

Predation risk, competition, and territorial damselfishes as drivers of herbivore foraging on Caribbean coral reefs

Laura B. Catano*, Andrew A. Shantz, Deron E. Burkepile

Marine Science Program, Department of Biological Sciences, Florida International University, 3000 NE 151st Street, North Miami, FL 33181, USA

ABSTRACT: Food availability, competition, habitat complexity, and territorial damselfish shape foraging decisions of herbivorous coral reef fishes. However, relatively little is known about how predators affect herbivore diet selection. We examined diets of 2 common reef herbivores, *Sparisoma aurofrenatum* and *Acanthurus coeruleus*, in the Florida Keys, across sites of varying predator biomass. We used stable isotope analysis to understand the importance of predation risk relative to other known drivers of herbivore foraging decisions. For *S. aurofrenatum*, we found that greater predator biomass was associated with an increase in the diversity of resources consumed within populations. In contrast, increasing densities of damselfishes, which aggressively defend resource-rich algal gardens, were associated with lower diet diversity. However, within *A. coeruleus* populations, diet diversity increased with damselfish abundance, but was unrelated to predator biomass. Stomach content analyses and direct observation of diet selection in the field corroborated the stable isotope analysis. Importantly, both predator and damselfish abundance impacted diet diversity in different ways for these 2 fishes, which may be linked to differences in sociality and group foraging. *A. coeruleus* is more likely to forage in schools, potentially reducing predation risk and allowing them to overwhelm damselfishes and access their territories. Interestingly, damselfish abundance was positively correlated with predator biomass, suggesting that predators may influence herbivore diets indirectly via altered densities or behavior of damselfishes. Our work argues for more emphasis on the role of predation risk in affecting herbivore foraging in order to understand the implications of human-mediated predator removal and recovery in coral reef ecosystems.

KEY WORDS: Stable isotope analysis · Predation risk · Herbivore · Diet · Food web · Coral reef · Marine protected area · MPA · Florida Keys

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INTRODUCTION

Animals often make tradeoffs to balance the conflicting demands of obtaining energy required for growth and reproduction while avoiding competitors or predators (Lima & Dill 1990, Houston et al. 1993). For instance, herbivores often avoid resource-rich but risky habitats in order to stay safe (Gilliam & Fraser 1987, Schmitz et al. 1997, Heithaus & Dill 2002). Tradeoffs like this are a fundamental organizing principle in ecological communities (Werner & Anholt 1993). Ultimately, it is important to under-

stand the determinants of foraging behavior, even when the consequences of any single foraging decision are small, because the cumulative effects of foraging decisions can alter community dynamics and ecosystem processes (Schmitz 2008).

Many abiotic and biotic factors determine the foraging behavior and diet of herbivorous fishes on coral reefs, including resource availability and quality, inter- and intraspecific competition, and habitat complexity. For example, herbivores must acquire enough algae of sufficient nutritional quality while avoiding species that are chemically or morphologi-

cally defended (Hay 1991). Thus, where palatable algae are more abundant, they will likely be more abundant in the diets of fishes. Also, both inter- and intraspecific competitive interactions can alter foraging behavior (Muñoz & Motta 2000), as resource overlap is often high among large herbivorous fishes (e.g. parrotfishes and surgeonfishes) (Bellwood & Choat 1990). Therefore, when competition for the same limiting resources is intense, inferior competitors may be forced to consume less-optimal resources (Milinski 1982). Interspecific competitors such as territorial damselfish can also affect how larger herbivorous fish forage (Foster 1985) by aggressively defending the algal gardens within their territories (Hixon & Brostoff 1983). Fishes that can invade defended algal gardens gain access to a greater diversity of algal resources (Klumpp & Polunin 1989). Finally, structural complexity (i.e. rugosity) can affect both algal cover (Graham & Nash 2013) and fish densities (Roberts & Ormond 1987), which in turn can affect density-dependent competitive interactions (Carr et al. 2002). Thus, in structurally complex areas, where fish are more abundant and resources are often scarce, herbivorous fish may be forced to consume less-optimal resources relative to those in low-complexity areas, which are less-preferred habitats and may have better-quality food sources.

Predation risk is likely also an important factor affecting foraging by herbivorous fishes in reef ecosystems; however, it has received relatively little empirical attention (but see Madin et al. 2010b). Evidence from many different ecosystems shows important and ubiquitous effects of predators on foraging behavior of their prey (termed non-consumptive effects [NCEs]) (e.g. Schmitz et al. 1997, Heithaus & Dill 2002, Preisser et al. 2005, Ripple & Beschta 2007). In coral reefs, predators have an important consumptive role in affecting the size structure and abundance of their prey (McClanahan & Muthiga 1988, Mumby et al. 2006, 2012); however, few studies have investigated the NCEs of reef predators on herbivorous fishes, especially the responses of multiple families of herbivores. In the central Pacific's remote northern Line Islands, Madin et al. (2010b) demonstrated that predation risk was associated with decreased excursion area of multiple prey fish species. This work suggests that NCEs may play an important but underappreciated role in consumer-prey interactions on coral reefs.

Large predatory fishes such as sharks and large grouper are rare on most modern reefs, except in relatively remote places (Sandin et al. 2008) or in well-established marine protected areas (MPAs) protected

from fishing (Russ & Alcala 2010) due primarily to overexploitation (Myers & Worm 2003). Such drastic declines in predator abundance may have profoundly altered foraging behavior of reef herbivores. This may be especially true for long-lived, iteroparous species such as parrotfishes (Scaridae) and surgeonfishes (Acanthuridae), as their life-histories may select for responses that minimize predation risk (Heithaus et al. 2008). Additionally, these herbivores are very versatile in diet (Bellwood et al. 2006) and social organization (van Rooij et al. 1996) across local environmental conditions, suggesting that they may respond to changes in predator abundance with alterations in foraging behavior or diet. Understanding the drivers of foraging behavior for these herbivores is important to reef health, as they are key for removing algae and facilitating coral settlement, growth, and survivorship (Hughes et al. 2007, Mumby et al. 2007, Burkepile & Hay 2008).

The influence of predation risk on the diets of herbivorous fish depends on how individuals alter their foraging behavior in response to intimidation. Prey could potentially respond to risk by shifting habitats and foraging only in safer areas (Werner et al. 1983). Prey could also respond by staying in riskier areas but limiting their movement or reducing their excursion area (i.e. area they move over during a given time period) (Madin et al. 2010b). Both of these responses could potentially decrease individual diet diversity because algal resources are heterogeneously distributed on reefs (Hay 1991), and thus reduced foraging area would likely reduce the diversity of potential diet items that are encountered. However, individual diet diversity could also increase under this scenario. If fishes are constrained to foraging in risk-free areas, they may be forced to broaden their diet by consuming the resources that are most available, but typically low-preference. In contrast, individuals in areas with low predator abundance that are unconstrained in foraging area would likely have a narrower diet consisting primarily of their preferred foods. Furthermore, the relationships between individual herbivorous fish foraging behavior and predation risk are likely species-dependent. Factors such as body size, physiology, and social behavior will likely shape different tradeoffs between food and safety across species (Wirsing et al. 2010, Preisser & Orrock 2012). For example, species that typically forage in groups may be less likely to change their behavior with increased predation risk due to the dilution of risk on individual foragers (Creel 2011).

