

# Predation risk influences feeding rates but competition structures space use for a common Pacific parrotfish

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**Abstract** In terrestrial systems it is well known that the spatial patterns of grazing by herbivores can influence the structure of primary producer communities. On coral reefs, the consequences of varied space use by herbivores on benthic community structure are not well understood, nor are the relative influences of bottom-up (resource abundance and quality), horizontal (competition), and top-down (predation risk) factors in affecting spatial foraging behaviors of mobile herbivorous fishes. In the current study we quantified space use and feeding rates of the parrotfish, *Chlorurus spilurus*, across a strong gradient of food resources and predator and competitor abundance across two islands with drastically different fisheries management schemes. We found evidence that while feeding rates of this species are affected by direct interference competition and chronic predation risk, space use appears to be primarily related to exploitative competition with the surrounding herbivore community. We found no evidence that predation risk influences diurnal foraging space use in this small bodied

parrotfish species. Additionally, we found the influence of chronic predation risk on feeding rates of this species to be less dramatic than the results of recent studies that used model predators to measure acute behavioral responses of other species of herbivorous fishes. Our results indicate that the non-consumptive effects of predators on the foraging behaviors of coral reef herbivores may be less dramatic than previously thought.

**Keywords** Herbivory · Coral reef · Territory size · Foraging behavior · Chronic risk

## Introduction

The spatial pattern of grazing by herbivores can have a dramatic influence on the structure of plant and algal communities in marine and terrestrial systems (Adler et al. 2001; Sommer 2000). Spatial interactions between herbivores and their resources have been shown to influence ecosystem dynamics, with grazing being a particularly important driver of space competition among primary producers (Palmer et al. 2005). Heterogeneity of grazing intensity across space can arise from variable distributions of grazers across habitats (Hay 1981; Hoey and Bellwood 2007), but at finer scales, it can arise from foraging behaviors and decision-making by individual herbivores (Parsons and Dumont 2003). The long-term effects of spatially heterogeneous grazing intensity has been modeled in a variety of systems, indicating the potential for consumers to significantly influence the strength and asymmetry of competitive interactions among basal resource species (Palmer et al. 2005; Weber et al. 1998). In particular, models indicate that the spatial pattern of grazing by coral reef herbivores can have a major impact

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on the long-term outcomes of interactions between corals and macroalgae on coral reefs (Eynaud et al. 2016; Sandin and McNamara 2012).

In the context of coral reef resilience, the competitive dynamics between reef-accreting corals and their algal competitors are of particular interest to scientists, managers, and members of coastal tropical communities. Multiple lines of evidence indicate that herbivorous fishes are important agents that affect competition between corals and algae on reefs (Carpenter 1986; Hixon and Brostoff 1996; Jackson et al. 2014; Lewis 1986; Lirman 2001; Mumby 2006, 2009; Mumby et al. 2006; Smith et al. 2010; Thacker et al. 2014; Williams and Polunin 2001). Sandin and McNamara (2012) modeled multi-decadal trajectories of coral reef benthic community dynamics, examining the impact of the spatial patterns of herbivory by grazers that differ in their foraging behaviors. The results suggested that the outcome of coral–algal competition is significantly influenced by the level of heterogeneity in grazing: (1) concentrated feeding by herbivores creates pockets of bare space that enhance coral recruitment, leading to coral-dominated reefs, while (2) scattered and homogenous feeding favored algal domination over corals. In contrast, other studies indicate that parrotfishes may damage and consume juvenile corals through inadvertent or intentional corallivory in the process of their natural grazing activities (Mumby 2009) and it is probable that the net effect of these positive and negative interactions between grazing and coral recruitment is largely dependent on the spatial and temporal patterns of foraging by parrotfishes. While theory and empirical observations suggest that variation in the density and distribution of grazers may have significant impact on coral reef benthic dynamics, we know much less about the drivers that lead to this variation. Because specific management actions aimed at preserving the ecosystem function of coral reef grazers may affect their space use differently (e.g., the effect of a fishing ban on predators versus a fishing ban on herbivorous competitors), there is an urgent need for a more comprehensive understanding of the various factors affecting spatial foraging behavior.

Territoriality theory suggests that territory sizes should be negatively related to population densities of competitors, as long as the costs of defending the territory do not outweigh the benefits gained by holding it (Dill 1978; Hixon 1980). This relationship between competitor density and territory size has been demonstrated in avian and aquatic systems (Morse 1976; Tricas 1989) and specifically for parrotfishes (Mumby and Wabnitz 2002; van Rooij et al. 1996). Additionally, many studies show how natural variability and experimental manipulation of resource abundance (i.e., food) affect animal movement behavior and territory size (Seastedt and MacLean 1979; Stenger 1958; Stimson 1973).

