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# Parrotfish movement patterns vary with spatiotemporal scale

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ABSTRACT: Herbivorous fishes are being increasingly valued for their ecological function in coral reef systems, and consequently they have become the focus of management actions on many reefs around the world. Because many conservation actions require an understanding of the space use patterns of species of interest, there has been an increased effort in recent years to study the movement patterns and home range sizes of many herbivorous taxa. Also of great interest are the fine-scale foraging patterns of parrotfishes and the spatial and temporal scale of their interactions with benthic organisms. In this study, we performed a comprehensive evaluation of the movement patterns of the parrotfish *Chlorurus microrhinos* at multiple spatial and temporal scales at Palmyra Atoll in 2013–2015. We found that these fish have large home ranges when accounting for migrations to spawning and night refuge sites, but that within feeding territories, their activity is highly non-random and is quite spatially constrained and temporally episodic, indicating a high level of feeding selectivity. These patterns of foraging activity result in the patchy removal of algae from the reef, which may have consequences for the space competition between algae and corals.

KEY WORDS: Space use · Telemetry · Parrotfish · Herbivory · Coral reef · Palmyra Atoll

## INTRODUCTION

Animal movements generally consist of directed responses to social and environmental cues, resulting in space use patterns that represent trade-offs between energy acquisition, survival, and reproduction (Lowe & Bray 2006) and directly linking movement patterns to individual fitness outcomes (Liedvogel et al. 2013). Animal movement data are critical for effective management and conservation (Allen & Singh 2016, Crossin et al. 2017) and can reveal patterns of important biological interactions between species (Westcott & Graham 2000, Fortin et al. 2005, Owen-Smith et al. 2010). Movement patterns and behaviors can be complex and vary strongly through ontogeny and across seasons (van Beest et al. 2011, Welsh et al. 2013). Thus, a snapshot view of animal movements at a given time point will be limited in its ability to explain the complex suite of biological interactions that influence movement over multiple spatial and temporal scales (e.g. Damgaard & Weiner 2017).

Parrotfishes (Family Labridae) have complex social and mating systems (Robertson & Warner 1978, Warner 1984) and their space use patterns can be tightly connected to interactions between their social status and environment (van Rooij et al. 1996, Mumby & Wabnitz 2002, Afonso et al. 2008b). Space use is partially governed by reproductive strategy, which ranges from pair spawning within a territory to migrations to group spawning sites (Buckman & Ogden 1973, De Girolamo et al. 1999, de Mitcheson & Colin 2012) and can even vary within a given species or population (Afonso et al. 2008b). Some species are highly site-attached (Ogden & Buckman 1973, van

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Rooij et al. 1996, Welsh & Bellwood 2012b, Howard et al. 2013), which may be explained by the predictable regeneration of resources, and habitat and resource partitioning among competitors (Mumby & Wabnitz 2002, Clements et al. 2016, Carlson et al. 2017, this volume). Other species exhibit both territorial and schooling behaviors (Afonso et al. 2008a, Welsh & Bellwood 2012a), the latter of which can also have a variety of fitness benefits (Robertson et al. 1976, Clifton 1991, DeMartini et al. 2011). The strong contrast in movement behaviors across the parrotfishes demonstrates potential benefits of this behavioral plasticity, in that there are clear trade-offs between these behaviors that can affect risk, energetic rewards, and reproductive success.

Over the past several decades, there has been a growing recognition of the ecological importance of herbivorous fishes, and they are now widely thought to be important mediators of competition between corals and algae on reefs (Bellwood et al. 2004, Mumby 2006, Hughes et al. 2007, Jackson et al. 2014), leading to targeted management of these taxa in many regions of the world. One of the most commonly employed conservation strategies for marine organisms is the application 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 safeguard individuals effectively (Lowe et al. 2003, Lowe & Bray 2006). In fact, most studies describing home ranges of tropical herbivorous fishes have been reported in the context of designing or evaluating a specific MPA (Eristhee 2001, Meyer & Holland 2005, Afonso et al. 2008a, Chateau & Wantiez 2009, 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 criteria for reef managers who are designing MPAs to protect specific taxa or functional groups (Kramer & Chapman 1999, Green et al. 2015, Nash et al. 2015). However, significant plasticity 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 study systems (Meyer & Holland 2005, Hardman et al. 2010). 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, and most studies to date do not delineate activities across home ranges. 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.

Variation in space use and the fine-scale distribution of grazing activities of coral reef fishes across reef habitat is related to a number of factors, including benthic composition (Nash et al. 2012, 2016, Tootell & Steele 2016, Carlson et al. 2017), competition (Mumby & Wabnitz 2002, Nash et al. 2012, Davis et al. 2017), and predation risk (Madin et al. 2010a). Variation in grazer abundance and identity both impact, and are impacted by, the distribution of resources across habitats (Williams et al. 2001, Hoey & Bellwood 2008, Russ et al. 2015), and space use patterns of individual grazers can also shape patterns of algal distribution (Madin et al. 2011). Recent compelling evidence indicates that large parrotfishes in particular may target autotrophic bacteria living on and within the calcareous reef substrate as their main source of protein, and that they preferentially target early successional pioneer species (Clements et al. 2016). Removal and consumption of algae that have been conventionally understood to be the primary food sources for these species may thus be somewhat incidental (though the feeding process results in the removal of algae from the reef regardless of whether the algae are the primary nutritional targets). These concepts are consistent with observations of population-level responses of parrotfishes that have been shown to increase in abundance after localized disturbances which cause decreases in coral cover (Adam et al. 2011, Russ et al. 2015). Rapid and predictable regeneration of nutritional resources could have a major influence on movement behaviors of individual parrotfishes as well, potentially resulting in fine-scale patterns of grazing that are highly non-random across space and time. This may, in turn, have a significant impact on spatial distributions of benthic species and large-scale benthic processes. Specifically, 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 influenced by the spatial distribution and temporal stability of feeding by the grazers in the system (Sandin & McNamara 2012, Eynaud et al. 2016).

