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N. P. Lemoine & J. F. Valentine

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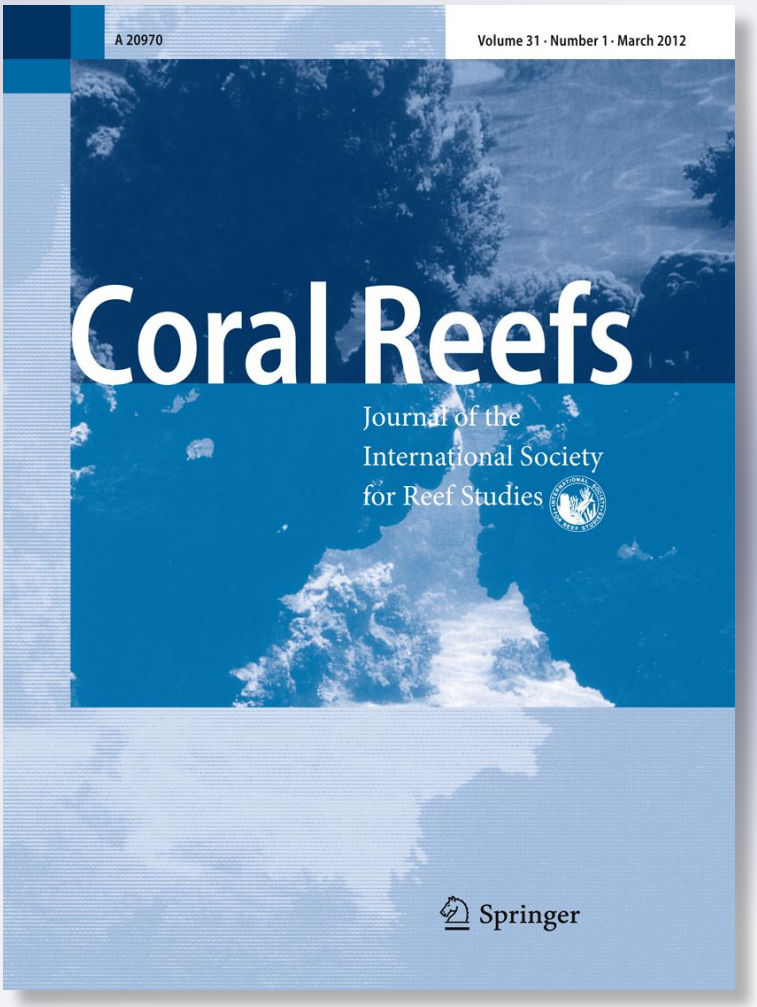

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REPORT

Structurally complex habitats provided by *Acropora palmata* influence ecosystem processes on a reef in the Florida Keys National Marine Sanctuary

N. P. Lemoine · J. F. Valentine

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Abstract The disappearance of *Acropora palmata* from reefs in the Florida Keys National Marine Sanctuary (FKNMS) represents a significant loss in the amount of structurally complex habitat available for reef-associated species. The consequences of such a widespread loss of complex structure on ecosystem processes are still unclear. We sought to determine whether the disappearance of complex structure has adversely affected grazing and invertebrate predation rates on a shallow reef in the FKNMS. Surprisingly, we found grazing rates and invertebrate predation rates were lower in the structurally complex *A. palmata* branches than on the topographically simple degraded reefs. We attribute these results to high densities of aggressively territorial damselfish, *Stegastes planifrons*, living within *A. palmata*. Our study suggests the presence of agonistic damselfish can cause the realized spatial patterns of ecosystem processes to deviate from the expected patterns. Reef ecologists must therefore carefully consider the assemblage of associate fish communities when assessing how the mortality of *A. palmata* has affected coral reef ecosystem processes.

