivores in an ecosystem.

Finally, the contributions of individual species to overall ecosystem function have been shown to vary relative to other species across time and functional space in grasslands (Isbell et al. 2011), the intertidal (Aguilera and Navarrete 2012), seagrass beds (Duffy et al. 2001), and the desert (Thibault et al. 2010). This pattern may be more pronounced or unpredictable in a changing world (Isbell et al. 2011). For coral reefs on Maui, many of which are exposed to chronic nutrient pollution (Dailer et al. 2010) and high fishing pressure (Williams et al. 2008; Edwards et al. 2014) as well as episodic algal blooms (Conklin and Smith 2005) and declines in coral cover (Rodgers et al. 2015), the potential importance of single species in changing environments further speaks to managing for a diverse fish assemblage (Rasher et al. 2013).

Our work demonstrates that individual species within a single herbivore community have different consumption patterns on a reef and are selecting for different types of available algae despite initial appearances of high functional redundancy. In situ observation combined with gut content analysis allowed us to differentiate within and between species' bite rates and substrates bitten within a given reef context. Thus, we are able to quantify the "rain of bites" (Hamilton et al. 2014) across a reefscape, with resolution to macroalgae genera and turf algae functional form. This detailed view of the herbivore community helps to inform how individual herbivores influence benthic community structure based on community algal composition, although importantly, the ecological fate of these bites has different implications. Increasing functional complementarity with additional ecological metrics emphasizes the importance of diverse herbivore communities for reef ecosystem function.

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Author contribution statement ELAK and JES conceived and designed the experiments. ELAK, SC, RT, IDW, and JES executed the field work and resulting additional research ideas. ELAK, SC, and MG analyzed samples in the lab. YE, ELAK, SC, MG and JES analyzed the data. ELAK wrote the manuscript with significant contributions and edits from all authors.

Compliance with ethical standards

Statement of animal rights All applicable institutional and/or national guidelines for the care and use of animals were followed.

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

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