In this study, we aim to quantify the movement patterns of *Chlorurus microrhinos*, a large-bodied, excavating Pacific parrotfish. This species is one of the dominant contributors to calcium carbonate bioerosion on Pacific coral reefs (Bellwood 1995a), and its large size means that it is particularly important to rates of algal removal from reefs, because parrotfish bite size scales non-linearly with body size (Lokrantz et al. 2008). Their bite scars, which are relatively large compared to those of other parrotfish species, can remain free of algae and sediment for several days, potentially increasing settlement habitat for other benthic space competitors (Bonaldo & Bellwood 2009, Carlson et al. 2017). *Chlorurus microrhinos* shows a strong preference for biting on substrate covered in algal turfs (Bellwood 1995b, Carlson et al. 2017); turfs, in turn, can have deleterious effects on living corals (Smith et al. 2006) and inhibit coral settlement (Ritson-Williams et al. 2009). In contrast, this species shows avoidance for biting calcareous red algae (Bellwood 1995b), some species of which are known to enhance coral settlement and post-settlement survivorship (Heyward & Negri 1999, Harrington et al. 2004). These physical and behavioral traits likely make this species of parrotfish an important moderator of space competition between corals and algal turfs on reefs.

Our multi-scale approach to evaluating the space use patterns of *C. microrhinos* utilizes 3 methods: (1) long-term passive acoustic monitoring to capture coarse-scale movements at the scale of kilometers over the course of months to years; (2) active acoustic tracking to characterize short-term, fine-scale (~5–10 m resolution) diurnal movement patterns; and (3) repeated behavioral observations consisting of mapping of spatially explicit activity distributions to determine the patterns of utilization intensity at the meter scale. Exploring the patterns of movement across multiple spatiotemporal scales provides a more comprehensive understanding of how biological and environmental drivers may interact to structure space use by these ecologically important animals, and enhances our understanding of the spatiotemporal patterns of interactions between this grazer and coral reef benthic biota.

## MATERIALS AND METHODS

### Study species

*Chlorurus microrhinos* is a large-bodied parrotfish that is abundant and widely distributed across the tropical Pacific (Choat et al. 2012). *C. microrhinos* primarily bite on substrates colonized by low-lying algal turfs (Bellwood 1995b, Hamilton et al. 2014, Carlson et al. 2017), scraping algae and other material from dead coral substrates and excavating large divots in surface algae and underlying calcium carbonate structure. This species is a sequential protogynous hermaphrodite (Randall & Choat 1980, Choat & Randall 1986), and males can be identified by their large size and coloration of the pectoral fin; otherwise it is difficult to visually distinguish between the sexes in this species (Ebisawa et al. 2016). Little has been published about their reproductive habits, except a report by Johannes (1981) that the species often aggregates to spawn at the edges of promontories on outer reef slopes and observations by Colin and Bell (1991) of group courtship with one observation of spawning directly after an afternoon high tide. Our observations of the social behaviors of *C. microrhinos* at diurnal feeding sites were mostly consistent with other observations (Welsh & Bellwood 2012b), in that they forage in social groups, with a large male associated with several smaller individuals within a shared home range (authors' pers. obs.).

### Study sites

We conducted this study at Palmyra Atoll (5° 53′ N 162° 5′ W; Fig. 1A) in the summers (July–September) 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 except during 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 1 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. 2016). 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 intact predator (Sandin et al. 2008, Bradley et al. 2017) and herbivore (Edwards et al. 2014) communities. The atoll consists of 3 large lagoons flanked by long, open reef terraces that extend to the east and west with a very gradual slope for 4–5 km before dropping off sharply at 20–30 m (Williams et al. 2013). The backreef habitats in Palmyra referenced here are somewhat dissimilar to typical lagoonal backreefs of other islands in the Pacific in that they are open to deeper water through the sloping terraces and they are generally made up of contiguous reef.

We performed an acoustic telemetry study at 2 sites on the shallow western reef of the atoll: Western Terrace (Fig. 1C) and Rubble Pile (Fig. 1D). The 2 sites are similar in depth range and structural complexity, but differ in benthic assemblage. The Rubble Pile 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*, which