In contrast to these bottom-up, resource competition-driven models of animal foraging behavior, the top-down, “landscape of fear” concept has gained substantial traction in both marine and terrestrial literature. The assumptions of this model are that prey alter their foraging behaviors in response to spatial and temporal heterogeneity in predation risk (Laundré et al. 2010). Modifying foraging activities in response to predation risk may result in behaviorally mediated trophic cascades, with significant effects on associated primary producer communities. In the classic example, the reintroduction of wolves into Yellowstone National Park resulted in shifts in the foraging behavior of elk from open habitats to safer wooded habitats (Hernández and Laundré 2005), ultimately resulting in the re-establishment of aspen tree stands in open habitats (Fortin et al. 2005). More recently, the landscape (seascape, reefscape) of fear effect has been documented in marine systems. Marine mammals and sea turtles are shown to minimize use of high-quality but dangerous foraging grounds in the presence of predators, although for sea turtles, the propensity for visiting areas of high resource quality (and high risk) is contingent on the energetic condition of the animal (Heithaus et al. 2007; Wirsing et al. 2008). The outcome of predator avoidance by these marine grazers can be measured in effects on seagrass community structure (Burkholder et al. 2013). For coral reef herbivorous fishes, past research demonstrates relationships between the movement extent of the grazer and predation threat, both in acute effects of actual predator presence as well as chronic effects measured by predator abundance (Madin et al. 2010a, b). Risk avoidance behaviors may be modified by the abundance and distribution of algal resources; fishes may be less risk adverse if energetic rewards in high-risk areas are high enough (Gil et al. 2016). These patterns sometimes result in patchy removal of the algal resources by the herbivorous prey species (Madin et al. 2011) because there is often heterogeneity in shelter availability for the prey species across habitats (Taylor 1988). Studies that used model predators to measure responses of coral reef herbivores suggest that the acute effect of predator presence may also substantially reduce foraging rates (Catano et al. 2016; Rizzari et al. 2014).

While there is a large body of evidence indicating varied effects of resource abundance, competition, and predation risk in structuring reef herbivore space use, most studies address only single factors without incorporating the potential for combined effects of multiple drivers or the possibility of covariation among them (Adler et al. 2001; for exception see Nash et al. 2012). Fear and energy landscapes are not mutually exclusive but are overlaid and trade off to modulate animal movements (Gallagher et al. 2016). Understanding the relative effects of each paradigm on particular aspects of an animal’s activity patterns can be valuable for forecasting how spatial behavior may change with

shifts in community structure, for example from benthic disturbances or fisheries management changes. The relative effects of these drivers in structuring parrotfish movements remain unclear.

If the variable of interest is phenotypically plastic, one way to gauge the relative importance of different candidate drivers is to monitor the expression of the variable under different states of the drivers (Warner 1991). For example, Nash et al. (2012) showed that habitat characteristics and competitor abundance best explained some spatial metrics of parrotfish foraging on the Great Barrier Reef, and they did not find any effect of predator abundance on foraging behavior. However, predator abundance was low and homogenous across their study sites. To effectively assess the relative influences of habitat, predation risk, and competition in structuring space use, it is essential to compare responses across a significant gradient of all potentially relevant drivers.

In the present study, we conducted comparative observations of foraging behaviors of a coral reef grazer at two islands that vary strongly in food abundance, competition, and predation risk because of dramatically different management regimes. One of these islands is essentially pristine and unfished, with relatively high herbivore and predator biomass and variation in these factors between two distinct reef habitats within the island, while at the other island both trophic groups are fished resulting in relatively low herbivore and predator biomass. We measured two components of foraging behavior, feeding rate and size of the feeding territory, for individual parrotfish across multiple sites at both islands. Within islands, sites varied in their abundances of piscivores and herbivore competitors as well as in the availability of food resources. We measured rates of acute responses to predators and direct interference competition by herbivore competitors. We then constructed models that combined the individual-level interactions with site-level abundance of predators, competitors, and resource abundance to evaluate the drivers of herbivore foraging behavior.

