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REPORT

Movement and spawning migration patterns suggest small marine reserves can offer adequate protection for exploited emperorfishes

B. M. Taylor · J. S. Mills

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Abstract A critical feature of effective marine reserves is to be large enough to encompass home ranges of target species, thereby allowing a significant portion of the population to persist without the threat of exploitation. In this study, patterns of movement and home range for *Lethrinus harak* and *Lethrinus obsoletus* were quantified using an array of 33 acoustic receivers that covered approximately three quarters of Piti Marine Reserve in the Pacific island of Guam. This array was designed to ensure extensive overlap of receiver ranges throughout the study area. Eighteen individuals (12 *L. harak* and 6 *L. obsoletus*) were surgically implanted with ultrasonic transmitters and passively tracked for 4 months. Both species displayed high site fidelity and had relatively small home ranges. The home ranges of *L. harak* expanded with increasing body size. Feeding of fish by humans, which was common but restricted to a small area within the study site, had little effect on the distribution of the resident populations. *L. harak* made nightly spawning migrations within the reserve between full moon and last quarter moon of each lunar cycle, coinciding with a strong ebbing tide. Results indicate that even small reserves can include many individual home ranges of these emperorfishes and can protect spawning sites for *L. harak*. These species are heavily targeted in Guam, and there are major demographic differences between fished and protected sites. This study shows the potential for protected areas to sustain reproductive viability in exploited populations.

Keywords Ultrasonic telemetry · Fish movement · Home range · Marine reserve · Lethrinidae · Spawning migration

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B. M. Taylor (✉)
School of Marine and Tropical Biology, James Cook University, Townsville, QLD 4811, Australia
e-mail: brettmtaylor@gmail.com

B. M. Taylor · J. S. Mills
Marine Laboratory, University of Guam, Mangilao, Guam 96923, USA

Introduction

The success of marine reserves in sustaining or rebuilding reproductively viable populations of reef fishes hinges on the ability to expand reproductive biomass and sustain natural age structures of exploited species (Palumbi 2004; Roberts et al. 2005). To do this, a significant portion of the population must exist without the threat of exploitation (Kramer and Chapman 1999). Small home ranges of many reef fishes facilitate protection within marine reserves (Meyer et al. 2000; Marshell et al. 2011), but having a defined home range does not necessarily ensure safety as temporary migration outside of protected boundaries (e.g., spawning) and ontogenetic habitat shifts can increase vulnerability to exploitation (Kramer and Chapman 1999). Therefore, it is imperative that reserve size and placement adequately encompass the variety of movement patterns of targeted species.

Movement remains a lesser-understood aspect of reef fish life history, largely because of the logistical difficulty of such studies (Sale et al. 2005; Heupel et al. 2006). In the past, studies of fish movement have been limited to tag-recapture methods where data consist of single points of capture and recapture, and the distance and time interval between events (Zeller 1999). Advances in technology have led to an increased use of telemetry as a means of tracking fish movements on coral reefs (Holland et al. 1996; Meyer and Holland 2005; Popple and Hunte 2005;

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Chateau and Wantiez 2009; Hutchison and Rhodes 2010). The passive tracking of individuals tagged with ultrasonic transmitters using an array of acoustic receivers can provide insight into home range size, diurnal and seasonal movement, and habitat use well beyond the scale achievable using conventional tagging (Heupel et al. 2006). Hence, a more recent objective of such studies is the design and evaluation of marine reserves regarding their ability to protect target species from exploitation.

Many studies have reported strong site fidelity among reef fishes (Meyer et al. 2000; Meyer and Holland 2005; Nanami and Yamada 2009) and a variety of maximum home range sizes spanning thousands to hundreds of thousands of square meters for medium- to large-bodied species (e.g., Zeller 1997; Meyer et al. 2000; Eristhee and Oxenford 2001; Meyer and Holland 2005; Popple and Hunte 2005; Hutchison and Rhodes 2010). Additionally, home range size has been found to increase significantly with body size both among (Kramer and Chapman 1999) and within species (Nanami and Yamada 2009; Marshell et al. 2011). For many species, migrations for the purpose of spawning may not be considered part of an individual's home range, as it does not represent normal daily activity patterns (Kramer and Chapman 1999). Such migrations occur at various scales up to hundreds of kilometers (Colin 1992). Rhodes and Tupper (2008) highlighted how spawning migration patterns in *Plectropomus areolatus* increase the capture vulnerability of individuals during reproductive seasons.

