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Author
Davis, Kathryn

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An evaluation of the drivers of movement and foraging behaviors of tropical parrotfishes across management regimes and spatiotemporal scales

A thesis submitted in partial satisfaction of the
requirements for the degree Master of Arts
in Ecology, Evolution & Marine Biology

by

Kathryn Davis

Committee in charge:
Dr. Jennifer Caselle, Research Biologist, co-chair
Professor Steven Gaines, co-chair
Professor Christopher Lowe, California State University Long Beach
Professor Douglas McCauley
Professor Robert Warner

March 2016

The thesis of Kathryn Davis is approved.

Robert Warner

Douglas McCauley

Christopher Lowe

Steven Gaines, Committee Co-Chair

Jennifer Caselle, Committee Co-Chair

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ABSTRACT

An evaluation of the drivers of movement and foraging behaviors of tropical parrotfishes across management regimes and spatiotemporal scales

by

Kathryn Davis

There is abundant evidence that herbivorous fishes play an important role in mediating the competitive interactions between corals and algae and that with the reduction or absence of these grazers there may be regime shifts from domination by reef-building corals to non-accreting turfs and fleshy algae. This topic is of particular interest because of the perceived, documented, and projected declines in coral abundances across the tropics and because of the myriad of ecosystem services that healthy coral reefs provide to coastal tropical communities. Parrotfishes in particular appear to be important for promoting coral recruitment, because they scrape away bare patches on the substrate creating suitable settlement habitat for coral larvae. Because of this unique function and its potential to influence long-term coral reef resilience, there have been many appeals from the scientific community for the conservation of parrotfishes.

In terrestrial systems the interactions between the spatial patterns of grazing and the spatial patterns of primary producers have been well explored, but we know less about the fine-scale spatial behaviors of individual coral reef herbivores and how these behaviors influence reef benthic dynamics. There is evidence from spatially explicit models of herbivore foraging behavior that the spatial patterns of feeding by individual herbivores may have a significant impact on the long-term outcomes of coral-algal competition. However, there are multiple drivers that have been identified as influential to the spatial behaviors of parrotfishes and there is no current consensus as to what the primary driver is. In the first chapter of this thesis, we explore the relative influences of competition, predation, and resource abundance on the short-term space use patterns and feeding rates of *Chlorurus sordidus*, an abundant and widespread Pacific parrotfish. We characterized the foraging behaviors of these fish across sites that vary strongly in the presence of piscivorous predators and herbivorous competitors. We found that feeding rates are mainly influenced by direct interference competition and chronic predation risk and that short-term space use is mainly influenced by exploitative competition from the herbivore community. We found little evidence that acute predator presence has any influence on the short-term diurnal foraging behaviors of these fish, even where predators are large, diverse, and abundant. This provides insight into how foraging behaviors may be affected with changing herbivore and piscivore populations, for instance within a Marine Protected Area.

In the second chapter of this thesis we evaluated the movement patterns of *Chlorurus microrhinos*, a large-bodied Pacific parrotfish, across multiple spatial and temporal scales to determine what biological and environmental driver influence space use patterns at each scale. We found evidence for the influences of reproduction and oceanographic conditions, habitat features, predation, resource abundance and competition, however these drivers operated at varying spatial and temporal scales to influence the movement behaviors of these parrotfish. Large-scale movement was driven by oceanographic conditions that influenced the spatial and temporal patterns of reproductive events, as well as night sheltering behavior that was likely related to habitat selection to mediate predation risk. Fine scale movement patterns appeared to be strongly related to resource abundance and competition. We found that measures of movement and the emergent patterns between movement and these drivers depend heavily on the scale of study.

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Chapter 1: Effects of predation risk, competition, and resource abundance on the short-term movement and feeding behaviors of *Chlorurus sordidus*

Introduction

The spatial pattern of grazing by herbivores can have a dramatic influence on the structure of vegetation communities (Sommer 2000, Adler et al. 2001). Spatial interactions between herbivores and vegetation can drive ecosystem dynamics, particularly in the context of primary producer competition (Palmer et al. 2005). Heterogeneity of grazing intensity can arise from variable distributions of grazers across habitats (Hay 1981, Hoey and Bellwood 2007) but at finer scales, heterogeneity can arise from foraging behaviors and decision-making by individual herbivores (Parsons and Dumont 2003). The long-term effects of heterogeneous grazing have been modeled in a variety of systems and are shown to have a significant influence in projected primary producer community structure (Weber et al. 1998, Palmer et al. 2005). In particular, models indicate that the nature of the spatial pattern of grazing by coral reef herbivores can have a major impact on the long-term outcomes of interactions between corals and macroalgae on coral reefs (Sandin and McNamara 2012, Eynaud et al. in review).

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. Herbivorous fishes have been identified as important mediators in the competition between corals and algae, determined with small-scale field experiments (Carpenter 1986, Lewis 1986, Hixon and Brostoff 1996, Lirman 2001, Smith et al. 2001, Smith et al. 2010, Thacker et al. 2014) as well as large-scale relationships between fish communities and benthic assemblages (Williams and Polunin

2001, Mumby et al. 2006, Jackson et al. 2014). In addition to removing algae that compete directly with adult corals, some herbivorous parrotfishes in particular provide an additional unique function in the manner in which they scrape algae from the reef, leaving behind bare spaces and small divots in the calcium carbonate substrate (Bellwood and Choat 1990). This mode of feeding has been positively related to rates of coral recruitment (Brock 1979, Mumby et al. 2007).

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. They suggested that the outcome of coral-algal competition is significantly influenced by the level of heterogeneity in grazing. Concentrated feeding by herbivores favored coral-dominated reef while scattered and homogenous feeding favored algal domination. Mechanistically, this is because constrained grazing creates pockets of space where a coral settler may have refuge from encroaching algae for a period long enough for it to become resistant to displacement by algae. In light of the potentially significant impact of spatial foraging behaviors of grazers on coral reef benthic dynamics, it is important to explore the potential drivers of variation in space use by coral reef herbivores.

Many factors have been shown to influence the extent and distribution of foraging space use by herbivores, including resource availability, predation risk, as well as social behaviors and intra- and interspecific competition (Adler et al. 2001). Often, studies of space use and foraging patterns focus on a single driver (e.g., predation risk only) without incorporating the potential for combined effects of multiple drivers or the possibility of covariation among them (e.g., predation risk and competition might covary because both predators and herbivores are harvested in some locations, or avoiding predation may increase competition in less risky areas). 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), we need a complete understanding of the various drivers of 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 in parrotfishes (van Rooij et al. 1996, Mumby and Wabnitz 2002). Additionally, many studies show how natural variability and experimental manipulation of resource abundance (i.e., food) and growth rates affect animal movement behavior and territory size (Stenger 1958, Stimson 1973, Seastedt and MacLean 1979, Kruuk and Parish 1981). Herbivorous fishes on coral reefs demonstrate the capability to adjust to spatial variation in local resource abundance and assemble around algal resources, resulting in positive relationships between herbivore biomass and algal abundance (Russ et al. 2015, Tootell and Steele 2015, Carlson et al. in prep). Ebersole (1980) proposes that most territorial animals are "food-maximizers" that guard territories that house food in excess of their metabolic needs in order to use surplus for reproductive fitness gains, increased survivorship, or selective size advantage. In this case, optimizing territory size requires balancing per-area benefit of increased food with costs of territorial defense.

In contrast to bottom-up, resource competition-driven models of animal foraging behavior, in recent years the “landscape of fear” concept has gained substantial traction in both marine and terrestrial literature. The assumptions of this model are that there is spatial and temporal heterogeneity in predation risk that is perceptible to prey species who in turn alter their foraging behaviors to decrease risk (Laundré et al. 2010). These modifications of foraging activities may result in behaviorally mediated trophic cascades with significant effects on the primary producer communities. In the classic example, the reintroduction of wolves into Yellowstone National Park resulted in shifting foraging behavior of elk from open habitats to safer wooded habitats (Hernández and Laundré 2005). While wolves were absent, the recruitment of aspen trees in open areas was virtually nonexistent due to herbivory by elk, and upon reintroduction of the wolves the aspen stands have reestablished. Increased recruitment and survival of aspen trees is attributed to these shifts in elk foraging behaviors as a response to spatial variation in predation risk (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 (Heithaus et al. 2007, Wirsing et al. 2008), with measured effects on seagrass community structure (Burkholder et al. 2013). However, in the turtle study (Heithaus et al. 2007) there is an evident trade-off between resource acquisition and risk. Avoidance of preferred-food habitat is dependent on the energetic condition of the turtle: when energy demands are high enough the animal risks exposure to the predator to acquire high quality food resources. In the context of coral reef herbivorous fish foraging patterns, research demonstrates relationships between movement extent of the grazer and both acute effects of predator presence as well as chronic effects measured by predator abundance (Madin et al. 2010a, Madin et al. 2010b). These patterns sometimes resulted 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). In addition to altering the spatial distribution of foraging, the acute effect of predator presence may also substantially reduce rates of foraging by coral reef herbivores (Rizzari et al. 2014, Catano et al. 2016).

As in the case of the elk in Yellowstone, the nature of the spatial patterning of herbivory can have major effects on the vegetation communities in a number of different systems (Olff and Ritchie 1998, Fine et al. 2004, Bagchi et al. 2006, Madin et al. 2011). While there is a large body of evidence indicating varied effects of resource abundance, competition, and predation risk on structuring reef herbivore space use, most studies address only single factors (except see Nash et al. 2012). The relative, additive, and interactive effects of these factors remain unclear. When addressed simultaneously in vervet monkeys, Willems and Hill (2009) showed that both resource acquisition and predation risk structure space use in South African forests. It is likely that there may be combined effects in reef herbivores as well. On the Great Barrier Reef, Nash et al. (2012) showed that habitat characteristics and competitor abundance best explained some spatial metrics of parrotfish foraging, 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 predation risk and competition on structuring space use, it is necessary to compare responses across a gradient of both drivers.

In order to evaluate the relative importance of food resource abundance, competition, and predation risk on structuring foraging behaviors of a coral reef grazer we conducted a comparative study at two islands that are subject to drastically different management regimes. One of the islands is essentially pristine and unfished, with high biomass of herbivores and predators, while at the other both trophic groups are fished. We measured two components of foraging behavior, feeding rate and size of feeding territory, for individual parrotfish across multiple sites at both islands. Sithin 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 explore their relationships with the two metrics of foraging behaviors. Working with a baseline of an undisturbed population allows us to assess the potential impact of fishing on the foraging behaviors of these potentially important herbivores.

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 has been 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, hosting a small number of researchers and island staff. There is no extractive fishing at Palmyra except limited offshore fishing for pelagic species (e.g. tuna, wahoo). 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 human-impacted reefs. The atoll consists of three large lagoons flanked by long, gradually-sloping reef terraces that extend to the east and west. We conducted this study at two sites on the forereef, and four sites across the backreef and shallow western terrace (Figure 1) 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), which unlike Palmyra has high levels of subsistence and small-scale commercial fishing activity (Walker and Robinson 2009, Leenhardt et al. 2012). Both piscivores and herbivores are fished in Mo'orea (Figure 2). Mo'orea 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 (e.g. fishes are very wary, and shallow depths place researchers too close to fish subjects, potentially affecting behavior). Thus we conducted our observations on the forereef habitat, which was similar to forereefs at Palmyra and where we could follow fish from an appropriate distance in order to affect their behavior minimally. We conducted observations at three sites on the north and western shores of Mo'orea (Figure 1) in May of 2015.

Study species

Chlorurus sordidus (classified in some references as *C. spilurus*) is a protogynous hermaphroditic small-bodied member of the family Scaridae (maximum size to 37 cm) and is one of the most abundant and widespread parrotfish in the tropical Pacific. There are two color phases present in the species: terminal phase (TP) males are green with pink or orange markings, usually with a lighter patch of green or tan on the caudal peduncle, and initial phase (IP) individuals are dark colored with some reddish markings on the head and light spots that appear on the body. IP individuals can be male or female. The larger (TP) males can be derived from (IP) primary males or a result of sex change from an IP female (Munday et al. 2004). The prevalence of IP males has been demonstrated to vary across habitats, and range from 4-12% of the population (Gust 2004). Though the social system of this species is not fully described, Gust (2004) observed that on the Great Barrier Reef, *C. sordidus* "displays loose groupings of IP fish in feeding schools attended by TP males that often interact aggressively". This description is consistent with our own observations of the social behaviors of these fish at our study sites, where TP individuals defend territories against other TP individuals while tolerating IP individuals, supposedly females. Occasionally, we observed some aggressive behavior by TP males toward larger IP individuals, supposedly males. Gust (2004) suggests that there can be plasticity in the social and mating systems over relatively small (10's of kilometers) spatial scales and that either pair or group spawning may be employed at frequencies dictated by local conditions. This is also consistent with our own observations at Palmyra because we witnessed both pair spawning (infrequent) in territories and group spawning (frequent); the latter appears to be confined to specific habitats (i.e. forereef and high-flow areas of the deeper reef terrace). Sancho et al. (2000) reported primarily group spawning with some pair spawning activity by *C. sordidus* at Johnston Atoll that peaked in the afternoon and was also related to current direction and tidal height. They suggest that spawning activity is not related directly to tidal height but to the influence of tidal movement on outgoing currents.

Chlorurus sordidus was the most numerically abundant species of parrotfish at both study islands and was present in both the forereef and backreef habitats. After an ontogenetic shift from omnivory at around 2 cm, *C. sordidus* are herbivores that primarily scrape algal material from dead coral. Hamilton et al. (2014) showed that in Palmyra, *C. sordidus* selectively target mixed algal turfs as their primary food source but that roughly half of their diet consists of an assortment of macroalgal species and a small amount of live coral. They classify *C. sordidus* as diet generalists, which likely explains their abundance and ubiquity across habitats. They must continuously feed throughout the day to maximize the nutrition gained from a low quality algal food source (Chen 2002). Bellwood (1995) estimated that they spend on average 83.6-91.0% of daylight hours feeding, and that each individual is responsible for 23.6±3.4 (SE) kg of bioerosion every year. Due to the non-linear relationship between fish body size and bite size (Lokrantz et al. 2008), larger individuals are especially effective at scraping the substrata. Because fishing efforts usually target the largest size classes of a population, this important ecosystem function may be especially vulnerable to the effects of fishing. However, because of smaller size and rapid growth, *C. sordidus* populations are relatively insensitive to fishing pressure relative to large bodied and slow maturing parrotfishes (Clua and Legendre 2008).

We observed two different foraging modes by individual *C. sordidus* at Palmyra. Some fish fed in small territories while others foraged in roving schools mostly composed of IP individuals. Dual foraging modes have also been recorded in other scarids (Welsh and Bellwood 2012). It is important to note that in this study we characterize only the spatial patterns of foraging by site-attached individuals of *C. sordidus* (i.e., ‘short-term foraging territories’) and do not attempt to estimate average home range size across the population, since we did not track fish to spawning grounds or sleeping sites, nor did we track fish associated with large roving schools.

Behavioral Observations

Behavioral observations of *C. sordidus* consisted of a SCUBA diver (forereef) or snorkeler (backreef/reef terrace) towing a surface floated GPS unit logging a position every fifteen seconds. 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 diver proximity. At both islands, prior to commencing data collections, we made several observations from varying distances from focal fish to gauge an appropriate distance from where there was no apparent disruption of normal feeding and movement activities. During 20 minute focal follows observers recorded: a) number of bites, and b) all inter- and intraspecific interactions including competitive chases, cleanings (our focal fish were cleaned predominantly by the cleaner wrasses *Labroides dimidiatus* and *L. rubrolabiatus*), territorial displays, and predator responses, in all cases noting the direction of the interaction (i.e., focal fish chased/focal fish was chased). Bites were later aggregated into five-minute bins and expressed as a rate (number of bites per min). Sample sizes are as follows: at Palmyra n=169 individual observations across four backreef sites and two forereef sites and at Mo’orea n=95 observations across three forereef sites, with roughly thirty observations per site. For each observation we estimated the total length of the focal individual and recorded its color phase as well of the time of day that the observation started. All observations were conducted between the hours of

08:00 and 17:00. Across the observations we attempted to observe sizes and color phases of focal individuals in proportion to the distributions observed at the sites, and were careful not to re-sample any individual fish.

Fish Community Surveys

In order to characterize the diurnal fish community assemblage (particularly predator and competitor abundance) at each site we conducted fish surveys using a belt transect method (n=9 transects per site). Divers swam out a 25 m transect line recording identity (to species), number, and the total length of each fish longer than 20 cm in a 4x25 m swath that extended to the surface (see Friedlander et al. 2016). Upon completion of the first 25 m swath, the diver swam back along the same transect and counted all fish less than 20 cm total length in a 2x25 m swath extending to the surface. We later assigned fishes to broad trophic categories and converted total length to biomass using trophic classifications and length-weight conversion compiled by the NOAA Coral Reef Ecosystem Division (CRED) from FishBase. For the Mo'orea sites we utilized fish community data from the Mo'orea Coral Reef Long-Term Ecological Research (LTER) program collected in the summer of 2014 (Brooks and LTER 2015). The LTER transect configuration differed from what we conducted in Palmyra (5x50 m transect for mobile taxa, 1x50 m along the same transect for cryptic and non-mobile taxa, n = 4 transects per site) so we converted all count data to biomass-density using the area surveyed and the length-weight parameters.

Benthic Surveys

In order to estimate the site-level abundances of the preferred food types of *C. sordidus,* we conducted benthic community surveys using uniform point contact (UPC) methodology. At each meter along eight, parallel, 25 m transect lines placed randomly throughout each site we recorded the identity of the space-holding organism living beneath the point. We then aggregated the four categories that made up the majority of *C. sordidus* diet from Hamilton et al. (2014) (mixed algal turfs, crustose coralline algae, *Lobophora*, and *Halimeda*) into a site-level average of percent cover of major food types. We defined algal turfs as any low-lying filamentous algae less than 2 cm in height.

Data Analysis

Kernel calculations

We computed kernel area metrics from all GPS tracks using the biased random bridge method using the "adehabitatHR" package in R (Calenge 2006). Improving on the traditionally used location-based distribution kernels calculated from density of point positions, bridge methods incorporate a temporal component to interpolate between successive relocations to create a movement-based utilization distribution (Figure 3). The application of the relocation history allows for the computation of utilization distributions from serially correlated raw tracking data. The biased random (advective-diffusive) bridge method allows for home-ranging behavior and habitat patch selection by the tracked animal, unlike the (purely diffusive) Brownian Bridge method (Benhamou 2011).