Keywords Damselfish · *Acropora palmata* · Grazing rates · Predation rates · Competition · Habitat

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Present Address:
N. P. Lemoine (✉)
Department of Biology, Florida International University, 3000 NE 151st, North Miami, FL 33181, USA
e-mail: nlemo001@fiu.edu

N. P. Lemoine · J. F. Valentine
Dauphin Island Sea Lab, 101 Bienville Blvd., Dauphin Island, AL 36528, USA

N. P. Lemoine · J. F. Valentine
Department of Marine Sciences, University of South Alabama, Mobile, AL 36688, USA

Introduction

Over the past several decades, coral reefs in the Florida Keys National Marine Sanctuary (FKNMS) have undergone substantial declines in the cover of live coral (Gardner et al. 2003; Schutte et al. 2010). In particular, elkhorn coral *Acropora palmata* once dominated shallow coral reefs of the FKNMS until suffering >95% mortality from an outbreak of white-band disease in the mid-1980s (Aronson and Precht 2001; Miller et al. 2002). As *A. palmata* was probably responsible for providing the majority of complex shelter on shallow patch reefs within the FKNMS, reefs within the FKNMS are now much more structurally homogenous (Alvarez-Filip et al. 2009). Given the large body of knowledge on how structural complexity modifies community composition on coral reefs (Almany 2004; Lee 2006), our objective was to assess how structurally complex habitats provided by *A. palmata* affect ecosystem processes on a reef in the FKNMS.

Herbivory and invertebrate predation are two important ecosystem processes that affect benthic community structure on coral reefs (McClanahan 1999; Burkepile and Hay 2008). Herbivory plays a critical role in structuring benthic communities, although the effect of herbivory on benthic composition depends on the number and type of herbivores present (Burkepile and Hay 2008). Increased scarid grazing rates have been correlated with declines in macroalgal cover

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and subsequent increases in coral recruitment (Mumby et al. 2006, 2007). In contrast, the effect of urchins on substrate composition appears to be density dependent. At intermediate densities, urchins indirectly increase coral survival by cropping macroalgae (Aronson and Precht 2001). At high densities, overgrazing by urchins can increase coral juvenile mortality (Sammarco et al. 1973).

Complex structure often harbors higher abundances of herbivores than structurally simple areas (Almany 2004). Macroalgal cover declines (Lee 2006) and coral cover increases (Aronson and Precht 1995) with increasing structural complexity, suggesting that herbivory rates are the greatest near complex structures such as those provided by *A. palmata*. Moreover, the association of many invertebrate predators with *A. palmata* suggests that *A. palmata* colonies may be sites of high invertebrate predation potential and thus have less grazing pressure from small-bodied invertebrates, such as sea urchins (e.g., McClanahan 1999). As *A. palmata* likely provided the majority of complex substrate within the FKNMS, *A. palmata* colonies might play a pivotal role as localized sites of intense herbivory and invertebrate predation pressure.

Three lines of evidence suggest that *A. palmata* colonies in the FKNMS may not be sites of intense grazing as with other structurally complex habitats. First, Lirman (1999) found that abundances of finfish grazers, scarids, and acanthurids, were higher in structurally degraded rubble fields than in living *A. palmata*. Second, abundances of territorial damselfish, *Stegastes planifrons*, were highest on living *A. palmata* (Lirman 1999). *S. planifrons* often antagonizes and territorially exclude herbivores, including scarids (Almany 2004) and *Diadema* urchins (Sammarco and Williams 1982). Third, Bennett et al. (2010) found that the caespitose morphology of some *Acropora* species presents a physical barrier to large-bodied herbivores and decreases rates of herbivory within the complex structures provided by acroporids. The studies of Lirman (1999) and Bennett et al. (2010) on acroporid species contrast the more general assumption that herbivore abundances would be greatest within the complex structure provided by *A. palmata*. Yet, there is little information on how *A. palmata* affects rates of herbivory and predation.

To assess how the complex shelter provided by *A. palmata* affects ecosystem processes within a reef in the FKNMS, we used comparisons of food-web structure and grazing and predation rates among three habitat types at Horseshoe Reef (see 'Methods' for site description). We hypothesized that *A. palmata* would harbor higher densities of herbivores and invertebrate predators than nearby structurally simpler rubble fields. As high densities of territorial damselfishes, particularly *Stegastes planifrons*, associate with *A. palmata* (Lirman 1999) and as damselfish aggression increase with size (Helfman 1989), we constructed a size-distribution of *S. planifrons* within each habitat as a proxy for the intensity of competitive interactions in each habitat. Following our hypothesis of higher grazer and invertebrate predator densities within *A. palmata*, we hypothesized that the *A. palmata* habitat would also have the highest localized grazing and predation pressure. To determine whether grazers perceived structurally degraded areas as potentially risky habitats, we quantified grazer attack rates in each habitat. We expected that attack rates would be lowest in structurally simple areas given the exposure of herbivores to predators.

