

Contribution to the Theme Section 'Tracking fitness in marine vertebrates'

Movement, habitat utilization and behaviour of coral trout *Plectropomus leopardus* during and after the reproductive period on the southern Great Barrier Reef

C. M. Bunt^{1,*}, M. J. Kingsford²

¹Biotactic Fish and Wildlife Research (Biotactic, Inc) 691 Hidden Valley Road, Kitchener, Ontario N2C 2S4, Canada

²School of Marine and Tropical Biology and ARC Centre of Excellence for Coral Reef Studies, James Cook University, Townsville QLD 4811, Australia

ABSTRACT: Coral trout *Plectropomus leopardus* (mean total length = 498.9 ± 19.7 mm, n = 10) were tagged and tracked with ultrasonic transmitters over 81 d at an intra-lagoonal location at One Tree Island, Great Barrier Reef, Australia (23.4979° S, 152.0712° E). Movement and habitat preferences were compared during the transition between the reproductive and post-reproductive period. Overall, mean movement was highest between 05:00 and 10:00 h, with the most movement during the crepuscular period and the least movement at night. There was no difference in nighttime movement during or after the reproductive period. Mean daily movement (14.48 ± 0.26 km d⁻¹) and fish depths (4.23 ± 0.02 m) during the post-reproductive period were significantly greater than both movement (10.63 ± 0.13 km d⁻¹) and depths occupied (3.38 ± 0.01 m) during the reproductive period, which was likely related to reallocation of bioenergetic resources to foraging related activities rather than spawning. Most fish movement was localized (within 0.04 km²), with some movements recorded outside of this area to a maximum distance of 0.6 km. Fish traversed sand and small scattered coral out-croppings to reach areas of continuous reef. The ranges of movement and habitat preferences described in this study are important for future research on habitat requirements and behavioural changes across the transition period between reproductive and post-reproductive states. Furthermore, this study provides additional information that may be used for focusing and delineating species-specific Marine Protected Area management plans.

KEY WORDS: *Plectropomus leopardus* · Serranidae · Movement · Habitat preference · Habitat requirements · Ultrasonic telemetry · Marine Protected Area

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INTRODUCTION

Common coral trout *Plectropomus leopardus* are epinephiline serranids (i.e. groupers) that form the basis of the commercial and recreational reef line fishery on the Great Barrier Reef (Russ 1991), and comprise 35–55% of the commercial catch, 20–25% of the charter catch and 15–20% of the recreational catch (Mapstone et al. 2004). In Queensland, Australia, alone, the *P. leopardus* fishery generates approximately \$35 million (AUD) in gross annual revenue

(Queensland Government 2011). However, previous studies have revealed evidence of population decline of this economically valuable species (Fulton et al. 1999, Morris et al. 2000, Graham et al. 2003, Little et al. 2005), and *P. leopardus* are now classified by the IUCN as Near Threatened (Cornish & Kiwi 2004).

Declines in *Plectropomus leopardus* populations have been attributed to life history patterns of the species (Bohnsack 1982, Russ 1991), specifically their tendency to form reproductive aggregations (Thresher 1984), which make them vulnerable to

*Corresponding author: cbunt@biotactic.com

overfishing (Samoilys 1997a). In the last 20 yr, the establishment of marine reserves in known *P. leopardus* aggregation locations has been identified as the most viable strategy for sustainable management of this species (DeMartini 1993, Rowley 1994, Russ & Alcala 1996a,b). Management programs designed to protect specific *P. leopardus* reproduction aggregation areas are more likely to succeed as additional information on reproductive behaviour, movement and habitat requirements becomes available (Zeller 1996, 1997, 1998, Samoilys 1997a,b, Zeller & Russ 1998).

In addition to fisheries-related economic implications, the sustainability of *Plectropomus leopardus* populations has ecological ramifications. This species feeds on fishes and invertebrates (Choat 1968, Kingsford 1992, St. John et al. 2001), and thereby influences mortality rates and population dynamics of other predators and their prey (Hixon 1991, Connell & Kingsford 1998, Mclean et al. 2011). Data on spatial and temporal scales of movement as well as habitat selection and habitat preferences of these higher-order predators are important for reef fisheries management and the maintenance of viable *P. leopardus* populations, and have implications for the balance of the entire reef ecosystem (Sluka et al. 1994, Ceccarelli & Ayling 2010).

Previous studies on *Plectropomus leopardus* spatial utilization have focused on counting individuals in aggregations, mapping aggregation sites (Aguilar-Perera & Aguilar-Dávila 1996, Samoilys 1997a) and enumerating intra-reef patterns of abundance (Connell & Kingsford 1998, Kingsford 2009). Habitat preferences and movement patterns during the reproductive and post-reproductive transition at aggregation sites are largely unknown.

Ultrasonic telemetry has been used with *Plectropomus leopardus* to determine the movement within home ranges (Zeller 1997), spawning aggregations (Zeller 1998) and across boundaries of Marine Protected Areas (MPAs) (Zeller & Russ 1998). However, data from these studies were not stratified to allow movement comparisons during reproductive and post-reproductive periods. Therefore, the purpose of this project was to enhance and build on previously acquired information by providing detailed data to: (1) characterize diel movement patterns (in 3 dimensions) of *P. leopardus* into and out of an aggregation site during the reproductive (November–December) and post-reproductive periods (January–February); and (2) evaluate diel habitat utilization patterns and habitat preferences during the reproductive and post-reproductive periods.

MATERIALS AND METHODS

Study site and sampling design

Plectropomus leopardus were collected, tagged and tracked at One Tree Island (OTI), southern Great Barrier Reef, Australia (23.4979° S, 152.0712° E; Fig. 1a). The tracking location was based on long-term SCUBA observations over 13 yr that identified an area with a pre-existing and presumably spawning-related aggregation site. Fish were monitored over 81 d from 13 November 2001 to 4 February 2002, spanning the typical reproductive (November–December) and post-reproductive (January–February) periods at OTI (M.J.K., pers. obs.). These periods are estimates based on definitions of reproductive periodicity by Domeier & Colin (1997) because the beginning and ending dates of spawning are usually not known for certain. However, there was distinct evidence that fish were in a reproductive state at the beginning of the study. This evidence included: unusual aggregation behaviour of mature fish (see Pet et al. 2005) during a time of the year when spawning of this species is known to occur; swollen gonads in females; and males that expressed milt on Analytical groups in this study did not contain fish from both reproductive states, and no data were included in the analyses from 18 December 2001 to 11 January 2002. This unintended but surreptitious buffer was the result of technical difficulties with the tracking system during a period when researchers were away from OTI. We euthanised one of the tagged fish (4591) on 18 January 2002 and there were no gametes present internally, suggesting that spawning was complete. It is unlikely that this was an immature fish, based on behavioural comparisons with other similarly sized mature fish in the spawning aggregation in November/December.