Commonly used metrics describing animal space use are the 50% and 95% utilization kernels. For example, a 50% kernel area encompass the smallest area in which the probability of locating the animal is 50%. In telemetry studies, 95% kernels are sometimes used to characterize home ranges or territories and 50% kernels are often used to characterize areas of core use within a home range or territory (Meyer and Holland 2005, Welsh and Bellwood 2011, La Mesa et al. 2012). Kernel estimation is highly sensitive to the bandwidth used for the smoothing parameter (Gitzen et al. 2006) as well as tracking techniques (Walter et al. 2015). Therefore the best application of kernel area estimates is for making comparisons within a study, using consistent data collection techniques and model parameterization. For this study we use the 95% kernel to approximate territory size and the 50% kernel to approximate areas of core use within the territory. To test whether the 20 min trial duration was sufficient to approximate territory size we truncated each trial (Palmyra only) to successive five min intervals and plotted the 95% kernel area against trial duration (Figure 4). Site-level boxplots as well as accumulation curves for individual trials showed that the kernel area levels off by 20 min indicating that these trial lengths were sufficient in capturing the short-term territory sizes of these fish. Two other observations led us to believe that 20 min was adequate: 1) Focal fish would swim repeated patterns, returning to a few specific food patches within the areas while we followed them; 2) Over the course of the trials, the TP individuals usually encountered other TP individuals 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 the short-term movement patterns (Mumby and Wabnitz 2002, Howard et al. 2013).

Foraging Behavior Models

We decomposed foraging behavior into two components, measured for every observation: feeding rates (bites/min) and space use (50 and 95% utilization kernels). We also calculated or measured the following predictors: competitive chase rate (chases/min), time of day, focal fish total length, and focal fish color phase. 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 used the residuals from these linear models to create a site mean for each response parameter to model relationships with the site-level predictors of piscivore biomass, herbivore biomass, and food abundance. Again best-fit models were selected using stepwise model selection and AIC. For each multi-term linear model we calculated the relative importance of each term using the "lmg" method of 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 ensure that the direction of the relationships within islands are consistent with the results found across islands.

To compare differences between islands in fish and benthic community composition, species interactions, and foraging behavior metrics we used Welch's two sample t-tests to test for differences in bite rate, 50% and 95% kernel area, piscivore biomass, herbivore biomass, food abundance, and chase rates. Space use metrics (kernel areas) were log transformed for all analyses to satisfy assumptions of normality. We performed all tests in R (R. Core Team 2014).

Results

Community Composition

There were large differences in the predator communities between islands. Mean piscivore biomass was almost 7 times greater at Palmyra compared to Mo'orea (Figure 5; Palmyra: 58.6 g/m^2 ± 8.7 SE; Mo'orea: 8.7 g/m^2 ± 2.3 SE; $t = -5.56$, $df = 79.02$, $p < 0.001$). There was variation in predator identity as well as abundance. At Palmyra sites the piscivore biomass is dominated by members of the families Lutjanidae, Carcharhinidae, Serranidae, and large bodied species of Carangidae. The piscivore biomass at survey sites in Mo'orea was dominated by members of Serranidae, Lethrinidae, and small bodied species of Carangidae. We did observe abundant sharks and snappers in Mo'orea at sites dived by tourism operations where provisioning is a common practice. This indicates that the differences are not strictly due to biogeography. Mean herbivore biomass was over 2.5 times greater at Palmyra compared to Mo'orea (Figure 5; Palmyra: 104.4 g/m^2 ± 6.4 SE; Mo'orea: 40.0 g/m^2 ± 5.5 SE; $t = -7.65$, $df = 47.98$, $p < 0.001$). However, the herbivore communities were similar at both islands, tending to be dominated by Scaridae and 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 (Mo'orea: 61.8% ± 3.2 SE; Palmyra: 50.3% ± 2.1 SE; $t = 2.99$, $df = 44.28$, $p = 0.0045$).

Inspection of size frequency distributions of *C. sordidus* from forereef sites at Palmyra and Mo'orea showed that the largest size classes of individuals were present in Palmyra but absent from Mo'orea (Figure 6). We observed fishing of large, TP *C. sordidus* by local fishermen (Figure 2).

Species Interactions

Competitive chase rates (number of times per minute that the focal individual interrupted feeding due to a chase by another fish) were roughly 3.5 times higher in Palmyra than in Mo'orea on average (Palmyra: 0.52 chases/min ± 0.028 SE; Mo'orea: 0.15 chases/min ± 0.018 SE; $t = -11.14$, $df = 253.47$, $p < 0.001$). In total, we observed more than 2000 competitive chases directed towards the focal individuals over the duration of the study at both islands. The families of the individuals involved in most chases were

Acanthuridae, Pomacentridae, and Scaridae (Table 1). The group primarily responsible for the large island differences in chase rate were the territorial acanthurids, 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 pomacentrids and other scarids did not vary as strongly between islands. The majority of scarid interactions were with other *C. sordidus,* with larger individuals usually 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 (when the focal individual interrupted feeding to move out of the way of an approaching predator) were extremely rare. Over the course of 264 observations (88 hours) 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 serranids, while in Palmyra responses were elicited by members of Lutjanidae (n = 4), Carangidae (n = 3), Serranidae (n = 2), Lethrinidae (n = 1), Muraenidae (n = 1), and Carcharhinidae (n = 1). We never observed an actual predation attempt on our focal individuals.

Foraging Behavior Metrics

Mean 50% and 95% kernel areas for all observations were 39.5 m^2 ± 2.0 SE and 184.8 m^2 ± 9.3 SE respectively. The average ratio of the 50% kernel area to the 95% kernel area was 22.6% ± 0.34 SE. Mean bite rate for all observations was 16.1 bites/minute (± 0.3 SE). Bite rates were higher in Mo'orea than in Palmyra (Figure 7; Mo'orea: 19.1 bites/min ± 0.6 SE; Palmyra: 14.4 bites/min ± 0.3 SE; $t = 7.12$, $df = 154.12$, $p < 0.001$). Log transformed 50% kernel areas were larger in Mo'orea than in Palmyra (Figure 7; Mo'orea:

3.7 ± 0.07 SE; Palmyra: 3.3 ± 0.05; $t = 4.36$, $df = 174.25$, $p < 0.001$), as were log transformed 95% kernel areas (Mo'orea: 5.24 ± 0.07 SE; Palmyra: 4.8 ± 0.05 SE; $t = 5.15$, $df = 180.45$, $p < 0.001$). Size structure of the populations varied by island and habitat, but the between-island differences in transformed 50% and 95% kernel areas were still significant when we adjusted the kernels for individual body size ($t = 2.90$, $df = 164.15$, $p = 0.0042$; $t = 3.80$, $df = 173.29$, $p < 0.001$ respectively).

Foraging Behavior Models

We tested the effects of observation-level predictors on both bite rates and area used in separate linear models. Variation in bite rate was best explained by models incorporating focal individual total length, color phase, time of day, chase rate, and the interaction between total length and color phase (Table 2). In this best fit model (AIC = 866.06), chase rate accounted for the majority (71%) of the explanatory power of the model, followed by time of day (12%). Observation-level variation in metrics of space use, territory size (Table 3), and core area (Table 4) were explained only by focal individual total length (AIC = -232.38 and -246.96 respectively).

We then tested the effects of site-level predictors (piscivore biomass, herbivore biomass, food abundance) on both bite rates and area used, using the residuals of the observation-level models described above. Site level variation in mean residual bite rate was best explained by a model incorporating piscivore biomass and food abundance (Table 5). In this model (AIC = 9.5), piscivore biomass accounted for the majority (82%) of the explanatory power (Figure 8). Site level variation in territory size was best explained by a model incorporating herbivore biomass and food abundance (AIC = -35.37, Table 6), with herbivore biomass accounting for almost all (94%) of the explanatory power (Figure 9).

Site level variation in core use area was explained only by herbivore biomass (AIC = -31.75, Table 7, Figure 10).

Finally, we modeled the within-island relationships for the site-level parameters that best explained variation for each foraging behavior metric: predator biomass vs. bite rate and herbivore biomass vs. area used. In all cases, the direction of the relationships were consistent with what was demonstrated in the models that included all sites across both islands. In some cases, the relationships remained significant and in some the within-island relationships were no longer significant (Figure 11), likely because the within-island analysis reduced sample sizes as well as variation across sites compared to the analysis that included all sites across both islands.

Discussion

Both predation risk and competition for resources appear to play a role in structuring foraging behaviors in the herbivorous parrotfish *Chlorurus sordidus*. However, they appear to play different roles in affecting various aspects of behavior. Feeding rates were affected primarily by direct interference competition and chronic level of predation risk, the latter measured by site level biomass of predators.

We hypothesize that the negative relationship between feeding rates and predator abundance found here is due 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 conclusion. First, we recorded extremely low rates of acute responses to predators by focal fish in behavioral observations (16 responses in 88 hours of observation), 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 the presence of actively swimming jacks (Carangidae) which frequently elicit strong responses from smaller fishes.

We acknowledge that predators may elicit strong behavioral responses from prey species at times of day when we were not conducting observations (i.e., crepuscular 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). Note that our results on the influence of predators on foraging rates were quite different from recent studies of coral reef fishes, which suggested up to 90% reductions in herbivory in the presence of model predators (Rizzari et al. 2014, Catano et al. 2016). Our results showed that at Mo'orea sites, where all predators are scarce and predators at a size large enough to pose a threat to a small parrotfish are virtually absent, average bite rates were 24% higher than in Palmyra, where large predators are abundant. After correcting for differences in individual observation-level factors (focal size, color phase, and chase rates) this difference was even smaller (19%). While this difference is non-trivial when extrapolated across larger time scales and populations, it was a much smaller decrease in grazing intensity compared to the model-based studies cited above. One potential explanation for the strong difference in results may be adaptive decision-making in response to frequent predator encounters at

Palmyra, as was shown in Costa Rican cichlids (Ferrari et al. 2010). In high predator environments it would be maladaptive for herbivores to halt feeding or flee every time a predator is present, especially when those predators may not always impose a threat. In fact, 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). Reef fishes react more strongly to humans in fished areas versus unfished areas where humans do not pose a threat (Gotanda et al. 2009, Januchowski-Hartley et al. 2012). 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. This effect of model predators could be exacerbated because models do not convey the same information as natural predators. 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 likely 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 ('chronic risk', Madin et al. 2010b), and this may 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 (Barnard 1980, 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. sordidus*. With such a 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 as shown for multiple species in Madin et al. (2010b). While there were significant differences in both the territory sizes and areas of core usage between islands (even when accounting differences in fish size structure) these differences were best explained by total herbivore biomass, not predator biomass. This indicates that space use by *C. sordidus* may be primarily related to levels of competition from other herbivores in the community, particularly large-bodied herbivores, because they contribute disproportionately to total biomass as well as total algal removal. 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.

Food availability appeared to have a small effect on bite rate and territory size. Further partitioning of benthic cover into the single primary preferred food (mixed algal turfs) produced similar results. Some studies have shown that algal growth rates are better predictors of parrotfish space use than algal abundances (Tootell and Steele 2015, Carlson et al. in prep), and in parrotfish species with more specialized diets we have observed much tighter linkages between preferred food abundance and space use (Carlson et al. in prep, Davis et al. in prep). However, it is possible that the generalist diet of *C. sordidus* may make the importance of any particular food source(s) less important for structuring space use at spatial scales of whole territories. 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 exhibit complex social behaviors, it is possible that resource acquisition could interact with social and/or reproductive behaviors to structure territoriality and space use.

At both islands we observed concentrated feeding within a few small patches compared with the whole area traversed. This was true for both TP and IP individuals and was similar between islands. This result of concentrated activity within a small portion of total space used is consistent with results of other studies on parrotfish (e.g. Welsh and Bellwood 2011). These concentrated areas of feeding may create areas of refuge for coral settlers that have a temporarily reduced amount of harmful algae (Smith et al. 2006), potentially facilitating coral recruitment. Both total area used and core area were negatively related to herbivore biomass, so when competition is high, feeding is particularly focused, potentially enhancing this coral settlement refuge effect.

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 rates of herbivory but that suppression may not be as dramatic as that suggested by model predator studies. Additionally, the suppression of rates of herbivory resulting from increases in piscivore abundance and size may be at least partially offset by the restoration of herbivore population size structures because large individuals remove more algae per bite than small individuals. Our results also indicate that the spatial patterns of herbivory are strongly linked to competitive dynamics, and that restoration of entire herbivore populations, such as suggested parrotfish fishing closures (Jackson et al. 2014), may increase the spatial concentration of feeding in parrotfish, coral recruitment, and long-term reef resilience. As management actions for coral reefs become more precise (e.g. managing specific trophic groups), a better understanding of the complex ecological relationships within coral reef communities will be required.

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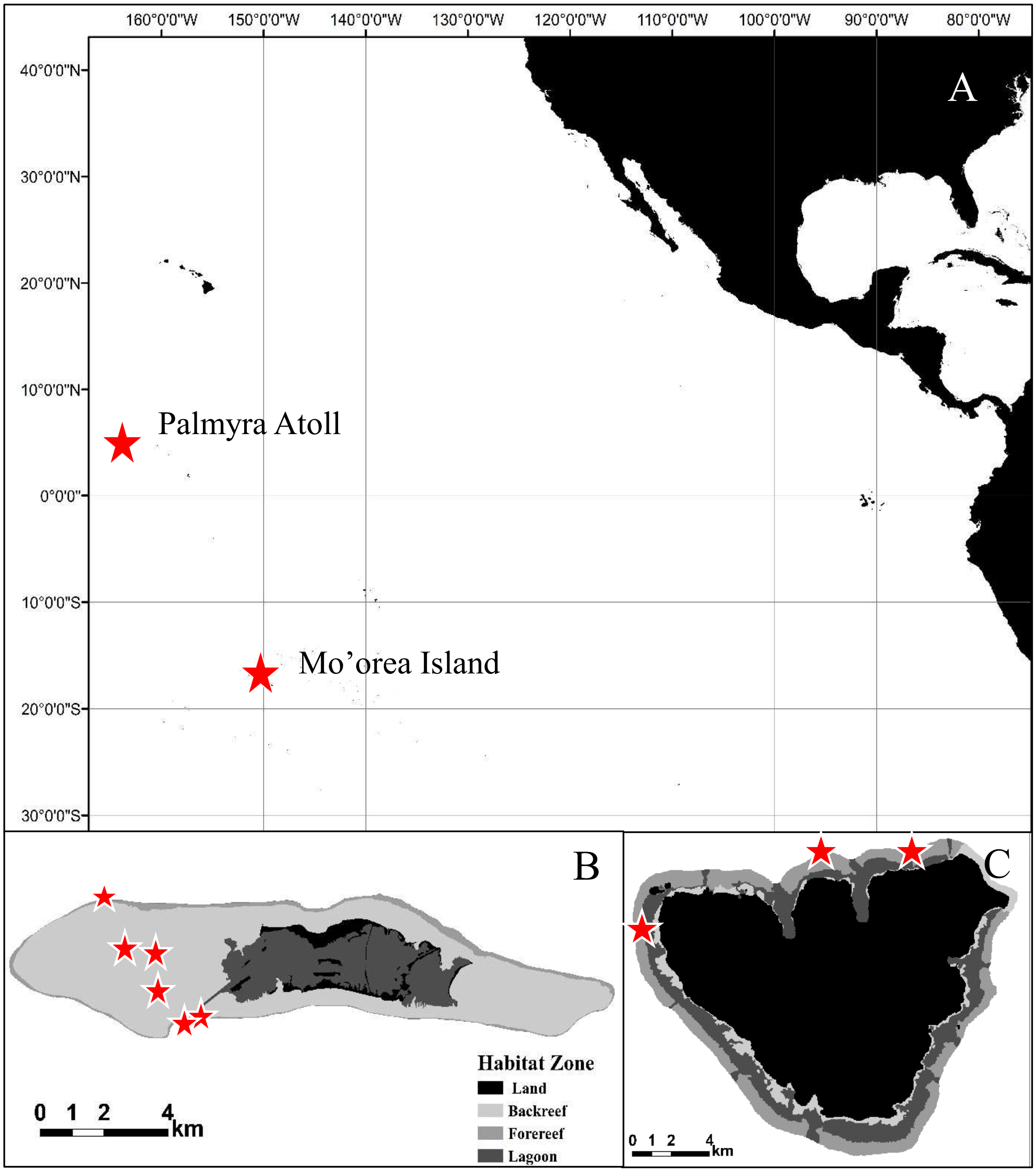

Figure 1: Map of the study sites. (A) Location of the islands in the tropical Pacific Ocean. Locations of the study sites at Palmyra Atoll (B) and Mo'orea Island (C).

Figure 2: Photos of the reef fish catch of local commercial spearfishermen in Mo’orea. (A) A container full of fish that were speared from a boat near one of our study sites. (B) Fish for sale on the roadside in Mo’orea. (C) Two terminal phase *Chlorurus sordidus* on display for sale.

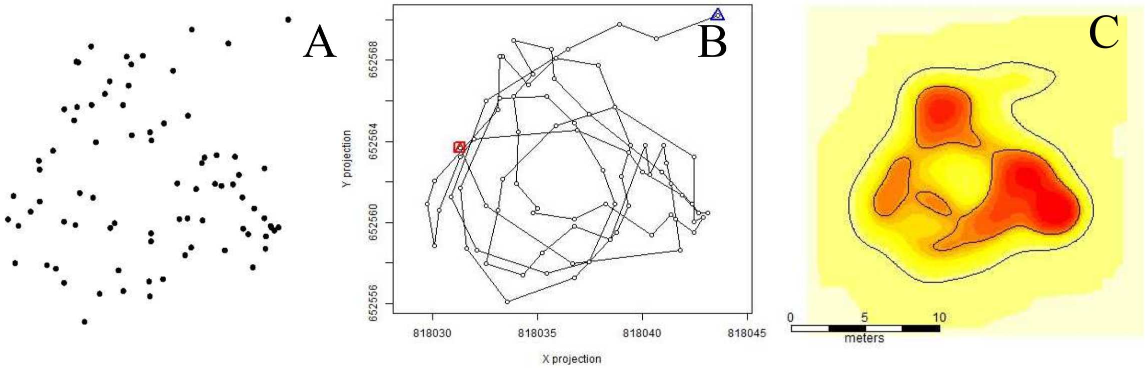

Figure 3: Example of Biased Random Bridge kernel estimation method for one 20 min track of a single individual *C. sordidus*. (A) Raw point positions for a 20-min track. (B) Trajectory created from the raw time-stamped points. Location data are projected meters using Universal Traverse Mercator. (C) Smoothed utilization distribution kernel with 95% and 50% contours outlined in black. Areas of highest intensity use (50% kernel) are depicted in redder colors.

