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UNIVERSITY OF CALIFORNIA, SAN DIEGO

Assessment of the functional complementarity among grazing Hawaiian surgeonfish:
A multi-pronged approach

A Thesis submitted in partial satisfaction of the requirements for the degree Master of
Science

in

Biology

by

Samantha Michelle Clements

Committee in charge:

Professor Jennifer E. Smith, Chair
Professor Jonathan Shurin, Co-Chair
Professor Carolyn Kurle

2015

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Co-Chair

Chair

University of California, San Diego

2015

DEDICATION

I dedicate this thesis first and foremost to my family – to my mom, who raised me to be the strong, curious, independent woman I am today; to my dad, who took me exploring in the tide pools as a kid, instilling a love of the ocean in my veins at a young age; and to all my family who taught me to love nature and to care for the planet, who made so many trips to Maui possible and taught me to snorkel and scuba dive. This thesis is dedicated to those who shaped me and inspired me to pursue the path I've chosen, and especially to those who taught me to keep my head up and keep moving when life gets tough. I can't imagine I would be here if not for them.

I would additionally like to dedicate this thesis to all my friends and colleagues who kept me sane throughout my time working on this project. I will never forget the infinite coffee dates, endless laughs (and some tears), trips to conferences, field sites, and campsites, innumerable social gatherings, holidays, and bonding opportunities, and hundreds of hours spent in, on, and under the water. These people have influenced and encouraged me in all the best ways.

Finally, I dedicate this thesis to my late friend and colleague, Rachel Anne Morrison. Though our time as friends was brief, she made a lasting impression on me. She was one of the few people who made me feel welcome as the new girl in the lab, a gift I hope to pay forward to others. In Rachel's mind, there was no shame in being free-spirited and wild and taking chances – we don't all fit into the same mold! In her words, "I am not wild; I am free."

EPIGRAPH

Earth and sky, woods and fields, lakes and rivers,
the mountain and sea, are excellent schoolmasters, and teach some of us
more than we can ever learn from books.

John Lubbock

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ABSTRACT OF THE THESIS

Assessment of the functional complementarity among grazing Hawaiian surgeonfish:
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by

Samantha Michelle Clements

Master of Science in Biology

University of California, San Diego, 2015

Professor Jennifer E. Smith, Chair
Professor Jonathan Shurin, Co-Chair

Herbivores on coral reefs are instrumental in mitigating the competitive interactions between reef-building corals and fleshy algae; however, not all herbivores provide the same ecological function. Grazers/ detritivores consume turf algae (and associated organic matter), which are the primary spatial competitors to corals in the Main Hawaiian Islands. This study highlights functional diversity among surgeonfishes through observations of foraging behavior, analysis of stomach

contents, and analysis of stable isotopic signatures of muscle tissue ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) for three common species (*Acanthurus nigrofuscus*, *Acanthurus olivaceus*, and *Ctenochaetus strigosus*) on the leeward side of Maui. Similar foraging behavior was observed in *A. nigrofuscus* and *C. strigosus*, with both biting primarily on turf; *A. olivaceus* grazed primarily sand in addition to turf. Diet composition based on stomach contents was different among species, and variation in composition was influenced by site. Measured $\delta^{15}\text{N}$ values indicate similar trophic position in the three species; however, $\delta^{13}\text{C}$ values varied among species at different sites, indicating consumption of different algal resources. Collectively, these data suggest that surgeonfish grazers exhibit significant within-guild functional diversity; however, the differences and degree of divergence revealed depend on the methods used.

Introduction

Coral reefs worldwide are experiencing declines in coral cover and subsequent increases in the cover of fleshy algae (Pandolfi et al. 2005). Grazing of these fleshy algae by the herbivore guild is believed to be particularly important on coral reefs for promoting coral dominance by reducing algal standing stock and thus minimizing coral-algal competition (Ogden & Lobel 1978, McCook et al. 2001). Intense grazing can also promote the abundance of other important reef builders such as crustose coralline algae (Smith et al. 2010), which are known to be important for coral larval settlement (Price 2010). However, coral reef herbivorous fish biomass and functional diversity are known to be globally impacted by fishing, with some feeding guilds experiencing more fishing pressure than others, thus there is a need to consider the role of individual species roles in reef dynamics (Edwards et al. 2014).

Given the global decline in the abundance of reef corals and the rise in the abundance of fleshy algae there has been more frequent discussion of the use of herbivore restoration or enhancement as a tool for reef management (Jackson et al. 2014). In order for this approach to be effective we need a better understanding of the roles of individual herbivores, including the amount of redundancy versus complementarity in their consumption of benthic algal assemblages. Benthic reef algae comprise a highly diverse and often complex group of photosynthetic organisms spanning several phyla. These algal groups 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 & Dethier 1994, Hay et al. 1987, Williams & Carpenter 1990, respectively). Thus not all algae are equally palatable to herbivores nor are all herbivores capable of extracting nutrition from all types of algae (Lobel 1981, Choat et al. 2004). As a result, different guilds within the herbivore assemblage have adapted to take advantage of various resource pools.

Many studies have investigated the functional diversity and partitioning of algal resources within the assemblage of herbivorous fishes on coral reefs in an attempt to better understand their role in controlling algal growth. These studies often test assumptions of function based on feeding behavior (Bruggemann et al. 1994) morphology (Bellwood & Choat 1990) and phylogeny (Bellwood 1994), and have led to categorization of species into functional guilds that include scrapers, excavators, browsers, and grazers/detritivores (Green & Bellwood 2009). There is evidence of the variation and complementarity among herbivore guilds (browsers, scrapers, etc.) and the positive effects of high inter-guild diversity in maintaining reef health. Thus far, findings indicate that areas with higher functional complementarity within the herbivorous fish community have less fleshy algal cover on the benthos than those with low functional diversity (Burkepile & Hay 2008, Rasher et al. 2013).

There is, however, significantly less information regarding within-guild functional diversity. Some studies have addressed within-guild diversity of browsers (Burkepile & Hay 2011), which typically consume macroalgae. They have found significant complementarity among species within the guild where individual taxa seem to prefer different components of the macroalgae assemblage. Studies that

exclusively focus on macroalgal groups, however, overlook turf algae, which are often the most common benthic competitors for space with corals (as reviewed in McCook et al. 2001, Barott et al. 2009). Turf algae are additionally fast colonizers of open space on reefs after disturbance events (McClanahan et al. 2001, Diaz-Pulido & McCook 2002), and are known to inhibit coral larval settlement (Birrell et al. 2005) and/or post settlement survival. Thus, grazing of turf algae is essential to maintaining low standing stock biomass of turf on reefs. Little is known about the functional redundancy of the grazer/ detritivore guild with regards to turf algae consumption, but these relationships are ecologically meaningful for reefs with high turf cover. There is a need to investigate the specific functional roles of common grazers/ detritivores on reefs to provide a greater understanding of how these important consumers interact with the benthos to alter benthic community dynamics.

Past studies have used various approaches with differing levels of resolution to investigate the individual and combined effects of certain taxa in the communities in which they exist. Investigation into herbivore gut contents (Choat et al. 2004), *in situ* observational bite rate data (Hamilton et al. 2014), and stable isotope analysis (SIA) of tissues (Bradley et al. 2015) can provide greater insight into the nutritional ecology of fishes. Specifically, these different approaches can inform variation that may exist with regards to growth, maturation, and reproduction (Clements et al. 2009) as well as the ecological impact of specific groups of fishes on the reef benthos.

Behavioral observations are simple and useful for providing information about the rate and frequency of foraging *in situ*, as well as what benthic groups an organism

is interacting with in its environment (Brandl & Bellwood 2014, Hamilton et al. 2014, Adam et al. 2015, Kelly et al. in review). These observational approaches are beneficial in that they are non-destructive and allow for high sample size without removal of the species of interest. However, the turf assemblage is highly variable and often contains material and organisms besides algae (microalgae, detritus & microbial consortia, sediment, invertebrates) (Wilson et al. 2003, Kramer et al. 2012, Max et al. 2014), making it very difficult to discern what an organism is actually targeting, removing from the environment, and ingesting.

In order to compare individual diets within and among fish species, higher resolution data are often needed, and stomach contents are commonly used. Analysis of stomach contents in coral reef herbivores can reveal food items that are often overlooked in the field, and can allow identification of prey at higher taxonomic resolution. Studies of stomach contents in herbivorous reef fish have revealed that apparent behavioral redundancy doesn't always imply redundancy in diet (Kelly et al. in review). Further, predictions based on phylogeny and oral morphology are also not always reliable predictors of diet (Choat et al. 2002 & 2004, Hoey et al. 2013). However, these analyses require destructive sampling of individuals, which can be difficult to carry out in systems where population densities are low. Additionally, gut content analysis may be biased, as many herbivorous use mechanical trituration by either pharyngeal jaws or a thick gizzard-like stomach to break down algal cells making identification of key groups in stomach contents nearly impossible (Choat et al. 2004, Rindorf & Lewy 2004).

Stable isotope analysis (SIA) can help to partition species across different trophic boundaries and may be useful for detecting within-trophic-level differences if species feed on prey items with different $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopic signatures in bulk tissues (as reviewed in Peterson 1999). Tissue isotopic analyses have the added benefit of measuring integrated information about nutrient assimilation over weeks to months (Vander Zanden et al. 2015), while behavioral observations and stomach contents provide only a snapshot of diet information on the scale of minutes to hours. The isotopic approach may be particularly useful for assessing the diet of flexible or opportunistic feeders. However, analysis of stable isotopes in tissues has very low taxonomic and functional resolution, and is often better for providing information about trophic position than exact diet. For this reason, stomach content analyses are frequently conducted in conjunction with isotopic analyses to elucidate details of feeding ecology of reef fishes (Bradley et al. 2015).

When investigating functional complementarity in a group of reef fishes that forages on a functional group of algae that are difficult to characterize, it can be useful and often necessary to use multiple approaches. This multipronged approach will allow for more accurate assessment of the complementary effects (or lack thereof) of grazing species on groups within the turf that have different intrinsic properties that make them unique (i.e. easily digestible, more complex, early successional settlers, highly competitive with corals, fast-growing/weedy, etc.). Use of only one method may underestimate the true complementarity between groups (Rosenfeld 2002). Many studies have embraced this approach of combining multiple measures of species

function and found that functional overlap is greatly reduced when multiple scales of function are considered (Brandl & Bellwood 2014, Adam et al. 2015).