## Materials and methods

### Study sites

Palmyra Atoll is a remote island in the northern Line Islands, roughly 1600 km south of the main Hawaiian Islands (5°53'N 162°5'W). Palmyra was virtually uninhabited before and after its occupation by the US military during WWII and has been managed as a US National Wildlife Refuge since 2001. There is currently no extractive fishing on Palmyra's reefs. Though the lagoon system was heavily altered by the military at the time of occupation,

the forereefs and reef terraces remain relatively pristine and host high predator (Sandin et al. 2008) and herbivore (Edwards et al. 2014) biomass compared with reefs affected by local human activity. The atoll consists of three large lagoons flanked by long, gradually sloping reef terraces that extend to the east and west (for further description see Papastamatiou et al. 2010). We conducted this study at two sites on the sloping forereef and four sites across the backreef and shallow western terrace between July and September of 2013.

Mo'orea is an inhabited island in the Society Islands of French Polynesia (17°32'S 149°50'W); unlike Palmyra, it has high levels of subsistence and small-scale commercial fishing activity of both piscivores and herbivores (Leenhardt et al. 2012; Walker and Robinson 2009). The island has a lagoon-backreef system and sloping forereefs. We restricted data collection in Mo'orea to the forereef for two reasons. First, the backreef habitat in Mo'orea is mostly very shallow and patchy and is highly dissimilar to the contiguous, variable-depth reef terraces at Palmyra; and second, both the shallow depths and the high levels of spearfishing activity on the backreefs at Mo'orea prevented us from making behavioral observations (i.e., fishes are very wary, and the shallow water forces divers to be closer to the fish subjects, potentially affecting behavior). We conducted observations at three sites on the north and western sloping forereef of Mo'orea in May of 2015 (see Electronic Supplementary Material Fig. 1 for a map of the study locations).

### Study species

*Chlorurus spilurus* (formerly *C. sordidus*) is a protogynous hermaphroditic small-bodied member of the family Labridae (subfamily Scarinae) and is one of the most abundant and widespread parrotfish in the tropical Pacific. *C. spilurus* is the most numerically abundant species of parrotfish at both study islands and was present in both the forereef and backreef habitats. *C. spilurus* are diet generalists, which likely explains their abundance and ubiquity across habitats, and they primarily bite mixed algal turfs, crustose coralline algae, a variety of species of macroalgae, and a small amount of live coral (Hamilton et al. 2014). They are functionally classified as scrapers for the majority of size classes though the largest individuals are classified as excavators/bioeroders (Green and Bellwood 2009).

### Behavioral observations

Behavioral observations of *C. spilurus* were conducted by a SCUBA diver (forereef) or snorkeler (backreef/reef terrace). In the backreef the snorkeler observed the fish from the surface and on the forereef the diver made observations from several meters above the fish in order

not to influence its behavior due to proximity (distance tested at both islands prior to data collection). In order to track the activity space of each individual, the diver towed a surface-floated GPS unit, logging positions every 15 s. During 20 min focal follows for each individual *C. spilurus*, observers recorded (a) number of bites, and (b) all inter- and intraspecific interactions including competitive chases, cleanings, territorial displays, and predator responses. Sample sizes are as follows: at Palmyra  $n = 167$  individuals across six sites and at Mo'orea  $n = 95$  observations across three sites, with roughly 30 observations per site. Two observations led us to believe that 20 min was adequate to characterize space use: (1) focal fish would swim repeated patterns, returning to a few specific food patches within the areas during the course of an observation; and (2) over the course of an observation, the terminal phase (TP) male individuals usually encountered other TP males at territory borders, indicating that they were limited in their ability to forage beyond those boundaries. Similar studies have shown that 20 min tracks of territorial parrotfish were adequate to characterize short-term movement patterns (Howard et al. 2013; Mumby and Wabnitz 2002).

For each observation we estimated the total length of the focal individual and recorded its color phase [terminal phase male (TP) or initial phase (IP)] as well of the time of day that the observation started. All observations were conducted between the hours of 08:00 and 17:00. We attempted to choose focal fish across sizes and color phases in proportion to the natural distributions of these variables observed at our study sites and were careful not to re-sample any individual fish.

### Fish community surveys

In order to characterize the diurnal fish community assemblage we conducted fish surveys at Palmyra using a belt transect method ( $n = 9$  transects per site,  $25 \times 4$  m for fishes greater than 20 cm total length,  $25 \times 2$  meters back along the same transect for fishes less than 20 cm total length; see Friedlander et al. 2016 for detailed methods). For the Mo'orea sites, we utilized fish community data from the Mo'orea Coral Reef Long-Term Ecological Research program collected in the summer of 2014 ( $n = 4$  transects per site,  $5 \times 50$  m transect for mobile taxa,  $1 \times 50$  m along the same transect for cryptic and non-mobile taxa, see Brooks 2015). We later assigned fishes to broad trophic categories and converted counts and total lengths to biomass density using trophic classifications and length-weight conversion compiled by the NOAA Coral Reef Ecosystem Program from FishBase (Heenan et al. 2014).