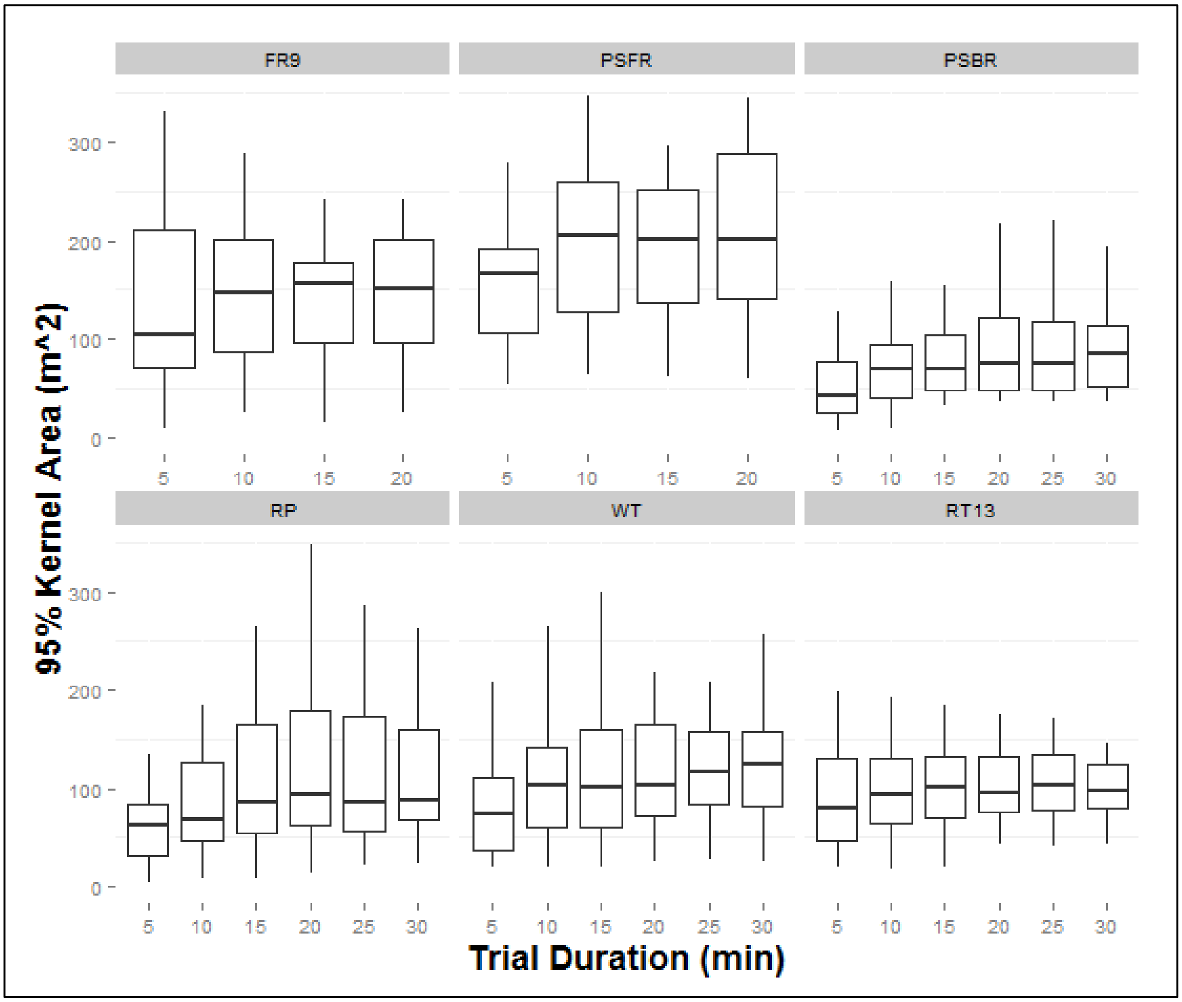

Figure 4: Boxplot showing area accumulation for observations truncated to 5, 10, 15, 20, 25, and 30 min. Generally areas do not increase significantly after 15 min. Research site codes are as follows: FR9 = Forereef 9, PSFR = Penguin Spit Forereef, PSBR = Penguin Spit Backreef, RP = Rubblepile, WT = Western Terrace, RT13 = Reef Terrace 13. Hinges show the first and third quartiles, whiskers extends from the hinge to the highest value that is within 1.5 * IQR.

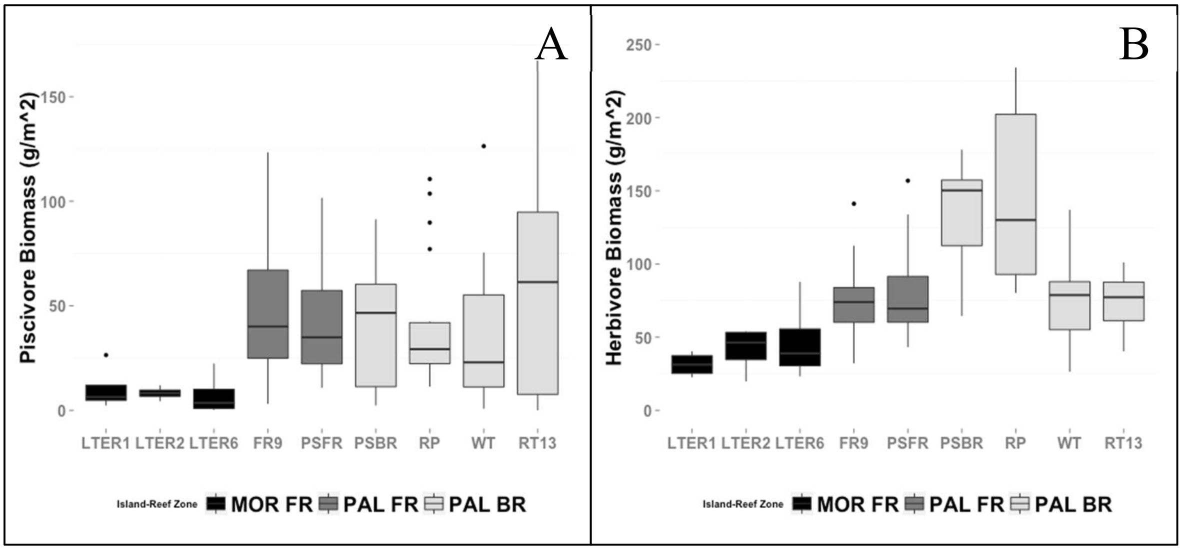

Figure 5: Piscivore (A) and herbivore (B) biomass densities (g/m^2) on Mo'orea forereef sites (black), Palmyra forereef sites (dark grey), and Palmyra backreef/reef terrace sites (light grey). Data are calculated from belt transect surveys. Hinges show the first and third quartiles, whiskers extends from the hinge to the highest value that is within 1.5 * IQR. See Figure 4 for site names.

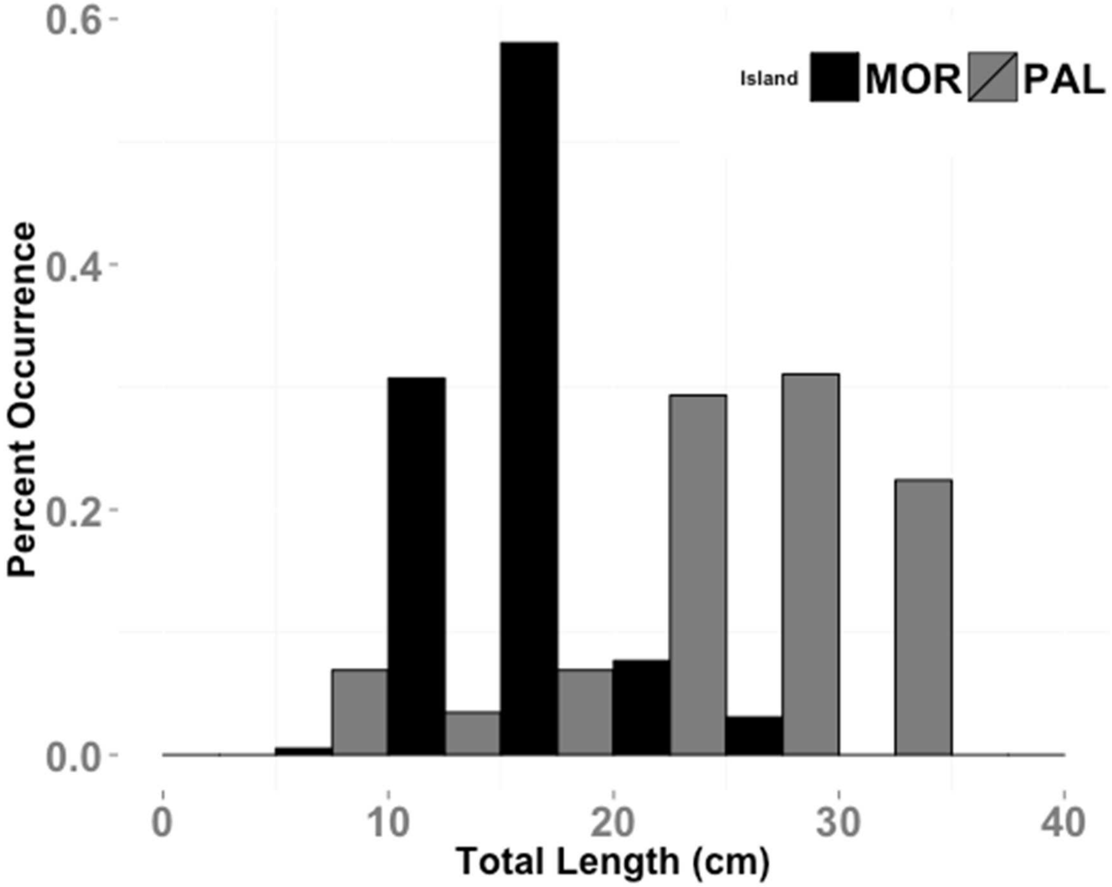

Figure 6: Length frequency distributions of *C. sordidus* from forereef sites at Mo'orea and Palmyra. The largest size classes that are represented in Palmyra (>30 cm) are absent from Mo'orea sites.

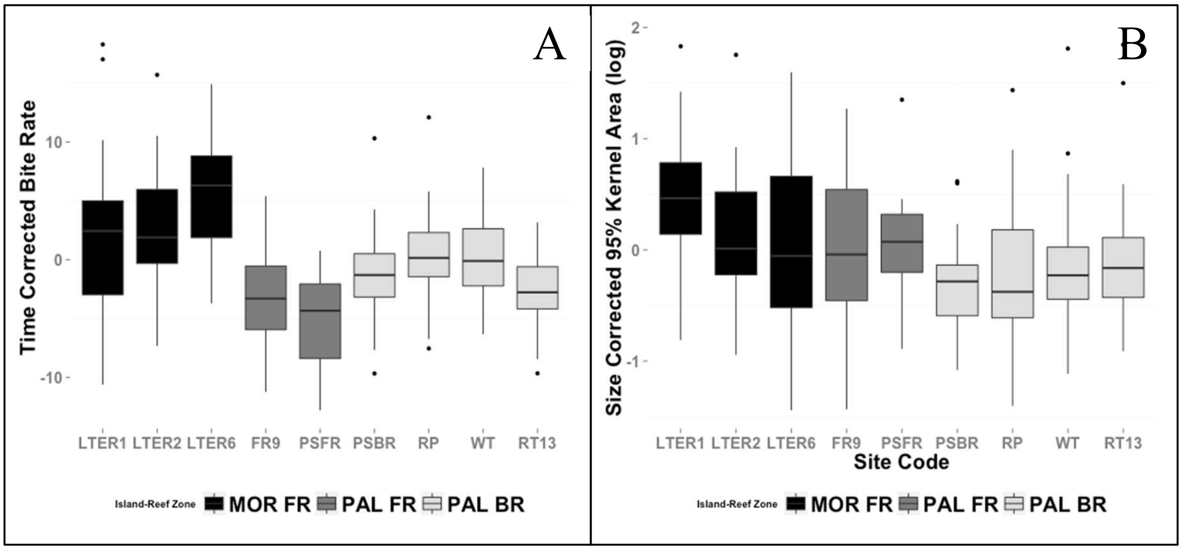

Figure 7: Bite rates (A) and transformed 50% kernel areas (B) across all study sites. Mo'orea forereef sites are in black, Palmyra forereef sites are in dark grey, and Palmyra backreef/reef terrace sites are in light grey. Bite rates are corrected for time of day (residuals: bite rate ~ time of day). Kernel areas are corrected for focal total length (residuals: log 50% kernel area ~ focal total length). Hinges show the first and third quartiles, whiskers extends from the hinge to the highest value that is within 1.5 * IQR. See Figure 4 for site names.

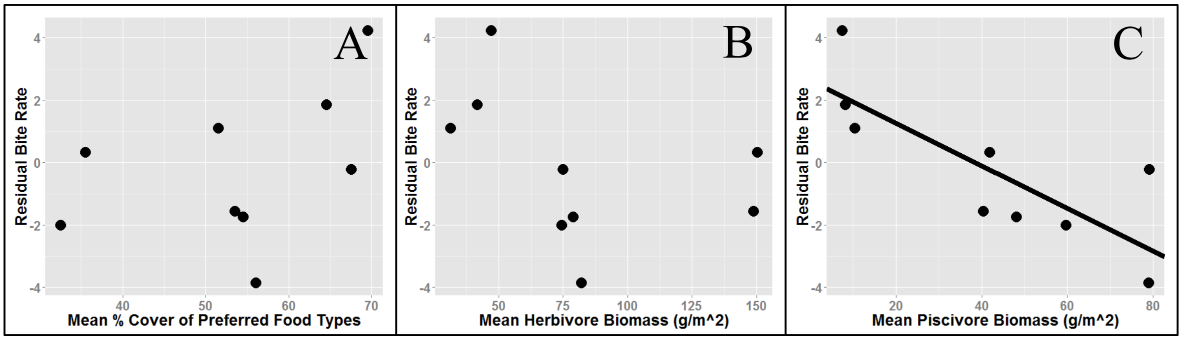

Figure 8: Individual relationships of site-level predictors (A) percent cover food, (B) herbivore biomass and (C) piscivore biomass with mean residual site bite rates across all sites. Trend line indicates a significant relationship. See Table 5 for combined model results.

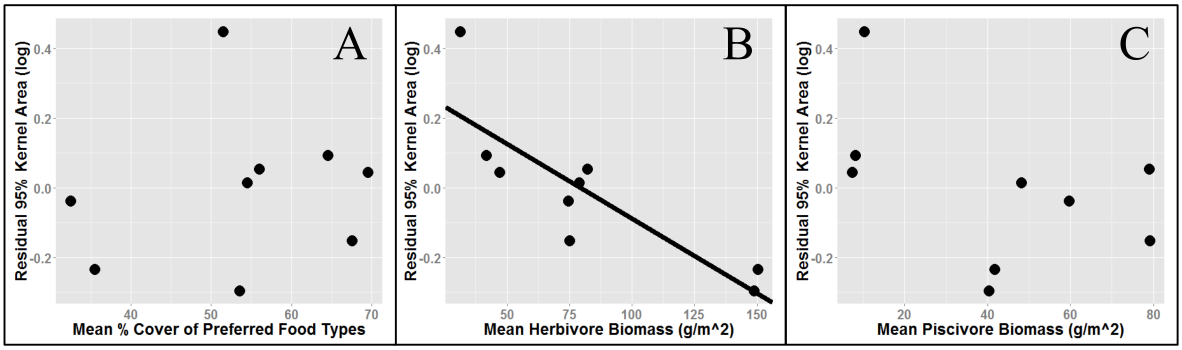

Figure 9: Individual relationships of site-level predictors (A) percent cover food, (B) herbivore biomass and (C) piscivore biomass with mean residual 95% kernel area (log) across all sites. Trend line indicates a significant relationship. See Table 6 for combined model results.

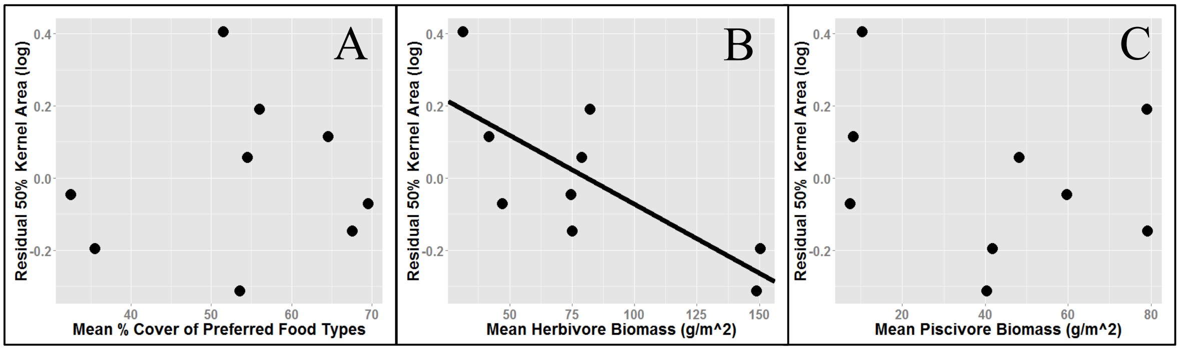

Figure 10: Individual relationships of site-level predictors (A) percent cover food, (B) herbivore biomass and (C) piscivore biomass with mean residual 50% kernel area (log) across all sites. Trend line indicates a significant relationship. See Table 7 for combined model results.

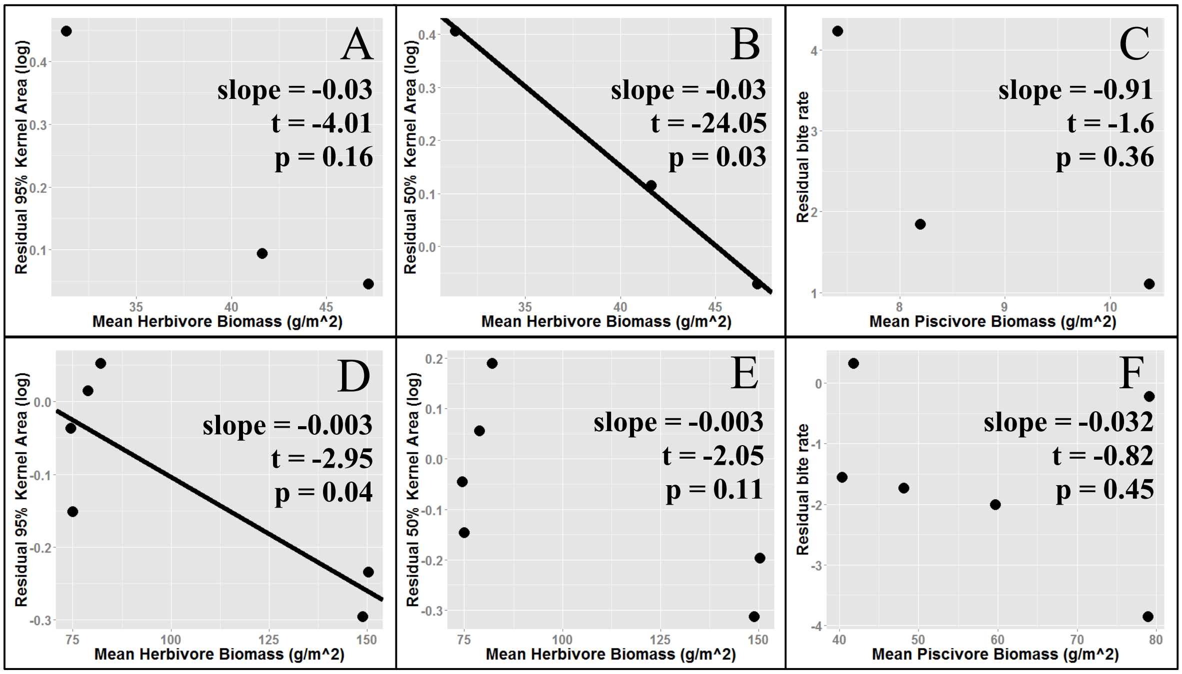

Figure 11: Within-island relationships: (A) residual 95% KUD vs. herbivore biomass at Mo'orea, (B) residual 50% KUD vs. herbivore biomass at Mo'orea, (C) residual bite rate vs. piscivore biomass at Mo'orea, (D) residual 95% KUD vs. herbivore biomass at Palmyra, (E) residual 50% KUD vs. herbivore biomass at Palmyra, and (F) residual bite rate vs. piscivore biomass at Palmyra. Trend line indicates a significant relationship.