Methods

Study site

Horseshoe Reef (25°08.30 N, 80°18.80 W) is a shallow (< 4 m) reef located in the northern FKNMS, containing a large ($\sim$50 m × 50 m) stand of healthy *A. palmata* bordered by structurally degraded rubble zones. To study within-reef dynamics, we conducted surveys and tethering experiments in three habitats: (1) 'Live' *A. palmata* stands representative of historical conditions, (2) 'Near-Rubble' algal covered rubble fields immediately adjacent to living *A. palmata*, and (3) 'Far-Rubble' habitat zones located over 50 m from the living *A. palmata.* 'Near-Rubble' sites were included to account for the possibility of edge effects, wherein resident herbivores within *A. palmata* forage in nearby habitats.

Complexity measurements

We estimated the structural complexity of all habitats using the fractal dimension (*D*), which provides an estimate of surface complexity and shelter availability for non-uniform surfaces (Sugihara and May 1990). The chain-link rugosity metric is commonly employed to estimate substrate complexity on coral reefs, but Beck (1998) found that the fractal dimension of a habitat is a better predictor of community structure.

Two perpendicular profile images of each tethering location (see 'Grazing Rates') were taken using a digital camera. *D* was calculated for the reef outline in each photograph using the grid method (see Sugihara and May 1990). *D* values calculated from the two images taken at each tether location were averaged prior to analysis to yield one fractal dimension estimate of each tether location.

Fish assemblages

Fish assemblages in 'Live', 'Near-Rubble', and 'Far-Rubble' habitats were assessed using replicate 15 m, non-overlapping belt transects haphazardly lain over the reef ($n = 5$ per treatment). All fishes encountered within 0.5 m

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on either side of the transect line were identified to species and recorded. To estimate damselfish size, we used a marked scale bar as a guide to record the number of damselfish falling into pre-defined size categories (0–5, 5–10, 10–15, 15+ cm) along each 15 m transect.

Grazing rates

As feeding preferences vary widely among reef herbivores (Burkepile and Hay 2008), grazing rates were estimated using both seagrass (*Thalassia testudinum*) and macroalgae (*Laurencia* spp.). Before each trial, ungrazed seagrass shoots (1–3 leaves) were scraped free of epiphytic calcareous algae. Percent loss of each *T. testudinum* blade was calculated by comparing pre- and post-trial photographs of leaf surface estimated using ImageJ Image Analysis software. Percent loss of *Laurencia* spp. was based on differences in pre- and post-trial wet weights (±0.01 g) of the tethered algal branches.

Lead disks, with three clothespins attached along the perimeter of each disk, were randomly assigned to hold either seagrass shoots or algal branches. Each clothespin held either a single shoot of seagrass or branch of algae. Based on our preliminary data, the duration of the grazing trials was limited to 1 h. Data were averaged for each disk so that each lead disk represented a single replicate. Four disks were deployed in each treatment each day for 3 days ($n = 12$ disks per habitat).

Invertebrate predation potential

We documented treatment impacts on invertebrate predation potential by tethering crabs (*Mithrax sculptus*) collected from Rodriguez Key (25°03.037 N, 80°26.597 W). *M. sculptus* is a commonly used prey to measure invertebrate predation potential in coral reef ecosystems (Valentine et al. 2008), and urchins were not readily available in the numbers necessary for this study. Carapace width (±1 mm) of each crab was measured using Vernier calipers. A single lead disk ($n = 12$ per habitat) held two crabs tethered with at least 20 cm of monofilament line. Predation trials also lasted 1 h and were conducted on the same days as the grazing trials.

Forager behavior

To provide indirect measures of how herbivores perceive risk in each treatment, we measured herbivore attack rates on seagrass and algal tethers placed in each habitat. In each trial, a tether group in each habitat was randomly chosen to document attacks via remote video ($n = 3$ per habitat). The number of attacks on each tether was recorded for the duration of all videos. Bites too close together to distinguish as separate attacks were recorded as one attack. The number of attacks per minute was summed for all species across seagrass and algal tethers to yield total herbivore attack rate (Bennett et al. 2010).