Fish tagging and tracking

Plectropomus leopardus were collected from the aggregation by precision angling, which involved the presentation of a pilchard to target fish by a diver who minimized entanglement of gear with coral, as an angler on a boat retrieved the hooked fish. These fish were then measured and anaesthetized with a 50 to 75 ppm solution of clove oil and ethanol. A depth-sensitive ultrasonic transmitter (VEMCO, 106 × 15 mm with a 2 s burst rate) was implanted into the body cavity through a 15 mm incision posterior to the left pelvic fin. The incision was closed with 2 simple

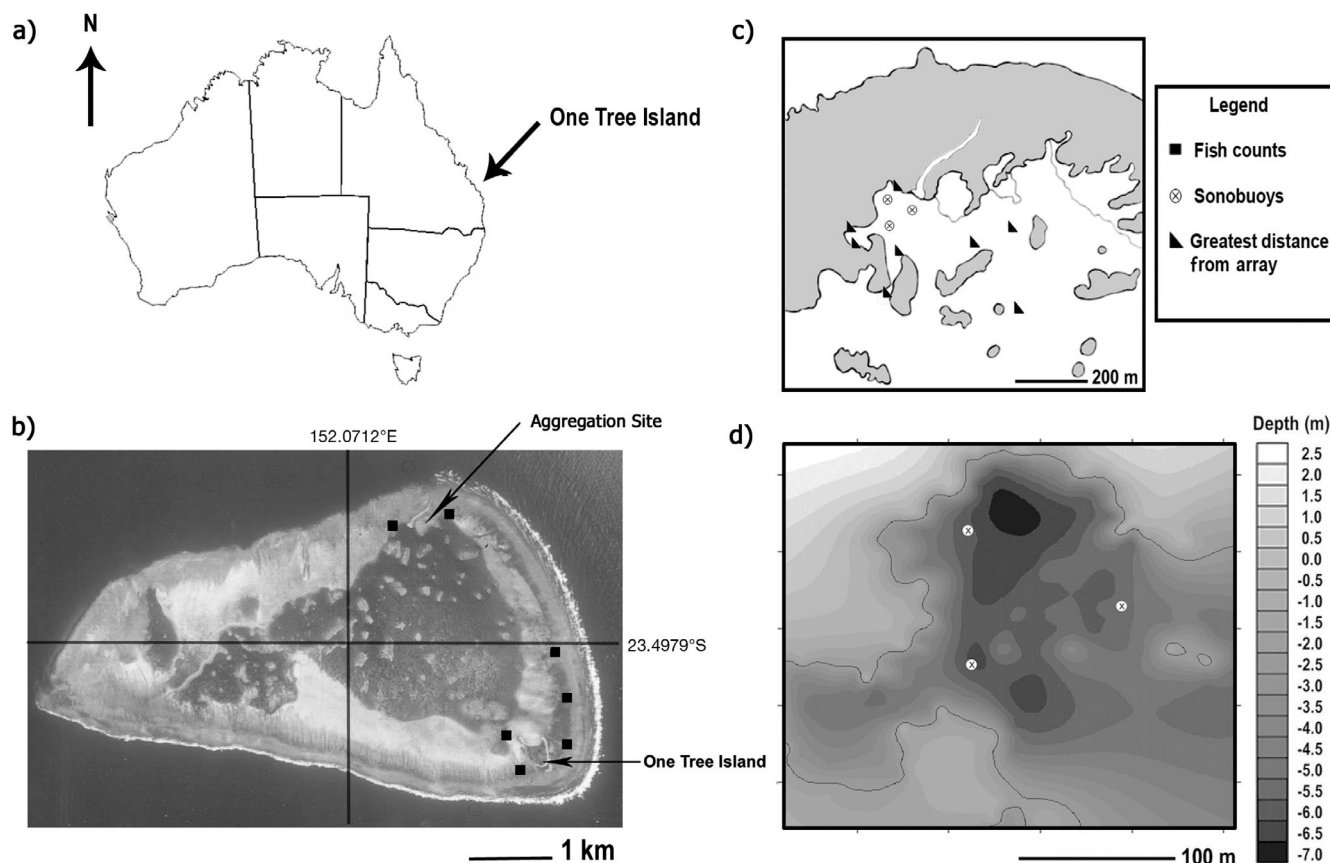


Fig. 1. (a) The approximate location of One Tree Island (OTI) on the Southern Great Barrier Reef. (b) OTI lagoon (14 km²), showing the aggregation site and fish count locations. (c) Aggregation area, with approximate positions of VRAP sonobuoys used to track *Plectropomus leopardus* and maximum distances fish moved from the array. (d) Enlargement of the aggregation site, showing tracking buoys and depth contours at high tide

interrupted braided silk sutures. Tagged fish were placed in flow-through pens for a recovery period of 3 to 6 h, and were then released near the site of original capture. Fish tracking was conducted with a radio-linked acoustic positioning sonobuoy array (VRAP System, Vemco) 1.5 km northwest of the OTI research station. Tracking system function and triangulation of transmitters is described in O'Dor et al. (2001). According to the manufacturer and verified with pre-study tests, locations were accurate to within 1 m (x , y dimensions) and depth data were accurate to within 0.2 m when transmitters were not hidden behind coral. During collection of VRAP data, telemetry data from areas outside the array were also recorded by boat using mobile VEMCO VR-60 receivers and a towed hydrophone. On occasion we used an underwater pinger locator (VEMCO VR-96) to track fish within the aggregation site with SCUBA. *Plectropomus leopardus* were also counted with SCUBA at the aggregation site and at 6 other sites along the lagoon edge to determine how representa-

tive the tagging site was (Kingsford 1992, 2009). Sites were separated by 0.3 to 5 km along the edge of the lagoon (Fig. 1b). At each site, fish were counted in 5 transects, each measuring 5 × 25 m. This sampling design was repeated January–February each year from 1995 to 2007.