Table 1: Mean per observation chase rates (chases toward the focal individual) by the major interacting families at Palmyra and Mo'orea. Other families that chased *C. sordidus* at very low rates included Balistidae (n=14), Blenniidae (n=7) and Holocentridae (n=1) in Mo'orea, and Cirrhitidae (n=1), Kyphosidae (n=1) and Labridae (n=2) in Palmyra.

	Mo'orea (Chases/20 min observation)	**Palmyra (Chases/20 min observation)**
Acanthuridae	0.43	7.57
Pomacentridae	0.57	1.33
Scaridae	1.70	1.46

Table 2: Model results for individual observation predictors of bite rate.

Term	**Estimate**	**p-value**	**Relative Importance**
(Intercept)	18.34	4.74e-09 ***	NA
Total Length	-0.19	0.0898 .	0.0593
Phase(TP)	-6.89	0.1615	0.0291
Time of Day	6.44	0.0703 .	0.124
Chase Rate	-4.06	1.55e-05 ***	0.712
Total Length * Phase(TP)	0.27	0.1578	0.0754

Residual standard error: 5.163 on 256 DF

Multiple R-squared: 0.08625

Adjusted R-squared: 0.0684

F-statistic: 4.833 on 5 and 256 DF

p-value: 0.0003058

Table 3: Model results for individual observation predictors of 95% kernel area (log).

Term	**Estimate**	**p-value**
(Intercept)	4.06	< 2e-16 ***
Total Length	0.0386	4.2e-08 ***

Residual standard error: 0.6394 on 260 DF
Multiple R-squared: 0.1094
Adjusted R-squared: 0.1059
F-statistic: 31.92 on 1 and 260 DF
p-value: 4.204e-08

Table 4: Model results for individual observation predictors of 50% kernel area (log).

Term	**Estimate**	**p-value**
(Intercept)	2.46	< 2e-16 ***
Total Length	0.042	1.12e-09 ***

Residual standard error: 0.6218 on 260 DF
Multiple R-squared: 0.1332
Adjusted R-squared: 0.1299
F-statistic: 39.96 on 1 and 260 DF
p-value: 1.124e-09

Table 5: Model results for site level predictors of mean residual bite rate.

Term	Estimate	p-value	Relative Importance
(Intercept)	-0.369	0.8903	NA
Piscivore Biomass	-0.0633	0.0156 *	0.817
% Cover Preferred Food	0.0519	0.2572	0.183

Residual standard error: 1.488 on 6 DF
Multiple R-squared: 0.7157
Adjusted R-squared: 0.6209
F-statistic: 7.551 on 2 and 6 DF
p-value: 0.02299

Table 6: Model results for site level predictors of mean residual 95% kernel area (log).

Term	**Estimate**	**p-value**	**Relative Importance**
(Intercept)	0.646	0.050 *	NA
Herbivore Biomass	-0.00494	0.00509 **	0.941
% Cover Preferred Food	-0.00469	0.262	0.0592

Residual standard error: 0.123 on 6 DF
Multiple R-squared: 0.7623
Adjusted R-squared: 0.6831
F-statistic: 9.621 on 2 and 6 DF
p-value: 0.01343

Table 7: Model results for site level predictors of mean residual 50% kernel area (log).

Term	Estimate	p-value
(Intercept)	0.309	0.0328 *
Herbivore Biomass	-0.00381	0.0209 *

Residual standard error: 0.1556 on 7 DF
Multiple R-squared: 0.557
Adjusted R-squared: 0.4937
F-statistic: 8.8 on 1 and 7 DF
p-value: 0.02091

Chapter 2: A comprehensive multi-scale analysis of the movement patterns of *Chlorurus microrhinos*

Introduction

Animal movements generally consist of directed responses to social and environmental cues that result in space use patterns that represent tradeoffs between energy acquisition, survival, and reproduction (Lowe and Bray 2006). Parrotfishes are characterized by complex social and mating systems (Robertson and Warner 1978, Warner 1984) and their space use patterns can be strongly linked to interactions between their social status and environment (vanRooij et al. 1996, Mumby and Wabnitz 2002, Afonso et al. 2008b). In the context of movement behaviors, there are some traits that are consistently observed across many species within the family, while other movement behaviors can be quite plastic even within a single species or population. For example, many species are active during daylight hours and transition to night refuging sites in reef crevices at dusk to conserve energy and avoid nocturnal predators (Winn and Bardach 1959, Hobson 1972, Ogden and Buckman 1973, Dubin and Baker 1982, Howard et al. 2013). Most species are primarily herbivorous and consume algal turfs and other forms of epilithic algae (Bellwood and Choat 1990, Hamilton et al. 2014). Some species show high levels of site attachment (Ogden and Buckman 1973, vanRooij et al. 1996, Mumby and Wabnitz 2002, Welsh and Bellwood 2012b, Howard et al. 2013) which may be partially explained by the predictable regeneration of algal resources (Carlson et al. in prep) combined with the need to constantly forage to maximize energy gained from low quality resources (Bellwood and Choat 1990, Chen 2002), as well as habitat and resource partitioning among competitors (Mumby and Wabnitz 2002). However, some species contain both territorial individuals and individuals who rove over larger areas in schools (Afonso et al. 2008a, Welsh and Bellwood 2012a), and schooling can be beneficial for food finding (Clifton 1991), reducing individual predation risk (DeMartini et al. 2011), and for circumventing the territories of other herbivores (Robertson et al. 1976). The strong contrast in behaviors between territoriality and schooling demonstrates potential benefits of this behavioral plasticity, because there are clear tradeoffs between these behaviors that can affect predation risk, energetic rewards, and reproductive benefits. Movement patterns are influenced by reproductive behaviors which vary across the Scaridae family and include territory spawning within a harem (Buckman and Ogden 1973, De Girolamo et al. 1999) and migrations to spawning aggregation sites (Johannes 1981, Domeier and Colin 1997). These behaviors can also be plastic within a given species or population (Afonso et al. 2008b). The high levels of plasticity in the movement behaviors within the Scaridae demonstrates that there may be many unique combinations of behaviors that these fishes can use in order to maximize individual fitness. These behaviors are likely to be highly context dependent and further investigation of the determinants of movement behaviors will improve our understanding of the ecological roles of these species and the chances for effective conservation.

Over the past several decades, there has been a growing recognition of the ecological importance of herbivorous fishes and they are now widely recognized as important contributors to the maintenance of coral-dominated reefs (Bellwood et al. 2004, Hughes et al. 2007, Jackson et al. 2014). When these fish are experimentally excluded, coral cover is reduced as turf algae and fleshy macroalgae overgrow living corals (Lewis 1986, Lirman 2001), and high algal cover prohibits the recruitment of new corals through direct competition for space on the substrate (Kuffner et al. 2006). Grazing fishes are therefore important in preventing existing coral colonies from being overgrown by competitive algae, and for creating space for new corals to settle by clearing away algae from dead coral substrates (Mumby et al. 2007). Parrotfishes are particularly important in the latter activity, because their feeding mode and jaw morphologies enable them to scrape algae completely from the substrate leaving bare spaces with microstructure (Bellwood and Choat 1990) that may enhance coral settlement (McCauley et al. 2014). The microstructure itself may further enhance coral settler survivorship (Nozawa 2008). The bite scars created by large excavating parrotfishes may be particularly beneficial because algae may take longer to regrow in large bite scars compared with those left by smaller scraping parrotfishes, extending the refuge period for newly settled corals (Bonaldo and Bellwood 2009). Large-bodied species are often preferentially targeted by fisheries (Clua and Legendre 2008), jeopardizing this unique function on many reefs worldwide. The widespread recognition of the importance of parrotfishes and other coral reef herbivores to coral reef resilience has recently led to targeted management of these taxa in many regions.

One of the most commonly employed protection strategies for marine organisms is the application of spatial management in the form of Marine Protected Areas (MPAs). Species home range information is crucial to inform strategic, science-driven, MPA design ensuring that the protected areas are large enough to effectively safeguard individuals from moving beyond their boundaries and being fished. In fact, most studies of space use by tropical herbivorous fishes have been reported in the context of designing or evaluating a specific MPA based on local movement and home range patterns of species of interest (Eristhee 2001, Meyer and Holland 2005, Afonso et al. 2008a, Chateau and Wantiez 2009, Garcia et al. 2010, Hardman et al. 2010, Meyer et al. 2010, Marshell et al. 2011, La Mesa et al. 2012). This information can be compiled to develop useful tools to advise reef managers who are designing future MPAs in order to protect specific taxa or functional groups (e.g. Green et al. 2015). However, significant plasticity (orders of magnitude) in home range size has been observed among individuals within a study (Afonso et al. 2008a, Marshell et al. 2011) and within a species across different study systems (Meyer and Holland 2005, Hardman et al. 2010). In addition, few home range estimation studies include contextual information linking movement patterns to the behavioral drivers that explain variation in home range size within and across systems. Thus, further understanding of the drivers of movement behaviors is needed in order to enable MPA designers to set target sizes more rationally for protecting specific taxa or functional groups. Additionally, most studies do not delineate activities across home ranges and thus, despite their utility for conservation applications, these descriptive studies can provide few insights into ecological processes such as those that regulate the spatial patterns of grazing.

In terrestrial systems the interactions between the level of heterogeneity of herbivore foraging and the structure of primary producer communities have been well studied (Adler et al. 2001), but on coral reefs these interactions and their implications are not as well understood. However, spatially explicit modeling of coral reef benthic states suggests that the spatiotemporal patterns of grazing on reefs are important to benthic dynamics and that the outcomes of coral-algal competition are largely influenced by the spatial distribution and temporal stability of feeding by the herbivores in the system (Sandin and McNamara 2012, Eynaud et al. in review). When herbivore mobility is low and individual feeding is constrained to small areas, corals are favored. When mobility is high and feeding is dispersed, algae are favored. These models suggest that herbivore mobility matters because when feeding is dispersed, cleared areas are not maintained at time scales long enough to allow settled coral to recruit to the adult population. Conversely, with low herbivore mobility, spatially concentrated and temporally stable feeding allows corals to settle and grow with refuge from encroaching algae. Nearby algae are harmful and sometimes lethal to neighboring corals (Smith et al. 2006, Box and Mumby 2007), so the formation and maintenance of many concentrated patches of bare space may be an important factor influencing coral recruitment (Arnold et al. 2010). While there are many studies quantifying gradients of overall grazing intensity across coral reef habitats (Hay 1981, Lewis and Wainwright 1985, Paddack et al. 2006, Hoey and Bellwood 2007), there is less information about space use intensity patterns for individual coral reef herbivores (except see Welsh and Bellwood 2012b) and we do not yet have a complete understanding of the drivers of variation in foraging behaviors at scales fine enough to be important to these reef processes.

In this study, we aim to quantify the movement patterns of *Chlorurus microrhinos*, a large-bodied, excavating, Pacific parrotfish. Our multi-scale approach utilizes three methods of monitoring: (1) long-term passive acoustic monitoring to capture movements at the scale of the whole reef over the course of months to years; (2) active acoustic tracking to characterize daily movement patterns; and (3) repeated behavioral observation consisting of mapping of spatially-explicit activity distributions to determine the patterns of utilization intensity at the scale of feeding territories. We predict movement may be driven by a variety of aspects of the animal's life history, ecology, and abiotic features of the environment and that space use may be related to different social and environmental drivers depending on the spatial and temporal scale examined. Exploring the patterns of movement across multiple spatiotemporal scales will provide a more comprehensive understanding of how these behavioral drivers interact to structure the space used by these ecologically important animals.

Materials and Methods

Study Species

Chlorurus microrhinos is a large-bodied (reported maximum total length of 80 cm) parrotfish that is abundant and widely distributed across the tropical Pacific (Choat et al. 2012). *C. microrhinos* is chiefly herbivorous (Hamilton et al. 2014) and scrapes algal material from dead coral substrates, excavating large divots in the benthos (Figure 1). Bellwood (1995) estimated that an average individual is responsible for 1017.7 kg ± 186.3 (SE) of bioerosion per year. The largest individuals at our study site (Palmyra Atoll, see below) are much larger than the *C. microrhinos* on the Great Barrier Reef site where the removal metrics were derived, so individual bioerosion contribution rates may be higher at our study site. *C. microrhinos* is highly targeted by fishermen throughout its range due to its large size. Because the ages of maturity and sex change are late relative to smaller parrotfish, the species has a higher than average sensitivity to fishing pressure (Clua and Legendre 2008).

C. microrhinos is classified as a sequential protogynous hermaphrodite (Randall and Choat 1980, Choat and Randall 1986), and recent studies indicate that there are some primary males in the species (Barba 2010). Dimorphism is weaker in this species than in other scarids, but initial phase (IP) individuals in the Pacific are characterized by green coloration and terminal phase (TP) individuals are blue with purple markings, and develop a bump on their head as they get large. Little is known about their reproductive behavior except a report Johannes (1981) received from a Palauan chief and scholar that the species often aggregate to spawn at the edges of promontories on the outer reef slope. Colin and Bell (1991) witnessed a single event in the Marshall Islands where a pair of fish from a large aggregation rose to spawn in the water column. This event was in the afternoon following a high tide. The authors reported that they observed courtship behaviors in this species throughout the year. Our observations of the social behaviors of *C. microrhinos* at diurnal feeding sites were mostly consistent with other observations (Welsh and Bellwood 2012b), in that they forage in social groups, with a large TP male associated with several IP individuals and smaller TP individuals within a joint home range. However, we did not observe mating within these groups, and one study site (Penguin Spit, see below) consisted of solitary TP males in small territories.

Study Sites

We conducted this study at Palmyra Atoll (5°53′N 162°5′W) in the summers of 2013 and 2014. Palmyra Atoll is a remote island in the northern Line Islands, roughly 600 km south of the main Hawaiian Islands. Palmyra has been 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. Palmyra experiences semidiurnal tides with a maximum tidal fluctuation of roughly one m. Current hydrodynamics at the atoll scale are primarily driven by tides and waves, and wind-driven flow also occurs across the shallow terraces (Rogers 2015, Rogers et al. in review). Although 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 human-affected reefs. The atoll consists of three large lagoons flanked by long, gradually-sloping reef terraces that extend to the east and west (Figure 2A).

We performed telemetry at two sites on the shallow western reef of the atoll: Rubblepile and Western Terrace. The two sites are similar in depth range and structural complexity but differ in their benthic assemblages. The Rubblepile site is a section of reef that lies adjacent to a large expanse of coral rubble. It has been affected by the spread of the corallimorph *Rhodactis howesii* (Work et al. 2008), which has recently increased in abundance and killed substantial amounts of living coral. However, there is still a high level of structural complexity from the dead coral skeletons and some remaining living corals. The Western Terrace site has high living coral and crustose coralline algal cover and is similarly structurally complex. We performed visual observations at the Western Terrace and an additional site, Penguin Spit. It is believed that the Penguin Spit was badly bleached in the major El Niño–Southern Oscillation event of 1998, which resulted in mass coral mortality. Currently, the site has a high percent cover of red algal turf, which makes up a majority of the diet of *C. microrhinos* (Hamilton et al. 2014) and is the preferred substrate type targeted by the species in Palmyra (Carlson et al. in prep). The site also has a great deal of structural complexity from the skeletons of dead corals as well as some living corals. At this site we observed a high density of large TP males and few IP individuals. Instead of the social system we observed at our other sites, at Penguin Spit the large TP males mostly maintained individual territories.

Passive Acoustic Monitoring

In order to assess the reef-scale movements, long-term (~ 1 yr) site fidelity, and seasonal variation in movement patterns of *C. microrhinos* we surgically implanted a total of nine individuals with coded transmitters (Vemco, V9-2L, 29 mm long x 9 mm diam., 4.7 g in air, 2.9 g in water, nominal delay 120 sec, battery life 484 d, power output 145 dB, 69 kHz) in 2013 and 2014 (See Appendix I for tagging procedures). The transmitters are programmed to transmit roughly every two minutes with some built-in variation in transmission interval to avoid interference caused by temporal overlap in multiple tag transmissions. Each transmission consists of a specific pattern that is identified and logged by moored underwater omnidirectional acoustic receivers (Vemco VR2Ws) when the transmitter is within the detection range of the receiver. The receiver stores the identity of the transmitter with the date and time (h:m) of the transmission. The detection range for both sites was roughly 60 m though detection efficiency dropped to a low level after 30 m. See Appendix II for detailed range testing methods and results.

There is a large array of Vemco VR2W receivers at Palmyra Atoll from previous telemetry projects. An extensive, high-density VR2W receiver array of eleven receivers spaced between 100 and 300 m apart was already in place at the Rubblepile (Figure 2C); we augmented the receiver array at the Western Terrace with five receivers placed 100 m apart in 2013 (Figure 2B), basing spacing of the receivers on reported receiver detection ranges in shallow coral reef habitat (Welsh et al. 2012) and reported extents of movement for this species (Welsh and Bellwood 2012b). After we identified some of the patterns of diurnal movements with active tracking we deployed additional receivers in 2013 and 2014 to capture movements outside of daytime feeding ranges.