In the Main Hawaiian Islands, coral cover has decreased and fleshy algae have become increasingly more abundant on many reefs (Rodgers et al. 2015). In some cases upward of 50% - 90% of the reef benthos is covered with turf algae (Jouffray et al. 2015). Herbivore populations have also declined from historic estimates as a result of fishing (Williams et al. 2008, Kittinger et al. 2011, Edwards et al. 2014). A negative relationship between macroalgal cover and herbivore biomass has been shown for reefs in the Main Hawaiian Islands (Friedlander et al. 2007) and the Caribbean (Williams & Polunin 2001). This strong relationship implies loss of ecosystem function by macroalgal consumers on reefs that have been overfished. However, we have limited data on the role of individual species of herbivores on these reefs, particularly with regards to variability in consumption of different functional groups of algae, such as the abundant turfs. It is therefore important to identify the feeding roles of individual grazers to understand how these species are utilizing specific groups within the turf assemblage and how herbivore communities may directly and indirectly influence the reef benthos.

The primary goal of this study was to evaluate the extent to which functional complementarity exists within the dominant members of the grazer/detritivore guild on the reefs of west Maui, Hawaii. We addressed this goal by examining the following questions: 1) Does foraging behavior (rates and bite choices) differ among species? 2) Does diet composition based on stomach contents differ among species? And, 3) Do

values of C and N stable isotopes differ among species, indicating different trophic positions or food sources? Comparing data across multiple methods of inquiry and scales of observation provides insight into the functional complexity of grazers in the Hawaiian Islands.

Methods

This study was conducted on the leeward side of the island of Maui, Hawaiian Islands, USA. Three species of Acanthurids (*Acanthurus nigrofuscus*, *Acanthurus olivaceus*, and *Ctenochaetus strigosus*) were chosen for this study because they represent a majority of the biomass of surgeonfish grazers in the study area (Hawaii Division of Aquatic Resources (DAR), unpublished data 2010). Behavioral observations of chosen fish species were conducted at three sites - the Kahekili Herbivore Fisheries Management Area (KHFMA), established in 2009 as a 2 km² no-take area for herbivorous fish and sea urchins, north of KHFMA at Kapalua Bay, and south of KHFMA at Olowalu mile marker 14 (Figure 1). Destructive sampling of fish guts and tissue for stable isotopes was conducted at Kapalua and Olowalu. These two sites were chosen because they have similar fish and benthic communities to KHFMA, and they are not no-take areas for herbivores.

Feeding Behavior

Grazing rates and substrate preferences for the chosen species were determined using timed behavioral observations. Divers followed individuals to record bite rates and type of substrate bitten by fish during 3-5 minute timed swims. This time period allowed for multiple forays (grazing episodes), as well as other social behavior (such as territoriality and mating), and has been successfully implemented in other studies (Bellwood & 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. At least 6, but up to 48 observations were made for each species at each site for a total of 46 to 113 observations per species, or 207 total observations. All observational data were taken between 2m and 10m depth, during a timespan from 2009 to 2012 (though a majority of data were collected in 2012).

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 (CCA), and other benthic groups were identified as functional groups. 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 of consumed turf algae was achieved through gut content analysis, explained below.

Differences in grazing intensity (bite rates) were described by comparing the absolute bite rates using a two-way crossed analysis of variance (ANOVA) in which fish species was treated as a fixed factor and site was treated as random. Post-hoc pairwise comparisons with Tukey’s honest significant difference (HSD) test were used to test for differences in absolute bite rates between species.

To describe the distribution of the observed bites on different benthic groups, the proportion of bites taken on each benthic group out of the total bites taken in an

observation for each individual fish was calculated. The proportional bite choice data were then averaged for each species at each site. Bray Curtis Similarity (BCS) distances (BCS – 1- Bray Curtis Dissimilarity distance) were then calculated for each pair. Non-metric multidimensional scaling (nMDS) plots were used to visualize the similarity within and among the different grazer species' proportional bite data on various benthic groups.

To determine whether the proportion of bites on various benthic groups within grazer species were more similar to each other than diets among species, we used a multifactorial permutation based multivariate analysis of variance (PERMANOVA; Anderson et al. 2008), in which fish species was treated as a fixed factor and site was treated as random, and a pseudo-F was calculated using 9999 unrestricted permutations of data. Post hoc pair-wise comparisons were used to test for significant differences in proportion of bites taken on particular benthic groups among species. We acknowledge the possibility of a Type I Error in using multiple pair-wise comparisons, but for consistency in evaluating the evidence of differences we did not calculate an adjusted p-value (Hurlbert and Lombardi 2009; Hurlbert and Lombardi 2012). When significant differences were found, Similarity percentage breakdowns (SIMPER) were used to identify the food types that contributed the most to the differences among grazer species.

The ANOVA, Tukey HSD test, and nMDS analyses were performed using R v3.2.2 © (R Core Team 2015) with the vegan add-on package (Oksanen et al. 2015). The PERMANOVA analyses were performed using PRIMER v6.1.11 ® (Clarke &

Gorley 2006) with the PERMANOVA+1.0.1. add-on package (Anderson et al. 2008).

Gut Contents: Functional Group Composition

To examine the composition of the diets of herbivorous surgeonfishes classified as grazers at a finer scale, gut contents were analyzed from all three species from Kapalua and Olowalu collected between 2011 and 2013. Fish were speared by snorkelers and stored on ice immediately upon return to shore. All fish were collected between 1000 and 1600 h. Specimens were collected during the northern hemisphere summer, so there is no effect of seasonality on stomach contents. Collected fish were dissected within two hours 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 spaced, pre-selected points on a gridded dish, contents were examined within a 5mm diameter circle using a dissecting microscope at 40x magnification. Gut contents were identified to morphological group according to functional-form groups adopted from Steneck & Dethier (1994) as follows: (1) filamentous, (2) foliose, (3) complex cylinder, (4) coenocytic, (5) jointed calcareous, (6) encrusting, (7) calcified crust, and (8) thick and leathery. It was possible to identify seaweeds into these categories

despite their often-small size or partially digested nature. Functional forms are known to reflect algal traits including the degree of grazing palatability (Padilla & Allen 2000). Cyanobacteria, detritus, sand, foraminifera, and invertebrates were also identified as functional groups. Contents were quantified using the proportion of algal functional groups in each stomach to eliminate variance due to differences in the volume of gut contents per sample (Choat et al. 2002).

Gut content functional form composition data are expressed as the mean proportion of gut contents by grazer species at different sites with standard error. BCS distances were calculated and data were visualized using nMDS plots. Potential differences in similarity of gut contents across species at different sites were evaluated using PERMANOVA, where fish species was treated as a fixed factor and site was treated as a random factor. Post-hoc pairwise comparisons were used to determine differences among species gut contents (Anderson et al. 2008), as in the analysis of observational data. When significant differences were found, we used the SIMPER procedure to identify the functional groups that contributed the most to the differences among stomach contents of grazer species.

Gut Contents: Composition of Algal Taxa

Contents from each stomach were subsampled for analysis at higher taxonomic resolution (to genus, when possible) of functional groups, excluding detritus and sand, under a compound microscope at 100x magnification. Five subsamples were randomly selected from the same gridded petri dish used for functional-group analysis. Each

subsample of gut contents was transferred by pipette from a 5mm-diameter circular area of the petri dish to a microscope slide. Semi-permanent slides of gut contents were made using methods for the preparation of semi-permanent slides with Karo Corn Syrup, as described by the Smithsonian National Museum of Natural History Department of Botany (<http://botany.si.edu/projects/algae/collpres/slides.htm>). One drop of 1% HCl was added to material, followed by a stain of 1% W/V aniline blue dye to reveal cellular structure of algal tissues. Finally, 1-2 drops of 25% Karo corn syrup with DI water were added and a cover slip was placed, taking care to eliminate air bubbles. Slides were allowed to dry for 1-3 days, and were finally sealed using a 50% Karo corn syrup and DI water solution.

All material on semi-permanent slides was photographed at 100x magnification using a Lumenera Infinity-1 scientific CMOS microscope camera mounted to an Olympus BX43 compound microscope. Photographs were analyzed for common genera of algae found in turf assemblages of the Hawaiian Islands and non-algal groups not easily distinguished at 40x on the dissecting microscope (such as diatoms, foraminifera, and small invertebrates, which are small and often embedded in detrital material). Analysis of stomach contents at higher taxonomic resolution allows for a more specific characterization of grazer diets, and may reveal biases for certain groups with morphological characteristics that make them more or less palatable or digestible (Lobel 1981, Padilla & Allen 2000).

Gut content taxonomic composition data were analyzed at the family level in order to reduce the total number of groups while preserving functional relevance.

Categorizing genera by family allows for combination of very similar closely related genera with similar functional and morphological form, while differentiating major taxonomic groups within a functional category (i.e. Rhodomelaceae within the turf). The very large family Rhodomelaceae contained numerous genera of differing morphology, and was therefore separated into “simple” and “complex” groups by morphological characteristics to preserve functional relevance. These data are expressed as the mean proportion of gut contents, excluding sand and detritus, by grazer species at different sites with standard error. BCS distances were calculated and data were visualized using nMDS plots. Potential differences in similarity of gut contents using fine-scale algal taxonomy across species at the two sites were evaluated using PERMANOVA, and post-hoc pairwise comparisons were used to determine differences among species gut contents (Anderson et al. 2008) as described above. Similarity percentage breakdowns (SIMPER) were used to compare the percentage contributions of the various algal families towards the within-species similarities and among-species dissimilarities.

Gut Contents: Diversity of Algal Taxa

To determine if there were differences in the diversity of algal taxa removed from the reef by grazers, the total number of genera was calculated for each individual and averaged for each species at each site. Further, Shannon-Wiener diversity (H') was calculated for each individual (stomach = community) at the genus level using R v3.2.2 © (R Core Team 2015) with vegan add-on package (Oksanen et al. 2015).