Statistical analyses

The fractal dimensions (D) of the tether sites in each habitat were compared using a one-way ANOVA. Each tether site was a single replicate ($n = 4$ per habitat).

Comparisons of fish species richness, total fish density (m^{-2}), and densities of fish families (scarids, acanthurids, pomacentrids, haemulids, lutjanids) among 'Live', 'Near-Rubble', and 'Far-Rubble' treatments were made using one-way ANOVAs. Fisher's exact test was used to determine whether damselfish size varied independently of habitat type. Differences in fish assemblage composition among habitats were examined using SIMPER and ANOSIM tests conducted on a fourth-root transformed, Bray-Curtis dissimilarity matrix. Post hoc multiple comparisons following ANOSIM tests were made by examining the R statistic among pairwise tests (Clarke, personal communication). The R statistic is a measure of dissimilarity among treatments; $R = 0$ indicates identical communities (complete overlap) and $R = 1$ signifies two entirely distinct communities (no overlap). In ecological communities, R values greater than 0.2–0.3 indicate non-negligible differences in community structure.

Differences in seagrass and algae grazing rates among habitat types were analyzed using one-way ANOVAs followed by Tukey's HSD test. To ensure that the size of the tethered crabs did not confound the interpretation of treatment effects on predation, the carapace widths of tethered *M. sculptus* were compared among habitat treatments using a one-way ANOVA. Invertebrate predation potential was analyzed using Fisher's exact test. A one-way ANOVA was used to compare attack frequency among habitats.

Univariate statistical analyses were conducted using R v2.10. PRIMER v6.0 was used for ANOSIM, SIMPER, and nMDS plots. Parametric assumptions of normality and homoscedasticity were verified using plots of the residuals. Data that failed to meet these assumptions were $\log(x + 1)$ transformed. Results were considered marginally significant at $p < 0.10$ and significant at $p < 0.05$. All graphs show untransformed data to standardize comparisons with other studies.

Results

Complexity measurements

'Live' sites were significantly more structurally complex than either the 'Near-Rubble' or the 'Far-Rubble' sites

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($n = 4$ per habitat, $F_{2,9} = 8.434$, $p = 0.008$). The 'Rubble' sites were statistically indistinguishable from each other. Thus, each 'Rubble' site represents a low-relief contrast to the highly branching morphology of *A. palmata*.

Fish assemblages

Total fish density was significantly higher in 'Live' habitats compared to 'Near-Rubble', and 'Far-Rubble' habitats (Fig. 1a, $n = 5$ per habitat, $F_{2,12} = 4.292$, $p = 0.039$). While fish species richness did not vary significantly among treatments (Fig. 1a), fish assemblage composition did (Fig. 1b, global $R = 0.548$, $p < 0.001$). The composition of fishes in the 'Live' treatment differed markedly from both 'Far-Rubble' and 'Near-Rubble' treatments (Fig. 1b, $R > 0.600$), while fish composition did not differ between 'Far-Rubble' and 'Near-Rubble' sites.