The collective responses of individual-level foraging decisions to increased predation risk may be

apparent at the population level (Araújo et al. 2011). For instance, in high-risk areas, if individuals are forced to change their foraging behavior and expand their diets beyond targeting preferred resources, the population trophic niche (i.e. diet variation among individuals) would likely increase. Where predation risk is low and individual diets converge on preferred resources, the trophic niche of a population would likely remain small. However, not all individuals may respond the same way to risk. If only some individuals are risk-averse and alter their foraging behavior while others do not (Coleman & Wilson 1998), it is plausible that the trophic niche of a population may not change much. Therefore, for a more complete understanding of the influence of predation risk, it is important to consider both individual and population responses.

We investigated the relative importance of multiple factors, including: (1) algal community structure, (2) territorial damselfish abundance, (3) competition with other herbivorous fishes, (4) habitat structural complexity, and (5) predation risk, in influencing the foraging behavior and diet selection of the blue tang *Acanthurus coeruleus* and redband parrotfish *Sparisoma aurofrenatum* across 12 reefs in the Florida Keys (USA). We used stable isotope analysis (SIA) (a time- and space-integrated metric of diet) in conjunction with stomach content analysis and observations of foraging fishes (which represent recent diet choices) to investigate how resource use differed for each species across sites. We then investigated the effect of site characteristics (e.g. predator biomass, damselfish abundance, algal cover) on individual diet selection and on diet diversity within populations. We hypothesized that increasing competitive interactions (i.e. with other large herbivorous fishes) and/or predation risk would restrict access to preferred food resources and force herbivores to consume a broader diet of less-preferred foods, thereby increasing diet diversity within populations. Additionally, we hypothesized that abundant territorial damselfishes would increase diet diversity within populations by increasing the diversity of resources available, but only for those herbivores that can gain access to these resources.

MATERIALS AND METHODS

Site description

The Florida Keys reef tract is a large bank reef ecosystem located approximately 8 km offshore of the

Florida Keys, USA. Fishing pressure in the region is high, with both commercial and recreational fisheries heavily exploiting carnivorous fishes (e.g. snapper, grouper, and barracuda) (Bohnsack et al. 2009). In 1997, however, 23 no-take zones were designated within the Florida Keys National Marine Sanctuary (FKNMS) to eliminate all fishing activity within those areas (Bohnsack et al. 2009). Within these protected areas, piscivorous fishes have increased in size and abundance (Bohnsack et al. 2009, Smith et al. 2011). Unlike most piscivores, herbivorous fishes (e.g. parrotfish, surgeonfish, etc.) are protected across the entirety of the FKNMS (i.e. in both protected and unprotected zones), and their populations are robust in the FKNMS relative to most other reefs in the wider Caribbean (Burkepile et al. 2013). FKNMS is an ideal region to test hypotheses about the functional impact of predators on herbivorous fish, as it does not confound predator effects (e.g. protected vs. unprotected areas) with vast differences in herbivore abundance across reefs, as herbivores are protected everywhere.

From June to August 2011, we sampled 12 forereef sites between 6 and 8 m depth along the northern reef tract off of Key Largo (Fig. 1, see Table 1). We chose reefs that were similar in physical parameters (e.g. depth and structure) and that were separated by at least 700 m to assure independence. With the exception of large, mobile predators such as jacks, most reef fishes are unlikely to move among reefs over such distances, particularly when separated by open areas (i.e. large expanses of sand or rubble) (Chapman & Kramer 2000), as was the case with the sites used in the present study. Sites included 8 protected and 4 unprotected areas. At each site, we sampled fishes for dietary analyses and conducted benthic and fish community surveys either on the same day or within a few days of each other. All surveys and sampling were conducted over the same time period (10:00–14:00 h) using SCUBA.

Characterizing fish and benthic communities

To quantify fish abundance and benthic cover at each site, we conducted surveys along eight 25 m transects that were laid out parallel to the main reef formation. On the initial pass, we identified all fish and visually estimated their fork length, with the exception of territorial damselfish species, within a 4 m wide window. We used 1 m long PVC T-bars to help estimate lengths to the nearest cm. We counted individuals of territorial damselfish species (i.e. *Ste-*

gastes and *Microspathodon* spp.) within a 2 m wide window on the second transect pass, because they have high site fidelity and are generally tolerant to diver presence. We used published length:weight relationships to convert fish lengths to biomass (Bohnsack & Harper 1988). The urchin *Diadema antillarum*, once a dominant reef herbivore, has remained rare since the mass mortality throughout the Caribbean in the early 1980s, and were not quantified (Lessios 1988, Chiappone et al. 2002). On a third pass over each transect, photographs of the benthos were taken every meter to produce 50 cm × 50 cm photo-quadrats (n = 25 per transect). These photographs were analyzed for cover of benthic organisms using Coral Point Count V4.1 (Kohler & Gill 2006). Categories were created for: (1) crustose coralline algae (CCA), short algal turf (algal filaments < 0.5 cm tall), and bare space (abbreviated CTB: 'crustose, turf, bare'); (2) turf algae (algal filaments > 0.5 cm tall) and sediment (abbreviated TAS: 'turf algae, sediment'); (3) sponges; (4) gorgonians; and (5) zoanthids. Macroalgae were classified to genus level and scleractinian corals to species.

Structural complexity (i.e. rugosity) of each reef was calculated for each site using a Lidar (Light Detection and Ranging)-derived bathymetric dataset provided by the US Geological Survey (USGS) (available online at <http://pubs.usgs.gov/of/2007/1395/start.html>). We used this dataset to create a raster of benthic rugosity (1 × 1 m resolution) with the Benthic Terrain Modeler (a collection of ESRI ArcGIS-based tools available online at [\[noaa.gov/digitalcoast/tools/btm\]\(http://noaa.gov/digitalcoast/tools/btm\)\). We used benthic habitat maps available from the FKNMS \(\[http://floridakeys.noaa.gov/fknms_map/maplibrary.html?s=about\]\(http://floridakeys.noaa.gov/fknms_map/maplibrary.html?s=about\)\) to distinguish reef from non-reef habitats \(e.g. seagrass, sand, rubble\). We then used the ArcGIS zonal statistics tool to calculate average rugosity of reef habitat within a 250 m radius of where fish were captured at each reef \(see the following subsection\).](http://csc.</p>
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Fish collection and processing for stable isotope analysis

We focused our research on the parrotfish *Sparisoma aurofrenatum* and surgeonfish *Acanthurus coeruleus* because they are often numerically dominant on reefs in the Caribbean (Lewis & Wainwright 1985) and are similar in size. While both species are known to feed on turf algae and macroalgae, they vary in their adaptations for herbivory. *S. aurofrenatum* possesses grinding dentition, which enables this species to target leathery algal forms and scrape calcareous sediment, whereas *A. coeruleus* has relatively weak mouth parts, a complex alimentary architecture, and symbiotic microbes for fermentative digestion (Choat 1998). Additionally, these species vary in their social organization. Adult *S. aurofrenatum* are generally solitary or move in small groups (Mumby & Wabnitz 2002), whereas *A. coeruleus* are often aggregate and forage in large schools (Morgan & Kramer 2005).