Movement and depths

All fish were simultaneously tracked within a 0.04 km² area within the OTI lagoon. Distances (m) between successive time-stamped locations were calculated from filtered telemetry data. Approximately 1% of movement data appeared to be related to signal bounces and erroneous reception based on visual examination of temporal and spatial aspects of the telemetry data. These data points were removed accordingly to minimize overestimates of movement. *Plectropomus leopardus* movement data were analyzed within and among 4 daily time periods (early

morning: 05:00:01–10:00:00 h; midday: 10:00:01–14:00:00 h; late afternoon: 14:00:01–19:00:00 h; and night: 19:00:01–05:00:00 h) during and after the typical reproductive period. Movement patterns as well as fish depths were analyzed using *t*-tests and a 3-factor general linear ANOVA with the factors defined as individual, time block (time of day) and spawning state (reproductive/post-reproductive).

Habitat mapping

A bathymetric map of the study site was developed using a combination of SONAR and differential GPS (Fig. 1d). Maps of physical habitat (coral, open sand, rubble substrate, coral formations or bommies) were created throughout the study period. Coral was identified to genus and species (when possible) and mapped over scaled images derived from the bathymetric map of the reef edge. After the telemetry study was complete, habitat within the study area was mapped using SCUBA. To create scaled maps of habitat availability, we used a novel technique with an acoustically-tagged diver and an assistant, who both tabulated substrate and coral along underwater transects (spaced approximately 3 m within the tracking array) while being tracked with the telemetry system. In this way it was possible to create a scaled map of habitat availability that could be superimposed on a similarly scaled map of fish movement for analysis.

Raw telemetry data were filtered and superimposed over maps of habitat availability using a Windows-based telemetry data analysis program called Biotrek, which was custom designed for this study. This software used pixel-coding to assign specific habitat characteristics on scaled maps, and then correlated pixel codes with locations occupied by fish when they were tracked. The program essentially recreated patterns of habitat/depth utilization by replaying scaled paths of movement over scaled maps of habitat in areas that fish occupied. The program calculated habitat utilization histograms related to the number of observations of each fish in each habitat category.

Total area and percentage of the total area for each habitat type was calculated using GE path v 1.4.6. Habitat preference was calculated by dividing habitat utilization by habitat availability, which was then standardized to a value of 1 by dividing by the highest preference value (Mäki-Petäys et al. 1997) for each respective time block across the reproductive and post-reproductive periods. Patterns related to habitat

utilization throughout the day and night during and after the reproductive period were analyzed with a *G*-test. All analyses ($\alpha = 0.05$) were conducted using JMP 7.0 (SAS Institute).

RESULTS

Movement

Tagged fish from the aggregation site slowly began to disappear from the OTI lagoon over the course of the study, which corresponded to the transition between the estimated reproductive and post-reproductive periods (Table 1). Of the 10 fish that were tagged in November 2001, Fish 4587 was last detected on 11 December 2001 and Fish 4590 was not detected after 18 January 2002, despite extensive mobile tracking efforts throughout and around OTI. By 31 January 2002, only 40% of tagged *Plectropomus leopardus* were located near the aggregation site.

Fish were absent from the array for more than an hour before returning to the aggregation on 5 occasions during the reproductive period and 45 occasions after reproduction (Table 1). Fish detected outside the lagoon moved to a maximum distance of 593 m from the aggregation (Fig. 1c). Some fish disappeared and reappeared periodically from the array area, indicating movements away from the aggregation site (verified using mobile tracking). Other fish used complex areas of coral habitat, and transmitter signals were undetectable even while they were in the array (as determined with SCUBA and portable underwater receivers), particularly during the reproductive period. Movement outside the array increased during the post-reproductive period as the aggregation began to disperse in late January (Table 1).

Plectropomus leopardus movement for all daily time segments combined increased significantly after the reproductive period ($F = 121.65$, $p < 0.0001$; Table 2, Figs. 2, 3a,c,e). During the reproductive period, mean daily movement was 10.63 ± 0.13 km d⁻¹; after reproduction, mean daily movement was 14.48 ± 0.26 km d⁻¹ (Fig. 2). The greatest movement occurred during crepuscular hours, and particularly in the morning both during (12.29 ± 0.17 km d⁻¹; Table 3) and after the reproductive period (17.14 ± 0.51 km d⁻¹, $t = 10.01$, $p < 0.0001$; Table 3). *P. leopardus* moved the least at night, and there was no difference in nighttime movement during the reproductive period (7.99 ± 0.16 km d⁻¹; Table 3) or after the reproductive period (7.77 ± 0.24 km d⁻¹, $t = -0.55$, $p = 0.58$; Table 3, Fig. 2).

Table 1. *Plectropomus leopardus*. Vital statistics of coral trout tracked at One Tree Island, with tagging date, capture and release location, number of days each fish was tracked inside and outside the array during and after the reproductive period, and the status of each fish at the end of the study

Tag code	Tagging date	Freq. (kHz)	Length (mm)	Sex	Capture and release	Days tracked in array		No. occasions fish tracked outside array		Final status
						Reproductive	Post-reproductive	Reproductive	Post-reproductive	
4587	13/11/01	51	565	-	Near aggregation	17	-	0	0	Off reef
4588	13/11/01	54	485	M (ripe)	Near aggregation	23	14	0	2	Array
4589	13/11/01	57	545	M (ripe)	Aggregation	19	10	0	11	Lagoon
4590	16/11/01	60	585	-	Aggregation	23	1	0	0	Off reef
4591	16/11/01	63	470	-	Aggregation	19	9	0	14	Euthanised ^a
4592	16/11/01	66	447	-	Aggregation	13	2	0	6	Array
4593	16/11/01	69	572	-	Aggregation	23	15	0	2	Array
4594	16/11/01	72	466	M (ripe)	Aggregation	22	14	0	0	Array
4595	17/11/01	75	412	M (ripe)	Aggregation	18	-	5	6	Off reef
4596	17/11/01	78	442	M (ripe)	Aggregation	20	5	0	4	Off reef

^aRecaptured in the array on 18 January 2002 so that the transmitter could be re-used to map habitat with SCUBA

Depth

The maximum depth of the study area was 7.5 m at high tide, and fish utilized almost the entire depth range. The mean depth occupied during the reproductive period (3.38 ± 0.01 m) was significantly shallower than the mean depth occupied during the post-reproductive period, 4.23 ± 0.02 m ($F = 1093.37$, $p < 0.0001$; Table 2, Table 3, Figs. 2, 3b,d,f, 4). Fish occupied deeper areas during the reproductive period at night, and the shallowest depths were occupied in the morning and afternoon. After the reproductive period, the opposite pattern was observed. Despite overall trends, tracks of individual fish indicated that there was a great deal of variation, with some fish making rapid changes in depth in the water column (>6 m), while other fish tended to maintain similar depths throughout the day and night (Fig. 4).