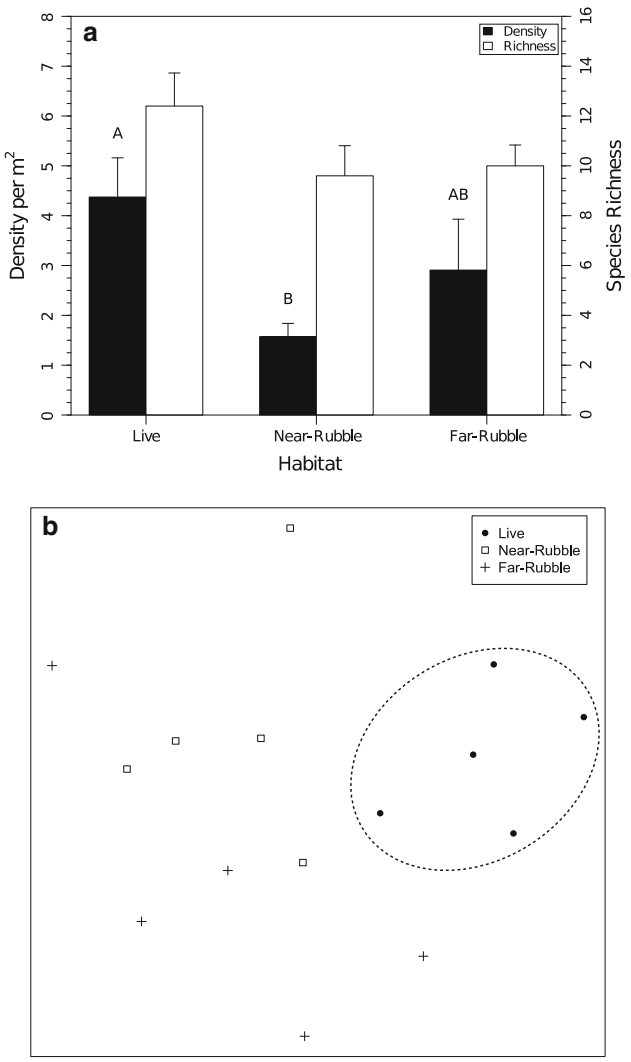

Fig. 1 **a** Fish species richness and density among 'Live' and 'Rubble' treatments. *Letters* denote significantly different groups. *Bars* are one standard error. **b** nMDS plot of fish assemblage composition on live *A. palmata* and 'Rubble' sites. *Dashed circle* encompasses all 'Live' sites

SIMPER analysis found that five fish families, pomacentrids, acanthurids, scarids, lutjanids, and haemulids accounted for the majority of the dissimilarity among treatments. Pomacentrid ($F_{2,12} = 16.086$, $p < 0.001$) densities were highest in the 'Live' habitats (Table 1). In particular, *S. planifrons* densities were significantly higher in the 'Live' treatment than in either of the 'Rubble' treatments (Electronic Supplemental Material, ESM Fig. S1 $F_{2,12} = 6.663$, $p = 0.011$). Damselfish were also significantly larger in the 'Live' *A. palmata* stand than in either the 'Near-Rubble' or 'Far-Rubble' sites (ESM Fig. S2, Fisher's Exact test, $p < 0.001$). Most of the individuals 5–20 cm in length were *S. planifrons*, although *Microspathodon chrysurus* accounted for a few of the largest individuals (i.e., ≥15 cm in total length).

Acanthurid ($F_{2,12} = 4.147$, $p = 0.042$) densities differed significantly among habitats, with a slightly higher densities individuals m^{-2} present in the 'Rubble' treatments (Table 1). Scarid densities were not significantly different among habitat treatments ($F_{2,12} = 1.828$, $p = 0.203$). The test of scarid densities, however, was characterized by low power due to the large variance compared to the observed effect size ($\beta = 0.33$). Even so, the 'Far-Rubble' sites had the highest average density of scarids while the 'Live' sites had the lowest scarid densities (Table 1). Lutjanid densities differed significantly among habitats ($F_{2,12} = 4.700$, $p = 0.031$) and were highest in the 'Live' habitats (Table 1). The difference in lutjanid densities between 'Live' and 'Far-Rubble' habitats was marginally significant ($p = 0.054$). Haemulid densities were marginally different among habitats ($F_{2,12} = 3.466$, $p = 0.065$), with the 'Near-Rubble' habitat having the lowest haemulid densities (Table 1). Overall, the general trend was that 'Live' *A. palmata* sites had the lowest herbivore densities, highest pomacentrid densities, and highest invertebrate predator densities compared to both 'Near-' and 'Far-Rubble' sites.

Grazing rates

Seagrass grazing differed significantly among treatments ($n = 12$ per habitat, $F_{2,29} = 14.791$, $p < 0.001$). Counter to our initial hypotheses, 'Live' habitats had significantly lower seagrass grazing rates than both 'Far-Rubble' sites ($p < 0.001$) and 'Near-Rubble' sites ($p = 0.031$) (Fig. 2). Grazing on seagrass tethers was significantly lower in 'Near-Rubble' sites than in 'Far-Rubble' sites ($p = 0.013$). Algal grazing rates did not differ significantly among habitats, although there was some indication that algal grazing rates were lower in the 'Live' habitats (Fig. 2).