Generic richness (S) and H' were compared within and among taxa using a two-way ANOVA, where fish species was treated as a fixed factor and site was random, with post-hoc Tukey HSD test to determine significant differences among species.

Stable Isotopic Analysis of Grazers

White muscle tissue samples were taken from the left side of each fish collected as described above, from the dense muscular area ventral to the dorsal fin. Muscle tissue was then rinsed, frozen, and freeze-dried in a LABCONCO Lyophilizer (24-48 hours). Once samples were completely dried, they were homogenized using a metal spatula. Subsamples of muscle tissue were weighed in tin capsules on a Sartorius Mettler Toledo AB265-S dual range analytical balance to the nearest $\pm 1\mu\text{g}$.

Algal sources were collected from each site for general prey characterization of $\delta^{15}\text{N}$ at sites in September 2013. Algal samples were collected from the same areas where behavioral observations were conducted and consisted of cyanobacteria, common macroalgae, and turf assemblages. Only taxa that were found at all three sites were analyzed (n=3 per site). Algal samples were rinsed in fresh water and frozen within 2 hours of collection. Macroalgal samples were examined in the lab for signs of calcification by epiphytic organisms under a dissecting microscope, and only clean portions were selected for SIA. All samples were freeze-dried in a LABCONCO Lyophilizer for 24-48 hours and subsequently homogenized using a mortar and pestle. Algal samples were treated with a weak acid solution of 5% HCl to remove inorganic carbon, and stirred intermittently, adding more HCl until bubbling ceased. Once

bubbling ceased, excess liquid was removed with a pipette and the sample was dried in a drying oven at 50-60°C until a constant weight was achieved (48-72 hours).

Carbon and nitrogen isotopic and elemental composition for all samples was determined by Dumas combustion using a Carlo Erba 1108 elemental analyzer coupled to a ThermoFinnigan Delta Plus XP isotope ratio mass spectrometer. Analyses were run at the University of California, Santa Cruz Stable Isotope Laboratory. Analytical precision of internationally calibrated in-house standards is better than 0.2 per mil for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. Sample isotopic values were corrected for size, drift and source stretching effects. Carbon and nitrogen elemental composition is estimated based on standards of known elemental composition. Precision of these known compounds is determined to better than 1%.

Values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in muscle tissues were compared among species using ANOVA in R v3.2.2 © (R Core Team 2015) with fish species treated as a fixed factor and site treated as random.

Results

Feeding Behavior

Bite rates significantly differed among species ($F_{2,2} = 17.58$, $p < 0.0001$) but not among sites. *Ctenochaetus strigosus* had a slower average bite rate than the other two species (21.9 bites min^{-1} versus 34.0 and 36.7 for *Acanthurus nigrofuscus* and *A. olivaceus*, respectively) (Figure 2). The proportion of bites taken on different substrate types was also significantly different among species (PERMANOVA Pseudo-F = 61.19, $p = 0.002$), though turf was the dominant substrate type targeted by all species (Figure 2). Pair-wise comparisons show that *A. nigrofuscus* and *C. strigosus* are between 85% and 100% similar (Figure 3). A majority of dissimilarity among species is driven by behavior of *A. olivaceus*, which took on average $> 50\%$ bites on sand. The nMDS plot (2D, stress = 0.03) using BCS distance shows that *A. nigrofuscus* and *C. strigosus* are highly similar, with substrate type bitten by *C. strigosus* nested within that of *A. nigrofuscus* and separation of these two species from *A. olivaceus* (Figure 4).

Gut Contents: Functional Group Composition

The composition of algal functional groups found in the guts of the grazers studied here was not significantly different among species or site, but there was a species by site interaction (PERMANOVA Pseudo-F = 2.8804, $p = 0.03$). This interaction can be explained by reduced consumption of algal functional groups by *A. olivaceus* at Olowalu compared to Kapalua (Figure 5). Pairwise comparisons revealed $> 60\%$ similarity between *C. strigosus* and *A. olivaceus*, due to ingestion of large

quantities of sand/sediment and organic material (detritus), and consumption of less filamentous algae than *A. nigrofuscus* (Figure 5). The nMDS plot (2D, stress = 0.07) shows that *A. olivaceus* and *C. strigosus* both consume more algal functional groups and demonstrate more within-species variation at Kapalua than conspecifics at Olowalu. The same trend is not seen for *A. nigrofuscus*, which demonstrates higher within-species variation at Olowalu than Kapalua; however the gut contents are dominated by algal functional groups at both sites for this species (Figures 5 & 6).

Gut Contents: Composition of Algal Taxa

The composition of algal families found in the guts of these grazers was significantly different among species (PERMANOVA Pseudo-F = 2.7998, $p = 0.02$), between sites (PERMANOVA Pseudo-F = 4.0820, $p = 0.0001$), and there was an interaction between species and site (PERMANOVA Pseudo-F = 2.4789, $p = 0.0018$). All three species consumed primarily red filamentous algae of the families Rhodomelaceae (simple) and Ceramiaceae, with gut contents of *A. olivaceus* containing proportionally more material from the Ceramiaceae than contents from the other two species (Average proportion: *A. olivaceus* = 0.26; *A. nigrofuscus* = 0.14; *C. strigosus* = 0.16) (Figure 7). Additionally, *A. olivaceus* consumed proportionally more jointed calcareous algae of the family Corallinaceae (especially at Olowalu) and brown foliose algae of the Dictyotaceae (though highly variable, and only making a small contribution), but consumed far less cyanobacteria than the other two species at both sites. The gut contents of *A. nigrofuscus* contained more of the complex red

corticated groups, especially Rhodomelaceae (complex), Gelideaceae, and Lomentariaceae than the other two species, but were also characterized by far fewer foraminifera and invertebrates than the other two, likely due to less ingestion of sand/sediment they are associated with. Gut contents of all species contained more diatoms at Olowalu than at Kapalua, but *C. strigosus* and *A. olivaceus* showed this response to a much higher degree than *A. nigrofuscus* (Figure 7).

Pairwise comparisons and nMDS revealed that grazers at Olowalu demonstrated more within-species variation in algal taxa consumed than Kapalua. This trend was particularly strong for *A. olivaceus* at Olowalu, which showed higher average similarity among conspecifics at Kapalua (66.3%) than locally (50.1%) as a result of very high variation among individuals at Olowalu (Figure 8). On the other hand, *C. strigosus* demonstrated decreased similarity between sites (Figure 8), indicating that fish were consuming different taxonomic groups at different sites (likely driven by consumption of more diatoms at Olowalu). The nMDS (2D, stress = 0.20) using BCS distance demonstrates that, despite site-effects and site by species interactions, species appears to be the strongest predictor of diet, though diets are somewhat flexible and may take advantage of ephemeral or spatially heterogeneous resources.

Gut Contents: Diversity of Algal Taxa

The number of algal genera found in gut contents of these grazer species differed (ANOVA $F = 4.207$, $p < 0.05$), as did the number of genera recorded in all

grazers from each site (ANOVA $F = 4.349$, $p < 0.05$). Tukey pairwise comparison revealed that *C. strigosus* consumed fewer algal genera than *A. nigrofuscus* ($p\text{-adj.} < 0.05$), and that overall fewer algal genera were found in fish from Olowalu than Kapalua ($p\text{-adj.} < 0.05$) (Figure 11; Table 1). No significant differences were seen in Shannon diversity values, implying that those species who consumed more genera tended to consume groups unevenly (i.e. focused on/ preferred one type), whereas those who consumed fewer genera did so non-preferentially (Table 1).

Stable Isotopes

Elemental comparisons revealed no significant difference in $\delta^{13}\text{C}$ values among species ($F_{2,1} = 2.214$, $p > 0.05$) or sites ($F_{2,1} = 0.595$, $p > 0.05$), however there was a significant species by site interaction ($F_{2,1} = 3.900$, $p < 0.05$). Values of $\delta^{13}\text{C}$ were lower for *A. olivaceus* at Kapalua (Figure 10B), suggesting that diet source for *A. olivaceus* varies by site. Dietary sources for *A. olivaceus* and *C. strigosus* may be more similar at Olowalu, but differ at Kapalua. Fish species did differ in $\delta^{15}\text{N}$ values ($F_{1,2} = 4.442$, $p < 0.05$), and there was a significant interaction between species and site ($F_{1,2} = 5.061$, $p < 0.05$) (Figure 10B). Algal groups at the two sites did not differ in $\delta^{15}\text{N}$ values ($F_{3,1} = 2.422$, $p > 0.05$), indicating that *A. nigrofuscus* is consuming a diet more enriched in $\delta^{15}\text{N}$ at Kapalua (Figures 9 & 10B). This shift, however, may not be ecologically relevant, as it is not large enough to represent a trophic shift. The difference may also be due to temporal variation, as fish tissue samples from Kapalua were collected in a different year than algal samples.

Discussion

Herbivores play an important role in the ecology of benthic coral reef communities by potentially preventing and reversing coral to algal phase shifts via consumption of various groups of algae (Hughes et al. 2007, Fox & Bellwood 2008, but see Cheal et al. 2010). On reefs where algal turfs are the primary spatial competitors with corals and where they also comprise a majority of benthic cover, grazers should be expected to play a critical role in mitigating algal overgrowth. Given the nature of turf algae as a spatially heterogeneous functional group at small scales (the scale at which most herbivores are grazing) (Harris et al. 2015) and the difficulty identifying various groups of turfs in the field due to their small size and high diversity (Adey & Steneck 1985), grazers can appear functionally redundant based on behavioral observations alone (Kelly et al. in review). It is therefore important to consider the fine-scale variations in foraging behavior and diet within the grazer guild to determine whether there is additional specificity within the grazer guild on different types of turf algae.