We collected 15 individuals of adult size class for *S. aurofrenatum* (mean: 20 cm, range: 15–27 cm, both terminal and initial phase) and *A. coeruleus* (mean: 18 cm, range: 12–27 cm) at each site using barrier and hand nets. We measured the total length (TL) and weight for each specimen. We then clipped a small portion of dorsal fin tissue, which was immediately frozen for later analysis. *S. aurofrenatum* individuals were released back onto the reef after fin sample collection, and *A. coeruleus* were euthanized with 95% eugenol, placed on ice, and transported back to the lab, where they were frozen for later stomach content analysis. Variation in isotopic composition among consumers could reflect variation in the isotopic composition of their algal

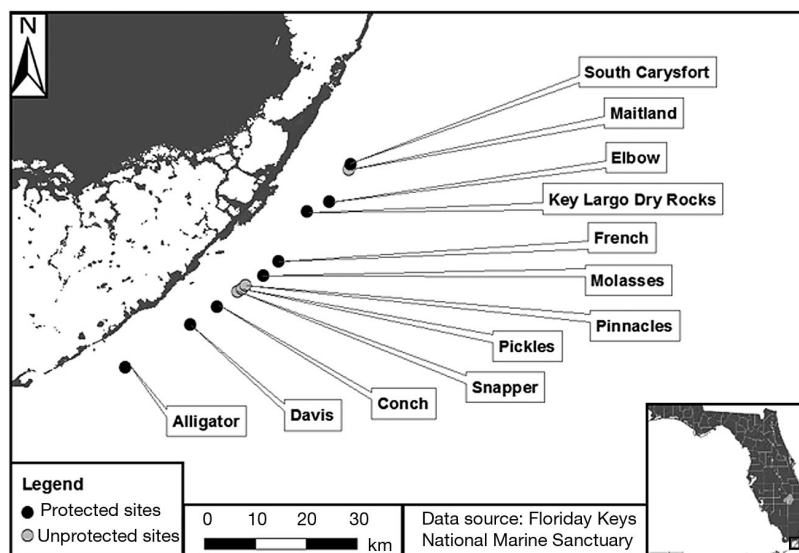


Fig. 1. Study sites in the northern reef tract of the Florida Keys National Marine Sanctuary (FKNMS) (inset: Florida) (see also Table 1)

diets (Post 2002). Therefore, to account for potential differences in isotopic baselines, we collected portions ($n = 8$ per species where possible) of 2 commonly consumed species of algae, *Halimeda tuna* and *Dictyota menstrualis*, at each site.

All fin and algal samples were dried at 60°C, ground to a fine powder with a mortar and pestle, and weighed into tin capsules for SIA of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. Prior to analysis of $\delta^{13}\text{C}$, ground samples of *H. tuna* (a highly calcified species) were washed in a 10% HCl solution, rinsed with deionized water, re-dried, and ground in order to remove inorganic carbon. All isotopic analyses were measured using standard elemental analyzer–isotope ratio mass spectrometer (EA-IRMS) procedures. Isotopic ratios (R) are reported in the standard delta notation (‰): δ (‰) = $[(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$. These results are presented with respect to the international standards of atmospheric nitrogen (AIR, N_2) and Vienna Pee Dee belemnite (VPDB) for carbon.

Characterizing fish diets

SIA of carbon and nitrogen was used to estimate individual trophic level and basal resource use, and population trophic niche. Trophic level (e.g. first-order or second-order consumer) can be estimated from the ratio of ^{15}N to ^{14}N (expressed as $\delta^{15}\text{N}$) because ^{15}N becomes enriched in the tissues of organisms with each trophic step (Peterson & Fry 1987). The basal source of carbon can be estimated by comparing the ratio of ^{13}C to ^{12}C (expressed as $\delta^{13}\text{C}$) in consumers and potential diet items because $\delta^{13}\text{C}$ changes very little with each trophic step (Peterson & Fry 1987). Therefore, by examining isotopic signatures separately, we can test hypotheses about the source of diet variation among individuals. We can infer if differences in diet are the result of differences in basal resource use and/or trophic level.

$\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values provide 2 dimensions of resource use that can be used in concert to assess the isotopic or trophic niche of a population (Newsome et al. 2007). At sites where individuals have a broader range of items in their diets, there would be greater isotopic variance (greater spread in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values) within those populations. Therefore, those populations would have increased diet diversity or a larger trophic niche. In contrast, at sites where individuals have similar diets, the population as a whole would have a smaller trophic niche. Therefore, by examining variation in trophic niche, we can test

hypotheses about differences in diet diversity among populations.

In addition to SIA, we analyzed stomach contents of *A. coeruleus* and feeding behavior of *S. aurofrenatum*. These 2 metrics give a snapshot of recent diet decisions that we could compare with isotope data, which provides a metric of foraging decisions that is integrated over larger spatial and temporal scales (Heady & Moore 2013). The grinding of food by the pharyngeal mill of *S. aurofrenatum* makes identification of stomach contents challenging, even under high magnification. Therefore, we used field observations of feeding behavior rather than gut contents to determine diet composition for this species. Alternately, field observations of *A. coeruleus* feeding behavior would have been challenging because of their high feeding rates. We used alternate methods for both species because we were not comparing these metrics between species, but rather we were using them to compare with and support inferences from SIA data.

A. coeruleus specimens were kept frozen until they were dissected in the laboratory. Their alimentary tract and associated viscera were dissected and materials from the stomach were preserved in 10% buffered formalin and stored in a 70% ethanol solution. Contents were sorted under 40× magnification and categorized as thallate red algae (e.g. *Laurencia*, *Hypnea*, *Botryocladia*), thallate green algae (e.g. *Ulva*, *Halimeda*), thallate brown algae (e.g. *Dictyota*, *Sargassum*), filamentous turf (e.g. *Polysiphonia*, *Cladophora*), calcareous sediment, animal material, or unidentifiable organic material (i.e. organic contents that lacked any structural form and could not be distinguished). After sorting, we dried samples at 60°C and weighed them to the nearest milligram. In cases where filamentous turf or organic material could not be physically separated from calcareous sediment, these samples were ashed at 500°C for 24 h, and the ash-free dry weight was subtracted from dried weight to determine the dry weight of turf or organic material. From these data, we calculated the percentage of the overall stomach contents that each diet category represented.

At each site, 30 *S. aurofrenatum* of adult size class (>15 cm TL), including terminal and initial phases, were followed on SCUBA by 1 diver for a total of 6 min, and observations of feeding behavior began after a 1 min acclimation period. Divers maintained a distance of at least 1 m behind and 1 m above the focal fish to limit diver influence on fish behavior. Bites were recorded as filamentous turf, macroalgae, coral, CCA, sponge, and other. Macroalgae were

identified to species level where possible, or to genus otherwise. From these data, we calculated the proportion of bites each fish took from each diet category.