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Table 1 Densities of the five major fish families in each habitat

	Scaridae	Acanthuridae	Pomacentridae	Haemulidae	Lutjanidae
Live	0.21 ± 0.11	0.07 ± 0.05[a]	0.91 ± 0.33[a]	1.97 ± 1.51*	0.77 ± 0.76[a]*
Near-Rubble	0.40 ± 0.32	0.21 ± 0.06[b]	0.32 ± 0.16[b]	0.23 ± 0.13*	0.08 ± 0.14[b]
Far-Rubble	0.65 ± 0.58	0.16 ± 0.12[ab]	0.16 ± 0.12[b]	0.81 ± 1.41	0.09 ± 0.14[b]*

Significant differences ($p < 0.05$) are denoted by letters

* Marginally significant differences ($p < 0.10$)

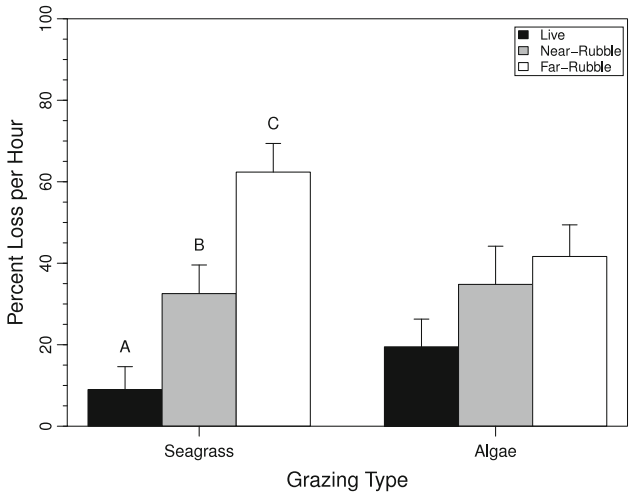

Fig. 2 Hourly grazing rates of seagrass and algae among habitats. *Letters* and *numbers* denote significantly different groups. *Bars* are one standard error

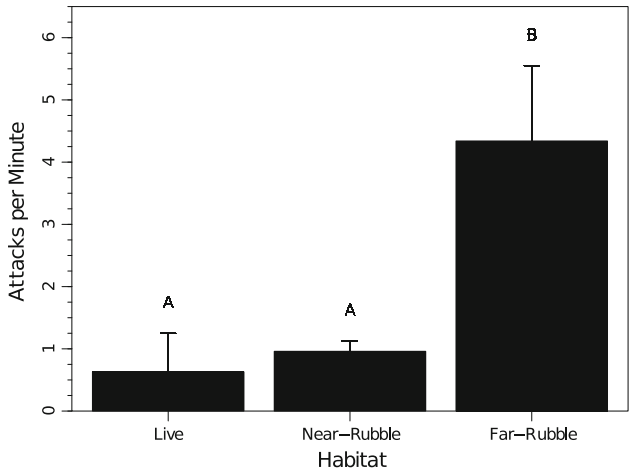

Fig. 3 Herbivore attack frequency (attacks × min^{-1}) among all habitats. *Bars* are one standard error

Invertebrate predation potential

There was no detectable difference in the size of tethered crabs placed among the treatments. Invertebrate predation rates varied significantly among habitats ($n = 12$ per habitat, $p = 0.032$). *M. sculptus* survival in 'Live' and 'Near-Rubble' habitats was higher than expected by chance, while the 'Far-Rubble' habitat had lower than expected survival (ESM Fig. S3). These results suggest that the 'Far-Rubble' habitat was a site of more intense predation, while areas in and around the live *A. palmata* were sites of higher invertebrate survival. Video recordings unexpectedly showed that the majority of attacks on invertebrates were made by parrotfishes (*Sparisoma viride* and *S. aurofrenatum*, 15% and 37% of attacks, respectively) and wrasses (*Halichoeres bivittatus*, 41% of attacks). Various haemulids were responsible for the remaining 7% of attacks. It should be noted that none of the attacks by *H. bivittatus* were lethal for the crabs, while *S. viride* and *S. aurofrenatum* accounted for nearly all lethal predation events.