### Benthic Surveys

In order to estimate the site-level abundance of preferred bitten substrates for *C. spilurus*, we conducted benthic community surveys using uniform point contact methodology. At each meter along  $n = 8$ , parallel, 25 m transect lines distributed across each site we recorded the identity of the space-holding organism living beneath each point. We then aggregated data from the four categories that made up the majority of *C. spilurus* bites at Palmyra from Hamilton et al. (2014) (mixed algal turfs, crustose coralline algae, the brown alga *Lobophora*, and the green alga *Halimeda*) into a site-level average of percent cover of these algal groups. Recently there has been compelling evidence presented that scarids may gain most of their protein nutrition from autotrophic bacteria (particularly cyanobacteria), not the underlying algae that has been conventionally understood to be their main food source (Clements et al. 2016). Thus we will refer to these algal types as 'preferred bitten substrates' as they may in fact not be the primary dietary targets but just suitable substrates for the colonization and growth of targeted bacteria. In either case, the effect of the bites on the substrate (i.e., removal of surface algae) occurs on this type of visible substrate. Algal turfs were defined as any low-lying filamentous algae less than 2 cm in height.

### Kernel calculations of space use

We computed space use metrics from all the diver-towed GPS tracks using the biased random bridge method in the *adehabitatHR* package in R (Benhamou 2011; Calenge 2006). We use the 95% utilization kernel to approximate feeding territory size and the 50% utilization kernel to approximate areas of core use within the feeding territory (see Electronic Supplementary Material Table 1 for a summary of space use metrics and see Electronic Supplementary Material Fig. 2 for examples of kernel utilization distributions from tracked fish).

### Foraging behavior models

We decomposed foraging behavior into two components, measured for every observation: feeding rates (bites/min) and space use (area of 50 and 95% utilization kernels). We log transformed all space use metrics (kernel areas) to satisfy assumptions of normality. For each observation we also calculated or measured the following predictors: bi-directional competitive chase rate, time of day, focal fish total length, and focal fish color phase (TP or IP). We constructed linear models for each of the response parameters using stepwise model selection and Akaike Information Criteria (AIC) using the *MASS* package in R (Ripley et al. 2015). We then used the residuals from these linear models

to create a site-level parrotfish foraging response variable, that controlled for the covariates described above, and tested for significant associations with the site-level predictors of piscivore biomass, herbivore biomass, and percent cover of preferred bitten substrate. For each multi-term best fit linear model, we calculated the relative importance of each term using the *relaimpo* package in R (Grömping 2006). This method partitions  $R^2$  into the relative contribution of each term. After identifying the strongest predictors of each foraging metric across all sites at both islands, we modeled the relationships within each island separately to test whether the direction of the relationships within islands are consistent with the results found across all sites at both islands.

## Results

### Community composition

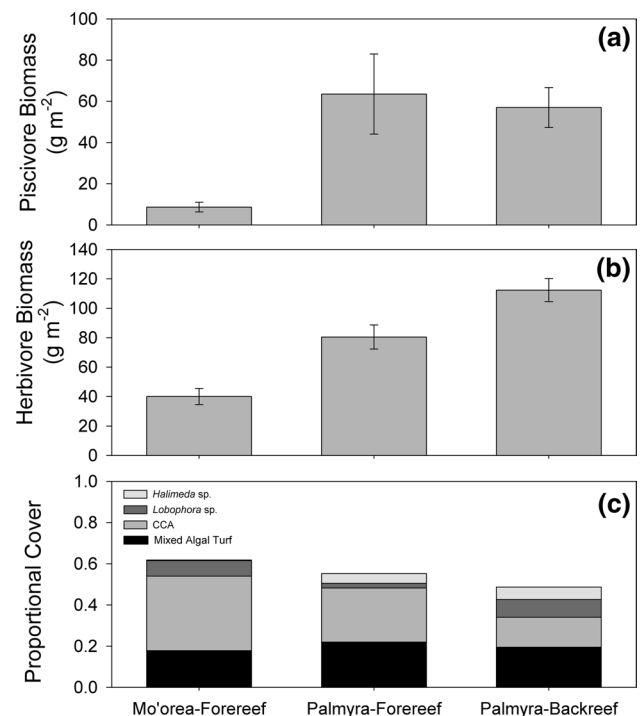
Mean piscivore biomass was greater at study sites at Palmyra compared to study sites at Mo'orea (Fig. 1a), and there was variation in predator identity as well as abundance. At Palmyra, piscivore biomass was dominated by snappers (Lutjanidae), sharks (Carcharhinidae), groupers (Serranidae), and large-bodied jacks (Carangidae). In contrast, the piscivore biomass at survey sites in Mo'orea was dominated by groupers, emperors (Lethrinidae), and small-bodied jacks. We did observe abundant sharks and snappers in Mo'orea at sites frequently visited by diving tourism operations, where fishing is discouraged and provisioning is a common practice (these sites were not included in our study). This suggests that the differences in piscivore identity seen at the study sites are not strictly due to biogeography.