Active Acoustic Tracking

In order to characterize the daily movement patterns of *C. microrhinos*, we surgically implanted eight individuals with continuous transmitters (Vemco, V9, 21 mm long x 9 mm diam., 4.7 g in air, 2.9 g in water, battery life 69 d, power output 145 dB) that transmitted with a two second interval at a specified frequency (78 - 84 kHz). Five frequencies are available in the V9 continuous active tracking tags (63, 75, 78, 81, 84 kHz) but there is potential for the 63 and 75 kHz tags to interfere with the 69 kHz coded tags transmitting to the VR2W receivers, so we did not use these frequencies within our receiver array. We recorded a location for each fish roughly every ten minutes throughout tracking days from approximately 06:20 to 18:10 for each track in accordance with the Palmyra Station operation regulations (no night boating is permitted on the reefs). We tracked each fish for three to six full tracking days spread out over a four to eight week period (Table 1). We also conducted several snorkeling observations of each tagged fish to verify their activities while they were at their foraging grounds (See Appendix III for detailed tracking methods).

Visual Observations

In order to characterize the fine-scale spatial and temporal patterns of feeding territory sizes and grazing intensity and we conducted repeated visual observations of individual *C. microrhinos* throughout the summer of 2014. We identified TP individuals of *C. microrhinos* with adjacent territories at two sites (Western Terrace and Penguin Spit, n = 5 individuals per site) and conducted observations on the same individual fish for a minimum of five times spread over two months. We chose to restrict observations to large, TP individuals to minimize confounding variation in behavior and territory size due to body size or sexual phase. We identified individuals by unique scar patterns, caudal color patterns, and other distinguishing markings. An observer towed a surface floated GPS unit positioned over the fish and logging a location every 5 seconds. With a watch synchronized to the GPS unit the observer recorded the start and end times of feeding, defecating, cleaning, and territorial disputes involving other TP fish outside of the social group of the focal fish. We then used these georeferenced activity locations to create activity maps for each track. Observations were two hours in duration and were randomized across time of day to account for any diel changes in activity.

We conducted fish counts and benthic surveys at both sites to measure predator density, conspecific density and food (red algal turf) availability. We conducted fish community surveys using 25 x 4 m belt transects (n = 9 per site) and benthic surveys using a point contact method quantifying the benthic cover type at each m of a 25 m transect (n = 8 per site). We conducted targeted surveys for *C. microrhinos* using 4 x 50 m belt transects (n = 6 per site) and we repeated these targeted surveys three times per site. Predator and conspecific biomass and percent cover turf differences between sites were compared between sites using Welch's two sample t-tests in R (R. Core Team 2014).

Spatial Data Analysis

Passive Acoustic Monitoring

Prior to analysis we filtered out any incidences of a single detection by a given transmitter on a particular receiver to exclude potentially spurious detections (there were few). We then used the receiver locations to calculate Minimum Convex Polygons (MCPs) for each fish to characterize the maximum movement extents detected over the study period (~ 1 year).

Many coral reef fish species are known to spawn at specific tidal heights, and preliminary data exploration revealed a pattern of excursions to the deeper western terrace that appeared to follow tidal cycles. To test for the influence of tidal height on the movement patterns of the tagged fish we analyzed the VR2W detection data using generalized additive mixed models (GAMMs). We selected these models because they allow for the temporal correlation in location data to be accounted for with the inclusion of a serial-autocorrelation structure. We selected a "home receiver" for each tagged fish based on the number and consistency of detections recorded by each receiver for a given individual. In one case (Fish 17470) the fish moved between a few closely located "home receivers" during its transmitter life so we pooled the data from those receivers. We then calculated the number of detections per hour at the "home receiver" as the response variable in order to identify periods of time when fish were leaving their home foraging grounds, hypothetically to travel to spawning grounds. We used hourly measured tide data (Rogers 2015, Rogers et al. in review) to assign a tidal height to each hour in the detection dataset. We truncated the datasets to the hours between 06:00 and 18:00 (when the fish are active) and ran separate GAMMs for each fish to test for the influence of tidal height on detection frequency. We used the continuous AR1 correlation function for the continuous time covariate and a cubic regression spline structure. We also included in all models the number of days since the VR2W was last cleaned and redeployed, as a measure of fouling. Biofouling has been demonstrated to decrease the detection ability of a VR2W (Heupel et al. 2008), and our receivers often become heavily encrusted with crustose coralline algae and other encrusting organisms on their hydrophone heads. We performed this analysis in R using the *mgcv* (Wood 2011) and *nlme* (Pinheiro et al. 2007) packages. We also conducted Welch's two-sample t-tests for each fish to test differences between the tidal height corresponding with offshore receiver detections in the VR2W dataset and a null distribution of all tidal heights from the measured tide dataset.

Active Tracking

We computed probabilistic kernel utilization distributions (KUDs) from all tracks (active acoustic tracking and GPS tracks from visual observations) using the biased random bridge (BRB) method with the *adehabitatHR* package (Calenge 2006, Benhamou 2011) in R. Improving on the classically used location-based distribution kernels calculated from density of point positions, bridge methods incorporate a temporal component to interpolate between successive relocations and create a movement based utilization distribution (Figure 3). The application of the relocation history allows for the computation of utilization distributions from serially correlated raw tracking data. The biased random (advective-diffusive) bridge method allows for home ranging behavior and habitat patch selection by the tracked animal, unlike the (purely diffusive) Brownian Bridge method and so this method allows for a more accurate estimation of high use, preferred patches within the territory or home range (Benhamou 2011).

Commonly used metrics describing animal space use are the 50% and 95% utilization kernels. For example, a 50% kernel area encompass the smallest area in which the probability of locating the animal is 50%. In tracking studies, 95% kernels are sometimes used to characterize home ranges and 50% kernels are often used to characterize areas of core use within a home range for herbivorous fishes (Meyer and

Holland 2005, La Mesa et al. 2012, Welsh and Bellwood 2012b), and we report them as such here. Benhamou and Riotte-Lambert (2012) developed analytical techniques to partition the utilization distribution into intensity (mean residence time per visit) and recursion (visitation frequency) distributions. We computed all three kernels (utilization, intensity, and recursion) and visually compared them with activity maps created for GPS tracked fish. We determined that the utilization kernel best characterized the areas where the fish was concentrating its feeding (Figure 3). This is logical considering that the fish spent the majority of time during focal follows feeding, with only brief intermissions for defecations, cleanings, and territorial disputes. We computed kernel metrics both for individual observations/tracking days and as a combined metric with all data for each fish (Table 2).

Visual Observations

We tested for differences in fine-scale space use between sites with linear mixed effects models, incorporating the individual fish as a random effect. We compared null models without site to models including site to test for a significant difference in space use between sites. For this analysis, we log transformed the spatial metrics to achieve normal residuals. We used the R package *lme4* (Bates et al. 2015) for this analysis.

Results

Passive Acoustic Monitoring

Tagged fish were detected for durations between 195-504 days (Table 1). Individual fish were detected on 95-100% of the days within their detection duration (most 100%). A few transmitters stopped being detected well before the time expected for transmitter life (See Appendix IV for discussion). Tagged fish displayed strongly diurnal activity patterns (Figure 4). Overall, the VR2Ws recorded 288,234 detections of our nine tagged individuals, and there were zero detections logged between the hours of 19:18 and 05:56. All fish tagged at the Rubblepile were detected at a shallow receiver (Figure 2B, receiver shown with blue circle) at the beginning and the end of most days, indicating that their sleeping sites are likely stable, and a relatively long distance (roughly 500 m) north of their diurnal foraging grounds. Some fish from the Western terrace were also detected at shallow receivers inshore and north of foraging grounds (also roughly 500 m, shown in blue in Figure 2C) on many days in the early mornings and evenings, indicating that they were swimming past on the way to and from night refuge sites. Three TP individuals (Figure 4D, H, I) appeared to have undergone home range shifts during the monitoring study. The receiver array at the Rubblepile was extensive and 11705 (4D) and 17470 (4I) were detected by a new "home receiver" after the shift. In the case of 17463 (4H) at the Western Terrace the fish continued to be detected but at a lower rate, indicating that it had shifted the core area of its home range out of the receiver array.

Visual inspection of the raw detection data showed that all individuals make repeated excursions past receivers greater than a kilometer west of their foraging grounds into deeper regions ("offshore") of the western terrace (Figure 2 B and C, receivers shown with dark pink circles). For some fish, these excursions appeared to track tidal cycles because the excursion occurred roughly one hour later each day and reset to earlier in the day when the high tides moved into the evening hours. However, there was extensive variation among individuals in the temporal patterns of offshore excursions. Some individuals visited offshore areas in the early mornings (Figure 4B, F, G), or late afternoons (see Figure 4G), and some had multiple offshore bouts clustered within a time period of a few weeks with sporadic visits at other times (Figure 4D, I). Some individuals displayed a combination of these patterns (Figure 4G). Generally, initial phase individuals were the most consistent offshore visitors with the most striking visual tidal signatures (Figure 4A, C, E, G) except for one terminal phase individual (Figure 4H). Terminal phase individuals were inconsistent in the timing of offshore detections with some clustered excursions (Figure 4D, I), another which showed mostly morning excursions (Figure 4B), and two showing excursions associated with the tidal cycle (Figure 4F, H). There were no apparent seasonal patterns to the offshore visitation frequencies, at least over the duration of the monitoring study. However, tidal height was a highly significant predictor of detection frequency on the "home receiver" for all tagged fish (Figure 5). Specifically, we found a decrease in detection frequency at positive (> 0 m) tides relative to negative (< 0 m) tides indicating that the fish were leaving their home foraging grounds during high tides more than during low tides. With one exception (11705) all fish were detected at "offshore" receivers more often on high tides than low tides and this differed significantly from the null distribution from tide data (Figure 5).

Minimum Convex Polygons (MCPs) calculated from VR2W detections ranged from 0.124 km^2 (Fish 11706) to 3.349 km^2 (Fish 17470). Fish 17470 had a much larger (order of magnitude) MCP home range than all of the other fish due to the fact that it was detected on the North Forereef on several separate occasions in the early morning throughout October and November of 2014 (all of the other detections from all fish throughout the study were logged on receivers on the reef terrace). This distant forereef site, over two kilometers from the normal foraging site, is a location where we have witnessed spawning aggregations of multiple species of parrotfishes. Remotely deployed video systems have also captured *C. microrhinos* in large aggregations at this site displaying behavior that appeared to be spawning related (Darcy Bradley unpublished data, Appendix V). Excluding this outlier fish, the next largest MCP home range was 0.419 km^2 (Fish 17462) and the average was 0.279 km^2.

Active Acoustic Tracking

Ninety-five percent kernel activity spaces calculated from active acoustic tracking (combining all tracks per individual) ranged from 4,860 to 117,480 m^2 (mean 28,524 ± 12,994 m^2). Fifty percent kernels ranged from 1,129 to 3,924 m^2 (mean 2425 ± 294 m^2, Figure 6). Only three of the nine individuals made excursions to offshore areas of the deep terrace while we were actively tracking them, which contributes largely to the variation in 95% activity space. The two fish that we tracked offshore from the Western Terrace site (Fish10 in 2013 and 17462 in 2014) both appeared to follow the same path offshore to a reef-rubble interface at 25 m depth (for reference the diurnal foraging grounds were at roughly 3-6 m depth). We made several dives in this area to install and swap VR2W receivers and each time we saw large aggregations of *C. microrhinos* in what appeared to be pre-spawning behaviors (e.g. TP males displaying in “loops” up in the water column). This behavior is consistent with courtship behavior described by Colin and Bell (1991) for this species.

All tracked fish appeared to seek nighttime refuge in areas that were several hundred meters from their diurnal foraging grounds. Due to research station curfew restrictions, we were unable to track fish to their precise sleeping holes each evening and could only roughly approximate the general area from where they were approaching in the mornings when they first became detectable. Two of the nine fish swam to what we believed to be their night sheltering sites while we were monitoring them on the day of the tagging procedure and both locations were characterized by very shallow, high relief reef.

All fish showed a high level of site fidelity over the course of the tracking study, utilizing the same general areas to forage each day. However, within those diurnal foraging grounds, fish had multiple, distinct, high-use areas. Sometimes this was reflected as separate highly utilized patches within the daily 50% KUD, separated by tens of meters, and the high use areas shifted somewhat between tracking days as well. While there was some overlap in daily 50% KUD between tracking days, there was substantial non-overlapping area as well (Figure 7). All observations of tagged fish by snorkelers during tracking and at other times revealed that these core use areas were in fact areas of intense feeding.

Visual Observations

Combined (all tracks per individual) 95% kernel areas for each of the ten fish ranged from 344 to 2,998 m^2. Combined 50% kernel areas ranged from 72 to 549 m^2. Areas of 50% and 95% kernels from individual tracks ranged from 9 to 300 m^2 and 56 to 1,580 m^2 respectively. Similar to the patterns detected using active acoustic tracking, the core use areas did not entirely overlap for each observation, and we observed that the focal individuals fed on different food patches during different observation periods. At Penguin Spit, feeding was generally concentrated in one or a few patches within the territory, while at the Western Terrace activity and feeding were more dispersed within the territory (Figure 8). *C. microrhinos* biomass and turf algal cover were significantly higher at Penguin Spit than at the Western Terrace ($t = 4.22$, $df = 2.34$, $p = 0.04$; $t = 6.24$, $df = 13.09$, $p < 0.001$ respectively, Figure 9B, C), and there was no difference in piscivore biomass between the sites (t = 0.36, df = 12.56, p = 0.72, Figure 9A). Linear mixed effects models showed a significant effect of site for both 50% (p = 0.019) and 95% (p = 0.0038) KUDs, with area used being larger at the Western Terrace than at Penguin Spit (Figure 10).

Discussion

Here we show that home range and space use estimations can vary considerably depending on the spatial and temporal scales of measurement and that the patterns of movement at various scales are related to different aspects of the life history and ecology of this large-bodied parrotfish. At the largest scale (the scale of the home range), movement behaviors are related to reproductive behaviors and crepuscular sheltering activities, while at fine scales (the scale of the feeding territory), movement appears to be closely related to food abundance and competition. Additionally, we estimated home ranges for this species that are much larger than those reported in previous studies, further demonstrating the huge amount of behavioral plasticity that may exist within a single species.

Passive acoustic monitoring provides data with low spatial resolution but it enables us to characterize movement over long periods of time (in this case roughly 1 year) at fairly high temporal resolutions. Fish movements at the largest scale (MCPs calculated from long-term receiver data) were largely influenced by routine offshore excursions to the deeper reef. In all individuals, these excursions were well predicted by the tidal cycle, indicating a high degree of synchronicity likely associated with spawning events. Because we observed large numbers of individuals at a handful of offshore sites, and because all fish tagged at a given site visited the same general offshore area, we believe that it is highly likely that large aggregations of fish form at these areas for spawning. It is notable that each time we visited these specific sites we also experienced unusually strong currents. Many reef fishes have been shown to make migrations to spawning sites at times when oceanographic conditions may favor movement of fertilized eggs from the reef (Johannes 1978), and several species of the scarids have been reported to form large aggregations at specific spawning sites (reviewed in Domeier and Colin 1997). Where spawning cycles have been linked to tidal dynamics, several labrids and scarids are known to spawn on or at some defined time after high tides (Robertson and Hoffman 1977, Robertson et al. 1982, Colin and Bell 1991). It is likely that it is the influence of the tide on current dynamics and not the tidal height itself that explains the tidally synchronized spawning in some species (Sancho et al. 2000). In their study on the Great Barrier Reef (GBR), using active tracking methods similar to ours, Welsh and Bellwood (2012b) observed only site attached behavior and did not detect long excursions away from feeding territories. It is possible that the species exhibits plasticity in their spawning behaviors (e.g. Gust 2004, Afonso et al. 2008b), and that spawning excursions occur in the Palmyra population but not in the GBR population studied previously. One possible hypothesis for this difference is that the hydrodynamic characteristics of each site dictate whether or not excursions are necessary for gamete transport (i.e. the animals tracked in the GBR study had home ranges centered on a reef crest and may have had proximate access to high flow conditions, making long excursions unnecessary). If this is true, then movement patterns and differences between populations may be strongly influenced by local oceanographic conditions that in turn affect reproductive behavior. Consequently, the long excursions like those documented here could potentially expose individuals to elevated risks associated with fish or human predators.

Another study that using long-term acoustic monitoring techniques (Chateau and Wantiez 2009) showed that a small percentage of tagged *C. microrhinos* made excursions up to a kilometer from tagging sites. These excursions were not believed to be related to spawning in this case because they did not coincide with the known reproductive season in New Caledonia where the monitoring study was conducted. In this case, these individuals moved from a reef within an MPA to a reef open to fishing. Therefore, regardless of the reason for the excursion, these fish were vulnerable to fishing despite the fact that their home range was thought to be encompassed by the MPA. This highlights the need for using large-scale, long-term datasets to characterize more realistically the variability of movements relative to differing habitats and conditions.

Another characteristic long-range movement seen here were the long distances (~ 0.5 km) travelled from an individual's diurnal foraging grounds to nighttime sheltering sites. Scarids are well known to shelter at night using mucous bubbles to prevent their scents from being detected by nocturnally hunting predators such as sharks and moray eels (Winn and Bardach 1959). Individual parrotfish have been shown to travel tens to hundreds of meters on consistent routes (Ogden and Buckman 1973) to areas with dense coral cover to seek night shelter (Dubin and Baker 1982). In some cases, large reef fishes appear to prefer to utilize particular coral morphologies, such as large tabular corals, as sheltering sites (Kerry and Bellwood 2011). The strong diurnal pattern evident in our passive receiver data indicates that these animals are sheltering at night, without exception, and that the transitions to night refuge sites usually happened near 18:00, concurrent with sunset in Palmyra. Because we were not able to observe tagged fish directly at their night refuge sites, we cannot assess here whether there are particular differences in habitat characteristics between sleep sites and foraging grounds. However, the general areas of the receivers that detected several fish in transition to and from night refuge sites were slightly shallower with higher relief than the diurnal foraging grounds of the fish. Our results contrast with those of Welsh and Bellwood (2012b), who found that their tagged individuals moved to consistent night refuge sites that were on average 34.8 ± 5.7 (SE) meters from their core use areas. Our individuals traveled much farther, potentially because of particular habitat or coral morphology requirements. Perhaps, in a predator-rich system like Palmyra, the particularities of the night sheltering sites are more critical for survival than in other locations where predators are not as abundant, and failure to take these night refuging site locations into account when designing an MPA may leave otherwise protected fish vulnerable during the nighttime hours. This is especially important because nighttime harvesting of parrotfish from their refuge sites is a common practice in many regions of the world (Aswani and Hamilton 2004, Dulvy and Polunin 2004, Taylor et al. 2014).