Vertical positions of *Plectropomus leopardus* in the water column were variable but did not appear to be influenced by daily tidal conditions during or after the reproductive period. OTI, including the area where the study was conducted, is a ponding lagoon, so the water level remains elevated and stable as sea level drops outside the reef. As such, the tidal fluctuation (for low tide) is truncated in the intra-lagoonal location where the tracking study took place. This confounds any statistical analyses designed to demonstrate that the fish responded to tidal fluctuations. Fig. 4 shows that as water elevation (or tide level) decreases, fish tended to occupy shallower areas; however, we believe that this is an artifact resulting from reduced hydrostatic pressure on the tag transducer rather than vertical movement in the water column. This also makes sense in light of the highly territorial nature of coral trout. Therefore, based on qualitative observations, *P. leopardus* tended to remain at specific locations relative to the bottom of the reef and did not appear to be affected by changes in surface water elevation (Fig. 4).

Habitat

Habitat was not distributed uniformly throughout the study area, and habitat utilization was not uniform throughout the day during or after the reproductive period (G -test, $G = 14.94$, all $p < 0.0001$). Sand was the most abundant habitat type (43%) and was utilized more than any other habitat type during the reproductive (36%) and post-reproductive periods (38%; Table 4, Fig. 5). However, in terms of pref-

Table 2. 3-factor ANOVA comparing movement and depth utilization throughout the day (time period) during and after the reproductive period (spawning status)

Factor	df	SS	F	p
Movement				
Spawning status	1	32850.71	121.65	<0.0001
Time period	3	86990.54	107.38	<0.0001
Individual	9	51386.29	21.14	<0.0001
Depth				
Spawning status	1	1894.26	1093.37	<0.0001
Time period	3	1001.45	192.68	<0.0001
Individual	9	21656.83	1388.93	<0.0001

Table 3. *t*-tests comparing movement and depth utilization throughout the day (time period) during and after the reproductive period. Movement, depth and estimate are mean (\pm SE)

	Movement (km d ⁻¹), or depth (m)		Estimate	<i>t</i>	p
	Reproductive	Post-reproductive			
Movement					
Night	7.99 \pm 0.16	7.77 \pm 0.24	-0.11 \pm 0.20	-0.55	0.58
Early morning	12.29 \pm 0.17	17.14 \pm 0.51	2.42 \pm 0.24	10.01	<0.0001
Midday	10.98 \pm 0.22	16.38 \pm 0.49	2.70 \pm 0.24	11.35	<0.0001
Late afternoon	11.91 \pm 0.35	15.03 \pm 0.45	1.56 \pm 0.33	4.78	<0.0001
Depth utilization					
Night	3.69 \pm 0.02	3.91 \pm 0.04	0.11 \pm 0.03	3.99	<0.0001
Early morning	3.23 \pm 0.02	4.38 \pm 0.04	0.58 \pm 0.02	23.44	<0.0001
Midday	3.28 \pm 0.02	4.25 \pm 0.03	0.48 \pm 0.02	19.53	<0.0001
Late afternoon	3.21 \pm 0.03	4.31 \pm 0.03	0.55 \pm 0.02	23.05	<0.0001

erence, live *Porites* coral, followed by large (>2 m wide, >1 m high) bommies, ranked as the most important habitat type during the reproductive period, regardless of time of day (Fig. 5a,c,e,g, Table 4). After spawning, there was a shift in habitat preference that varied depending on the time of day. At night, *Plectropomus leopardus* preferred to use coral rubble, whereas in the early morning they preferred large bommies >2 m wide and >1 m high. At night and in the late afternoon they preferred smaller bommies, 1 and 2 m wide and >0.5 m high (Fig. 5b,d,f,h).

Patterns of abundance

Twenty *Plectropomus leopardus* were observed near or within the aggregation area by SCUBA on 15 November 2001. Nine *P. leopardus* were observed together in an area measuring only \sim 1 m². The abundance of fish found at the aggregation site during the study was typical of previous years. Average density at the aggregation site was higher than the average density for all 7 sites along the edge of the lagoon. Fewer *P. leopardus* were counted throughout the lagoon from 2002 to 2004 (Fig. 6). This decrease

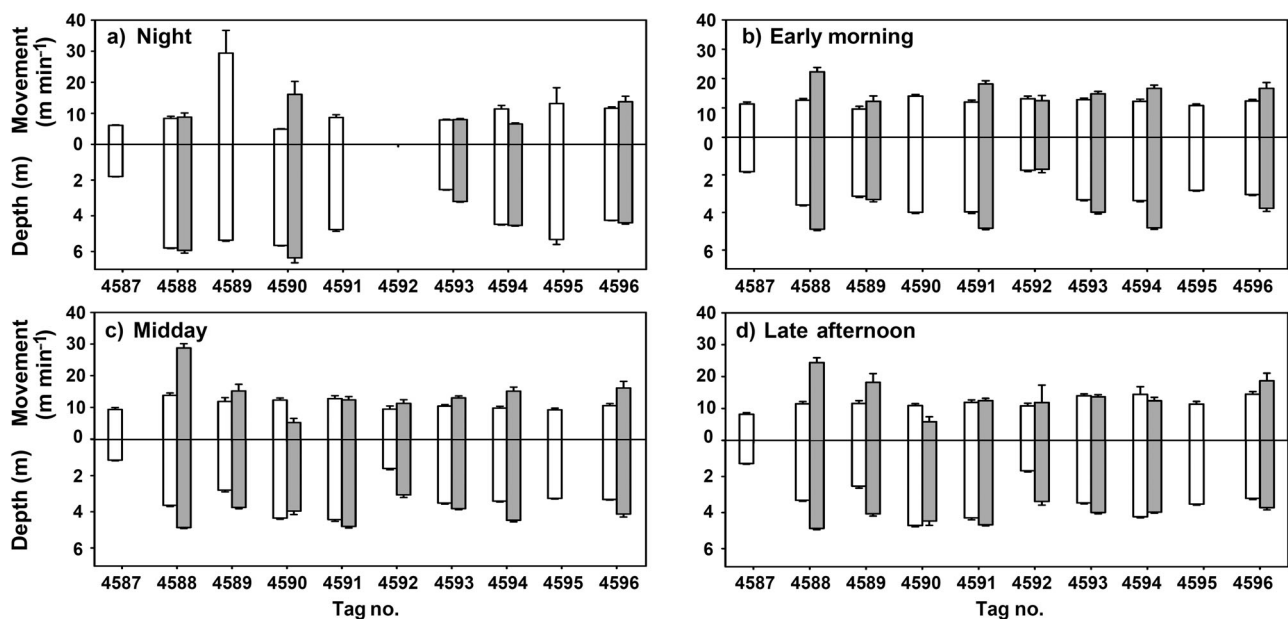


Fig. 2. *Plectropomus leopardus*. Mean movement (\pm SE) and mean depth utilization (SE) of coral trout during the reproductive period (white, November–December 2001) and after the reproductive period (grey, January–February 2002) across all daily time periods near the aggregation site