Forager behavior

The number of attacks per minute by herbivores differed significantly among habitats ($n = 3$ per habitat, $F_{2,6} = 6.337$, $p = 0.033$). Attack rate was highest in the 'Far-Rubble' habitat and did not differ between 'Live' and 'Near-Rubble' sites (Fig. 3). Seagrass and algal tethers were fed on by exclusive guilds of herbivorous fishes. Scarids accounted for all observed grazing on seagrass tethers and were never observed grazing on the algae tethers. In contrast, acanthurid grazers fed exclusively on algae tethers. Pomacanthids were witnessed feeding on algal tethers, albeit only twice. This suggests that seagrass and algal tethers offer information on the two dominant guilds of grazing fishes, scarids, and acanthurids, with no observed instances of these guilds feeding on multiple tether types.

Discussion

The complex shelter provided by acroporid corals can have significant effects on reef ecosystem structure and function (Beukers and Jones 1998), yet there has been relatively little work assessing how the structure provided by *A. palmata* specifically might affect trophic processes. Our comparisons of structural complexity among habitat zones of Horseshoe Reef demonstrate that our study site has two distinct habitat types, highly complex and nearly planar. The absence of complex shelter can increase the mortality

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of small, lower trophic level fishes (Shima et al. 2008). Reductions in the population sizes of these species can adversely affect critical ecosystem processes, such as grazing and predation rates (Kramer and Heck 2007; Valentine et al. 2008). Our data suggest that complex structure provided by *A. palmata* may not positively affect grazing and predation rates on a shallow reef in the FKNMS.

Based on previous work describing the importance of topographically complex habitats as predation refuges for many vulnerable reef fishes (Beukers and Jones 1998), we predicted that densities of herbivorous fishes would be higher in the structurally complex *A. palmata* stand than in either the 'Near-Rubble' or 'Far-Rubble' reef zones. Although we found no evidence to support this hypothesis, our findings are largely consistent with other studies. Lirman (1999) found that scarids were twice as abundant in low relief, low coral cover environments than in living *A. palmata* stands. At our study site, scarid densities were, on average, 88% higher in the 'Near-Rubble' and 206% higher in the 'Far-Rubble' habitat than in the 'Live' *A. palmata* habitat. High variances associated with these measurements, possibly related to schooling behavior of some scarids, prohibited a statistically significant result.

Lirman (1999) also found that acanthurid densities were just over 4× higher in low relief, low topography areas than in living *A. palmata* stands. Our study site, Horseshoe Reef, had low abundances of acanthurids regardless of habitat type (0.15 individuals m^{-2}); on average no individuals were encountered along a 15-m transect. Thus, ubiquitously low densities of acanthurids at our study site probably obscured this herbivore's habitat occupancy patterns. For invertebrate predators, our data corroborate results of other studies showing that haemulids and lutjanids aggregate within *A. palmata* (Lirman 1999). Common grunt species *Haemulon sciurus* (bluestripe grunt), *Haemulon plumieri* (white grunt), and *Haemulon aurolineatum* (tomtates) were more abundant in the 'Live' *A. palmata* stands than in either 'Rubble' site. *Lutjanus apodus* (schoolmaster snapper) was the only lutjanid species encountered during daylight visual surveys and was found almost exclusively within the living *A. palmata* branches.

Based on the expectation that herbivore and invertebrate predator densities would be the highest within the *A. palmata* stand, we hypothesized that grazing and predation rates would also be the highest in the live *A. palmata* stand. Yet, contrary to our expectations, seagrass grazing rates followed a pattern of 'Far-Rubble' > 'Near-Rubble' > 'Live'. As scarids were responsible for nearly 100% of seagrass consumption, it is not surprising that seagrass removal rates match scarid densities. As acanthurids consumed nearly 100% of the algae, it is also not surprising that algal grazing did not differ among habitats, similar to densities of acanthurids. Unexpectedly, invertebrate predation rates did not match the distribution of invertebrate predators (haemulids and lutjanids); predation rates were the highest where densities of these predator species were lowest. This is probably because scarids were unexpectedly the dominant consumers of *M. scultpus*, resulting in similar patterns of seagrass grazing and invertebrate mortality: highest in 'Far-Rubble' and lowest in 'Live' habitats. Our observed grazing and predation patterns are therefore likely related to the densities of herbivorous and omnivorous fishes in each habitat.