Active acoustic tracking provided us with data of high spatial resolution to form a probabilistic kernel metric that characterizes the daily activity space used by *C. microrhinos*. We found that at Palmyra, core areas of use within daily activity spaces were fairly small and were similar across individuals (50% KUD = 2425 m^2 ± 294 SE), but that overall diurnal activity spaces were large and more variable (95% KUD = 28,524 m^2 ± 12,994 SE). The large average size of the activity space estimations from active tracking methods is again driven by large-scale movements between foraging territories, offshore sites, and night refuging sites. The large variation in home range estimated from active tracking is due to the fact that only three of the nine individuals made offshore excursions on days that we were tracking them. Passive monitoring data suggest that all animals utilize offshore spawning sites, so our active tracking data underestimates the actual home ranges for several of our fish. Our findings of small core use areas is consistent with the findings of Welsh and Bellwood (2012b). However, our overall estimations of diurnal activity space differed strongly from theirs, which were much smaller and less variable than ours; this again indicates that there is significant plasticity in large-scale movement behaviors within the species.

One of the most interesting observations in terms of daily activity spatial patterns was related to the temporal stability of the core use areas of our tracked fish. We found that the core use areas were rather small and shifted slightly within the home range of the animal between each day of active tracks. We observed the same pattern in the behavioral following bouts, where we observed fish to graze one food patch on one day and a different nearby patch on a subsequent day, and that they sometimes returned to a previously observed grazing patch at some later date (Carlson et al. in prep). This contrasts with the findings of Welsh and Bellwood (2012b) who found high levels of temporal stability of core use areas over the course of their tracking study. One explanation for this may be that the fish from their study had home ranges centered on a prominent habitat feature (reef crest) while our sites were characterized by variable-depth contiguous reef. Perhaps the preferred food resources on the reef crest are concentrated on a more defined area than those on a contiguous reef and the temporal patterns we observed reflect those differences. These two behavioral scenarios (consistent grazing in the same localized area vs. graze, abandon, regraze) could have different effects on coral settlement and survivorship. Highly concentrated feeding creates localized areas with low levels of algae and abundant bare space which may positively influence rates of coral settlement. However, parrotfish can damage or consume coral settlers and recruits in the process of grazing (Bak and Engel 1979, Box and Mumby 2007), and they may negatively affect coral settler survivorship when they return to graze on a patch that had been grazed previously. In addition, Carlson et al. (in prep) found that areas of concentrated feeding were also areas of rapid algal regrowth. The overall net effects of these positive and negative interactions may vary depending on fine-scale spatial and temporal differences in fish foraging behaviors. Explicit testing of the localized effects of these different grazing behaviors on coral recruitment is needed in addition to further testing of how small-scale localized effects scale up to the level of entire reefs.

Though limited in the ability to provide overall space use estimates due to limitations on tracking for extended periods, GPS tracking data provided the finest-scale spatial and temporal resolution data of fish foraging patterns. We observed several major differences in the spatial behaviors of individuals within feeding territories across the two sites. At the Western Terrace site, fish had larger feeding territories and feeding was more distributed throughout the territory. Fish at Penguin Spit had small territories and concentrated feeding within fewer patches of their territories. There was no apparent difference in the abundance of diurnally present piscivorous fish at the two study sites (though the Penguin Spit site is closer to the forereef so it is possible the area is affected more by transiting large predators such as sharks). Variation in the foraging behavior of some smaller reef prey species has been shown to be influenced by predator abundance (Madin et al. 2010a, Madin et al. 2010b), but we find little evidence here for those effects on the diurnal foraging habits of these large-bodied herbivores. In another study of a smaller (so presumably more vulnerable) species of parrotfish, we also found no evidence that predation risk effects diurnal foraging space use patterns (Davis et al. in prep). In contrast, there are strong differences among sites in the percent cover of mixed algal turfs (preferred food) and the biomass of conspecifics, which were both higher at Penguin Spit. We hypothesize that food resource abundance may have strong bottom-up influences on fish behavior and movement patterns, and that it is the abundance of this resource that also explains the high biomass of this species at Penguin Spit. Other research has shown that parrotfish populations can respond to temporal or spatial variation in their algal resources, resulting in positive relationships between biomass or production of algae and biomass of parrotfishes (Adam et al. 2011, Russ et al. 2015, Tootell and Steele 2015, Han et al. 2016). We propose that the combination of competitor abundance and large and abundant patches of preferred food results in the style of constrained, localized feeding that we documented at Penguin Spit. These hypotheses are further investigated in greater detail in Carlson et al. (in prep). Again, future studies should concentrate on the effects of these distinct foraging modes on coral-algal interactions.

Our results suggest that movement behavior of *C. microrhinos* is influenced by multiple drivers. Predation risk, reproductive behavior, oceanographic conditions, habitat characteristics, resource abundance, and competition all affect the movement behavior of *C. microrhinos* to various degrees, but importantly, these drivers affect movement at varying spatial and temporal scales. At the scale of the home range, movement of *C. microrhinos* is dictated by reproductive behavior that is spatially and temporally driven by oceanographic conditions (tides and currents) and by night sheltering behavior that is likely resulting from habitat selection related to in predator avoidance. At the scale of feeding territories, the spatial and temporal patterns of activity appear to be strongly related to resource abundances and competition. Because a high level of plasticity and context dependency are evident in the movement behaviors of these fish, we argue that proper application of animal movement data depends on an understanding of the underlying behaviors that influence movement over multiple spatial and temporal scales.

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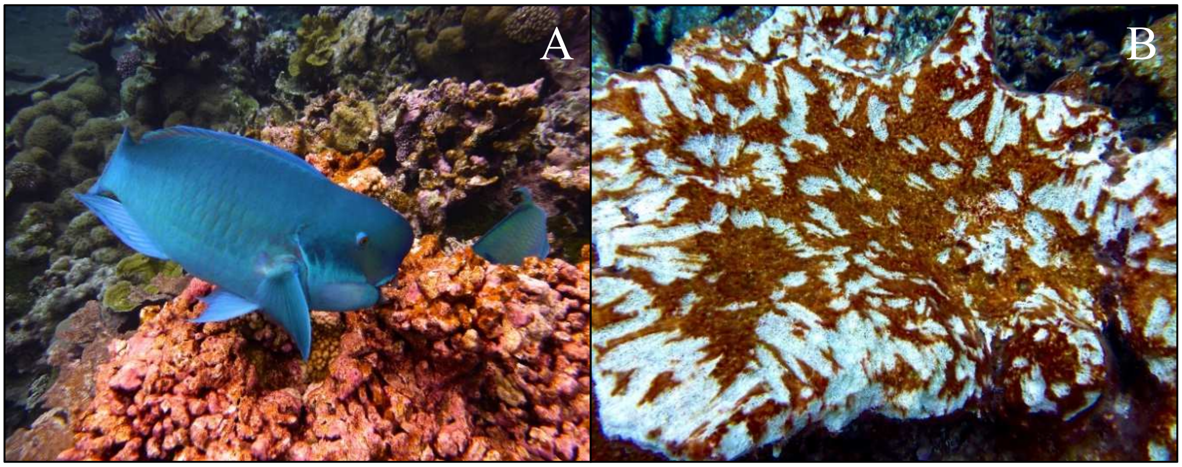


Figure 1: (A) A terminal phase *Chlorurus microrhinos* feeding. (B) feeding divots in red turf algae.

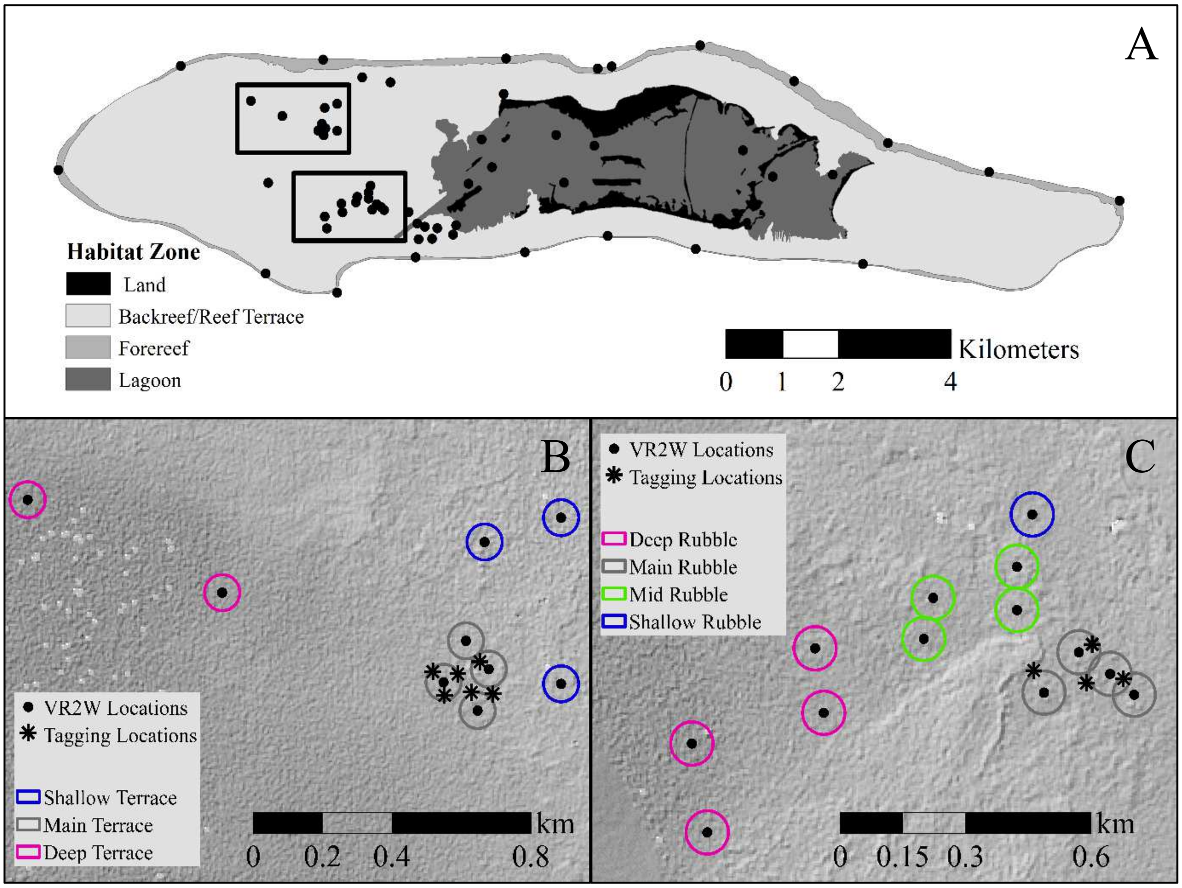


Figure 2: (A) Map of Palmyra Atoll habitat zones and VR2W receiver array. Rubblepile and Western Terrace areas are shown with black boxes. Black dots show locations of VR2W receivers. (B) VR2W configuration at the Western Terrace with bathymetry, (C) VR2W configuration at the Rubblepile with bathymetry. Asterisks indicate fish tagging locations. Colored circles indicate approximate receiver detection ranges (50 m). Pink circles indicate locations later described as offshore sites. Grey circles indicate diurnal foraging grounds. Green circles indicate transition zones between foraging grounds and offshore sites. Blue circles indicate shallow sites near night sheltering sites. Map layers: Gaia Geo-Analytical in collaboration with Davey Jones Locker GIS Laboratory, Oregon State University for Coral Reef Ecosystem Division, NOAA Pacific Islands Fisheries Science Center, Pacific Islands Benthic Habitat Mapping Center.

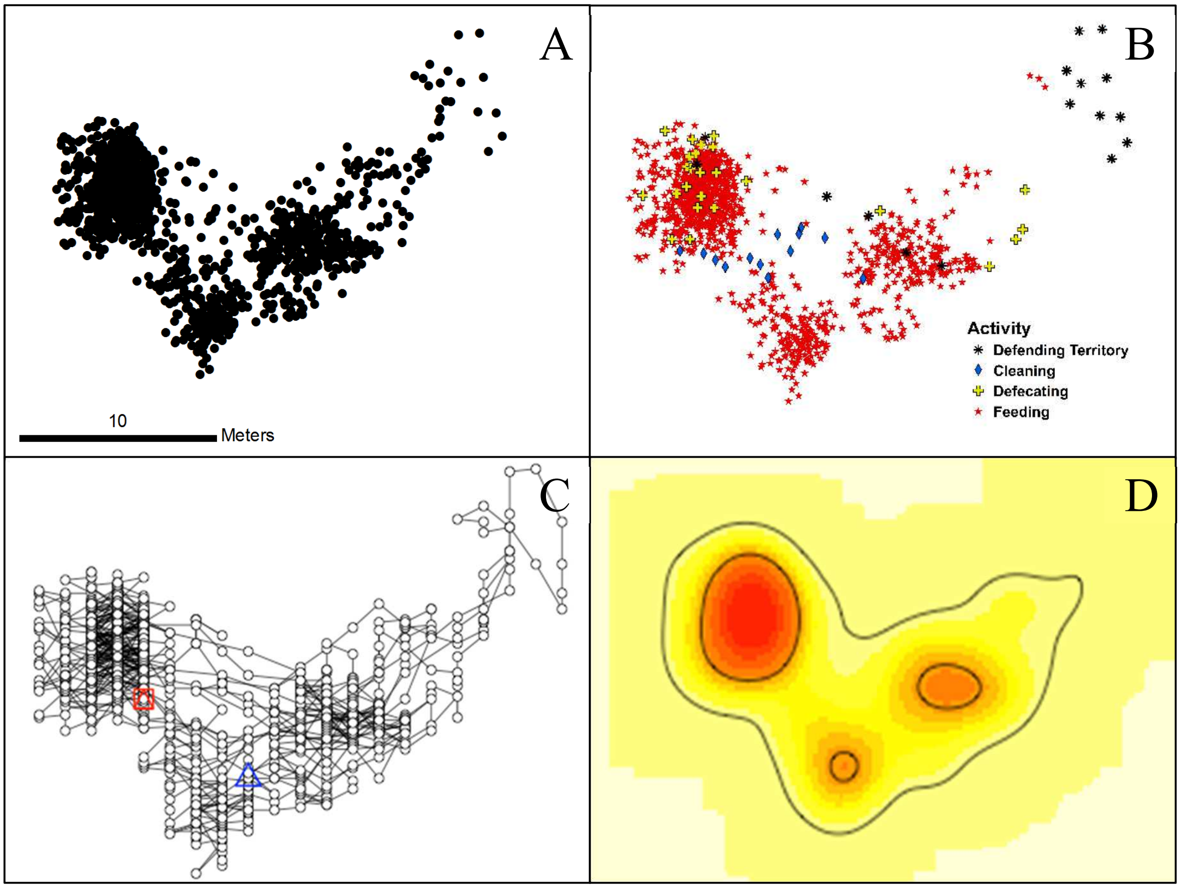
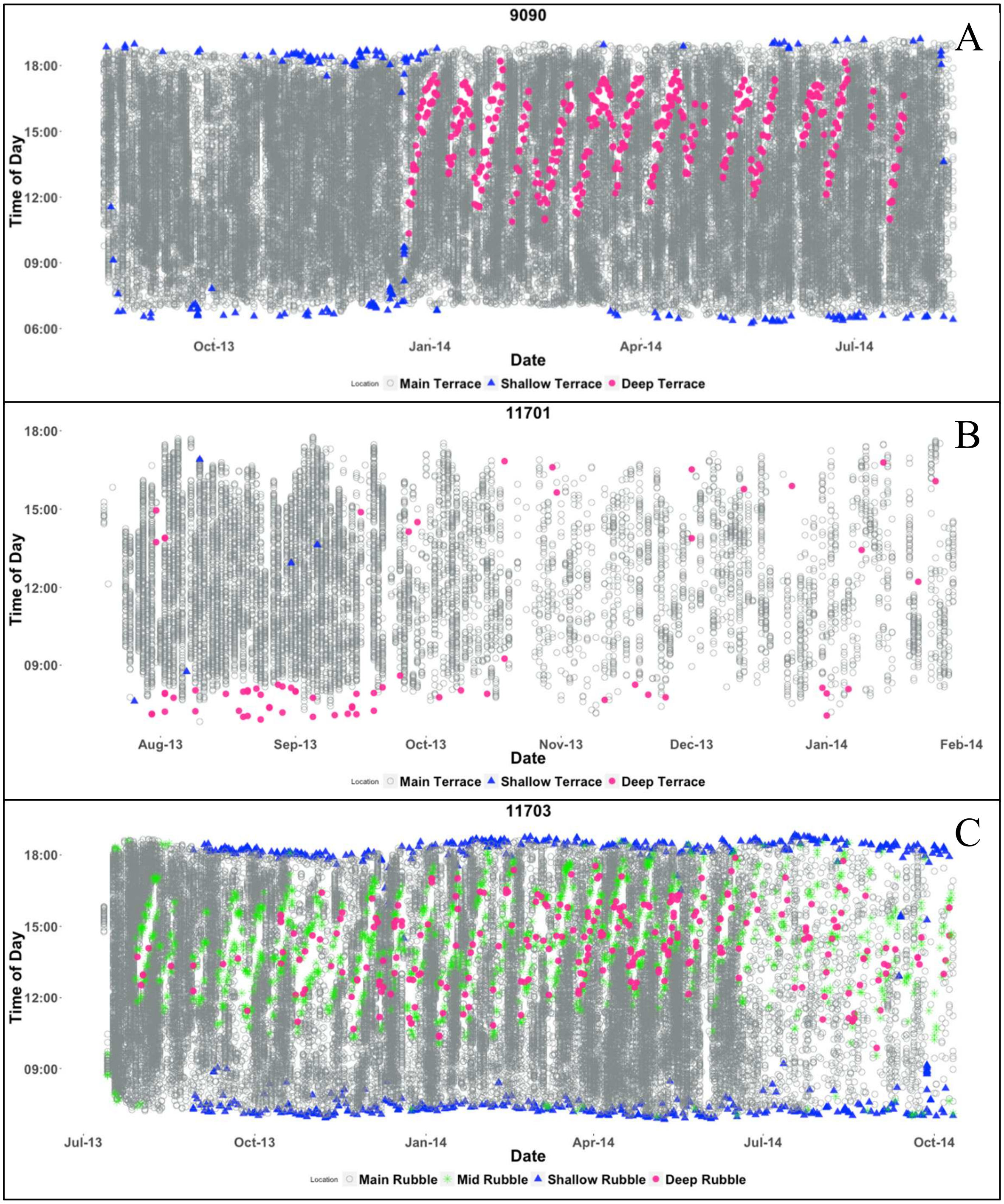