Emperorfishes (Family Lethrinidae) are an important component of coral-reef fisheries throughout the Indo-Pacific (Carpenter and Allen 1989). Despite their importance, relatively little is known regarding their adult life history (but see Ebisawa and Ozawa 2009; Currey et al. 2013) or movement patterns, with the exception of reproductive biology (e.g., Young and Martin 1982; Ebisawa 2006; Sumpton and Brown 2004; Bean et al. 2003; Williams et al. 2006; Grandcourt et al. 2010). Two species in particular, *Lethrinus harak* and *Lethrinus obsoletus*, are common on reefs throughout their range and are valued in both commercial and subsistence fisheries. Nanami and Yamada (2009) found that *L. harak* individuals have small and well-defined home ranges that were influenced by interspecific competition among similar-sized individuals. However, their study was limited to daylight hours at a small scale and did not consider potential diurnal movements or migrations related to spawning. On Guam, there are significant demographic differences (greater longevity, mean size and spawner biomass, and lower mortality within reserves) between *L. harak* populations within and outside of protected areas, suggesting protected populations are recovering from high exploitation (Taylor and McIlwain 2010; Taylor et al. 2012).

Understanding movement patterns of targeted reef fishes is a fishery management priority, especially in the context of spatial management procedures such as marine reserves. Here, we aim to quantify home range size, timing and location of spawning, and movement to and from spawning sites for *L. harak* and *L. obsoletus* on Guam. We then assess the present capacity of the marine reserve to protect targeted lethrinids, in terms of both their home range size and potential migration patterns.

Methods

Study site

Piti Marine Reserve (Fig. 1a, b) is one of five marine reserves on Guam. The reserve was established in May 1997, but not fully enforced until January 2001. No harvesting of lethrinids is permitted. Piti Marine Reserve contains a diverse habitat assemblage consisting of reef flat, lagoonal back reef, and fore-reef habitats (Fig. 1c). Reef flat habitats consist of expansive sea grass beds (*Enhalus acaroides*), uncolonized sandy bottom, pavement covered with turf algae, and pavement colonized by reef-building corals. Lagoonal back reef regions are characterized by reef-building corals (predominantly *Porites rus*) often adjacent to sandy bottoms up to ~10 m in depth. Fore-reef habitats range from low-to-high relief and have low-to-moderate coral cover. The reef flat ends at the western boundary of the reserve but is narrowly connected to adjacent Asan Bay at the eastern boundary.

The northeast section of Piti Marine Reserve contains the greatest diversity of habitats and has a high density of *L. harak* and *L. obsoletus*. *Lethrinus harak* is common across all backreef and lagoonal habitats except turf-covered pavement, with mean densities ranging from 3 to 16 individuals per 1,000 m^2 (Taylor et al. 2012). *Lethrinus obsoletus* is most common in areas of high coral cover. Fish feeding by divers is common in a limited area surrounding an underwater observatory (near receiver 3 in Fig. 1).

Acoustic array

We used passive acoustic telemetry to examine movement patterns and quantify home range sizes of *L. harak* and *L. obsoletus* in Piti Marine Reserve over a 4-month period. Fish were tracked using individually coded acoustic transmitters (V9-2L®, 60 s delay, 275-d battery life, Vemco). An array of 33 omnidirectional VR2W® acoustic receivers was deployed in a pattern to ensure near-complete overlap of receiver ranges across the study area (Fig. 1d). The functional range of transmitters was estimated prior to deploying the array using in situ trials at a range of depths. A V9-2L® equivalent range-test transmitter (same power output, faster transmission rate) was