Statistical analyses

All statistical analyses were conducted using R version 3.0.1. Parametric assumptions of normality and homoscedasticity were verified using plots of the residuals. In one of our analyses, for a simple linear regression between predator biomass and damselfish abundance, predator biomass was ln-transformed to meet normality assumptions. Biomass of large predators and competitors were used as proxies for the level of predation risk and the degree of competition, respectively. We chose biomass because it incorporates both fish size and abundance and has been shown to be meaningful for detecting the direct and indirect effects of fishing on coral reefs (Madin et al. 2010b). We defined competitor biomass as the combined biomass of Acanthuridae and Scaridae. We estimated large predator biomass by summing all primarily piscivorous fishes of the families Carangidae, Lutjanidae, Serranidae, and Sphyraenidae that were >30 cm FL and known to consume adult parrotfishes and surgeonfishes (based on Randall 1967). We tested for the effect of protection status on predator biomass using a Welch 2-sample *t*-test.

Because of the large number of predictors we wanted to incorporate in the analysis relative to the limited number of sample reefs, we performed a principal component analysis (PCA) on site-level predictors (including: rugosity, cover of *Halimeda* spp., cover of *Dictyota* spp., cover of TAS, territorial damselfish abundance, large predator biomass, and herbivorous fish biomass) to create uncorrelated principal components that described the different reefs (Graham 2003). We standardized each variable prior to the PCA by centering and scaling (i.e. subtracting each observation by the group mean and dividing by the standard deviation). We used scores of principal components in subsequent analyses and made interpretations based on correlations between principal component axes and original variables (Husson et al. 2010). We investigated how fish diet (based on isotopic data and observational/stomach content data) varied along principal component axes for each species. It is important to note that although certain reef characteristics (e.g. predator biomass, damselfish abundance) were correlated more or less strongly with the PCA axes, the axes represent composite variables that are loaded on >1 of the original vari-

ables. Thus, multiple reef characteristics likely influence the correlations between PCA axes and our metrics of fish diets, even if only a limited subset of these characteristics strongly influenced the PCA.

Prior to analyzing fish isotopic data, we tested and corrected for differences in isotopic baselines. We used ANOVA to test for differences in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ among sites using 2 species of algae, *H. tuna* and *D. menstrualis*. We did not find a significant difference among sites in $\delta^{15}\text{N}$ values of *H. tuna* (ANOVA, $F_{11,39} = 1.39$, $p = 0.21$) or *D. menstrualis* (ANOVA, $F_{11,56} = 1.68$, $p = 0.11$). Therefore, we attributed variation in consumer $\delta^{15}\text{N}$ values to differences in diet, not differences in baselines. We did find significant differences in $\delta^{13}\text{C}$ values of *H. tuna* (ANOVA, $F_{11,39} = 4.64$, $p < 0.001$) and *D. menstrualis* (ANOVA, $F_{11,56} = 2.06$, $p = 0.04$) among sites. We used a simple linear regression to investigate the relationship between $\delta^{13}\text{C}$ values for both algal species and found them to be significantly positively related ($p < 0.001$, $R^2 = 0.76$), suggesting that these were true differences in isotopic baselines among reefs. Therefore, we used the relationship between these 2 algal resources to develop a baseline relationship across all sites and then corrected consumer $\delta^{13}\text{C}$ values accordingly ($\delta^{13}\text{C}[\text{corrected}] = \delta^{13}\text{C}[\text{consumer}] - \delta^{13}\text{C}[\text{baseline}]$) (VanderZanden et al. 2003).

To test the hypothesis about the effect site characteristics (e.g. large predator biomass) on the diets of individuals, we used a hierarchical modeling framework (Gelman & Hill 2007). This approach allowed us to partition variance in isotopic metrics among individual-level predictors (e.g. fish size) and site-level predictors (e.g. large predator biomass). To understand if differences in diet were the result of differences in basal resource use and/or trophic level, we created 2 hierarchical models for each species to analyze $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ separately. We assessed the relative importance of each site characteristic's influence on each isotope signature based on values of parameter estimates. To assess model performance, we calculated conditional and marginal linear mixed-effect model (LMM) R^2 values. Conditional R^2 values ($R^2_{\text{LMM}(c)}$) describe the variance explained by the entire mixed-effects model (including fixed [i.e. fish size, large predator biomass, etc.] and random [i.e. Site] factors), while marginal R^2 values ($R^2_{\text{LMM}(m)}$) describe variance explained by only fixed factors (Nakagawa & Schielzeth 2013).

Next, we tested the hypothesis that site characteristics affect trophic niche within populations (i.e. the similarity in resource use among individuals at a site). For each herbivore, we calculated Bayesian

standard ellipse area (SEA_B) for each site. SEA_B is a metric similar to convex hull area (Layman et al. 2007), which uses the area encompassed by isotope data points to estimate the extent of diet diversity among individuals of a population. To calculate SEA_B metrics that were unbiased by unequal size distributions of fishes captured among sites, we used residuals from each site's relationship between isotope values and fish length. Residuals were added to the intercepts from each regression and used to calculate SEA_B . We used linear regressions to evaluate relationships between SEA_B and the principal component scores. The R package SIAR was used to calculate SEA_B (Parnell & Jackson 2011).

Finally, we tested the hypothesis that acute differences in diet diversity among individuals (i.e. measured from stomach content and behavioral data) correlated with chronic differences in trophic niche (i.e. measured from isotope data). To calculate diversity indices at each site, we used the exponential of the Shannon–Wiener diversity index [$\exp(H')$] using the proportions of diet items consumed (from stomach data for *A. coeruleus* and behavioral data from *S. aurofrenatum*). We used Spearman rank correlation to determine if there was a relationship between site diversity indices [$\exp(H')$] and site trophic niche measurements (SEA_B). Positive correlation would indicate that trophic niche inferred from isotopes reflected true differences in feeding choices within populations.

Because isotope data suggested strong ontogenetic shifts in diet for *A. coeruleus* (see 'Results'), we used simple linear regressions to assess relationships between proportions of major individual stomach components and total length. We also performed

logistic regressions on several diet components to assess their probability of occurrence with fish size, and evaluated model fit using the Hosmer–Lemeshow goodness-of-fit test. These analyses helped confirm that the differences across size classes in the isotopic data reflected true differences in diet. Although fish length was strongly related to isotopic composition for *S. aurofrenatum*, we did not perform these same analyses because we did not have diet data on the same individuals from which we also had stable isotope data.

Finally, because we found that damselfish abundance was significantly related to diet composition (see 'Results'), we assessed if an increase in large predators may be influencing damselfish abundance, as others have shown (Harborne et al. 2008, Mumby et al. 2012). We used simple linear regression to examine the relationships between biomass of large predators and mesopredators known to consume damselfish (e.g. *Cephalopholis fulvus*, *C. cruentatus*, and *Epinephelus guttatus*) and between large predator biomass and damselfish abundance.