Figure 3: Example of biased random bridge method of kernel calculation. (A) Raw GPS location data for a two hour track of a fish at Penguin Spit projected in Universal Transverse Mercator Zone 3N, (B) points colored by activity, (C) trajectory of the fish, and (D) resulting kernel utilization distribution. Contours for the 50% and 95% utilization kernel are outlined in black.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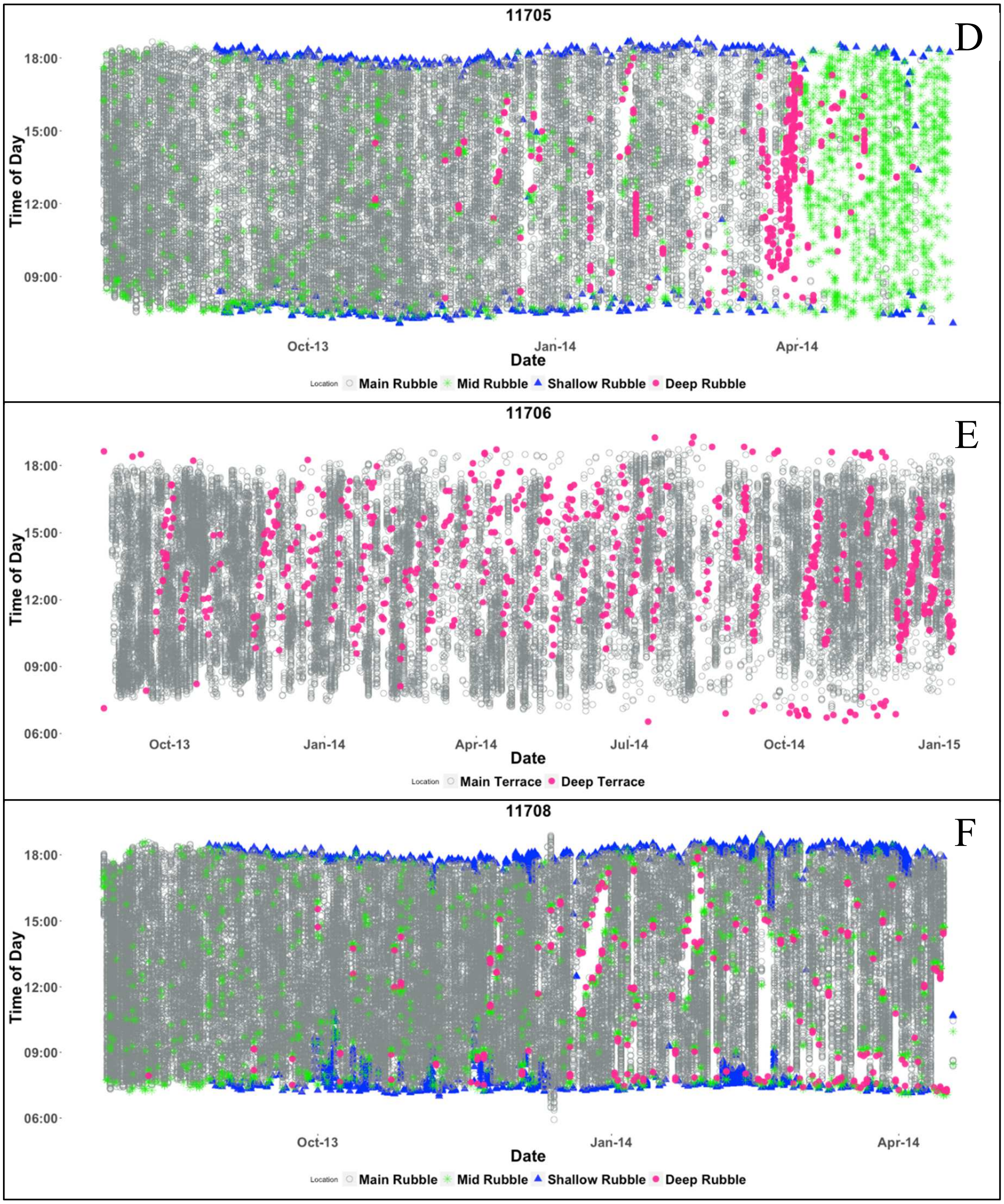
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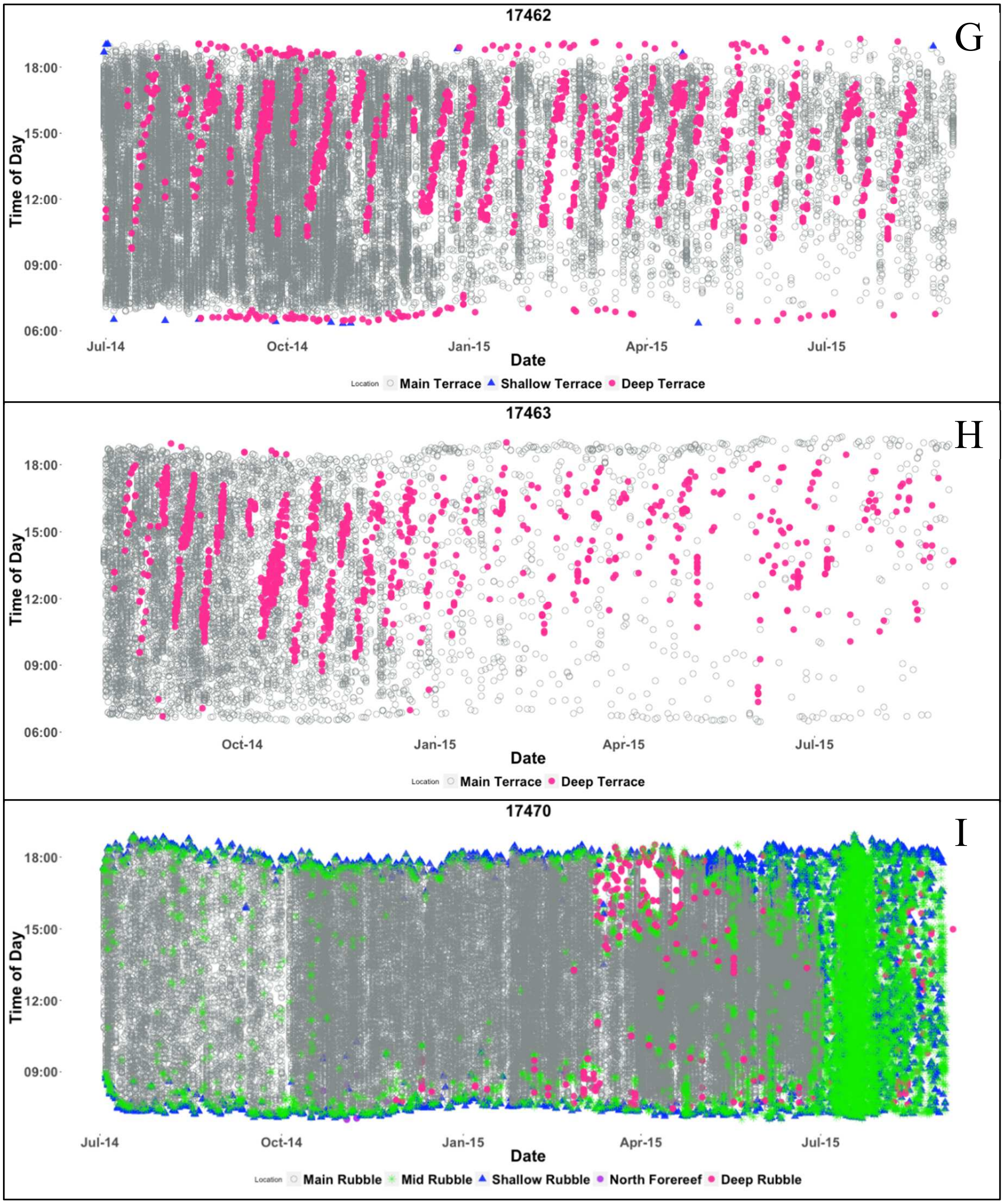


Figure 4: Raw VR2W detection data from each tagged fish. Each point is a detection logged at that specific date and time on a particular receiver. Colors correspond with the locations of receivers from the maps on Figure 2.

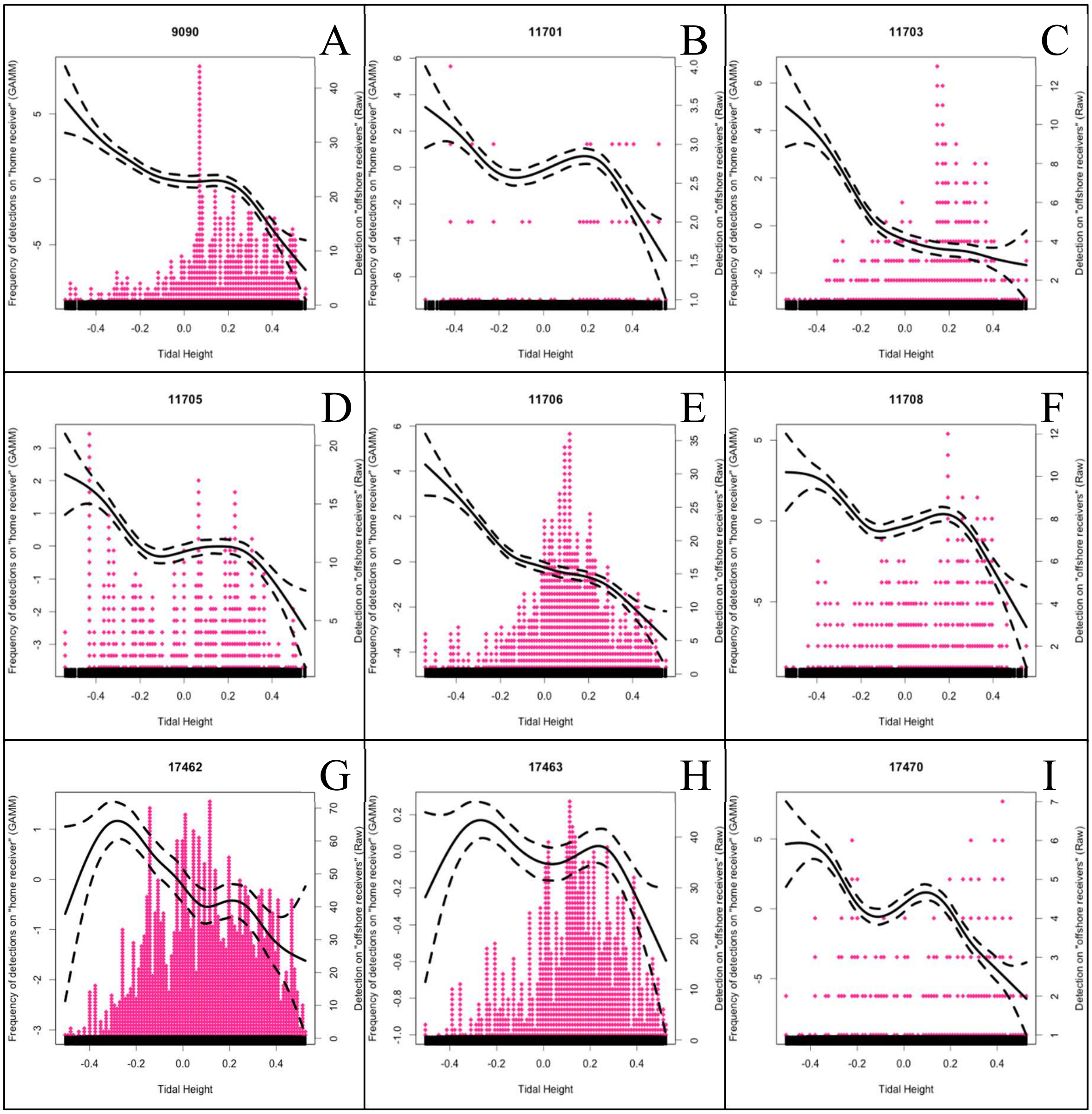


Figure 5: GAMM results for individual fish. X-axis shows tidal height measured in meters. The left axis and smoothed spline show frequency of detection at home receivers with tidal height. Right axis and raw data overlaid in pink show frequency of detection at offshore receivers. P-values for tidal height GAMM smooth terms and t-test comparing tidal height at offshore detections and null tidal height distributions respectively are as follows: A: <2e-16, <-2e-16; B: 5.55e-15, 1.99e-05; C: <2e-16, 9.35e-12; D: <2e-16, 0.0087; E: <2e-16, 2.2e-16; F: <2e-16, 4.68e-12; G: 1.03e-12, <2e-16; H: 0.00027, <2e-16; I: <2e-16, 1.02e-10. Letters correspond to the letters from the previous figure.

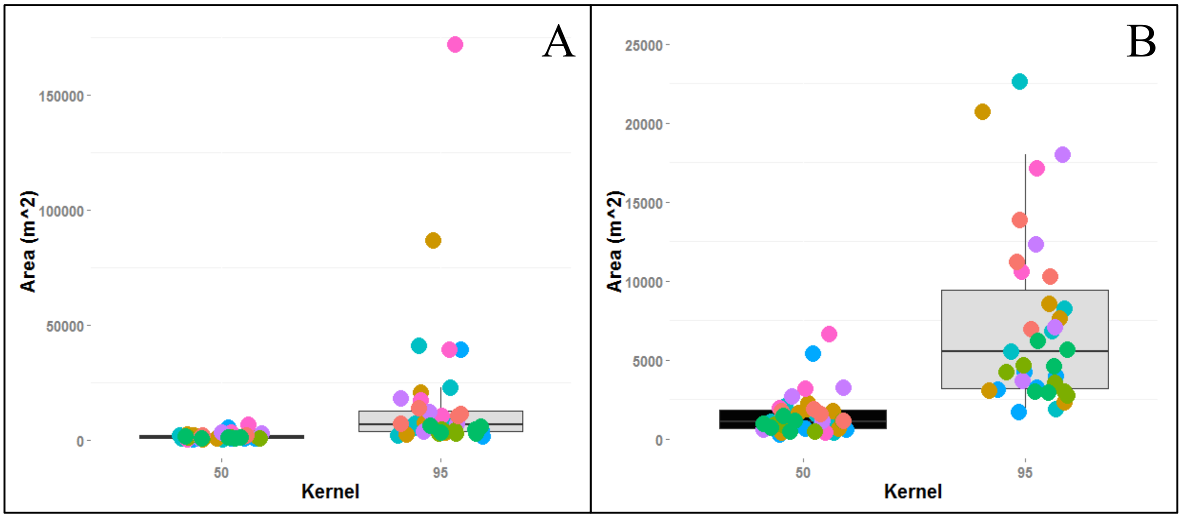


Figure 6: Boxplots showing the distribution of kernels calculated from each day of active tracking. Colors represent different individual fish. (A) All data including outliers showing all of the variability in the 95% kernel. (B) Data excluding the five largest 95% kernels so that the spread of the remaining data is visible. Boxplot hinges are first and third quartiles and whiskers are highest/lowest values within 1.5x the interquartile range.

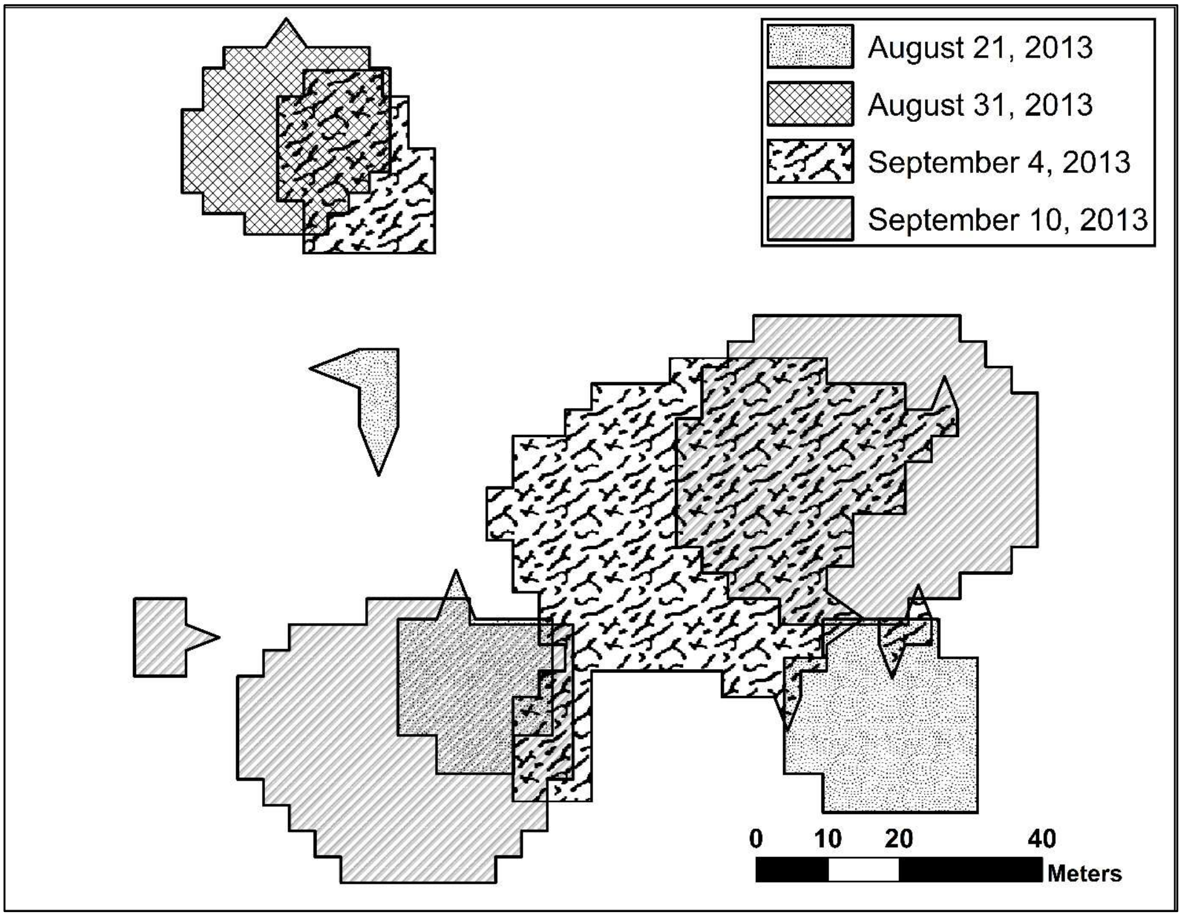


Figure 7: Example of 50% KUDs for one actively tracked fish (9090) on four tracking days.