The data presented here demonstrate that fishes within the grazer guild take advantage of different resources in ways that may have different functional effects on the competitive relationship between turf algae and reef building corals. While many studies have explored the extent of functional complementarity within the herbivorous fish functional group on coral reefs (Choat et al. 2002 & 2004, Crossman et al. 2005, Adam et al. 2015, Kelly et al. in review), this work is unique in that it adds to our knowledge of within-guild functional complementarity for the often-abundant

grazer/detritivore group. Further this work includes detailed analysis of the diets of 3 of the most common grazer/detritivores in the Hawaiian Islands using multiple metrics. The results presented here show that even within the grazer/detritivore guild there are clear differences in bite rates, bite choice, food types ingested, and integrated diet elucidated from C and N isotopic values. These results have important implications for grazing ecology and herbivore management and identify that there is differentiation even within herbivore feeding guilds.

Oral morphology and phylogenetic relationships are common predictors of foraging behavior and diet (Bellwood & Choat 1990, Rosenfeld 2002, Bellwood 1994). Some studies have found that prediction factors such as jaw morphology and phylogenetics do not hold true for dietary differentiation (Choat et al. 2002 & 2004, Hoey et al. 2013), however we found that morphology, physiology, and phylogenetic relationships all appear to contribute to trends on some level. Oral morphology has been used in previous studies of parrotfishes (Bellwood & Choat 1990) and surgeonfishes (Purcell & Bellwood 1993) to compare the potential for algal removal by different mouth types. *A. nigrofuscus* and *A. olivaceus* have very similar oral jaw morphology, with a straight row of serrated, robust spatulate teeth in a uniform line that can be used for cutting and cropping various algal groups (Tyler 1970, Purcell & Bellwood 1993, Fishelson & Delarea 2014). Due to larger size and slightly more robust jaw and teeth, *A. olivaceus* may more easily take advantage of physically defended algal turf taxa as demonstrated by the higher proportion of jointed calcareous algae found in the guts of this species. In contrast, *C. strigosus* has elongate, flexible

teeth that resemble bristles of a comb, which are expected to be used more for scooping detritus and combing organic matter out of the turf matrix (including benthic diatoms, foraminifera, and invertebrates) than for cutting algal filaments and blades (Purcell & Bellwood 1993, Fishelson & Delarea 2014). In an experimental context, Marshall & Mumby (2012) observed significant algal removal by *C. striatus*. Here we observed some algae in the stomachs of *C. strigosus*, indicating that it is capable of removing algae from the reef. However, algae were a minimal component of overall *C. strigosus* diet (Figure 5) and consisted primarily of groups that are simple and delicate, likely epiphytic or early-successional taxa (i.e. easily torn if they were caught in the bristle-like teeth) (as seen in Purcell & Bellwood 1993). Though nearly all bites by *C. strigosus* were on turf-covered substrate (Figure 2), it is not consuming primarily turf, but is likely using its unique comb-like oral morphology to scrape detritus from the epilithic algal matrix (EAM), as observed in previous studies (Choat et al. 2002, Max et al. 2013). In this study, oral morphology explains much of the variation in turf algal functional groups found in stomach contents of the study species.

Stomach morphology may be another predictor of diet in Acanthurid fishes. All members of the genus *Ctenochaetus* have a thick-walled, gizzard-like stomach, as do their closest phylogenetic relatives of the genus *Acanthurus* (Sorenson et al. 2013), including *A. olivaceus*. This similar stomach morphology explains the high levels of sand in the stomachs of both *A. olivaceus* and *C. strigosus* (Figure 5), as sand and grit are used as an effective method of food trituration in herbivores that do not have the

stomach chemistry to break down cellulose in plant walls to access critical nutrients (Lobel 1981). Based on behavioral observations, *A. olivaceus* expended a great deal of effort consuming sand, whereas *C. strigosus* appeared to spend no time consuming sand (Figure 2). The sand found in the stomachs of *C. strigosus* generally consisted of smaller grain size particles than sand in stomachs of *A. olivaceus* (pers. obs.), and was likely ingested as fine grit and sediments (Montgomery et al. 1989) trapped in the turf communities which were grazed by *C. strigosus*. The large proportion of bites on sand by *A. olivaceus* could have been in pursuit of microalgae or small invertebrates (as observed in goat fishes in Hawaii) in the sand, however isotopic analyses do not indicate a higher trophic position that would be obtained by consumption and subsequent digestion of invertebrates (Table 2; Figure 9). It is also possible that *A. olivaceus* must consume a large amount of sand to replace material lost by frequent defecation due to relatively short gut transit time (Choat et al. 2004, Hamilton et al. 2014). *A. nigrofuscus*, conversely, has a softer muscular stomach with proportionally longer intestines and uses stomach acid to break down food items (Jones 1968, Lobel 1981, Montgomery & Pollak 1988). This stomach morphology is characteristic of herbivores that do not use mechanical trituration to break down cellulose. Lobel (1981) found that different types of algae were affected differently by low pH conditions, with *Lophosiphonia* (a member of the simple Rhodomelaceae group) being easily lysed in solutions more acidic than seawater. More complex groups, like *Gelidium* (Gelidiaceae) and *Dictyota* (Dictyotaceae), were highly resistant to acid lysis, but vulnerable to trituration. This difference in algal digestibility by various gut

morphologies explains the high proportion of simple Rhodomelacea in stomachs of *A. nigrofuscus* in contrast with the higher proportion of Dictyotaceae (more complex) in stomachs of *A. olivaceus* (Figure 7). This provides additional insight into trends in the diversity of stomach contents. Since the gizzard-like stomach is capable of digesting all food sources *A. olivaceus* and *C. strigosus* may be less selective, indiscriminately consuming what their mouths are able to remove from their environments, resulting in low diversity and high evenness. *A. nigrofuscus* may need to be more selective, specifically targeting algae that can be digested by their morphology, consequently reducing evenness of groups consumed. The combination of these trends result in very similar values of Shannon diversity (H') despite differences in generic richness (S) among species (Figure 11).

Overall, algal groups and proportions in stomach contents appear to reflect a combined response to morphological ability to remove and digest algal groups, with *A. nigrofuscus* removing primarily red wiry turf groups, *A. olivaceus* removing more robust and complex algal groups that are most effectively broken down by mechanical trituration, and *C. strigosus* removing very little, usually delicate, algal material or recycling previously consumed algae as detritus (Figure 5). While it is important to know that fish consume different components of the turf community in different proportions, it is difficult to extrapolate this information to infer impact on the benthic reef communities. Though we have information about bite rate, a metric of the amount of material removed with each bite would be necessary to infer the quantity of material removed from the reef per bite per species. Additionally, we can make no

inferences about fine-scale selectivity or preference within the turf groups, as it would be necessary to sample the turf communities to get information about natural abundances in those groups.

Grazers and detritivores have been split in classifications in the literature numerous times (Choat et al. 2002, Crossman et al. 2005, Brandl & Bellwood 2014). *A. olivaceus* is frequently classified as a detritivore based on similar stomach morphology and contents to *C. strigosus* (Lobel 1981, Choat et al. 2002 & 2004, Sorenson et al. 2013) and small functional niche volume (Brandl & Bellwood 2014), but it has also been classified as a generalist grazer based on behavioral observations (Hamilton et al. 2014) at Palmyra atoll. Studies that focus on external morphology tend to label *A. olivaceus* as an algivore (Hamilton et al. 2014), while studies that focus on internal morphology label it as a detritivore (Choat et al. 2002). This study provides additional insight to this debate by considering both internal and external morphological traits.

Based on the combined methods used in this study, it seems that there is a spectrum between true grazer and true detritivore groups, at least among the species studied. *A. olivaceus* falls somewhere in the middle of the spectrum, consuming almost equal proportions of both algal and detrital material on Maui (Figure 5). However, because *A. olivaceus* is highly cosmopolitan and found on coral reefs worldwide (Choat et al. 2002 & 2004, Crossman et al. 2005, Brandl & Bellwood 2014), it is possible that it adjusts its behavior and diet in response to resource availability and intraspecific competition, thereby avoiding redundancy in its local

environment, resulting in niche partitioning in different reef communities (Hutchinson 1959, Chase & Leibold 2003). Interestingly, Hamilton et al. (2014) observed few bites on sand by *A. olivaceus* on Palmyra Atoll in the Northern Line Islands (there is little sand present in the environment (J. Smith pers. Com.)), but very high consumption of the green calcified alga *Halimeda*, while studies elsewhere on the Great Barrier Reef report high consumption of sand (Brandl & Bellwood 2014). Though Brandl & Bellwood (2014) report very little within-species variation (and therefore small niche volume) for *A. olivaceus* at Lizard Island, it is possible that in the absence of sand (the preferred trituration material) *A. olivaceus* adjusts its diet, consuming other calcified material to serve as trituration media in the stomach (e.g., *Halimeda*).

Variation in isotopic ratios of carbon and nitrogen do not necessarily reflect observed dissimilarities in composition of groups found in stomach contents among the 3 species of grazers studied here. While stomach contents tend to indicate higher levels of within-species than among-species similarities (Figures 6 & 8), isotopic signatures of these species appear to vary more within species at different sites than among species (Figure 9). All species appear to be more similar to each other at Olowalu than at Kapalua, indicating that diets may vary by site based on environmental variables that lead to niche partitioning under certain conditions. Given the proportions of consumed functional groups for these species, we would expect to see trends in isotopic similarity that reflect similarity of stomach content composition. However, despite variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ within and among species, isotopic differences are small and do not reinforce differences seen in stomach contents.

Though there was remarkably higher detrital consumption by *C. strigosus* than the other two species (Figure 5), it does not appear to affect $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$. This is likely due to the fact that detritus on these reefs is a product of the diet and waste of the overlying community, so likely consists of broken down or decomposing benthic algae (Max et al. 2013). Haines & Montague (1979) showed through lab experiments that microbial degradation of dead plant material caused negligible further fractionation of $\delta^{13}\text{C}$ in marsh plants, which may explain why detritivores and grazers in this study did not differ in $\delta^{13}\text{C}$ signatures (Table 2; Figure 9). The exception to this trend is seen in *A. olivaceus* with a significantly lower $\delta^{13}\text{C}$ value at Kapalua than Olowalu. Based on SIA of algal sources commonly found at sites in this study and $\delta^{13}\text{C}$ values from the literature (Max et al. 2013 supplement) in conjunction with stomach content analysis from this study, this difference in $\delta^{13}\text{C}$ does not appear to be explained by differences in algal consumption (Table 2; Figure 9). However, to gain a better understanding of contribution of individual functional groups and taxa to the isotopic ratios of these fish, SIA would need to be conducted for each of these groups independently, which was not feasible for this study. Additionally, results of such analyses would likely not provide increased diet resolution due to high frequency of overlap among signatures of algal types.