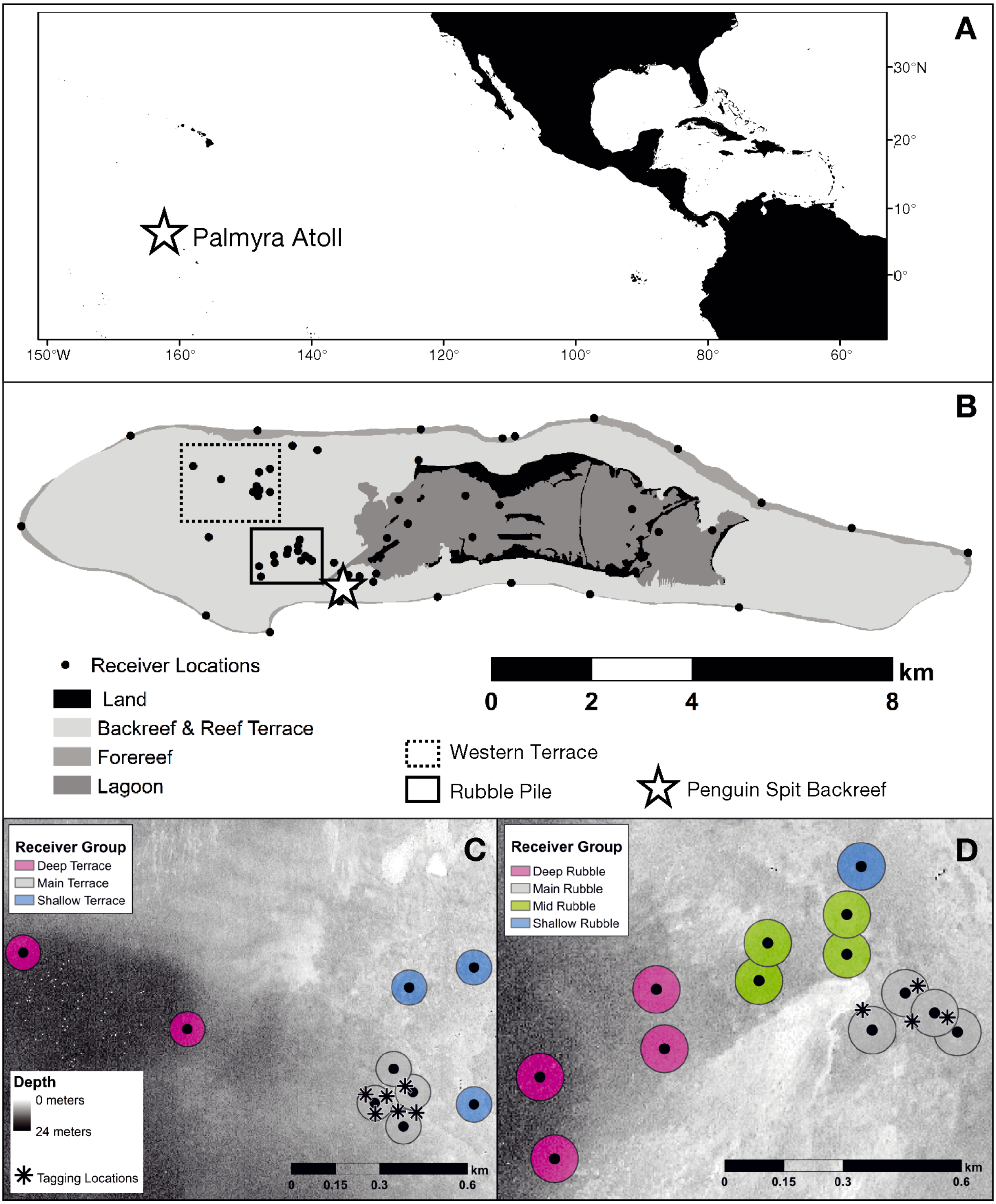

Fig. 1. Location of (A) Palmyra Atoll in the Pacific Ocean, (B) Palmyra Atoll habitat zones and VR2W receiver array and study locations, (C) VR2W configuration at the Western Terrace with bathymetry, and (D) VR2W configuration at the Rubble Pile with bathymetry. Asterisks indicate fish tagging locations. Colored circles indicate approximate receiver detection ranges (60 m). Map layers: bathymetry data are from NOAA ship 'Hi'ialakai' and R/V 'AHI' multibeam bathymetry, and IKONOS image is by Space Imaging. Benthic habitat map is from the National Centers for Coastal Ocean Science Data Collections at NOAA

has recently (beginning around 2005) increased in abundance and killed substantial amounts of living coral in some parts of the western terrace near the site of the wreck of a longline fishing vessel (Work et al. 2008). There is a high level of structural complexity from a combination of dead coral skeletons and living corals, and dead corals are colonized by a combination of algal turfs, macroalgae, and corallimorphs. The Western Terrace site has high cover of living coral and crustose coralline algae (Carlson et al. 2017) and is similarly structurally complex. We performed visual behavioral observations at the Western Terrace and an additional site, Penguin Spit Backreef (Fig. 2B). Penguin Spit Backreef lies in the southwestern backreef of Palmyra, between a dredged channel and inside of the reef crest. The southwestern backreef habitat was particularly affected by the bleaching associated with the El Niño–Southern Oscillation events of 1998 and 2009, resulting in a shift in benthic community structure (Williams et al. 2010). Currently, the site has a high percent cover of red algal turf, which is the primary benthic type bitten by *C. microrhinos* (Bellwood 1995b, Hamilton et al. 2014), and is the preferred substrate type targeted by the species in Palmyra (Carlson et al. 2017). 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 very high density of large males, and small individuals were rare. Unlike the social system we observed at our other sites, at Penguin Spit Backreef the large males mostly maintained small individual territories (authors' pers. obs.).

### Passive acoustic monitoring

To assess the large-scale (km) movements, long-term (~1 yr) site fidelity, and seasonal variation in movement patterns of *C. microrhinos*, we implanted a total of 9 individuals with coded transmitters (Vemco, V9-2L, 29 mm long × 9 mm diameter, 4.7 g in air, 2.9 g in water, nominal delay 120 s, battery life 484 d, power output 145 dB, 69 kHz) in 2013 and 2014 (for tagging procedures and tag specifications, see Supplement 1 at www.int-res.com/articles/suppl/m577p149_supp.pdf, this link applies for all supplements herein). The transmitters are programmed to transmit every 2 min 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 receiver's detection range. The receiver stores the identity of the transmitter with the date and time (h:min) of the transmission. The detection range for both Rubble Pile and Western Terrace was roughly 60 m, although detection efficiency dropped to a low level beyond approximately 30 m (see Supplement 2 for detailed range testing methods and results).