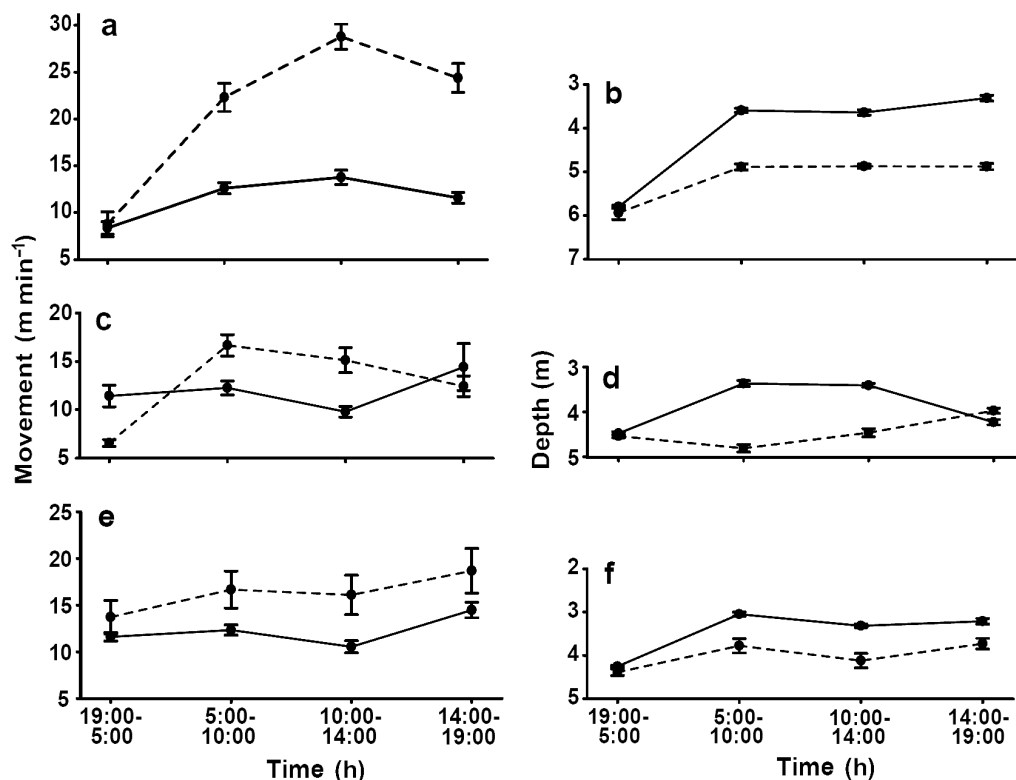


Fig. 3. *Plectropomus leopardus*. Detailed examples of (a,c,e) mean movement (\pm SE) and (b,d,f) mean depth (\pm SE) of Individuals 4588 (a,b), 4594 (c,d) and 4596 (e,f) within the aggregation site during the reproductive period (solid line, November–December 2001) and after the reproductive period (dashed line, January–February 2002)

in abundance appeared to be related to loss of live coral cover that followed strong El Niño conditions in 1998 and 2001.

DISCUSSION

MPAs and fishing restrictions are essential for the recovery and sustainability of *Plectropomus leopardus* and other serranids that are heavily targeted and exploited in the Indo-Pacific and the Great Barrier Reef (Williams et al. 2008). There is ample evidence that MPAs replenish fish populations (Graham et al. 2003, Nardi et al. 2004, Williamson et al. 2004, Watson et al. 2007, Russ et al. 2008) and are a promising global fisheries management option. Despite concerns of economic consequences associated with sequestering reef habitats for the sole purpose of conservation (Russ 1991), recent work has shown no net loss in revenue in commercial fisheries, with the losses of some fishers balanced by the gains of others (Jeffrey et al. 2012).

Identification of preferred habitats, movement capabilities and site fidelity within both home ranges and aggregation sites must be considered during de-

lineation of MPAs, and should be a focus of conservation objectives. Although data are limited for most species, it is important to determine whether *Plectropomus* spp., as well as other serranids, can be effectively managed using multi-species rather than species-specific conservation strategies.

In this study, *Plectropomus leopardus* moved significantly greater distances, utilized significantly deeper habitat and preferred different habitat during the post-reproductive compared with the reproductive period. In comparison with other studies on *P. leopardus*, the intralagoonal site at OTI is somewhat unique within the Great Barrier Reef. This location is at the southern end of the *P. leopardus* distribution, and as such, the data collected for this study may be more relevant to southern populations than northern ones, and may partially explain differences in behaviour considering that the tracking methods that we used were similar to those used by Zeller (1996), Zeller & Russ (1998) and Samoilys (1997a). Large amounts of data are typically collected with these types of VRAP telemetry projects, and this may have resulted in inflated distances moved due to the cumulative effect of minor signal bounces or variation in signal transmission. However, it is important to note that most of