Values of $\delta^{15}\text{N}$ were on average higher for *A. nigrofuscus*, and this trend appears to be driven by significantly higher values at Kapalua (Table 2; Figure 9). Given the similarity and low variance in diet contents from *A. nigrofuscus* individuals in this study from 2011 and 2013 (Figure 8), this bump is very likely due to a

combination of spatial and temporal effects on $\delta^{15}\text{N}$ values in the environment. Individuals of *A. nigrofuscus* collected from Olowalu in 2011 do not show the same trend, indicating a site-based effect rather than an island-wide event that caused enrichment of algal material in 2011. Unfortunately, since no individuals of *A. olivaceus* or *C. strigosus* were collected at Kapalua in 2011, there is no way to verify the presence of a site effect. It is notable that despite increased $\delta^{15}\text{N}$ values in *A. nigrofuscus*, all individuals in this study fell within the same trophic range, and this range reflected a standard trophic discrimination factor (TDF) for coral reef fishes (Wyatt et al. 2010) with respect to the algal groups sampled here (Figure 9).

At the broad resolution of isotopic ratios with respect to diet, the differences among these species are small enough that they are likely not ecologically significant. Therefore, these fish can all be considered functionally similar in trophic level and diet source, as they are all herbivores that primarily consume and contribute to the nutrient cycling of benthic-derived algal tissues (or remnants thereof). Regardless of this apparent functional redundancy at the trophic level, data from field observations and stomach contents provide evidence of differing impacts on the benthos, based on total number of bites impacting different benthic groups and functional removal of various benthic groups from the reef. These results provide further evidence that use of multiple metrics more effectively captures functional redundancy, or lack thereof (Rosenfeld 2002, Adam et al. 2015).

Analysis of the foraging behavior and diets of these Acanthurid grazer species using a multipronged approach allows for multiple considerations of species function

and aids us in defining the most important ecological function of each species individually. Through specialized consumption of simple wiry turfs of the Rhodomelaceae (Figure 7), which can be extremely competitive, sometimes directly overgrowing live coral (i.e. *Corallophila*) (Jompa & McCook 2003, Titlyanov et al. 2009), *A. nigrofuscus* is actively mitigating direct physical competition of the turf community with corals. While *C. strigosus* does not directly remove competitive turf groups from the reef benthos, it may play a critical role in removing detritus and sediment from turf communities that would otherwise deter grazers like *A. nigrofuscus* (Bellwood & Fulton 2008). This consumption of detrital material by both *C. strigosus* and *A. olivaceus* also enhances energy transfer efficiency through the trophic web by recycling detrital material, which has been found to be more nutritious than the benthic algae within which it sits and is largely derived (Wilson & Bellwood 1997, Crossman et al. 2001, Max et al. 2013). Despite the fact that *A. olivaceus* focuses half of its bites on sand rather than the reef (Figure 2), it may possess the capacity to shift its diet to adapt to changing environmental conditions and competitors, making it a valuable member of the herbivore community in the face of rapidly changing environmental conditions due to anthropogenic impacts.

With each method of diet assessment, we found significant functional differences between species within the grazer/detritivore guild. However, use of multiple metrics reveals varying levels of functional divergence. It's important to consider these results when assessing within-guild differences of any group of functionally similar organisms, as these differences may only be apparent at different

spatial, taxonomic, or temporal scales. The main reason that the topic of functional diversity within the grazer guild is of interest from a management of conservation perspective is because of their potential to reverse coral-to-turf-algae phase shifts that have occurred on coral reefs in Maui, Hawaii. Given the abundance and the varying levels of functional complementarity among the grazers studied here, the depletion of any one of these species could result in the loss of important functions, which could have serious implications for the future of benthic interactions and coral reef health. By understanding the foraging niches of the predominant herbivores on a fine scale, we can more effectively build targeted management plans that take into account how each of these fish interacts with the reef, their target food sources, and the cycling of nutrients through the system.

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APPENDIX

Table 1: Genus richness (S) and Shannon's index (H') of stomach contents (\pm standard error). Overall, genus richness (S) varies among species, with *A. nigrofuscus* consuming the highest number of different genera. All species consumed higher numbers of genera at Kapalua than Olowalu. Shannon's index did not differ among species, despite differences in richness.

Species	Kapalua		Olowalu		$H' \pm se$
	n	$S \pm se$	n	$S \pm se$	
<i>Acanthurus nigrofuscus</i>	5	25.6 \pm 1.5	10	20.1 \pm 1.6	2.49 \pm 0.06
<i>Acanthurus olivaceus</i>	5	20.8 \pm 3.5	5	17.4 \pm 3.5	2.23 \pm 0.10
<i>Ctenochaetus strigosus</i>	4	17.0 \pm 1.8	6	14.0 \pm 2.1	2.23 \pm 0.12

Table 2: Mean values (\pm standard error) of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ from stable isotope analysis. Fish from Kapalua showed more variation in isotopic values than fish from Olowalu. Algal samples showed varied $\delta^{13}\text{C}$ in different genera/ groups, but consistent $\delta^{15}\text{N}$ by site (excluding cyanobacteria, which fixes atmospheric nitrogen).

Species	Kapalua			Olowalu		
	n	$\delta^{13}\text{C} \pm \text{se}$	$\delta^{15}\text{N} \pm \text{se}$	n	$\delta^{13}\text{C} \pm \text{se}$	$\delta^{15}\text{N} \pm \text{se}$
<i>Acanthurus nigrofuscus</i>	6	-13.90 \pm 0.62	7.49 \pm 0.27	9	-15.05 \pm 0.52	6.53 \pm 0.16
<i>Acanthurus olivaceus</i>	5	-16.14 \pm 0.18	6.42 \pm 0.22	5	-14.38 \pm 0.89	6.33 \pm 0.22
<i>Ctenochaetus strigosus</i>	4	-13.02 \pm 0.30	6.24 \pm 0.27	6	-14.48 \pm 0.64	6.55 \pm 0.14
<i>Turbinaria sp.</i>	3	-10.76 \pm 0.60	3.46 \pm 0.28	3	-9.57 \pm 0.26	2.58 \pm 0.18
<i>Amansia sp.</i>	3	-19.26 \pm 1.50	3.02 \pm 0.05	3	-17.79 \pm 0.57	2.34 \pm 0.20
Turf	5	-15.77 \pm 0.89	3.37 \pm 0.61	5	-18.23 \pm 0.61	3.24 \pm 0.19
Cyanobacteria	3	-9.77 \pm 0.87	-0.05 \pm 0.19	3	-10.40 \pm 0.73	-0.15 \pm 0.11

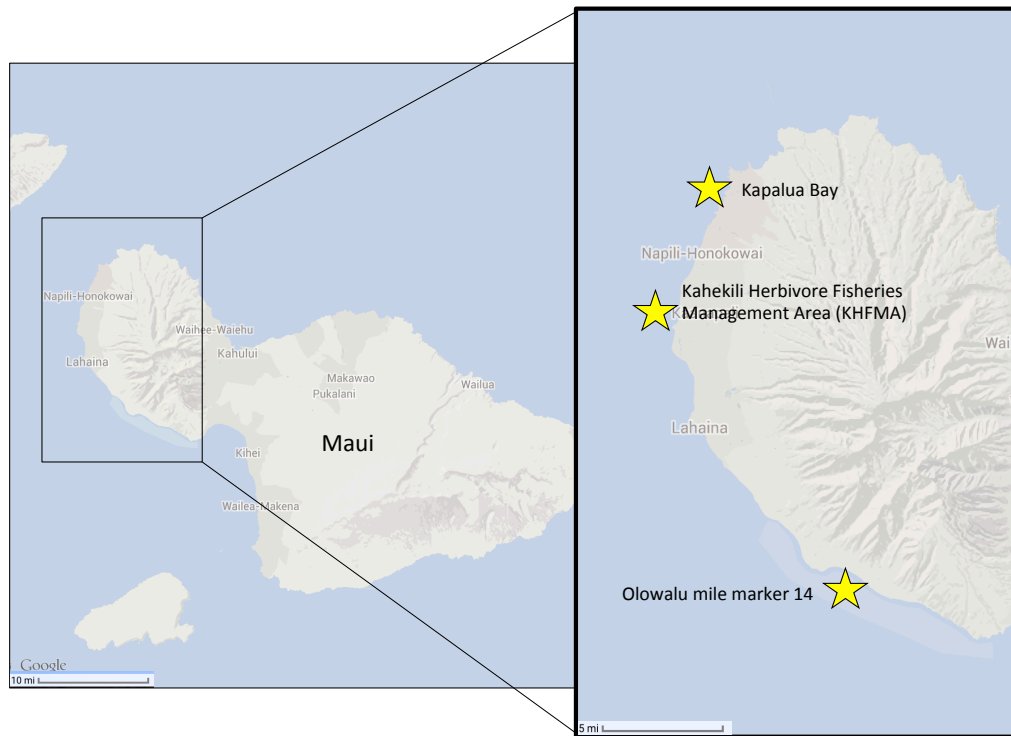
Figures

Figure 1: Observational studies were conducted at all three sites with gut content and stable isotope data from Kapalua Bay and Olowalu mile marker 14, all on West Maui, Hawaii.