We maintain a large array of Vemco VR2W receivers at Palmyra Atoll (Weng et al. 2015). We increased the receiver array (from that shown in Weng et al. 2015) at the Western Terrace with 5 receivers placed 100 m apart in 2013 (Fig. 1C), 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 & Bellwood 2012b). An extensive, high-density VR2W receiver array of 11 receivers spaced between 100 and 300 m apart was already in place at Rubble Pile (Fig. 1D). 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, for a total of 9 receivers at Western Terrace and 13 receivers at Rubble Pile, including their respective offshore areas.

### Active acoustic tracking

To characterize the daily movement patterns of *C. microrhinos*, we also surgically implanted 8 of the above-described individuals with continuous transmitters (Vemco, V9, 21 mm long × 9 mm diameter, 4.7 g in air, 2.9 g in water, battery life 69 d, power output 145 dB) that transmitted with a 2 s interval at a specified frequency (78, 81, or 84 kHz). We recorded a location for each fish roughly every 10 min throughout tracking days from approximately 06:20 to 18:10 h for each track in accordance with the Palmyra Station operation regulations. We tracked each fish for 3 to 6 full tracking days spread out over a 4 to 8 wk 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 Supplement 3 for detailed tracking methods).

### Visual behavioral observations

To characterize the fine-scale spatial and temporal patterns of feeding territory sizes and grazing inten-

Table 1. Summary of detections and tracking hours for each tagged fish. Fish are named for their coded tag ID (except Fish 10, which only had an active tracking tag and no coded tag ID). Fish 11706 and 17463 only had coded tags and were not actively tracked. The remainder of fish were double tagged. TL: total length; NA: not applicable

| Fish ID | TL (cm) | VR2W |  |  | Active tracking (h) | Tagging site |
|---|---|---|---|---|---|---|
|  |  | No. of detections | Duration (d) | No. detected by |  |  |
| 9090 | 50 | 47 467 | 362 | 6 | 41.5 | Western Terrace |
| 11701 | 64 | 9709 | 195 | 7 | 39 | Western Terrace |
| 11703 | 44 | 31 232 | 456 | 16 | 53 | Rubble Pile |
| 11705 | 43 | 28 161 | 316 | 15 | 44.5 | Rubble Pile |
| 11706 | 44 | 22 498 | 504 | 6 | NA | Western Terrace |
| 11708 | 65 | 50 592 | 266 | 15 | 43 | Rubble Pile |
| 17462 | 41 | 29 989 | 542 | 8 | 60 | Western Terrace |
| 17463 | 62 | 9125 | 533 | 8 | NA | Western Terrace |
| 17470 | 39 | 75 181 | 543 | 19 | 57 | Rubble Pile |
| 10 | 62 | NA | NA | NA | 32.5 | Western Terrace |

sity, we conducted repeated visual behavioral observations of individual *C. microrhinos* throughout the summer of 2014. We identified individuals with adjacent territories at 2 sites (Western Terrace and Penguin Spit Backreef, n = 5 individuals per site) and conducted observations on the same individual for a minimum of 5 times spread over 2 mo. We restricted observations to large males 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, which logged a location every 5 s (Nanami & Yamada 2008, Howard et al. 2013). With a watch synchronized to the GPS unit, the observer recorded the start and end times of each bout of feeding, defecating, cleaning (by cleaner wrasses), and territorial disputes. We then used these georeferenced activity locations to create activity maps for each track. Observations were 2 h in duration and were randomized across time of day to account for any diel changes in activity.

## 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 100% minimum convex polygons (MCPs) for each fish to characterize space use over the study period (~1 yr).

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 reef that appeared to track 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 (Papastamatiou et al. 2015). We selected a 'home receiver' for each tagged fish based on the number and consistency of detections recorded by each VR2W for a given individual. We then calculated the number of detections per hour at the 'home receiver' as the response variable to identify periods of time when fish were leaving their home foraging grounds, potentially to travel to spawning grounds. We used hourly measured tide data (Rogers 2015, Rogers et al. 2016) 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 h (when 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 control, because accumulation over time of fouling organisms has been demonstrated to decrease the detection ability of a VR2W (Heupel et al. 2008), and our receivers often become 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 packages (Pinheiro et al. 2007). We also conducted Welch's 2-sample *t*-tests for each individual fish to test for differences between the tidal height corresponding with offshore receiver detections and a null distribution of all tidal heights from the measured tide data.

### 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. 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; thus 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. Ninety-five percent kernels are often used to characterize overall activity space and 50 % kernels are used to characterize areas of core use for herbivorous fishes (Meyer & Holland 2005, La Mesa et al. 2012, Welsh & Bellwood 2012b), and we report them as such here. We computed kernel metrics both for individual observations (GPS tracks) and tracking days (acoustic tracks) and as a combined metric with all tracks for each fish (Table 2).