Mean herbivore biomass was greater at Palmyra compared to Mo'orea (Fig. 1b). The herbivore communities were similar at both islands, tending to be dominated by parrotfish and surgeonfish (Acanthuridae).

Mean percent cover of major food types (sum of mixed algal turfs, crustose coralline algae, *Lobophora*, and *Halimeda*) was slightly higher in Mo'orea compared to Palmyra (Fig. 1c).

### Species Interactions

In total, we observed nearly 3000 competitive chases between our focal individuals and other herbivorous fishes over the course of the study. Competitive chase rates were roughly twice as high in Palmyra as in Mo'orea on average (Palmyra:  $0.65 \pm 0.029$  chases/min,



**Fig. 1** Mean **a** Piscivore biomass with standard error, **b** herbivore biomass with standard error, and **c** proportional cover of preferred bitten substrates across islands and habitat types

SE; Mo'orea:  $0.38 \pm 0.032$  chases/min, SE;  $t = -6.36$ ,  $df = 225.45$ ,  $P < 0.001$ ). The taxonomic groups involved in most chases were surgeonfishes, damselfishes (Pomacentridae), and parrotfishes. The group primarily responsible for the large island differences in chase rate were the territorial surgeonfishes, particularly the highly territorial species such as *Acanthurus nigricans* and *A. lineatus*, which are abundant in Palmyra and rare in Mo'orea. Chase rates by damselfishes and other parrotfish species did not vary strongly between islands. The majority of parrotfish interactions were with other *C. spilurus*, usually involving larger individuals chasing smaller individuals in an apparent size-structured pecking order. TP males were highly aggressive towards each other at territory boundaries.

Compared to competitive chases, acute reactions to predators were extremely rare. Over the course of 264 observations (88 h) we recorded a total of 16 acute responses to a predator (4 in Mo'orea, 12 in Palmyra). In Mo'orea all four responses to predators were elicited by groupers, while in Palmyra responses were elicited by snappers ( $n = 4$ ), jacks ( $n = 3$ ), groupers ( $n = 2$ ), an emperor ( $n = 1$ ), an eel (Muraenidae) ( $n = 1$ ), and a shark ( $n = 1$ ). We never observed an actual predation attempt on any focal individual.

## Foraging behavior metrics

Bite rates were higher in Mo'orea than in Palmyra (Fig. 2a). Areas of core use were larger in Mo'orea than in Palmyra (Fig. 2b), as were overall territory areas (Fig. 2c).