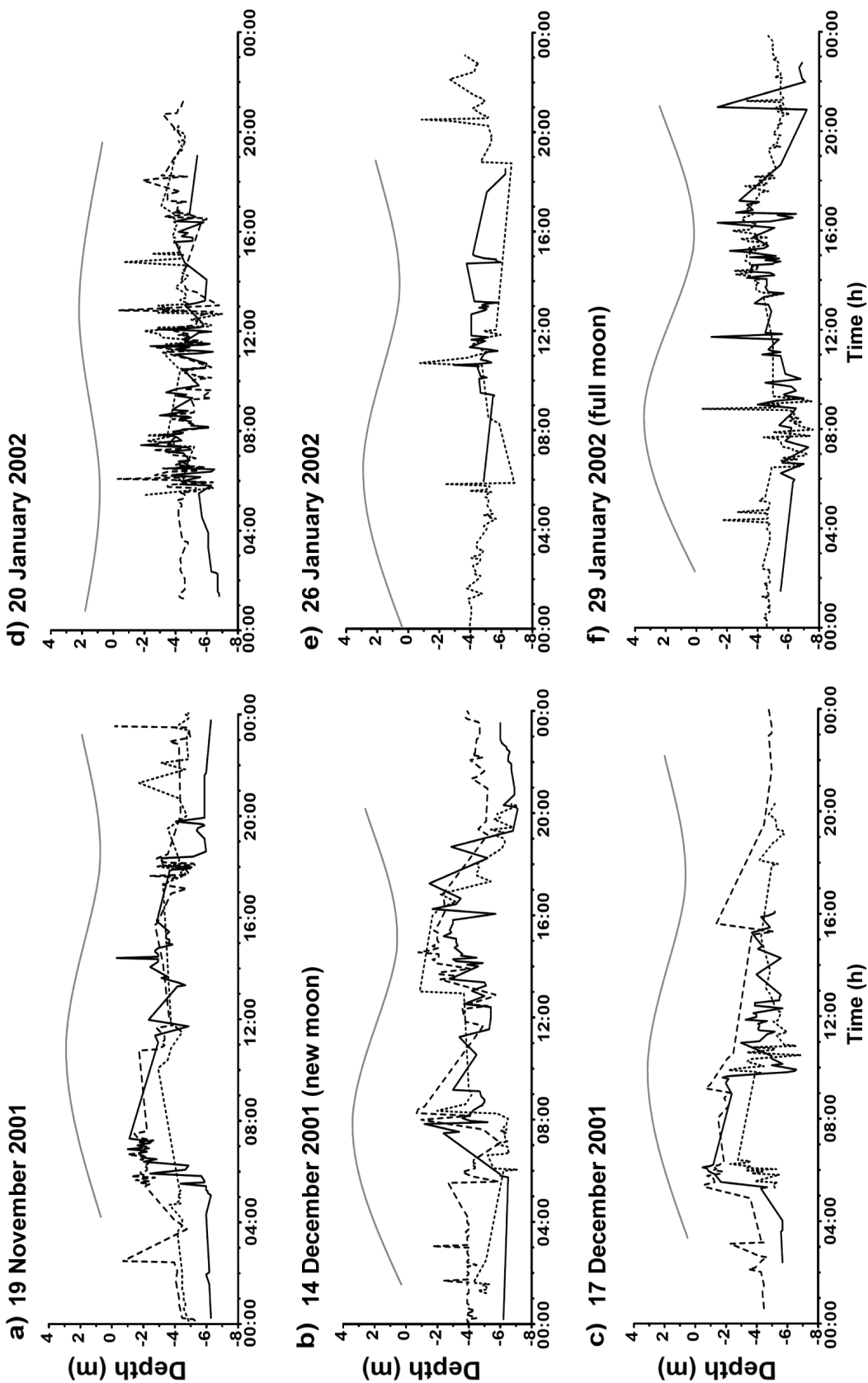


Fig. 4. *Plectropomus leopardus*. Depth data from Individuals 4588 (solid line), 4594 (dotted line) and 4596 (dashed line) over several days during the reproductive period ([a] 19 November 2001, [b] 14 December 2001 and [c] 17 December 2001) and post-reproductive period ([d] 20 January 2002, [e] 26 January 2002 and [f] 29 January 2002), in relation to the tide height above sea level outside the lagoon (grey curved line). New moon and full moon: 14 December 2001 and 29 January 2002, respectively

Table 4. Habitat type, number of sites surveyed, total area and percentage of total area of each habitat type within the receiver array, as well as coral trout utilization of each habitat type pooled across daily time blocks during and after the reproductive period

Habitat/substrate type	Number of sites	Total area (m ²)	% Available	Habitat utilization (%)	
				Reproductive	Post-reproductive
Sand	276	16803	43	36	38
Rubble	118	7163	19	17	27
Live <i>Porites</i> coral	85	5304	14	27	14
Bommie ^a > 2 m wide, >1 m high	27	1626	4	8	7
Bommie 1–2 m wide, <0.5 m high	23	1394	4	3	6
Bommie 1–2 m wide, >0.5 m high	33	2013	5	3	3
Bommie <1 m wide, <0.5 m high	72	4414	11	6	5
Total	634	38717	100	100	100

^aA bommie is a vertical coral out-crop or a distinct congregated coralline mound usually surrounded by sand