Table 2. Summary of space use metrics derived from GPS tracks, active acoustic tracks, and passive monitoring (fixed acoustic receivers) data. Kernel utilization distribution (KUD) data were computed per day (acoustically tracked fish) or per direct visual observation (GPS-tracked fish) as well as for a combined metric for each tracked fish for both methods. Passive acoustic monitoring data were used to calculate 100 % minimum convex polygons (MCPs)

| Method | Spatial metric | Area (mean ± SE) |
|---|---|---|
| Visual observation (GPS) | Per observation 50 % KUD | 63 ± 8 $m^2$ |
| | Per observation 95 % KUD | 512 ± 52 $m^2$ |
| | Combined 50 % KUD | 162 ± 44 $m^2$ |
| | Combined 95 % KUD | 1154 ± 246 $m^2$ |
| Active acoustic tracking | Daily 50 % KUD | 1499 ± 206 $m^2$ |
| | Daily 95 % KUD | 15850 ± 4714 $m^2$ |
| | Combined 50 % KUD | 2425 ± 294 $m^2$ |
| | Combined 95 % KUD | 28524 ± 12994 $m^2$ |
| Passive acoustic monitoring | MCP | 0.620 ± 0.342 $km^2$ |
| | MCP (excluding 17470) | 0.279 ± 0.315 $km^2$ |

### Visual behavioral observations

We tested for differences in fine-scale space use between sites with linear mixed effects (LME) models, incorporating the individual fish as a random effect. We compared null models without site to models including site to test for a 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 and 504 d (Table 1) and were detected on 95–100 % of the days within their detection duration (i.e. time of tagging to time of last detection, most were 100 % of days). A few transmitters stopped being detected well before the expected transmitter battery life (see Supplement 4 for discussion). Tagged fish displayed strongly diurnal activity patterns (for examples, see Fig. 2A,B; for data from all fish, see Supplement 5). Overall, the VR2Ws recorded 288 234 detections of our 9 tagged individuals, and there were zero detections logged between the hours of 19:18 and 05:56 h. All fish tagged at the Rubble Pile site were detected at a shallow receiver (Fig. 1D, 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. Most fish tagged at the Western Terrace site were also detected at shallow receivers inshore and north of foraging grounds (also roughly 500 m, shown in blue in Fig. 1C) in the early mornings and evenings, indicating that they were swimming past on the way to and from night refuge sites. A few fish appeared to have a shift in home