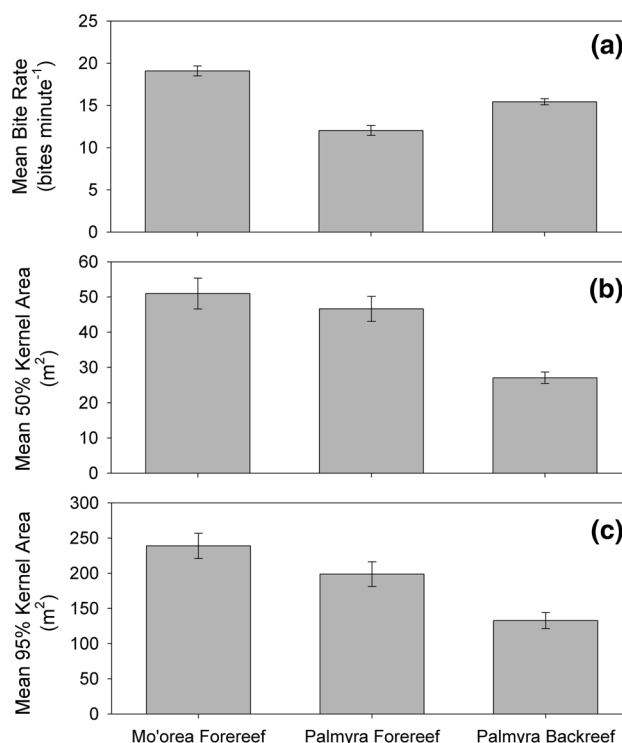
## Foraging behavior models

Individual-level variability in bite rates was best explained by models incorporating time of day and competitive chase rates (Table 1a). Bite rates positively correlated with time of day and negatively correlated with chase rates. In this best fit model, chase rate accounted for the majority (77.5%) of the explanatory power of the model, indicating that direct interference competition has a significant effect on foraging rates. Individual-level variation in metrics of space use (territory size, and core area; Table 1b, c) was explained only by focal individual total length. Space use metrics were positively correlated with body size. Site-level variation in mean residual bite rate was best explained by piscivore biomass (Table 1d) indicating that levels of chronic predation risk affect foraging rates. Site-level variation in territory size was best explained by a model incorporating herbivore biomass and food abundance, with herbivore biomass accounting for almost all (94%) of the explanatory power (Table 1e). Site level variation in core use area was explained only by herbivore biomass (Table 1f) indicating that exploitative competition is the primary factor affecting diurnal space use. Bite rates were negatively related to piscivore biomass and space use metrics were both negatively related to herbivore biomass. The univariate relationships between all site level drivers and behavioral responses are shown in Fig. 3.

Within-island models of bite rate and area use were directionally consistent with the full model that included all sites across both islands. In some cases, the relationships between predator biomass vs. bite rate, as well as herbivore biomass vs. areas used remained significant, but in other cases they did not. This is likely due to the fact that within-island analyses had reduced sample sizes as well as variation across sites compared to analyses that included all sites across both islands.

## Discussion

Both predation risk and competition for resources appear to play unique roles in structuring foraging behaviors in the parrotfish *Chlorurus spilurus*. We found evidence that feeding rates were affected by direct interference competition and chronic levels of predation risk, both of which reduced feeding rates. We hypothesize that this negative relationship between feeding rates and predator abundance is due



**Fig. 2** Mean **a** bite rates, **b** 50% kernel (core use) areas, and **c** 95% kernel (feeding territory) areas of *Chlorurus spilurus* on Mo'orea forereef sites ( $n = 95$ ), Palmyra forereef sites ( $n = 50$ ), and Palmyra backreef sites ( $n = 117$ )

to increased vigilance at sites where predators are present, as opposed to direct interruption of feeding due to predator avoidance (chronic vs. acute risk, sensu Madin et al. 2010b). Two observations support this hypothesis. First, we recorded extremely low rates of acute responses to predators by focal fish during behavioral observations, despite the fact that large predators are abundant at Palmyra and were frequently observed swimming in close proximity to our focal individuals. Second, in many hundreds of hours of diving and observations on the reefs at Palmyra, we very rarely observed any reaction of herbivorous fishes to the approach or presence of the majority of predators on those reefs, including sharks, snappers, groupers, and emperors. The exception to this is actively swimming jacks, which frequently elicit strong responses from smaller fishes.

We acknowledge that predators may elicit behavioral responses from prey species at times of day when we were not conducting observations (e.g., crepuscular and night sheltering behaviors that are well known in parrotfishes and other coral reef prey species; Dubin and Baker 1982) and that predation risk may structure the distribution of species and ontogenetic phases across habitats (e.g., recruits and juveniles inhabiting shallower, high-structure habitats and moving to deeper habitat as they grow to some size refuge; Dahlgren and Eggleston 2000; Laegdsgaard and Johnson

2001). Recent studies that used model predators to simulate the acute responses of different herbivore taxa to perceived threats showed extreme reductions in feeding rates in the vicinity of the models (Catano et al. 2016; Rizzari et al. 2014). Our results demonstrate that the effects of chronic