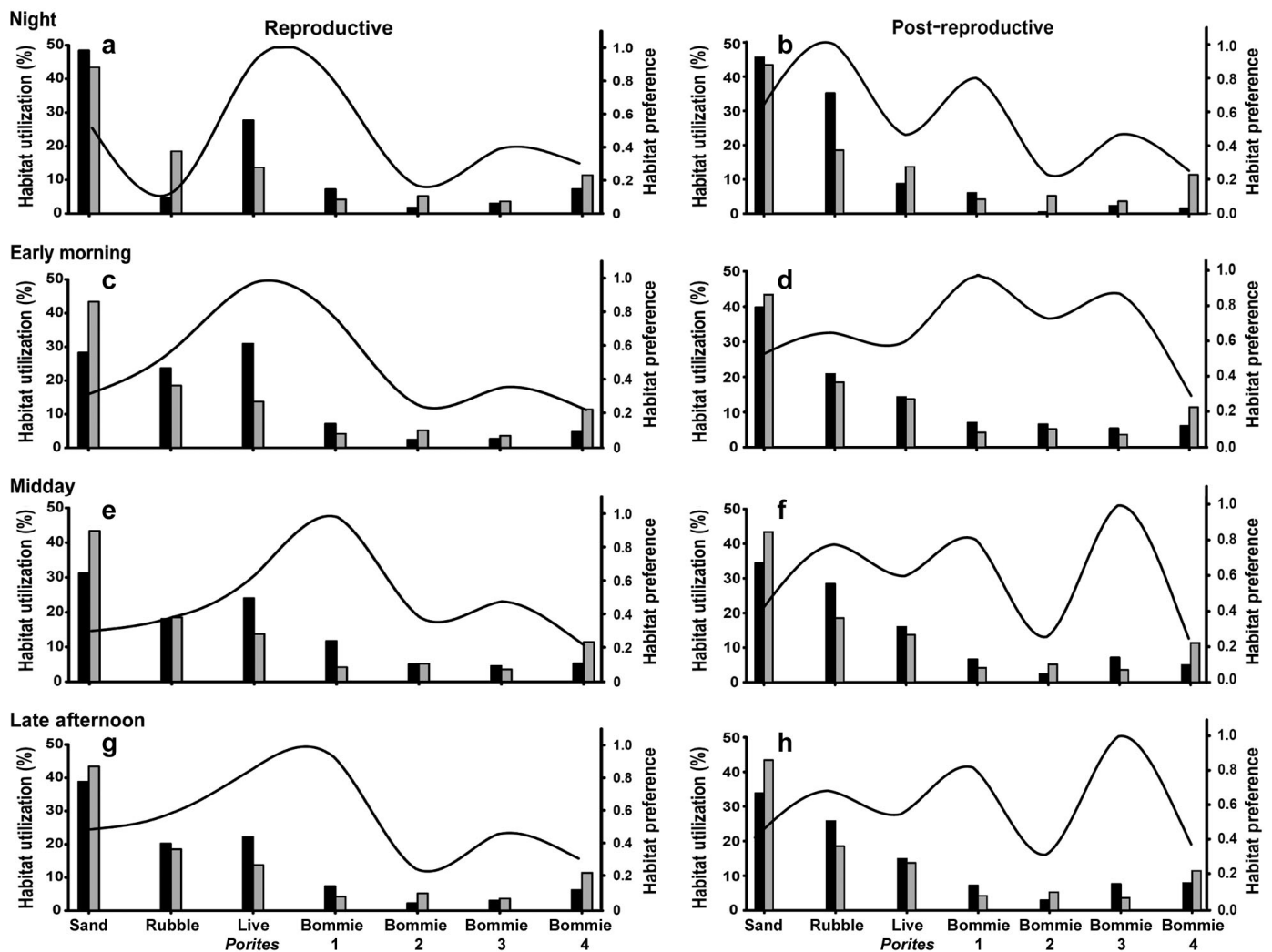


Fig. 5. *Plectropomus leopardus*. Habitat utilization (black bars), habitat availability (grey bars) and habitat preference curves for coral trout during the (a,b) night, (c,d) early morning, (e,f) midday and (g,h) late afternoon, during the reproductive period (a,c,e,g) and post-reproductive period (b,d,f,h). Bommie habitat types are as follows: Bommie 1: > 2 m wide, >1 m high; Bommie 2: 1–2 m wide, <0.5 m high; Bommie 3: 1–2 m wide, >0.5 m high; and Bommie 4: <1 m wide, <0.5 m high

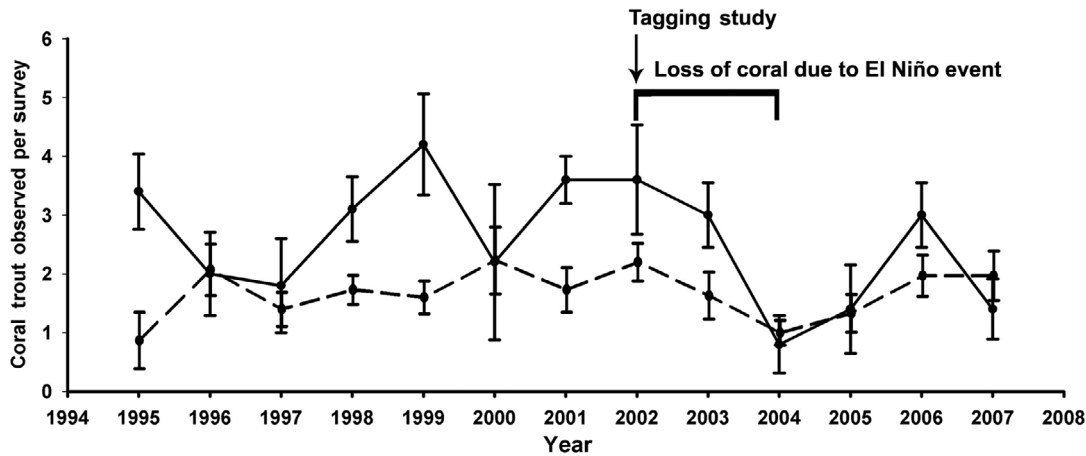


Fig. 6. *Plectropomus leopardus*. Changes in January abundance of coral trout observed per 125 m² at One Tree Island from SCUBA counts (1995–2007). Solid line: mean (\pm SE) number of observations near the lagoon aggregation; dashed line: mean (\pm SE) number of observations at all other count sites combined (count locations shown in Fig. 1)

the potential biases in our data would have been consistent across the 2 periods (reproductive and post-reproductive), and therefore the relative differences that we observed are significant and inferentially valuable. Despite the caveats, the differences in movement and habitat preferences between reproductive and post-reproductive periods from this study complement previously documented patterns and trends of *P. leopardus* behaviour that are essential for the development of effective management strategies.

As with many other species in the grouper family, this study showed that *Plectropomus leopardus* use a mosaic of habitats such as sand, rubble, live coral and bommies of varying dimension (Syms & Kingsford 2008). They also use lagoon reef environments including reef slope, areas of strong water currents (Kingsford 1992, 2009) and live coral such as *Acropora* and *Porites* (Morris et al. 2000, Manson et al. 2005). The preference for live corals was evident at the aggregation site, particularly during the reproductive period, as also described by Connell & Kingsford (1997). However, after reproduction, a shift away from live coral was noted at small spatial scales, with an increase in the use of coral rubble. This trend has also been documented for other heavily exploited and potentially threatened species such as black grouper *Mycteroperca bonaci* in Florida (Eklund et al. 2000), Nassau grouper *Epinephelus striatus* in the Bahamas (Eggleston 1995, Sadovy & Eklund 1999, Bolden 2000), red hind *E. guttatus* in the US Virgin Islands (Nemeth 2005), *Cephalopholis urodeta* in the Indo-West Pacific (Donaldson 2002) and *P. areolatus*, *P. labevis* and *P. maculatus* on the Great Barrier Reef (Hutchinson & Rhodes 2010).