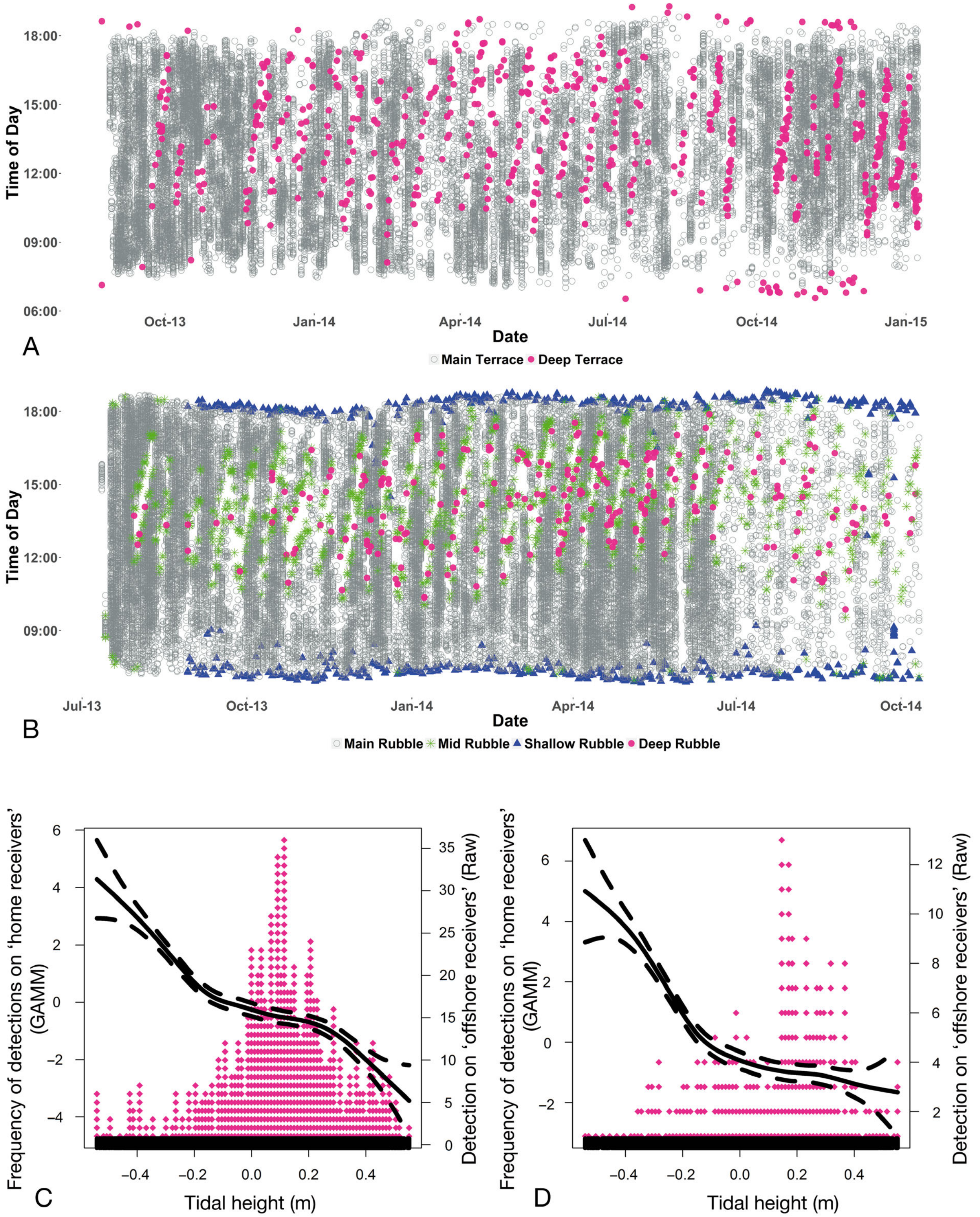

Fig. 2. (A,B) Examples of raw VR2W detection data from 44 cm fish at (A) Western Terrace (Fish 11706) and (B) Rubble Pile (Fish 11703). Each point is a detection logged at that specific date and time on a particular receiver. Colors correspond with the locations of receivers from the maps in Fig. 1. (C,D) Examples of GAMM results for corresponding fish in (A) and (B), respectively. The left axis and smoothed spline show frequency of detection at home receivers with tidal height with a 95% confidence interval shown with the dashed line. Right axis and raw data overlaid in pink show frequency distribution of detection at offshore receivers. Probability values for tidal height GAMM smooth terms and *t*-test comparing tidal height at offshore detections were <<0.001

range over the course of the study, indicated by either a reduction in overall detection rate or a shift in detections to a different set of receivers (see Supplement 5).

Visual inspection of the detection data showed that all individuals make repeated excursions past receivers >1 km west of their foraging grounds into deeper regions of the terrace (Fig. 1C,D, receivers shown with dark pink circles). For some fish, these excursions appeared to track tidal cycles because the excursion occurred roughly 1 h 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. There were no apparent seasonal patterns to the offshore visitation frequencies, at least over the duration of the observations. However, tidal height was a highly significant predictor of detection frequency on the 'home receiver' for all tagged fish (for examples, see Fig. 2C,D; for data from all fish, see Supplement 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 tide periods. With one exception (ID 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 (Fig. 2C,D).

Mean MCPs calculated from VR2W detections ranged from 0.12 to 3.35 km$^2$ (Table 2). Note that one individual (ID 17470) had an MCP home range that was an order of magnitude larger 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 hours throughout October and November 2014 (all of the other detections from all fish throughout the study were logged only on receivers on the reef terrace). This distant forereef site, over 2 km from the fish's foraging site, is a location where we have witnessed spawning aggregations of multiple species of parrotfish. Remotely deployed video systems have also captured *Chlorurus microrhinos* in large aggregations at this site displaying pre-spawning behavior (D. Bradley unpubl. data, Supplement 6).

### Active acoustic tracking

Ninety-five percent kernel activity spaces calculated from active acoustic tracking ranged from 4860 to 117 480 m$^2$. Fifty percent kernel core use areas ranged from 1129 to 3924 m$^2$ (means reported in Table 2). Only 3 of the 9 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. Two fish that we tracked offshore from the Western Terrace site 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). While diving to install and swap VR2W receivers at this site, we saw large aggregations of *C. microrhinos* in what appeared to be pre-spawning behavior (e.g. males displaying in 'loops' up in the water column). This behavior is consistent with courtship behavior described by Colin & Bell (1991) for this species.

Consistent with passive monitoring results, all tracked fish traveled to nighttime refuge in areas that were several 100 m 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. 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 10s of m, and the high use areas shifted somewhat between tracking days as well (for an example, see Fig. 3). 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.

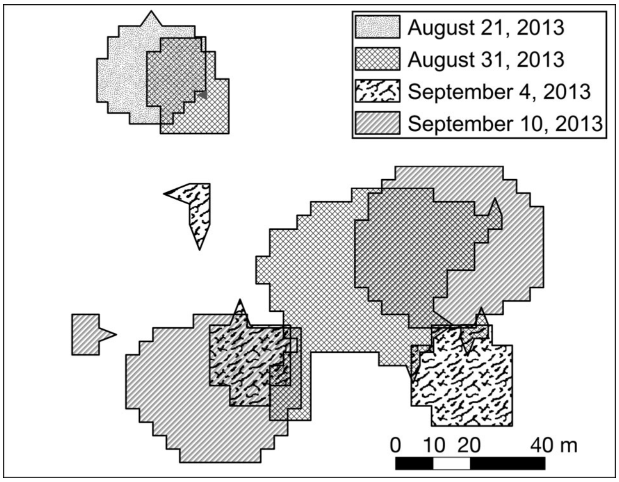

Fig. 3. Example of 50% kernel utilization distributions (KUDs; core use areas) for one active acoustic tracked fish (ID 9090) on 4 full tracking days

### Visual behavioral observations

Combined 95% kernel areas ranged from 344 to 2998 m$^2$. Combined 50% kernel areas ranged from 72 to 549 m$^2$. Areas of 95% and 50% kernels from individual tracks ranged from 56 to 1580 m$^2$ and 9 to 300 m$^2$, respectively (means reported in Table 2). 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 patches during consecutive observation periods. At Penguin Spit Backreef, feeding was generally concentrated in one or a few patches within the smaller territory, while at Western Terrace, activity and feeding were more dispersed across the larger territory (Fig. 4). Linear mixed effects models showed that both 95% ($p = 0.0038$) and 50% ($p = 0.019$) KUDs were larger at Western Terrace than at Penguin Spit Backreef.