Our study was conducted at one reef within the FKNMS, making it difficult for us to extrapolate our results into a broad context. Our results do corroborate previous work on this subject. As mentioned above, the distributions of herbivorous and omnivorous fishes at Horseshoe Reef are nearly identical to those reported by Lirman (1999). Other high-relief reefs within the FKNMS exhibit lower herbivore densities (<2 m^{-2}) than Horseshoe Reef (~4 m^{-2}) (Paddack et al. 2006). Thus, the presence *A. palmata* may increase herbivore densities on the whole reef scale above other structurally complex reefs in the FKNMS, but not necessarily grazing rates, as patterns of herbivore density and grazing rates were spatially partitioned between complex and planar habitats within a single reef.

Bennett et al. (2010) found that macroalgal grazing rates and herbivore attack rates were lowest within *Acropora* stands on inshore patch reefs of the Great Barrier Reef; they suggested that the branching morphology of acroporid species restricts herbivore movement, limiting grazing. Though incursions of large scarids into *A. palmata* were rare, we did record large *Scarus guacamaia* and *S. coelestinus* within the *A. palmata* colony. Therefore, we cannot conclude that the absence of herbivores from within *A. palmata* at Horseshoe Reef was due to size limitation.

Alternatively, the differences in herbivore abundances and grazing rates among topographically complex and flat areas at Horseshoe Reef may be driven by predation risk. On coral reefs, structurally complex habitats can act as a refuge for medium-bodied predators (coney *Cephalopholis fulva* and graysby *Cephalopholis cruentata*) and restrict prey visual line-of-sight (Rilov et al. 2007; Stallings 2008). High densities of intermediate predators would lead to both the reduced densities and risk-averse behavior of herbivorous fishes that we noted within *A. palmata* at Horseshoe Reef. Yet, no piscivores (except trumpetfish, *Aulostomus maculatus*) were observed in the 'Live' habitat. Several large piscivores (black grouper *Mycteroperca bonaci*, bar jacks *Caranx ruber*, and reef sharks *Carcharhinus melanopterus*) were seen swimming over the 'Near-Rubble' site, though sightings of these predators were infrequent and *C. melanopterus* were clearly transitory. This would suggest that herbivores in 'Rubble' habitats should be more exposed to predation, yet the safer, 'Live' habitat was clearly a site of reduced feeding rates and foraging efficiency for these herbivores.

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We believe that territorial behavior of *S. planifrons* led to the competitive exclusion of scarids and acanthurids from the *A. palmata* at Horseshoe Reef. High densities of large *S. planifrons* occupied the colonies of *A. palmata.* Moreover, damselfish within *A. palmata* were significantly larger than individuals in the other habitats. In damselfish, aggression often increases with body size (Robertson 1998), suggesting that competition in the *A. palmata* stand was more intense per individual. Accordingly, *S. planifrons* individuals were observed aggressively attacking many herbivores, including larger parrotfish, around the tether sites. *S. planifrons* can reduce the number of settling herbivores (Almany 2004), affect the home range size and resource use of other species (Jones 2005), and attack any herbivorous species with significant diet overlap, particularly scarids (Thresher 1976; Brawley and Adey 1977).

A causal link between damselfish and grazing rates cannot be established without measuring the response of herbivores to the removal of *S. planifrons* from *A. palmata*; however, Almany (2004) has shown increases in scarid abundances in complex habitats following the removal of damselfish. Removal of damselfish also increased the density of urchin grazers, resulting in lower algal biomass within stands of *A. cervicornis* (Williams 1981). Our data suggest that grazing rates and herbivore abundances have a positive relationship at our study site. It would therefore not be surprising if the removal of damselfish from *A. palmata* were followed by an increase in both herbivore abundances and grazing rates within the *A. palmata* stand at Horseshoe Reef.

Our data show that the structural complexity provided by *A. palmata* may have profound impacts on patterns of grazing and predation at Horseshoe Reef. At this particular reef, low-relief areas may be a refuge from interspecific competition, increasing herbivore feeding rates and foraging efficiencies. Many studies assume that increasing topographic complexity will lead to an increase in grazing rates. This assumption may not hold if highly territorial damselfishes rapidly colonize the available shelter, as was the case at our study site. Careful consideration of interspecific interactions within and among trophic levels is necessary in order to assess whether *A. palmata* mortality has rearranged trophic processes on reefs within the FKNMS.

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