RESULTS

Overall, benthic communities of sites were characterized by high macroalgal cover ($34.9 \pm 3.9\%$, mean \pm SE), dominated by *Dictyota* spp. ($29.9 \pm 3.9\%$), and low coral cover ($1.5 \pm 0.4\%$) (Table 1). Mean Scarid and Acanthurid biomass was $10.9 \pm 1.6 \text{ g m}^{-2}$ and $4.2 \pm 0.4 \text{ g m}^{-2}$, respectively. The mean biomass of large predators (>30 cm TL) known to consume adult surgeonfishes and parrotfishes (based on Randall 1967) was $10.7 \pm 5.1 \text{ g m}^{-2}$ (range: 0.2–108.6) and included:

Table 1. Study sites with GPS coordinates, protection status (P: protected, NP: not protected), and means of fish biomass, abundance, rugosity, and benthic community (% cover) (see also Fig. 1)

Site	°N	°W	Status	Macro-algae (% cover)	Coral (% cover)	Competitor biomass (g m^{-2})	Predator biomass (g m^{-2})	Damselfish abundance (ind. m^{-2})	Lidar-derived rugosity
Alligator	24.97	80.71	P	40.1	0.49	15.5	108.6	0.81	3.59
Conch	24.96	80.46	P	42.5	0.50	7.3	4.2	0.21	3.54
Davis	24.93	80.51	P	24.5	0.54	16.0	14.4	0.32	3.46
Dry Rocks	25.12	80.29	P	32.2	4.66	13.3	11.3	0.09	2.92
Elbow	25.14	80.26	P	20.9	1.10	17.5	5.3	0.18	5.39
French	25.04	80.36	P	37.0	3.27	16.3	6.3	0.23	3.66
Maitland	25.19	80.23	NP	60.6	0.81	5.1	1.2	0.35	3.96
Molasses	25.01	80.38	P	9.8	1.46	10.4	87.2	0.41	3.52
Pickles	24.99	80.41	NP	26.3	1.10	21.3	3.4	0.36	3.42
Pinnacles	24.99	80.41	NP	40.4	0.96	13.8	3.0	0.36	3.15
South Carysfort	25.21	80.22	P	34.2	2.76	31.7	0.2	0.22	4.52
Snapper Ledge	24.99	80.42	NP	50.2	1.02	13.6	35.0	0.44	2.84

Table 2. Correlation between 4 principal components (PC) and 7 site-level predictors. **Bold:** significant correlations at the $\alpha = 0.05$ level. Parentheses: percent of variance explained by each PC axis

	Rugosity	<i>Dictyota</i> cover	<i>Halimeda</i> cover	Turf algae/ sediment	Competitor biomass	Damsel fish abundance	Predator biomass
PC1 (29%)	0.601	-0.585	0.400	-0.559	-0.062	-0.831	-0.266
PC2 (26%)	0.276	0.418	0.517	0.028	0.887	0.299	-0.428
PC3 (17%)	-0.526	0.552	0.380	-0.588	-0.348	-0.097	0.010
PC4 (14%)	0.241	-0.068	0.122	-0.337	0.178	0.269	0.828

Table 3. Effects ($\beta \pm SE$) of principal component 1 (PC1) (damsel fish abundance), PC2 (competitor biomass), PC3 (turf algae/sediment [TAS] cover), PC4 (predator biomass), and fish total length on $\delta^{13}C$ and $\delta^{15}N$ values for *Sparisoma aurofrenatum* and *Acanthurus coeruleus* based on hierarchical models with site as a random effect (intercept only). Conditional R^2 values ($R^2_{LMM(c)}$) describe the variance explained by the entire mixed-effects model, while marginal R^2 values ($R^2_{LMM(m)}$) describe variance explained by only fixed factors.
* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Parameter	<i>S. aurofrenatum</i>		<i>A. coeruleus</i>	
	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$
PC1	0.18 \pm 0.07	-0.07 \pm 0.02*	-0.08 \pm 0.10	-0.10 \pm 0.03*
PC2	-0.24 \pm 0.08*	0.05 \pm 0.02	-0.13 \pm 0.11	0.04 \pm 0.03
PC3	0.18 \pm 0.1	-0.02 \pm 0.03	0.01 \pm 0.13	-0.003 \pm 0.04
PC4	0.63 \pm 0.10***	0.03 \pm 0.03	-0.06 \pm 0.15	-0.11 \pm 0.04
Total length	0.10 \pm 0.01***	0.09 \pm 0.01***	0.03 \pm 0.01**	0.09 \pm 0.01***
$R^2_{LMM(m)}$	0.24	0.35	0.36	0.45
$R^2_{LMM(c)}$	0.54	0.42	0.58	0.53

Caranx ruber, *C. bartholomaei*, *Lutjanus jocu*, *L. griseus*, *L. apodus*, *Sphyraena barracuda*, *Epinephelus morio*, and *Mycteroperca bonaci*. Protected sites had higher large-predator biomass ($14.3 \pm 7.3 \text{ g m}^{-2}$) relative to unprotected sites ($3.6 \pm 3.1 \text{ g m}^{-2}$); however, this difference was not statistically significant (t -test, $t = 1.34$, $p = 0.21$). Territorial damselfishes averaged $0.33 \pm 0.05 \text{ ind. m}^{-2}$, with *Stegastes partitus* being the most abundant damselfish (representing 88% of all observations).

From the PCA on site-level predictors, we retained 4 uncorrelated principal components that explained 88% of the total variance. Although the principal component axes are composites of all of the original variables, they each correlated most strongly with a single individual variable. Damsel fish abundance, competitor biomass, TAS cover, and large predator biomass were correlated more strongly with principal component axes 1 through 4, respectively, relative to the other original variables (Table 2).

Isotope values for both fish species were consistent with herbivores in this system based on algae isotope values (not shown) (see Fig. 2 for species biplots of

$\delta^{13}C$ and $\delta^{15}N$). Hierarchical models showed that $\delta^{13}C$ values (an index of basal resource use) for *Sparisoma aurofrenatum* were positively related to total length and PC4 (large predator biomass) and negatively related to PC2 (competitor biomass) (Table 3). Therefore, larger *S. aurofrenatum* and those at sites with more abundant large predators and fewer competitors chose diets that were less depleted in $\delta^{13}C$. $\delta^{15}N$ values (an index of trophic level) for both *Acanthurus coeruleus* and *S. aurofrenatum* were positively related to total length and negatively related to PC1 (damsel fish abundance) (Table 3). Therefore, larger fish at sites with numerous damselfish occupied higher trophic levels. For *A. coeruleus*, total length was positively related to $\delta^{13}C$ (Table 3). We did not include protection status (MPA vs. non-MPA) in these models because it explained $<0.01\%$ of the variance in $\delta^{13}C$ and $\delta^{15}N$ for both species based on null hierarchical models (i.e. intercept-only models).

For *S. aurofrenatum*, PC4 (large predator biomass) ($\beta = 0.11$, $p = 0.001$) and PC1 (damsel fish abundance) ($\beta = 0.04$, $p = 0.03$) were positively related to trophic niche area (SEA_B) in a multiple regression model ($p = 0.002$, $R^2 = 0.68$; Fig. 3a,b). This indicates a greater degree of diet diversity within populations where large predators were abundant and damselfish were not. For *A. coeruleus*, SEA_B was negatively related to PC1 (and hence positively related to damselfish abundance) ($\beta = 0.11$) in a simple linear regression model ($p = 0.02$, $R^2 = 0.42$; Fig. 3c). This indicates greater diet diversity within populations where damselfish were abundant. Other PC axes were unrelated to trophic niche and were therefore not included in these models.