## DISCUSSION

Here we show that 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 fine scales, movements and foraging activities are highly non-random, and feeding activities are tightly concentrated, consistent with the idea that parrotfish are highly selective in the substrate and successional state of targeted resources (Clements et al. 2016). At the largest scale, movement behaviors are related to reproductive behaviors and crepuscular sheltering activities, and these excursions can be quite long and frequent. We estimated home ranges for this species that are much larger than previously reported (Welsh & Bellwood 2012b), demonstrating the large amount of plasticity in movement behaviors 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 yr) at fairly high temporal resolutions. Fish movements at the largest scale 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. 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 parrotfish have been reported to form large aggregations at specific spawning sites (reviewed in Domeier & Colin 1997, de Mitcheson & Colin 2012). Where spawning cycles have been linked to tidal dynamics, several labrids are known to spawn at or immediately after high tides (Robertson & Hoffman 1977, Robertson et al. 1982, Colin & Bell 1991). In their study (conducted on the fringing reef of Orpheus Island, part of the inner shelf system of the Great Barrier Reef) using active tracking methods similar to ours, Welsh & Bellwood (2012b) observed only site-attached behavior and did not detect long excursions away from core use areas. This demonstrates that this species exhibits plasticity in its spawning behaviors (e.g. Gust 2004, Afonso et al. 2008b): spawning excursions occur in the Palmyra population but not in the Orpheus Island population. One hypothesis for this difference is that the hydrodynamic characteristics of each site dictate whether excursions are necessary for gamete transport. Another possible explanation for differences in spawning behavior may be differences in the abundance and identity of egg predators. Variation in mating strategy in labrids can also be driven by local population size (Warner & Hoffman 1980), and the inner reef system of the Great Barrier Reef supports a lower density of *Chlorurus microrhinos* than the backreef and terrace at Palmyra (Hoey & Bellwood 2008, Carlson et al. 2017). Variation in movement patterns between populations may be strongly influenced by local biotic and oceanographic conditions that in turn affect reproductive behavior, with ramifications to energetics and risk in individual fishes. It is worth noting that the long excursions such as those documented in Palmyra could potentially expose individuals to elevated risks associated with natural or human predators and are likely to be energetically costly.

Another characteristic long-range movement seen here were the long distances travelled from an individual's diurnal foraging grounds to night-time sheltering sites. Scarids are well known to shelter at night to avoid nocturnally hunting predators such as sharks and moray eels (Winn & Bardach 1959). Individual parrotfish have been shown to travel 10s to 100s of meters on consistent routes (Ogden & Buckman 1973) to areas with dense coral cover to seek night-time shelter (Dubin & 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 & Bellwood 2012). The strong diurnal pattern evident in our passive receiver data indicates that these animals are shelter-