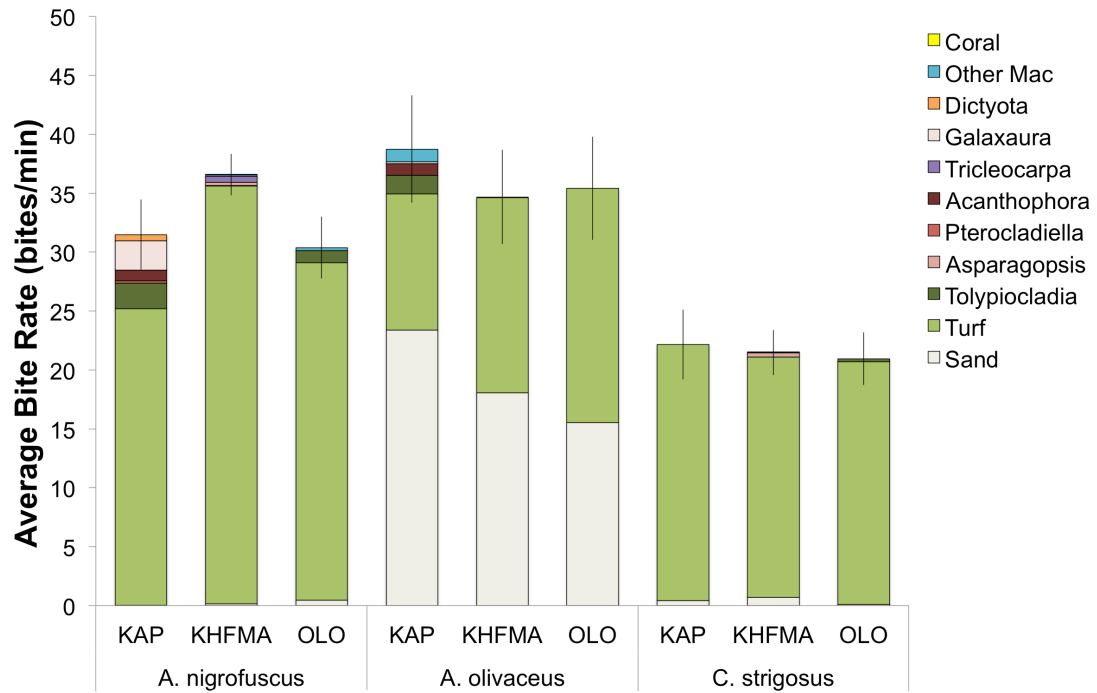


Figure 2: Bite rates and substrates bitten by grazers varied by species among the three sites, with *Ctenochaetus strigosus* showing slower bite rate than the other two species ($F_{2,2} = 17.58$, $p < 0.0001$). All grazers were observed biting primarily on turf algae, though *Acanthurus olivaceus* took many more bites on sand than the other two species (PERMANOVA Pseudo-F = 61.19, $p = 0.002$). There was no effect of site on bite rate or composition. Error bars are \pm SE of bite rate.

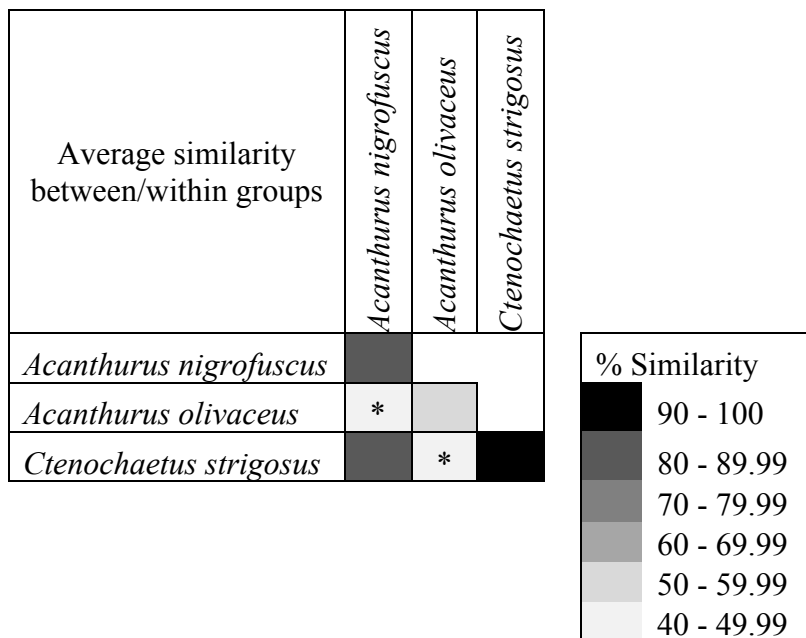


Figure 3: Percent similarity of bite proportion and composition between and within grazer species. * indicates pair-wise comparison in which $P(\text{perm}) < 0.05$.

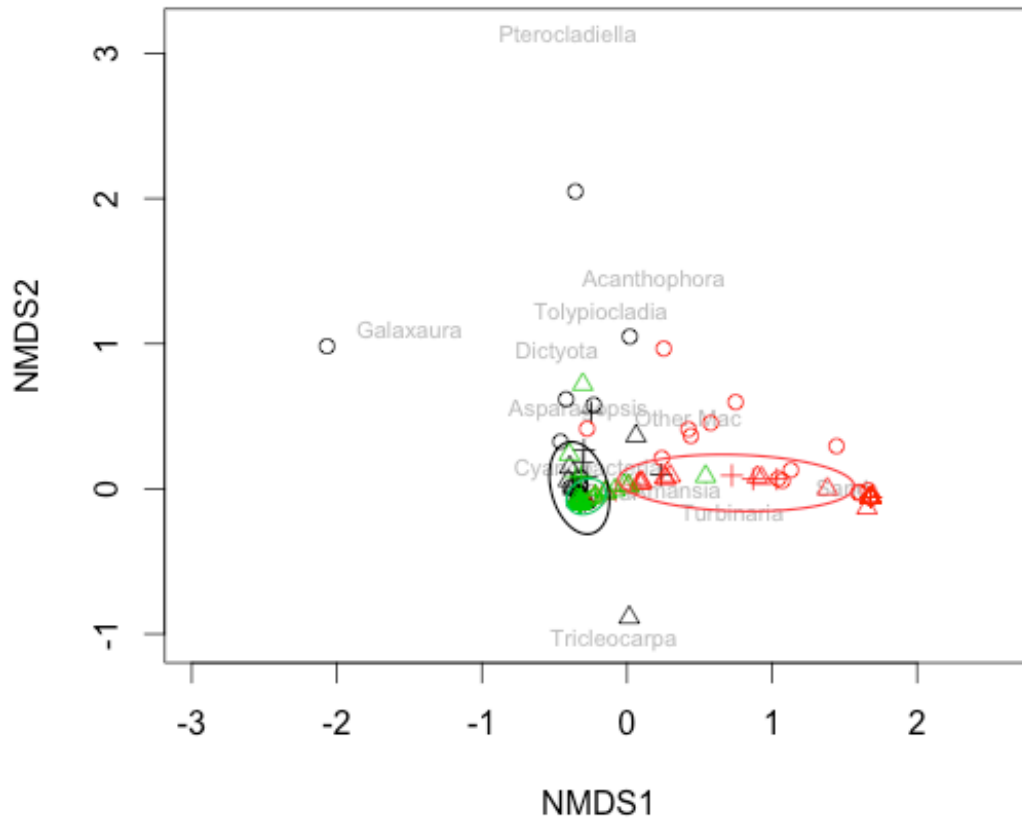


Figure 4: nMDS of observed bites by grazers on all benthic groups shows dissimilarity of *Acanthurus olivaceus* (red) from *Acanthurus nigrofuscus* (black) and *Ctenochaetus strigosus* (green) driven by its high proportion of bites on sand (grey). Data are the proportion of observed bites for each individual. Distance is Bray Curtis Similarity. No differences were observed among sites. Gray text represents benthic groups bitten.

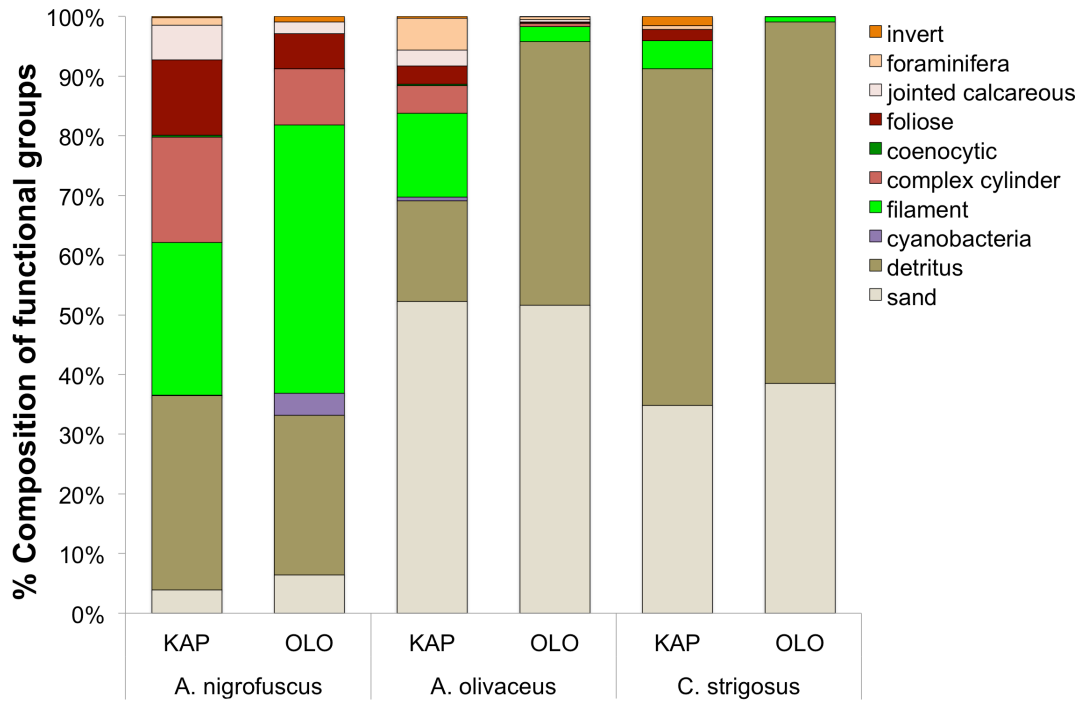


Figure 5: Results of stomach content analysis showing the proportion of different functional groups in grazer stomachs. *Acanthurus nigrofuscus* was significantly different from *Ctenochaetus strigosus*, and there was a significant species by site interaction, with *Acanthurus olivaceus* consuming groups in different proportions at different sites (PERMANOVA Pseudo-F = 61.19, $p = 0.002$).