Based on follows of 293 individuals, the major diet components of *S. aurofrenatum* were TAS and

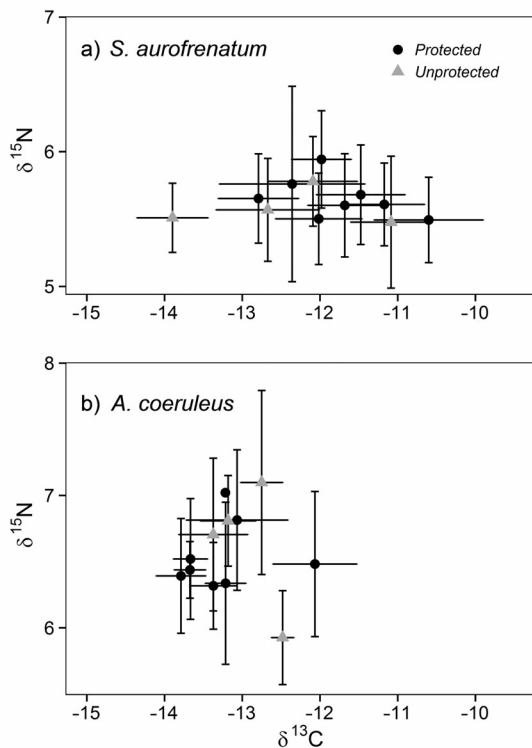


Fig. 2. Biplots of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values ($\pm\text{SD}$) for (a) *Sparisoma aurofrenatum* and (b) *Acanthurus coeruleus*, with baseline-corrected $\delta^{13}\text{C}$ values

macroalgae (Table 4). Brown thallate species included *Dictyota* spp. ($27.8 \pm 1.5\%$) and *Styopodium* spp. ($2.5 \pm 0.4\%$), and green thallate was comprised exclusively of *Halimeda* spp. Minor categories that comprised an average of $<1\%$ of diet included: CCA, scleractinian corals, sponges, *Millepora* spp., fecal material, and zoanthids. Diet diversity based on proportions of diet items consumed [$\exp(H')$] at each site was positively correlated with isotopic measurements of trophic niche (SEA_B) at each site (Spearman rank correlation, $r = 0.76$, $p = 0.006$). Based on the analysis of 157 *A. coeruleus* stomachs, we found the average gut to include primarily filamentous turf algae and macroalgae (Table 4). Animal material comprised a small proportion of diet ($<1\%$). Diet diversity based on proportions of average stomach contents [$\exp(H')$] at each site was positively correlated with isotopic measurements of trophic niche (SEA_B) (Spearman rank correlation, $r = 0.64$, $p = 0.04$).

We found significant, but relatively weak, positive relationships using simple linear regressions between *A. coeruleus* length and the proportions of macroalgae (red: $p < 0.001$, $R^2 = 0.06$, green: $p < 0.001$, $R^2 = 0.11$, and brown: $p < 0.001$, $R^2 = 0.08$, thallate species) and the proportion of calcareous sediment ($p < 0.001$, $R^2 =$

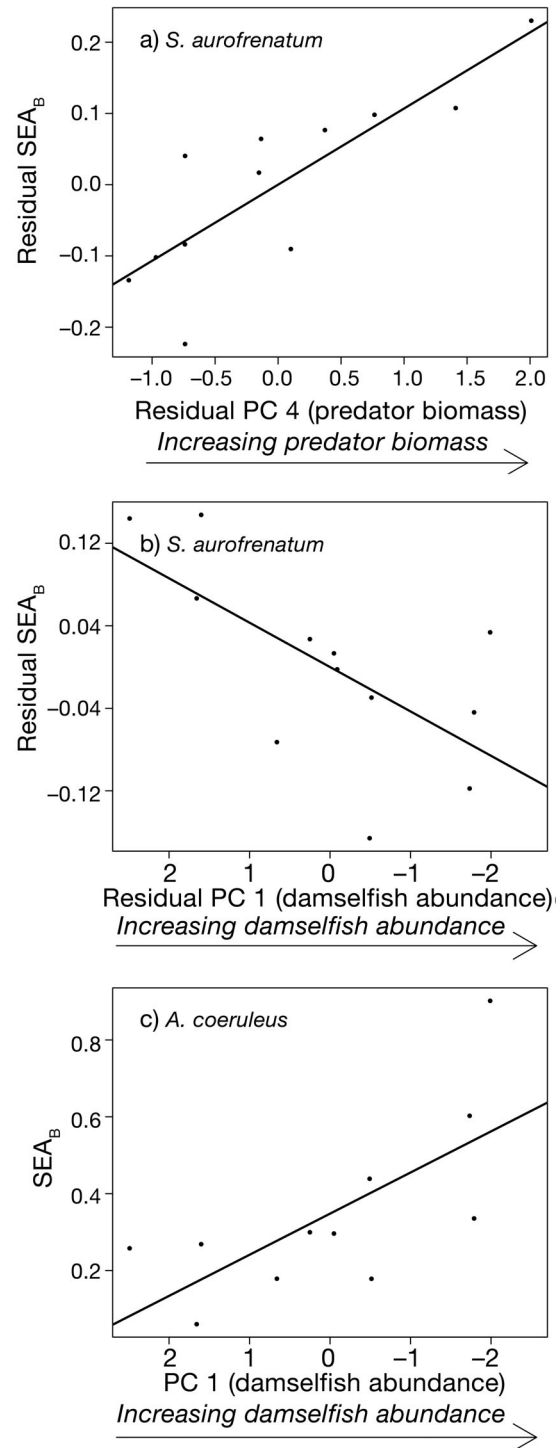


Fig. 3. Partial regression plots for *Sparisoma aurofrenatum* showing the effect of (a) principal component 4 (PC4) (predator biomass) and (b) PC1 (damselfish abundance) on Bayesian standard ellipse area (SEA_B). (c) Simple linear regression of PC1 (damselfish abundance) and SEA_B for *Acanthurus coeruleus*. Note that because of the negative relationship between PC1 and damselfish abundance, the x-axis has been reversed in (b) and (c) to represent increasing damselfish abundance from left to right. Solid lines: fitted linear regressions

Table 4. Diet components (% \pm SEM) of *Sparisoma aurofrenatum* based on behavioral follows and *Acanthurus coeruleus* based on stomach contents. Minor components are listed in the 'Results' section. Unidentified organic material (UOM) was not categorized (nc) for *S. aurofrenatum*

	Brown thallate	Green thallate	Red thallate	Turf algae	Sand/sediment	Gorgonians	UOM
<i>S. aurofrenatum</i>	30.3 \pm 1.5	8.2 \pm 0.7	<1	50.0 \pm 1.6	1.9 \pm 0.4	1.3 \pm 0.3	nc
<i>A. coeruleus</i>	11.6 \pm 0.7	3.3 \pm 0.9	10.7 \pm 0.9	55.1 \pm 2.3	9.9 \pm 1.2	<1	9.3 \pm 1.3

0.24) in stomachs. There was a strong negative relationship between fish length and the proportion of turf algae ($p < 0.001$, $R^2 = 0.40$) in stomachs. Additionally, using logistic regression, we found a significant decrease in the probability of occurrence of filamentous turf ($\beta = -0.34$, $SE = 0.09$, $p < 0.001$) that coincided with a significant increase in the probability of occurrence of animal material ($\beta = 0.24$, $SE = 0.09$, $p < 0.05$) as fish size increased (Fig. 4). A Hosmer–Lemeshow test for goodness of fit showed a good fit for both logistic regression models (turf algae: $\chi^2 = 12.18$, $p = 0.16$; animal: $\chi^2 = 11.71$, $p = 0.20$).