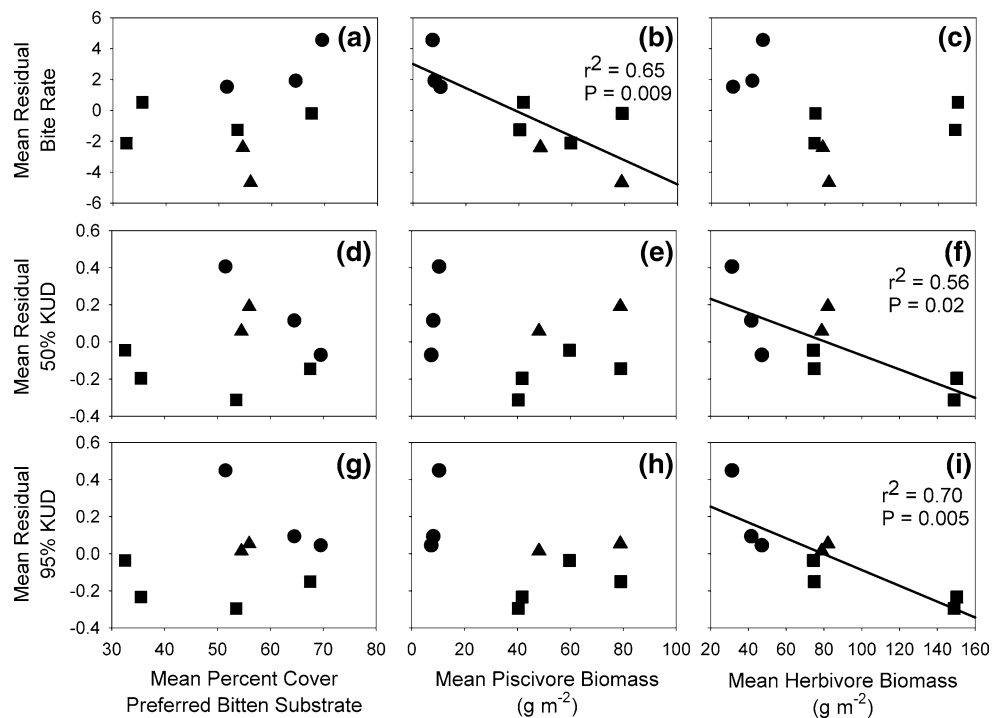
risk may reduce feeding rates for this particular species as well, but less drastically overall. In locations where predators are abundant, there may be adaptive decision-making by prey species in response to high encounter rates, as was shown for cichlids (Ferrari et al. 2010). In high predator environments it would be maladaptive for herbivores to suspend feeding or flee every time a predator is present, especially when those predators may not always impose a threat. Guppies have been shown to be able to differentiate between and alter their responses to hungry versus satiated predators (Licht 1989), and coral reef prey species show variable responses to predators based on predator size, proximity, and body posture (Helfman 1989). Lima and Bednekoff (1999) formulated the Predation Risk Allocation Hypothesis in which they stated that “the need to feed leaves an animal with little choice but to decrease its allocation of antipredator effort to high-risk situations as they become more frequent or lengthy.” They also suggest that studies which present model predators to prey species may overestimate the magnitude of natural responses when the background level of risk is low. Given that prey species have the ability to gauge whether a response is warranted based on cues from the predator and past experience, and the fact that an over-reaction to predator presence is energetically costly, it may be the case that most encounters will not result in a response from the prey species when encounter rates are high. This is consistent with what we observed at Palmyra. However, to perceive predator behavioral cues, prey species may have to be more alert and vigilant where predators are present (Madin et al. 2010b), and this may

**Table 1** Linear model results for **a–c** observation level and **d–f** site level predictors of bite rates and space use for *Chlorurus spilurus* across nine sites at Palmyra Atoll and Mo’orea Island

	Estimate	P value	Relative Importance
<b>(a) Bite rates—observation level predictors</b>			
Time of day	7.0	0.048*	0.225
Chase rate	−3.0	<0.001***	0.775
<b>(b) 95% kernel area—observation level predictors</b>			
Total length	0.039	<0.001***	na
<b>(c) 50% kernel area—observation level predictors</b>			
Total length	0.042	<0.001***	na
<b>(d) Bite rates—site level predictors</b>			
Piscivore biomass	−0.078	0.0087*	na
<b>(e) 95% kernel area—site level predictors</b>			
Herbivore biomass	−0.0049	0.0051**	0.941
% cover food	−0.0047	0.26	0.059
<b>(f) 50% kernel area—site level predictors</b>			
Herbivore Biomass	−0.0038	0.021*	na

Metrics of space use are log transformed. Site level models are created using the site mean of the residual values from the observation level models

**Fig. 3** Univariate plots of the relationships between site-level predictors and foraging behavior metrics. Foraging behavior metrics are represented as the residual value from the models including observation-level predictors. Mo’orea forereef sites are circles, Palmyra forereef sites are triangles, and Palmyra backreef sites are squares. Trend line indicates a significant relationship



account for the differences in feeding rates that we documented across these systems. Tradeoffs between energy acquisition and vigilance in relation to predator abundance, presence, or threat have been documented across many animal groups including reptiles (Cooper 2000), fish (Milinski and Heller 1978), passerine birds (Lendrem 1983), ducks (Pöysä 1987), rodents (Kotler et al. 2010), and primates (Hirsch 2002).