Changes in habitat preference and vertical shifts in

position within the water column did not appear to occur, as indicated by the lack of consistent response to tidal stage (Fig. 4). The results of Connell & Kingsford (1998) also showed little temporal variation in position within the water column. However, Samoily & Squire (1994) linked movements into and out of reproductive aggregation sites with lunar cycles. They also noted an increase in abundance at aggregation sites during the 3rd and 4th phases of the moon, and reproduction occurred around the new moon, when fish released gametes during strong tidal flow. According to Zeller (1998), the highest total count of *Plectropomus leopardus* was in aggregations during the new moon periods in October and November. In addition, Zeller (2002) also found that the upcurrent side of reefs and smaller structures were preferred, and that fish moved with changing upcurrent positions through the tidal cycle.

Previously examined movements of *Plectropomus leopardus* indicate site fidelity to both home ranges and aggregation sites (Zeller 1997, 1998, Zeller & Russ 1998). Such behaviours must be considered in MPA delineation. In the present study, movements away from the aggregation site were 9 times more likely after the reproductive period. However, at OTI, fish only moved a maximum distance of 0.6 km from the aggregation within the lagoon (Fig. 1). In comparison, these values differ greatly from those documented by Hutchinson & Rhodes (2010) for *P. areolatus* (23 km), *P. leopardus* (5.2 km), *Epinephelus striatus* (240 km) and *E. guttatus* (33 km). Zeller (1998) found that the distance between home ranges and aggregation sites ranged from 0.2 to 5.2 km (mean = 0.9 ± 0.2 km), and that movement back and forth between these sites ranged from 0.6 to 17 km.

In the present study, the mean distance moved by *P. leopardus* was less during the reproductive period ($10.63 \pm 0.13 \text{ km d}^{-1}$) and greater ($14.48 \pm 0.26 \text{ km d}^{-1}$) during the post-reproductive period, which contrasts with observations by Samoily (1997a). However, Zeller & Russ (1998) also showed that *P. leopardus* moved much less (mean = 0.2 km d^{-1}) during reproduction. These observations probably have a bioenergetic explanation, with re-direction of resources primarily towards reproduction. During the reproductive period, movement rates may have been reduced as fish conserved energy, remained relatively aggregated and devoted bioenergetic resources to gamete production and spawning. After reproduction, movement rates may have increased and proximity to the bottom of the reef (i.e. fish depth) may also have increased as fish became more engaged in foraging activities to replace resources lost during reproduction. In our study, fish moved most in the morning segment of the post-reproductive period, and this was likely related to visually oriented foraging activity. The least amount of movement was observed during the night throughout the study, and there was no significant difference in nighttime movement between the reproductive and post-reproductive period. Zeller (1998) found that 60% of departures from aggregation sites occurred in the morning and minimal movement occurred at night. Pastor et al. (2009) observed peak hours of activity between 08:00–09:00 and 19:00–20:00 h, with decreased activity at sunset for *Epinephelus marginatus* in the Mediterranean. The variation in movement and distance traveled between home ranges and aggregation sites by *P. leopardus* and other species of serranids is large. In this context, general protection of all serranids may require a maximum distance of 240 km from aggregations to be protected; however, for *P. leopardus* a maximum distance of 5.2 km may be sufficient at OTI, but this may not be appropriate for other areas.

It is important to note that several fish disappeared entirely during the study, which may be related to detection efficiency within a complex reef habitat or inter-reef movement. Hutchinson & Rhodes (2010) tested the efficiency of tag detection and found that in open water with no obstructions, detection ranges were 0.25 km, but when fish were associated with reefs, distances dropped to 0.1 km, and in complex coral, reception dropped to under 40 m with the worst detection ranges of 10–20 m. In addition to complex coral habitat, wind, sea state and biological noise (e.g. pistol shrimp) may also interfere with detection of ultrasonic transmissions, meaning that the

effects of these factors on signal detectability and orientation need to be considered to minimize directional bias and error (Zeller 1999, Farmer et al. 2013).

When considering inter-reef movements for the creation of MPAs, Zeller (1998) found that multiple aggregation sites do exist, and there was circumstantial evidence to suggest that inter-reef movements may have occurred in the present study. However, this contradicts results from Davies (1995), who found minimal movement between reefs even during reproductive periods. Zeller (1998) reported that only 31% of tagged fish returned to an aggregation, and one male utilized a spawning site 0.7 km away on a neighboring patch reef even though there were closer well-established aggregations. In a similar study, an individual Nassau grouper was caught at an aggregation 220 km away from the reef, where it was tagged in the Bahamas, although there were many other aggregations much closer (Bolden 2000). Bolden (2000) suggested that the locations of aggregations may be learned through social cues from older individuals. Evidence suggests that inter-environmental and inter-reef movements likely do occur and should be incorporated into the delineation of MPAs.

Consistent movements out of the aggregation indicate that fish were seeking one or a combination of the following: (1) better feeding conditions on the reef edge (Connell & Kingsford 1997) due to lack of significant resources within the aggregation site (Samoily & Squire 1994), or (2) cleaning stations and/or social interactions with conspecifics (e.g. courting, Kingsford 2009). However, *Plectropomus leopardus* in the OTI lagoon remained within 2.6 ha for over 81 d, suggesting a preference for particular smaller areas within a larger home range. Previous studies have shown that *P. leopardus* maintain a small number of sites for access to shelter and cleaning stations, and may move along the reef slope in search of prey (Samoily 1997a, Zeller 1997). Samoily (1997a) tracked *P. leopardus* that moved a mean distance of 2 km, to a maximum of 7.5 km, along the reef slope before returning to an aggregation site. Displacement experiments and observations of aggregation fidelity indicate that *P. leopardus* can and will move across the reef crest, and they have the ability to rapidly return to previously occupied areas over distances of several kilometers (C.M.B. & M.J.K. unpubl. data). This indicates strong site fidelity and exceptional homing abilities in highly complex reef habitats.

In conclusion, although the cumulative distances moved per day were high, *Plectropomus leopardus* often moved within a relatively small area and had specific habitat preferences that differed across the

reproductive and post-reproductive periods. Comparisons between *P. leopardus* and other serranids show that variation in movement is great and therefore multiple species cannot be effectively protected using similar management measures. Unless maximum movements of species (e.g. *Epinephelus striatus*) are used, species-specific and site-specific management plans should be developed. Therefore, to effectively protect and sustain *P. leopardus*, research on site-specific aggregations, migratory corridors and adjacent home range habitats must be conducted to determine appropriate sizes and placement of areas where *P. leopardus* could be protected from exploitation.

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