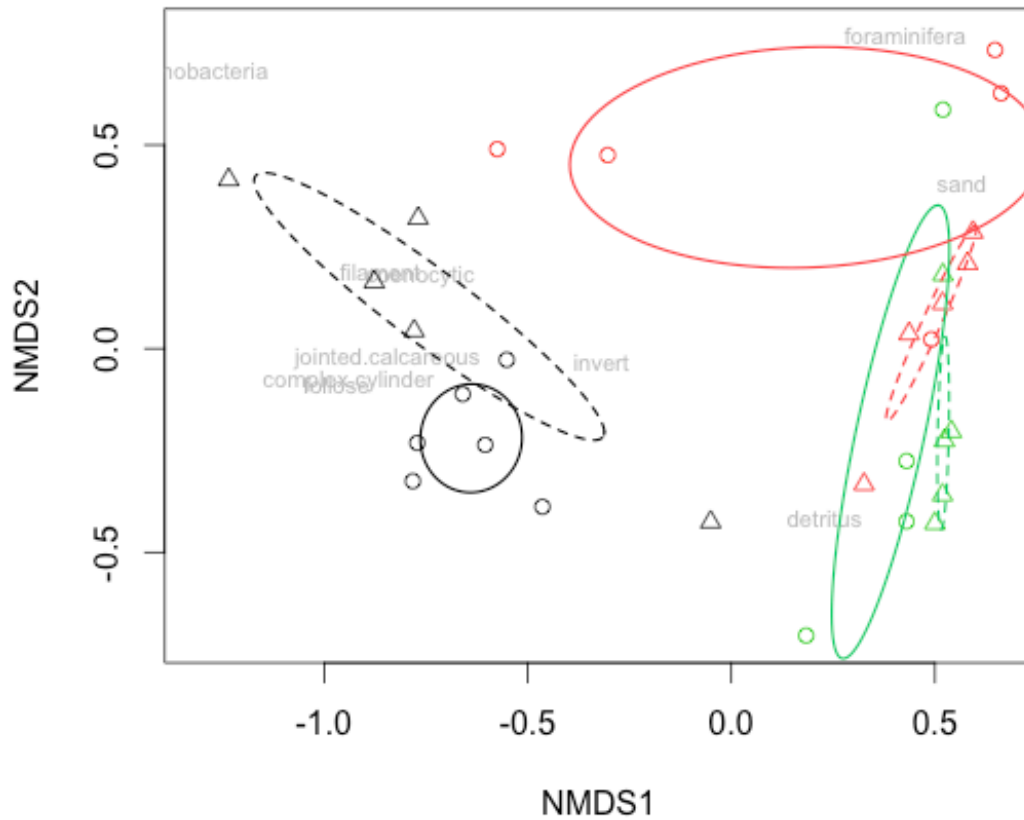


Figure 6: nMDS of proportion of functional groups in grazer stomachs shows that dissimilarity of *Acanthurus nigrofuscus* (black) to *Acanthurus olivaceus* (red) and *Ctenochaetus strigosus* (green) is driven by higher proportion of algal functional groups (grey) in stomach contents. *A. olivaceus* and *C. strigosus* have high proportions of sand and detritus in stomach contents, though *A. olivaceus* consumes more algal groups and shows much higher within-species variation at Kapalua (circles/ solid ellipses). Distance is Bray Curtis Similarity. Grey text represents functional groups found in stomach contents.

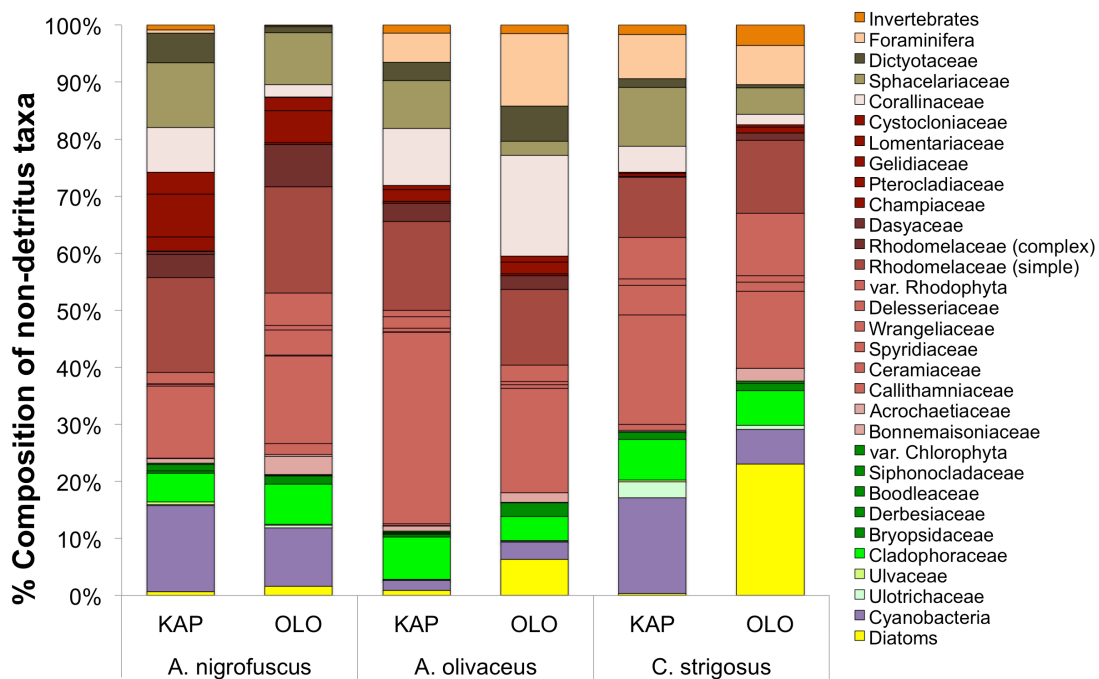


Figure 7: Results of fine-scale analysis of algal functional groups at the family level showing the proportion of non-detritus groups, including algal taxa and other benthic organisms found in the turf assemblage. Though all species show dominance by similar groups, differences in a few key groups drive significant differences among species (PERMANOVA Pseudo-F = 2.4789, $p = 0.0018$). Higher consumption of the complex Rhodomelaceae and cyanobacteria by *A. nigrofuscus*, Corallinaceae and invertebrates by *A. olivaceus*, and of diatoms and invertebrates by *C. strigosus* are the primary drivers of dissimilarity among species.

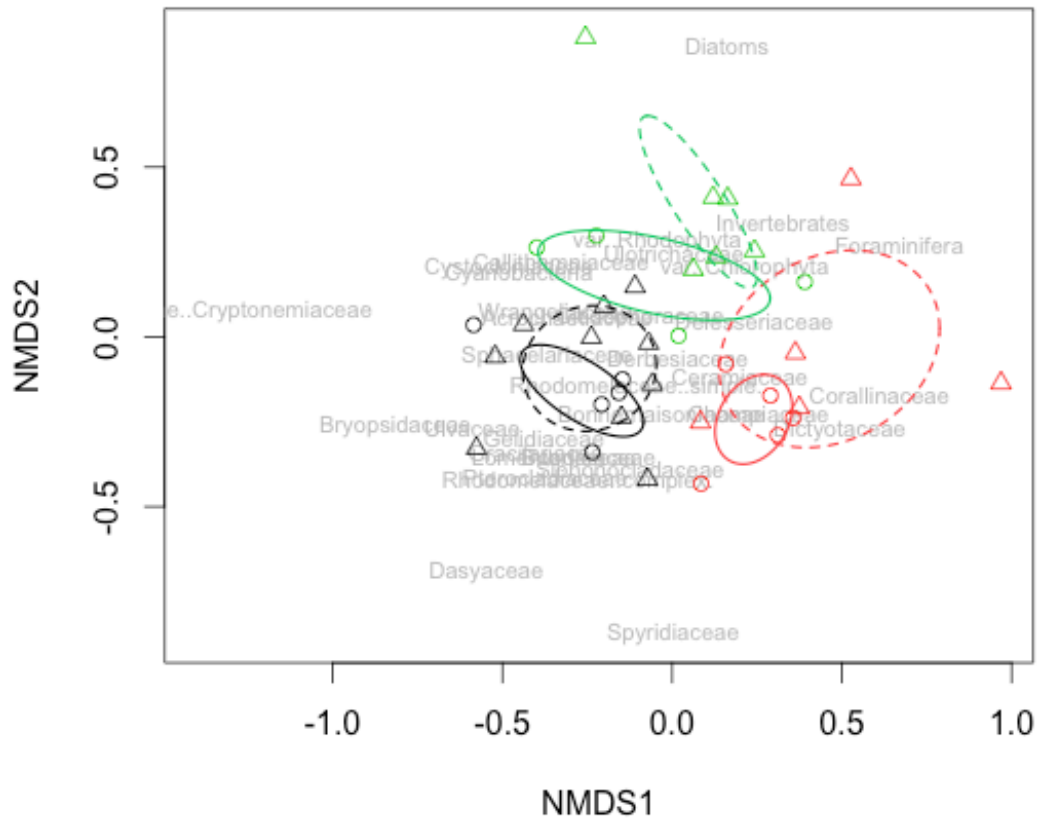


Figure 8: nMDS of proportions of non-detritus groups, including algal families and other benthic organisms found in the turf assemblage (grey text). Taxa found in stomach contents appear to be primarily dictated by species, though site does significantly contribute to within-species variability. Grazers at Olowalu (dashed ellipses) demonstrate more within-species variation in taxa consumed than at Kapalua (solid-line ellipses). Position with respect to gut taxa (grey text) reflects higher consumption of the complex Rhodomelaceae and cyanobacteria by *A. nigrofuscus* (black), Corallinaceae and invertebrates by *A. olivaceus* (red), and of diatoms and invertebrates by *C. strigosus* (green). Distance is Bray Curtis Similarity.