Finally, when we examined how large predators might impact damselfish abundance, we showed a significant positive relationship between large predator biomass and damselfish abundance across sites ($p = 0.05$, $R^2 = 0.25$; Fig. 5). We did not find a relationship between large predator and mesopredator biomass ($p = 0.12$, $R^2 = 0.13$).

DISCUSSION

On coral reefs, food availability (Muñoz & Motta 2000), competition (Nash et al. 2012), habitat struc-

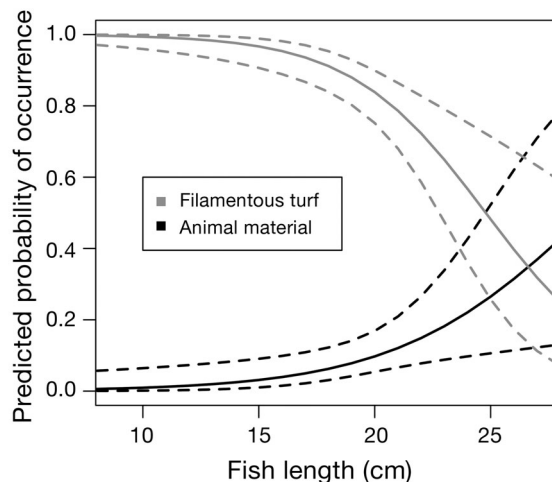


Fig. 4. Predicted probability of occurrence of animal material and filamentous turf in stomachs of *Acanthurus coeruleus* as a function of fish length based on logistic regression model. Dashed lines: 95% confidence intervals

tural complexity (Hixon & Beets 1993), and territorial damselfish (Foster 1985) can influence foraging decisions of large mobile herbivorous fishes. However, much less is known about the influence that predators have on their diet selection. Using complementary techniques including stable isotopes, behavioral observations, and stomach contents, we showed that the diets of 2 species of reef herbivores are influenced by different factors, likely depending on their susceptibility to predation and their ability to access defended food resources. For *Sparisoma aurofrenatum*, we found the basal resource use (carbon isotope ratios) was positively related to predator biomass and negatively related to competitor biomass, while trophic level (nitrogen isotope ratios) was negatively related to damselfish abundance. *S. aurofrenatum*'s trophic niche was partially positively correlated with large predator biomass and negatively correlated with damselfish abundance. For *Acanthurus coeruleus*, trophic level and trophic niche were positively related to the abundance of territorial damselfish. Importantly, damselfish abundance influenced the diet of both herbivore species but in slightly different ways, likely dependent on how different foraging behaviors lead to differential access to damselfish

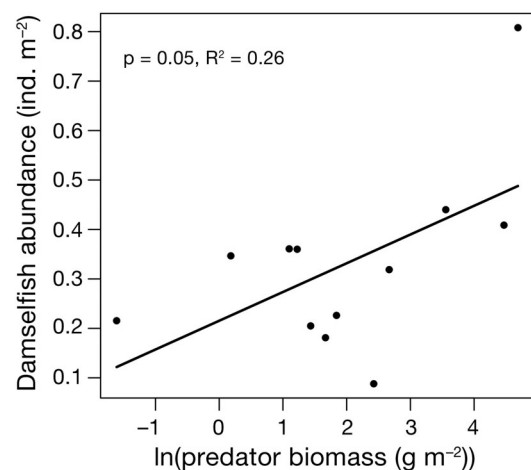


Fig. 5. Regression plot for territorial damselfish abundance and ln-transformed predator biomass across sites. Line: fitted linear regression

territories. The effect of damselfish may have been influenced by large predator abundance, as damselfish abundance showed a positive correlation with large predator biomass. Thus, abundant large predators may influence herbivore diets in a variety of direct and indirect mechanisms.

Effect of site and individual characteristics on individual diets

We found that fish size as well as multiple site characteristics influenced individual diets. In particular, our isotopic data show a shift towards omnivory in larger fish, which is contrary to what other studies suggest for many herbivorous fishes (Cocheret de la Morinière et al. 2003). Our stomach content data support our isotopic data, suggesting our result represents a true ontogenetic shift. Specifically, *A. coeruleus* incorporated more animal material and macroalgae and less filamentous algae with increasing size, suggesting that they may target more energetically rich animal material to meet their higher metabolic demands. However, they may simply be ingesting more animal material incidentally as they target more macroalgae, which may be fouled by epifauna more frequently than filamentous algae. Overall, the variation in isotopic values with fish length support the need for researchers to consider variation among individuals, and take appropriate steps to account for those differences as we have here, prior to making inferences about differences in isotopic composition among populations (Reum & Marshall 2013).

In addition to the strong effect of fish size, we found that certain site characteristics also correlated with individual diets, but that the important site characteristics differed for the different herbivore species. For *S. aurofrenatum*, partial correlations with the principal component axes suggested that the biomass of competitors and large predators influenced the type of food resources consumed (i.e. $\delta^{13}\text{C}$), whereas these factors were unrelated to diet for *A. coeruleus*. It is not surprising that competitive interactions could influence *S. aurofrenatum* diet because of the extensive overlap along multiple dimensions of diet (e.g. jaw morphology, feeding modes, microhabitat use) of the family Scaridae (Bellwood & Choat 1990). Additionally, others have shown that aggression can be intense, particularly towards conspecifics, for *S. aurofrenatum* (Mumby & Wabnitz 2002), suggesting strong inter- and intraspecific competition for food resources. In contrast, adult *A. coeruleus* rarely

engage in aggressive interactions (Lawson et al. 1999), suggesting that interference competition may play a lesser role in influencing diet for this species, as our data indicate. The effect of competition may also have been greater for *S. aurofrenatum* because parrotfishes, and thus potential competitors, were more abundant at our sites relative to surgeonfish.