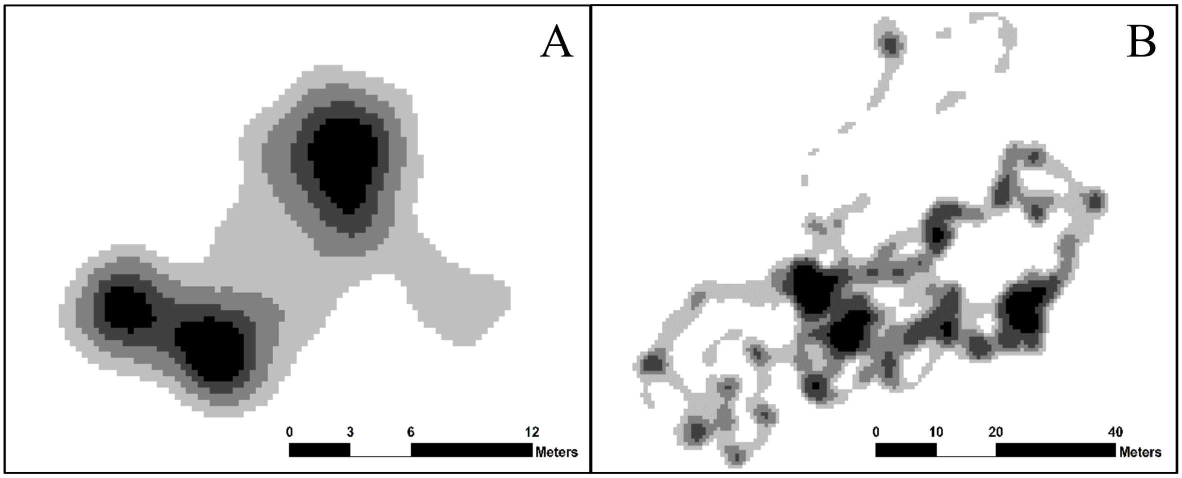


Figure 8: Kernel utilization distribution estimated from GPS tow data from a two hour track of a fish at Penguin Spit (A) and Western Terrace (B). Note the difference in scale bars.

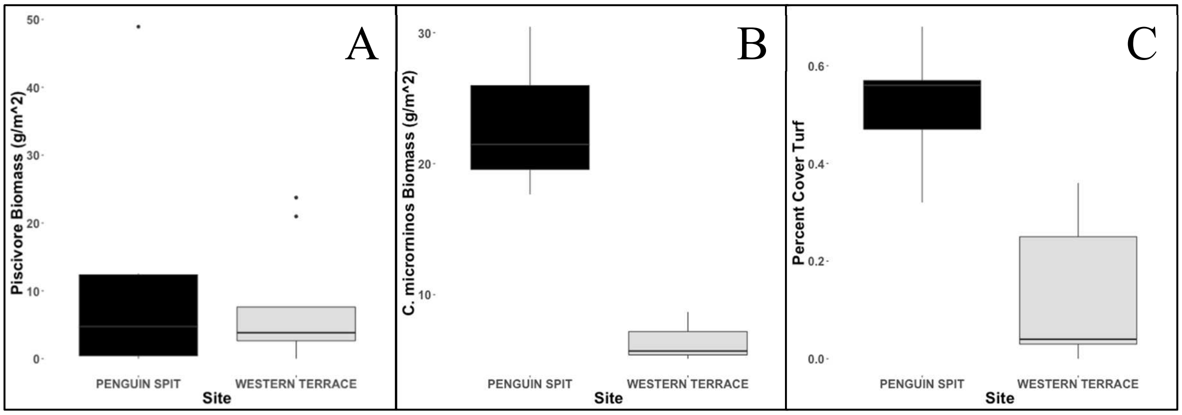


Figure 9: Boxplots showing site level differences in (A) piscivore biomass, (B) *Chlorurus microrhinos* biomass, and (C) percent cover turf at Penguin Spit and Western Terrace. Boxplot hinges are first and third quartiles and whiskers are highest/lowest values within 1.5x the interquartile range.

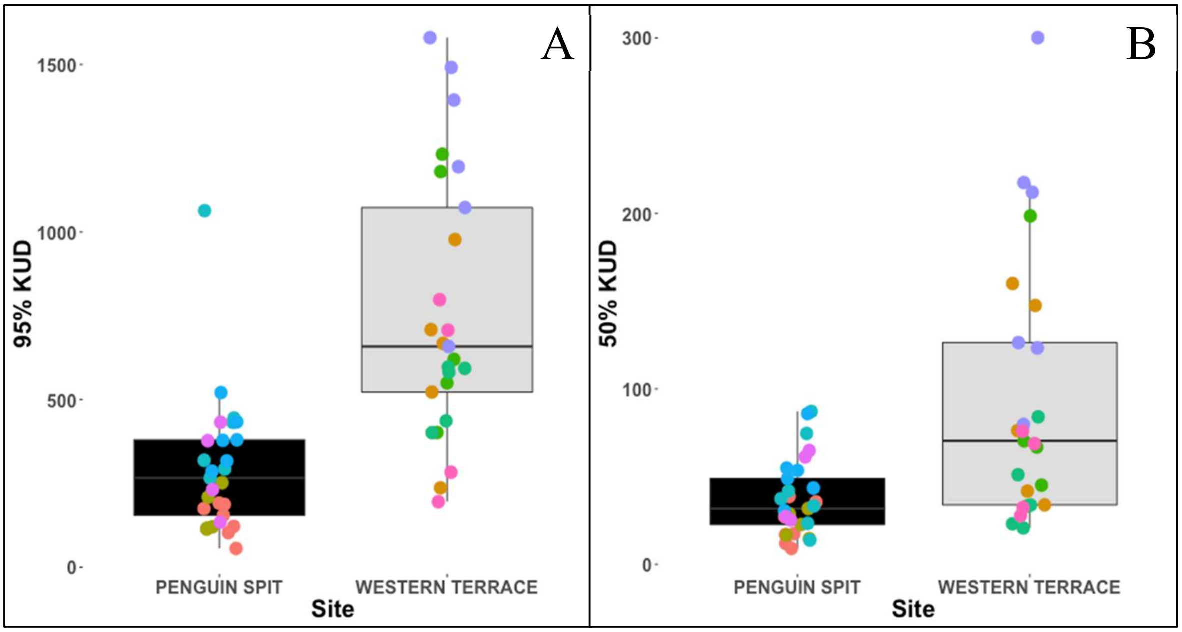


Figure 10: Boxplots showing site differences in (A) 95% and (B) 50% kernel areas for fish repeatedly tracked with GPS. Colors represent different individual fish. Boxplot hinges are first and third quartiles and whiskers are highest/lowest values within 1.5x the interquartile range.

Table 1: Summary of detections and tracking hours for each tagged fish. Asterisks indicate fish that still had an active tag when the final data was collected. Fish are named for their coded tag ID. Fish 10 only had an active tracking tag and no coded tag ID. Fish 11706 and 17463 only had coded tags and were not tracked. The remainder of fish were double tagged.

Fish ID	Color Phase	TL (cm)	Total VR2W Detections	VR2W Detection Duration (days)	# of VR2Ws Detected by	Active Tracking Hours	Tagging Site
9090	IP	50	47,467	362	6	41.5	Western Terrace
11701	TP	64	9709	195	7	39	Western Terrace
11703	IP	44	31,232	456	16	53	Rubblepile
11705	TP	43	28,161	316	15	44.5	Rubblepile
11706	IP	44	22,498	504	6	NA	Western Terrace
11708	TP	65	50,592	266	15	43	Rubblepile
17462	IP	41	28,966	430*	8	60	Western Terrace
17463	TP	62	8489	405*	7	NA	Western Terrace
17470	TP	39	61,120	430*	19	57	Rubblepile
Fish10	TP	62	NA	NA	NA	32.5	Western Terrace

Table 2: Summary of space use metrics derived from GPS follows, active tracking, and passive receiver data. Kernel data was computed per day or per observation as well as for in a combined metric for each fish.

Method	Spatial Metric	Mean Area ± SE
Focal Observation	Per observation 50% KUD	63 ± 8 m^2
Focal Observation	Per observation 95% KUD	512 ± 52 m^2
Focal Observation	Combined 50% KUD	162 ± 44 m^2
Focal Observation	Combined 95% KUD	1154 ± 246 m^2
Active Acoustic Tracking	Daily 50% KUD	1499 ± 206 m^2
Active Acoustic Tracking	Daily 95% KUD	15,850 ± 4714 m^2
Active Acoustic Tracking	Combined 50% KUD	2425 ± 294 m^2
Active Acoustic Tracking	Combined 95% KUD	28,524 ± 12,994 m^2
Passive Acoustic Monitoring	MCP	0.620 ± 0.342 km^2
Passive Acoustic Monitoring	MCP (excluding 17470)	0.279 ± 0.315 km^2

Appendix I: Acoustic tagging methods

We captured fish in large wall nets, then transferred them to soft mesh bags. Once a fish was secured in a bag, one diver would slowly ascend with the fish to the boat while a second diver would ascend and fill a large holding tank with ~150 L of seawater. We transfered the fish to the holding tank and begin pumping fresh seawater with a hand pump for the remainder of the holding time. We then drove offsite several hundred meters in order to minimize the attraction of predators due to spillage of water from the holding tank. We recorded the capture location coordinates, fish total length, standard length, and color phase, tag types, serial numbers, and frequencies, and any physical markings or features on the fish that would aid in future visual identification. One person held the fish in position for surgery with a chamois cloth with head and gills submerged and just a small amount of the underside exposed for surgery. We then used sterile forceps to remove two scales on the underside of the fish, just off of the midline between the pelvic fins and the anus. We used a sterile scalpel blade to make a small incision through the skin just large enough to insert the transmitters. We inserted a Vemco V9 continuous and/or coded transmitter (both in most cases) into the peritoneal cavity of the fish and performed two discontinuous surgical sutures to close the incision. We then returned to the capture site, and checked to ensure that there were no sharks in the area before we released the fish down into a crevice in the reef. Five frequencies are available in the V9 continuous active tracking tags (63, 75, 78, 81, 84 kHz) but there is potential for the 63 and 75 kHz tags to interfere with the 69 kHz coded tags transmitting to the VR2W receivers, so we did not use these frequencies within our receiver array. Thus we were limited to three frequencies per site at a given time. Tag life was approximately 69 days. We allowed at least four d for recovery from tagging before commencing tracking.

Appendix II: Range Testing

Methods

To range test the VR2W acoustic array we moored a Vemco V9 69 kHz coded test tag at 15, 30, 45, and 60 m from the moored VR2Ws at one m from the bottom. We then estimated the percent of expected detections for each distance position, calculated from the number of detections at that position and the transmission rate of the tag tested in the lab.

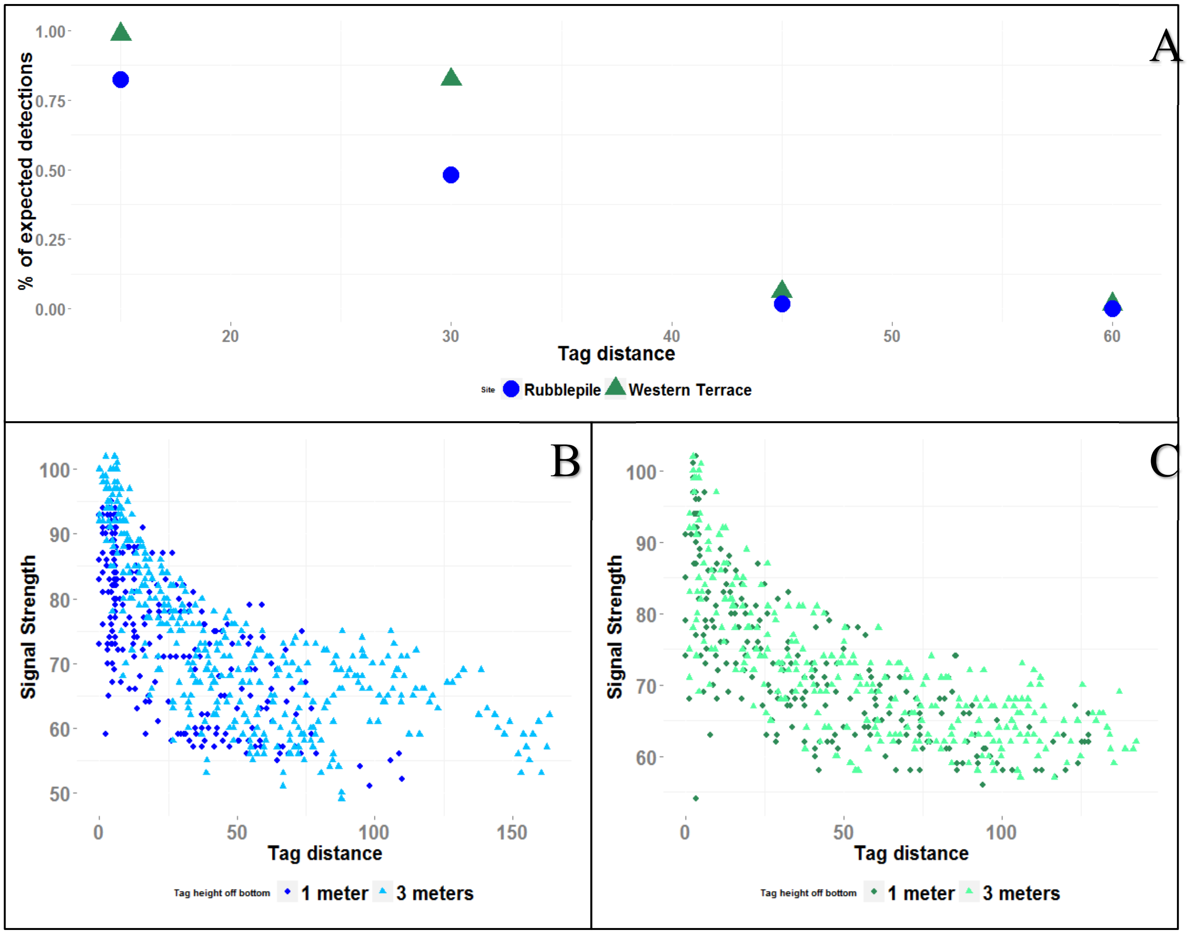
To range test the active acoustic tracking equipment at each tracking site we used a Vemco V9 continuous tag, 75 kHz, connected to a weighted float-line marked with a surface buoy. We ranged tested at each location at two tag heights: 1m off of the bottom (to mimic a tag inside of fish feeding on the benthos) and 3m off of the bottom (to mimic a tag inside of a fish swimming in the water column). For each test, we moored the tag and took a GPS recording of its position then drove the boat to a position out of detection range. Then we slowly drove the boat in a straight line toward the marker buoy with the directional hydrophone pointed at the buoy until reaching it. We drove 4 transects (from each cardinal direction) for each location and each tag height. Using the Point Distance tool in the Analysis toolbox in ArcGis we calculated the distance of each recorded detection to plot against signal strength.

Results

Consistent with the literature reporting typical detection ranges in highly complex coral reef environments (Welsh et al. 2012), our VR2W detection ranges were quite small. Detection rate dropped precipitously between 15 and 45 meters. At 15 meters distance the

Rubblepile and Western Terrace receivers recorded 82% and 98% of expected detections respectively. By 45 meters the detection rates had dropped to 1% and 6% respectively and at 60 meters to 0% and 1% respectively (Appendix Figure 1A). We did not test the Deep Terrace receivers but we hypothesize that the detection ranges in that location are slightly larger because the receivers are moored in deeper water and our observations indicate that the fish were engaging in behaviors that likely make them more detectable while offshore (e.g. swimming in the water column as opposed to benthic foraging). However with the small, low power transmitters that we used it is likely that detection ranges were consistently <100 meters.

Testing of the VR100 to estimate potential error in active tracking locations showed that the hydrophone was within just a few meters of the tag when the detection decibels read greater than 95 dB (our target lower threshold for recording a detection), even when the tag was fixed in the water column, three meters from the bottom (Appendix Figure 1B, C). This indicates that our positional error was relatively low (less than a few meters) when tracking fish in their shallow, highly complex diurnal foraging grounds. We also performed additional procedures to try to minimize our positional error including frequent visual confirmations of the position of the tagged fish, and slowly driving over the point of the highest signal until the signal dropped off indicating where exactly the fish was passed over.



Appendix Figure 1: Range testing results for the VR2Ws at both sites (A) and VR100 at the Rubblepile (B) and Western Terrace (C). Plots indicate the distance between the tag and the receiver and the percent of expected detections (A) or signal strength (B, C).

Appendix III: Tracking methods

We tracked fish at the same sites where we conducted the passive monitoring observations (n=4 fish per site). We tracked fish from a flat-bottom 16-foot outboard motor Carolina Skiff outfitted with a hydrophone bracket mount. We bolted a Vemco VH110 directional hydrophone to a 1-m section of PVC pole and inserted it into a pole bracket mounted to the side of the boat. The upper end of the PVC pole had an elbow joint and a perpendicular 30 cm piece of PVC that acted as a turning handle for the tracker. We plugged the hydrophone into a Vemco VR100 acoustic receiver that logged the location coordinates, time, frequency, signal strength, gain, and detection interval for each signal detected belonging to the preset frequencies. Approximately every ten minutes the tracker drove the boat slowly in the direction of the signal until the highest possible signal was detected and the detection strength was high from all directions. When the highest signal was achieved the tracker or an additional data recorder logged the time, coordinates, signal strength, compass heading, and depth. We generally only recorded a location when we could achieve at least 95 dB of signal strength to ensure that we were positioned above the fish. We made frequent visual confirmations (sometimes with a snorkeler and sometimes it was possible to see the fish from the boat without entering the water) that the fish was under the boat when signal strength was high, in addition to extensive range testing (see Appendix I for range testing methods and results). We also observed fish behavior when the boat was maneuvering overhead and did not perceive behavior that indicated that the fish were reacting to or avoiding the boat.

Appendix IV: Discussion of premature transmitter loss

Three scenarios that could have caused tags to stop being detected before the time expected from their estimated transmitter battery life include premature failure/ejection of the transmitter, emigration of the fish from the receiver array, or a mortality event. Transmitter failure is extremely uncommon (C. Lowe, personal communication) and Vemco reports malfunctioning transmitter return rates at less than 1% (Khan et al. 2015). Transmitter ejection is a possibility but we have not seen any reports of ejection from a live fish and our observations of fish several weeks post-tagging showed that tagging scars had all healed and appeared normal. Emigration from the receiver array is a potential explanation for the disappearance of a transmitter, and we did observe home range shifts for some individuals. However, each fish was detected on multiple receivers related to various activities within their home range so the spatial shift would have occurred for all activities in order for the fish to cease getting detected entirely. Mortality of the tagged fish is the most likely cause of tag disappearance. Because these disappearances happened at least a few months after tagging and we observed all fish to resume normal feeding and social activities after tagging, it is unlikely that tagging induced mortality was occurring. Khan et al. (2015) used passive receiver data to estimate potential mortality rates in adult coral reef herbivorous fishes (including some large bodied species) and estimated a mortality rate of 59% of individuals per year. They concluded, based on the specifics of the transmitter disappearances, that many of these mortality events were best explained by predation. In a large bodied species like *C. microrhinos*, it is likely that predation-induced mortality would be lower than for smaller species, but Palmyra is a predator-heavy system and it is possible that some predation may have occurred.

Appendix V: Aggregations of *C. microrhinos* on the North Forereef