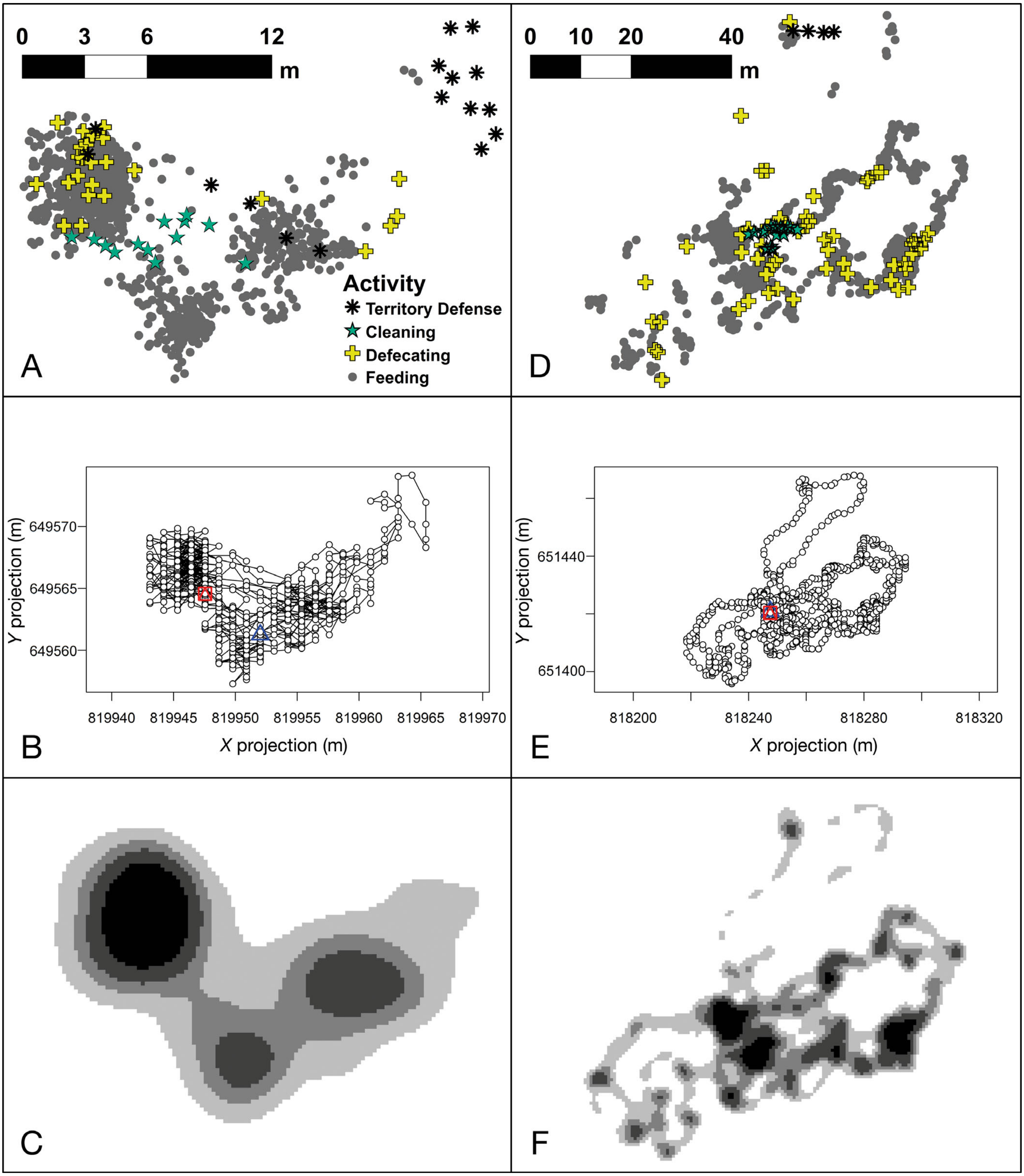

Fig. 4. Example of biased random bridge method of kernel calculation for (A–C) a fish at Penguin Spit Backreef and (D–F) fish from the Western Terrace. (A,D) Raw GPS location data for a 2 h track projected in Universal Transverse Mercator Zone 3N, with points colored by activity; (B,E) path networks of tracks, with the beginning of the track marked with a blue triangle and the end of the track marked with a red square; and (C,F) resulting kernel utilization distributions, with darker colors indicating higher utilization. Note the difference in scale bar between the 2 sites

ing at night, without exception, and that the transitions to night refuge sites usually happened near 18:00 h, 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 & Bellwood (2012b), who found that their tagged individuals moved to consistent night refuge sites that were roughly 35 m on average from their core use areas. Our individuals traveled much farther (>500 m). Perhaps in a predator-rich system such as Palmyra, the particularities of the night sheltering sites are more critical for survival than in other locations where predators are less abundant. Failure to take the potential distances travelled to night refuging site locations into account when designing an MPA may leave otherwise protected fish vulnerable during the night-time hours. This is especially important because night-time harvesting of parrotfish from their refuge sites is a common practice in many regions of the world (Aswani & Hamilton 2004, Dulvy & 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 in size across individuals, but that overall diurnal activity spaces were large and highly variable. The large average size of the activity space estimations from active tracking methods is again driven by large-scale movements between foraging territories, offshore spawning sites, and night refuging sites. 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 movement behaviors within the species.

One of the most noteworthy 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 area of core use shifted around the activity space of the animal between each track. We observed the same pattern in the behavioral following bouts, where we observed fish to graze one patch on one day and a different nearby patch on a subsequent day, returning to a previously observed grazing patch at some later date (Carlson et al. 2017). This contrasts with the findings of Welsh & 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 contiguous reef. Perhaps the preferred substrates for growth of nutritional resources on the reef crest are concentrated in a more defined area than those on a contiguous reef and the temporal patterns we observed reflect those differences. These 2 behavioral scenarios (consistent grazing in the same localized area versus graze, abandon, regraze) could have contrasting 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 (Sandin & McNamara 2012, Eynaud et al. 2016). However, parrotfish can damage or consume coral settlers and recruits in the process of grazing (Bak & Engel 1979, Box & 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. (2017) 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 localized effects scale up to the level of entire reefs.

Space use estimates from GPS tracks were much smaller in this study than those estimated from active tracking. Discrepancies between tracking techniques have been documented, with visual methods often providing smaller estimates of space use than acoustic tracking methods (Nash et al. 2015). This is logical in the context of the present study because our visual methods did not include excursions to sleep sites or spawning sites, movements that contributed greatly to the overall estimates of space use in the acoustically tracked fish. GPS tracking methods also are likely to incorporate substantially lower positional error, because the observer is able to continually validate the accuracy of each position. Thus, despite restrictions in the ability to provide overall space use estimates, GPS tracking data provided the highest resolution spatial and temporal data on fish foraging patterns. We observed some differences in the spatial behaviors of individuals within feeding territories across the 2 sites. At the Western Terrace site, fish had larger feeding territories overall and feeding was more dispersed throughout the territory, though still concentrated in many small patches. Fish at Penguin Spit Backreef had small territories and concentrated feeding within very few patches, resulting in dense aggregations of bite scars (Carlson et al. 2017). Variation in the foraging behavior of some smaller reef prey species has been shown to be influenced by predator abundance (Madin et al. 2010a,b), but in a study of a smaller (so presumably more vulnerable) species of parrotfish, *Chlorurus spilurus*, we found no evidence that predation risk effects diurnal foraging space use patterns (Davis et al. 2017). We did document strong differences between sites in the percent cover and growth rates of mixed algal turfs and the biomass of conspecifics, which were both higher at Penguin Spit Backreef (Carlson et al. 2017). We hypothesize that food resource abundance may have strong bottom-up influences on fish behavior and movement patterns. It has been 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, Han et al. 2016, Tootell & Steele 2016). It may be that the combination of conspecific competitor abundance and large and abundant patches of preferred substrate results in the style of constrained, localized feeding that we documented at Penguin Spit Backreef. These hypotheses are further investigated in great detail in Carlson et al. (2017).

The patterns of movement revealed by active tracking and visual behavioral observations indicate that feeding in this species is highly localized, intensely concentrated, and temporally punctuated. These observations are quite consistent with the suggestion of Clements et al. (2016) that large excavating parrotfishes are highly selective and target protein-rich bacterial autotrophs to support rapid growth rates and high reproductive output. Regardless of the actual source of nutrition to the parrotfishes, the foraging patterns observed here resulted in patches with temporarily suppressed levels of algal turfs, which has strong implications for benthic dynamics. Bare space may possibly provide a settlement refuge for larval corals and other benthic space competitors, and enhance reef resilience, while extensive regrazing of localized areas may mitigate that affect. Relationships between the fine-scale spatial drivers of parrotfish grazing and their effects on coral settlement and survivorship must be the focus of future research in order to reasonably manage coral reefs into the future.

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