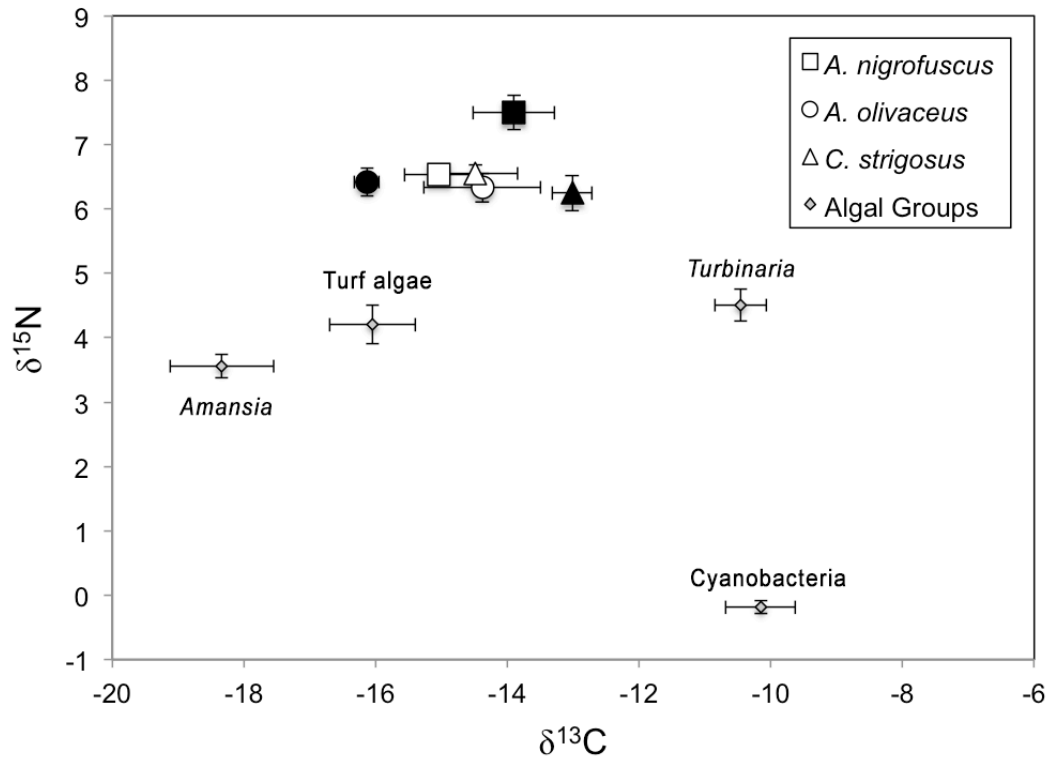


Figure 9: Stable isotope biplot showing signatures of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios for grazers collected from Kapalua (black symbols) and Olowalu (white symbols). Delta (δ) values indicate the difference between the sample measurement and standard. Also shown are stable isotope signatures of common algal groups (grey circles) collected at both sites, including *Turbinaria* sp., *Amansia* sp., cyanobacteria, and turf algae. Error bars = \pm SE.

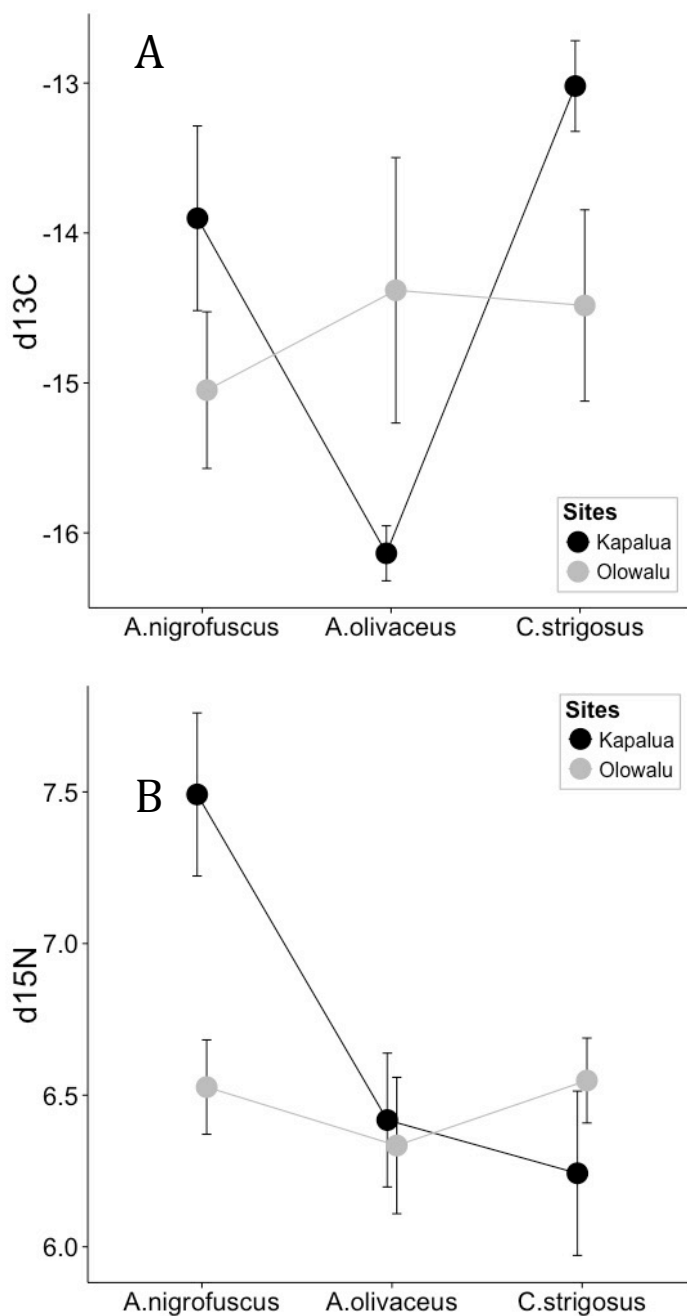


Figure 10: Interaction plots showing variation in (A) $\delta^{13}\text{C}$ and (B) $\delta^{15}\text{N}$ for grazers collected from Kapalua (black circles) and Olowalu (grey circles). *Acanthurus olivaceus* had significantly lower $\delta^{13}\text{C}$ than all other groups at Kapalua than at Olowalu (ANOVA $F_{2,1} = 8.157$, $p < 0.05$). *Acanthurus nigrofuscus* had significantly higher $\delta^{15}\text{N}$ than all other groups (ANOVA $F_{2,1} = 4.442$, $p < 0.05$).

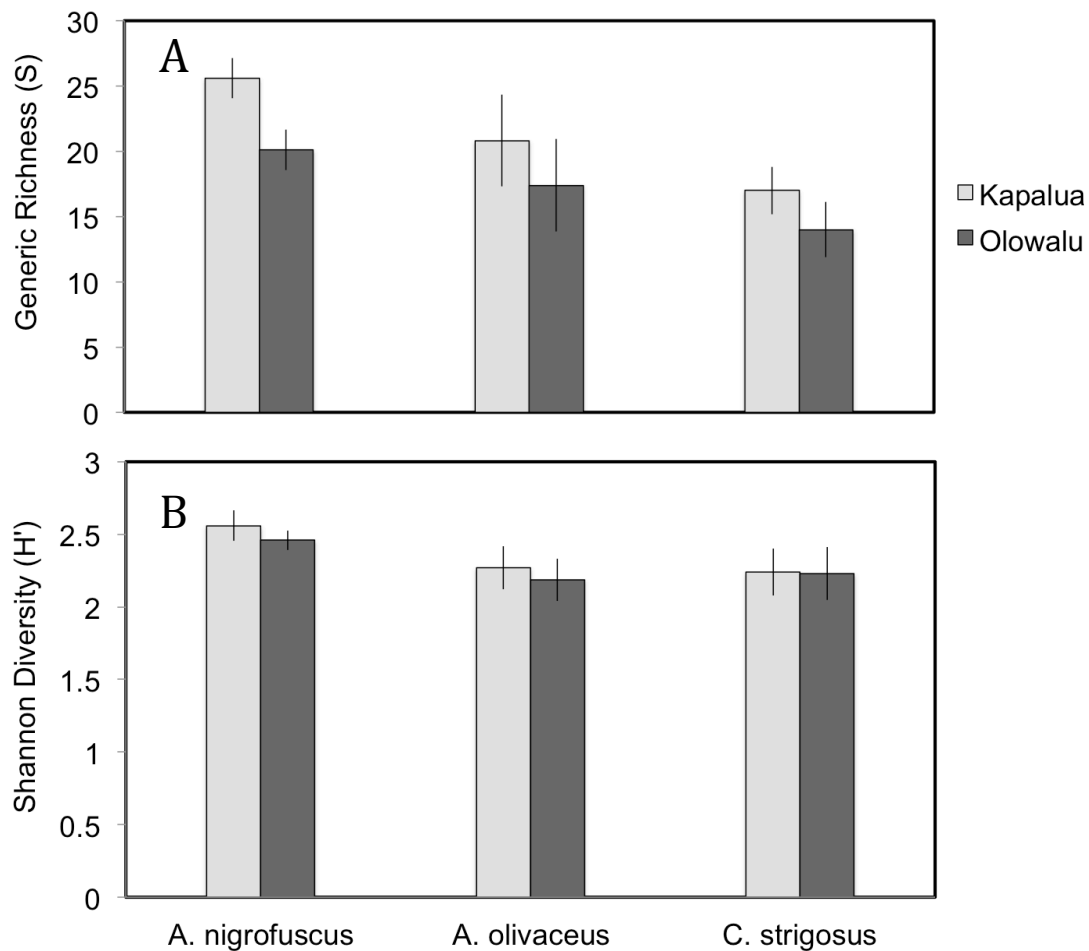


Figure 11: (A) Genus richness (S) of algae in stomach contents was higher for *A. nigrofuscus* than *C. strigosus* ($F = 4.207$, $p < 0.05$), and all species consumed more genera at Kapalua than at Olowalu ($F = 4.349$, $p < 0.05$). No significant differences were observed in (B) Shannon diversity (H'), indicating that those species who consumed more genera tended to consume groups unevenly.

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