Despite the apparent effects of predator abundance on feeding rates, we found no evidence that predator abundance has any effect on space use by *C. spilurus* across our study sites. With such striking differences in predator biomass between islands, we would predict large differences in space use to result if fishes were limiting their movement in response to risks associated with predators, which has been shown for a variety of small-bodied prey species in the Line Islands (Madin et al. 2010b). While there were significant differences in both the territory sizes and areas of core usage between islands (even when accounting for differences in fish size structure), these differences were best explained by total herbivore biomass, not predator biomass. This indicates that space use by *C. spilurus* may be primarily related to levels of competition from other herbivores in the community. Interspecific interference competition between coral reef herbivores has been shown to be a strong force structuring distributions and habitat partitioning among competitors (Robertson and Gaines 1986). Asymmetrical interspecific competition can also control local abundances and territory positions in strongly territorial damselfish (Robertson 1996). Our results indicate that exploitative interspecific competition also acts to structure space use patterns of individual site-attached grazers. In addition to the partitioning of space between close competitors, our data are suggestive of a high level of resource partitioning within the herbivore community, in that within these highly diverse primary consumer communities the majority of competitive interactions we observed were between a small subset of species. Interestingly, the parrotfish species that our focal individuals directed most competitive chases toward (after intraspecific interactions) was *Chlorurus microrhinos*, a large excavating scarid that preferentially bites red turfing algae (Carlson et al. in revision), the primary resource of *C. spilurus*, which comprises roughly half of bites taken (Hamilton et al. 2014).

Surprisingly, food availability appeared to have only a small effect on territory size. However, there were limitations in our ability to precisely measure resource abundance in this study. For example, standing stocks of algae may not necessarily translate to food availability or nutritional quality, and there are challenges in determining the exact targets of foraging through visual observations of feeding activity due to the complexity of the benthic algal turf and microbial assemblages (Clements et al. 2016). Our recent

work has shown that resource regeneration rates are better predictors of parrotfish space use than standing algal abundances, and in other parrotfish species with more specialized diets we have observed much tighter linkages between preferred food abundance and space use (Carlson et al. in revision). We were not able to measure precise differences in nutritional quality of the benthic resources across sites or islands in this study and it is quite possible that variation in bite rates were effected by differences in nutritional gains that we could not perceive. It is also possible that the generalist diet of *C. spilurus* may make the importance of any particular food source(s) less important for structuring space use at spatial scales of whole territories, though more work is needed to determine precise dietary targets in piscine herbivores. In sunbirds, it has been shown that territorial behavior depends on reproductive status in addition to resource quality and quantity within a territory (Evans 1996). In parrotfish that also exhibit complex social behaviors, it is likely that resource acquisition interacts with social and reproductive behaviors to structure territoriality and space use.

The relationship between space use and competitor abundance indicates that as herbivore biomass increases feeding becomes more concentrated in space. These concentrated areas of feeding may create areas of refuge for coral settlers that have a reduced amount of harmful algae (Smith et al. 2006), potentially facilitating coral recruitment. Alternatively, repeated and concentrated feeding may reduce coral recruitment through incidental removal (Box and Mumby 2007). Both total area used and core area were negatively related to herbivore biomass, so when competition is high, feeding is particularly focused, potentially enhancing the combined effects of concentrated feeding. Future work will focus on the relationships between constrained feeding, temporal trends in grazing site visitation, and coral recruitment.

As reef managers attempt to restore degraded reefs and manage specifically for the resilience of reefs in the face of many global and local stressors, it is critical to understand how the restoration of particular components of fish communities may affect fundamental reef process such as herbivory (Madin et al. 2012). This study indicates that restoration of piscivore communities, as commonly occurs within Marine Protected Areas, may result in some suppression of grazing pressure, but that overall suppression may not be as dramatic as that suggested by some recent studies. Our results also indicate that the spatial patterns of herbivory are strongly linked to competitive dynamics, and that restoration of herbivore populations, such as the parrotfish fishing closures suggested by Jackson et al. (2014), may increase the spatial concentration of feeding in parrotfish. In some cases, this could theoretically enhance coral recruitment and long-term



reef resilience. However, we must be cautious in broadly applying these management strategies without a robust understanding of how they may impact the complex suite of interactions and feedbacks between predator, grazer, and benthic communities.

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**Author contribution statement** KD, PMC, and JEC conceived of and designed the study. All authors performed fieldwork. KD performed analysis and wrote the manuscript. All authors provided editorial advice.

#### Compliance with ethical standards

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

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