Large predator biomass was also correlated with individual diets of *S. aurofrenatum*, but was unrelated to *A. coeruleus* diet. This result supports the hypothesis that there are species-specific responses to predation risk (Creel 2011). The schooling behavior often observed for *A. coeruleus* may function to decrease their per capita susceptibility to predation via group vigilance or diluting per capita predation risk (Parrish 1999). Additionally, *A. coeruleus* have a sharp scalpel on their caudal peduncle, which is presumably used in anti-predatory defense. Madin et al. (2010b) showed that *Acanthurus nigricans*, a congener of *A. coeruleus*, which also possesses a physical anti-predator defense and is known for its schooling behavior (Allen & Erdmann 2012), did not alter its foraging behavior in response to acute predation risk. These results together suggest that schooling Acanthuridae may be less likely to alter their behavior in response to higher risk of predation. In contrast, schooling is rarely observed for adult *S. aurofrenatum*, nor do they have a physical anti-predatory defense, potentially making them more likely to alter their behavior in areas with abundant predators. Patterns in social structure and group foraging often influence the vulnerability of different species to predation and predation risk (Wirsing et al. 2010) and could potentially explain the differences in diet between *A. coeruleus* and *S. aurofrenatum*.

The abundance of territorial damselfish influenced diets of both herbivores. It is unsurprising that damselfish had a strong influence on diet because on average, 34 % of the reef was occupied by damselfish territories at our sites (calculated based on territory sizes from Hata & Kato 2004 and references therein). As opposed to competitor and large predator biomass, which influenced the basal source of resources consumed (i.e. $\delta^{13}\text{C}$), damselfish influenced the trophic level of resources consumed (i.e. $\delta^{15}\text{N}$). Many territorial damselfishes modify benthic communities by preventing fleshy macroalgae growth via weeding within their territories, which they defend vigorously from larger herbivorous fishes (Hixon & Brostoff 1983). Even though the most common species we observed, *Stegastes partitus*, is primarily planktivorous and not known to cultivate algae within its territories, it can still increase algal diver-

sity by aggressively defending areas of the benthos (De Ruyter Van Steveninck 1984). Furthermore, the influence of 'farmer' species (i.e. *Stegastes fuscus*, *S. diencaeus*, *S. planifrons*, *S. leucostictus*, and *Microspathodon chrysurus*) may be greater than would be expected based on their low abundance relative to *S. partitus*, because of the larger territory areas they defend (Hata & Kato 2004). Yet, it is unclear how territorial damselfish may alter the isotopic composition of food resources. Our data show that greater damselfish abundance was associated with lower $\delta^{15}\text{N}$ values of both fish species. By eliminating macroalgae (which is often fouled with epifauna) from their territories, damselfish may lower the overall $\delta^{15}\text{N}$ signal of resources in their territories. However, algal communities within damselfish territories vary among fish species, substrata, and localities (Hata & Kato 2004), making it difficult to isolate the specific mechanism to explain our result. However, it is clear that damselfish play an important role in influencing the individual diets of larger herbivores.

Ultimately, we showed that individual and site-level factors influenced the isotopic signatures of individual herbivores. However, without isotopic information on a multitude of potential food resources, we cannot attribute specific changes in consumer isotopic signatures with specific changes in diet. This level of information, while useful, was not feasible for us to obtain considering the magnitude of sampling that would have been required over the large spatial scale of our study.

Effect of site characteristics on diet diversity within populations

We found that diet diversity within populations varied among sites based on SIA and other metrics of diet (i.e. stomach content analyses and observations of feeding behaviors). For *S. aurofrenatum*, we found that greater predator biomass was positively associated with population trophic niches, whereas damselfish abundance showed a negative relationship with trophic niche. However, for *A. coeruleus*, the trophic niche of a population was positively correlated with damselfish abundance, but unrelated to large predator biomass. Thus, territorial damselfishes appeared to have the opposite effect on the trophic niche of *A. coeruleus* relative to *S. aurofrenatum*. Therefore, the diverse algal resources inside damselfish territories appear differentially available to *A. coeruleus* versus *S. aurofrenatum*. Schooling by *A. coeruleus* may allow them to overwhelm damselfish

aggression and gain greater access to defended algal territories and therefore to a greater diversity of resources (Foster 1985). However, adult *S. aurofrenatum* are generally solitary or move in small groups that are likely too small to consistently overcome aggressive damselfishes (Mumby & Wabnitz 2002).

For *S. aurofrenatum*, there was also a positive relationship between trophic niche and large predator biomass. This could indicate that herbivores at sites with fewer large predators, and hence less risk, have larger excursion areas in which to seek out their preferred foods resulting in similar diets. In contrast, herbivores at sites with more large predators may decrease their excursion area (Madin et al. 2010b) or decrease the time devoted to foraging by increasing vigilance (Lima & Dill 1990), thereby restricting their access to preferred diet items. This could result in divergence of individual isotopic signatures and increase a population's trophic niche as our data suggest. Trophic niche was unrelated to large predator biomass for *A. coeruleus*. This supports our suggestion that this species is less susceptible to the behavioral impacts of predation risk, likely due to their schooling behavior and physical anti-predatory defense.

Our data also suggest that the effect of large predators on foraging may be mediated through their effect on damselfish abundance. As we show above, damselfishes were correlated with changes in diet metrics for both *S. aurofrenatum* and *A. coeruleus*. There was also a positive relationship between damselfish abundance and large predator biomass, suggesting that predators may indirectly affect herbivore foraging via their positive effect on damselfish abundance. Yet, we did not find a relationship between the abundance of large predators and mesopredators, as would be expected if the effect of large predators on damselfishes was mediated via a reduction in mesopredator abundance (e.g. Harborne et al. 2008, Mumby et al. 2012). However, we may not have captured the full extent of mesopredator biomass from diurnal surveys because many predatory species are most active during crepuscular periods and at night (Holbrook & Schmitt 2002). Predation risk from large predators could also lower foraging efficiency of mesopredators, resulting in increased abundance or aggression of damselfish (Stallings 2008, Madin et al. 2010b) and more interference with larger herbivorous fishes. The abundance of large predators is likely not the only factor driving differences in damselfish abundance across sites, as other factors such as available shelter (Holbrook & Schmitt 2002) and differences in recruitment (Sponaugle &

Cowen 1996) could also play a role. However, our data suggest that the indirect effects of large predator abundance on territorial damselfishes may be a common, yet overlooked, effect of predators on herbivore foraging.

CONCLUSIONS

Herbivorous fishes are functionally important to coral reef ecosystems because their grazing facilitates coral settlement, growth, and survivorship (Hughes et al. 2007, Mumby et al. 2007, Burkepile & Hay 2008). Understanding the factors that shape their foraging decisions will be a key to knowing their impact on reef resilience and recovery in the face of global change. We demonstrated that multiple factors, from body size to large predator abundance, can have important species-specific influences on herbivore diets both at the individual and population scale. Furthermore, our research is among the first to specifically address the nonconsumptive effects of predators on foraging of other reef fishes. Our data suggest that an increased abundance of large predators can alter herbivore diets directly by influencing foraging behavior via risk and indirectly by influencing food availability via positive indirect effects on damselfishes. A crucial question that remains is what cascading influences such predator-herbivore interactions can have on the reef community. Emerging evidence from other reef ecosystems suggests that increased predation risk lowers rates of herbivory and results in areas of increased macroalgal cover (Madin et al. 2010a). But it is yet unclear how this can, in turn, affect corals. It is increasingly clear that the non-consumptive effects of predators will be important for understanding the ecology of coral reefs in an era of human-mediated predator removal and recovery.

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