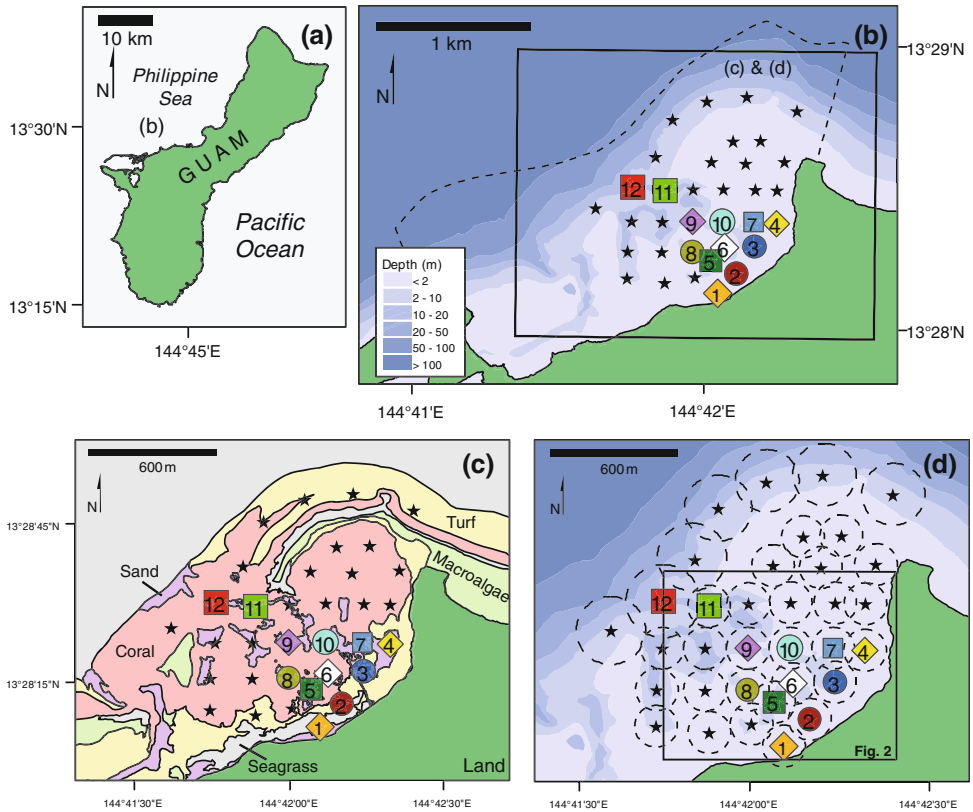

Fig. 1 **a** Map of the study site (*black rectangle*) on the central-west coast of Guam. **b** Depth contour plot of Piti Marine Reserve indicating the locations of receivers within the study array. *Dashed line* represents the marine reserve boundary. **c** Distribution and diversity of habitat types within Piti Marine Reserve. **d** Receiver positions with mean detectable ranges for receivers highlighted as *dashed circles*. *Color*- and *shape*-coded receivers correspond to Fig. 4

submerged at various distances from receivers for a fixed period of time over a range of depths from <1 to >10 m. Further range testing was carried out after array deployment to obtain receiver-specific range estimates by slowly moving the range-test transmitter throughout the array in a zigzag pattern tracked by a handheld GPS unit. Final detection ranges in backreef and lagoonal habitats averaged 111 m, with a minimum range of 60 m and maximum of 234 m. Outer-reef receiver ranges all exceeded 200 m.

The receiver array covered nearly 200 ha of reef area, with considerable overlap between adjacent receivers. Overall, there was 88 % coverage within the array (93 % excluding the surf zone) and a 91 % detection rate from in situ range tests throughout backreef habitats. Receivers were deployed using three methods: backreef receivers were mounted antenna-up, either attached to rebar fixed in cement-filled concrete blocks or within concrete blocks (in very shallow habitats); outer-reef receivers were moored to the reef in antenna-down position using stainless steel cable and subsurface buoys.

Fish capture and transmitter implantation

Fish were captured from Piti Marine Reserve using hook-and-line during early morning hours and immediately transported back to the laboratory where they were placed in an outdoor holding tank. A total of twelve *L. harak* and six *L. obsoletus* were surgically implanted with transmitters (Table 1). Fork length (FL) and total weight (TW) were measured for each individual, but sex was not determined because we decided nonlethal procedures for determining sex (cannulation) caused too much stress to fish and may have reduced survival rate. Fish were anesthetized using a 0.75 g L^{-1} solution of tricane methanesulfonate (Finquel MS-222) in an aerated tank. After anesthesia, fish were fitted internally with a sterile coded transmitter, surgically inserted into the abdomen through a small incision (<2 cm) in the body wall. Incisions were closed with a surgical stapler and covered with topical antibiotic cream. Each fish was also fitted externally with a T-bar anchor tag imprinted with a phone contact. Following surgery, fish were immediately placed in an aerated holding tank where they were monitored for 3 to 6 d prior to being released close to where they were originally captured. Captive recovery periods up to 3 weeks (Zeller 1998) have commonly been used to ensure optimal post-surgery survival rates. Incisions of all tagged individuals were fully healed before being returned to the study site. Fish lengths and release dates are given in Table 1.

Spawning activity and validation

Migrations of *L. harak* were monitored over eleven lunar cycles (October 17, 2009–August 21, 2010) using a single

Table 1 Summary of tagging, release, and detection data as well as home range area estimates (50 and 95 % kernel utilization distributions [hectares]) for *L. harak* and *L. obsoletus* in Piti Marine reserve

Code	Species	Fork length	Release date	Detection span (d)	Total detections	50 % KUD	95 % KUD
LH-1	*L. harak*	219	October 17, 2009	166	90,974	0.069	1.122
LH-2	*L. harak*	293	October 17, 2009	16	12,648	0.181	1.206
LH-3	*L. harak*	316	October 17, 2009	117	74,411	1.386	8.222
LH-4	*L. harak*	260	October 17, 2009	257	33,005	0.994	5.250
LH-5	*L. harak*	197	October 17, 2009	167	112,000	0.071	0.737
LH-6	*L. harak*	256	October 17, 2009	22	11,878	0.283	0.259
LH-7	*L. harak*	245	October 17, 2009	273	16,200	0.569	7.930
LH-8	*L. harak*	200	October 17 2009	5	2,247	(1.359)	(12.760)
LH-9	*L. harak*	195	October 17, 2009	196	20,648	0.051	0.447
LH-10	*L. harak*	234	November 3 ,2009	270	49,410	0.086	0.770
LH-11	*L. harak*	242	November 3, 2009	100	24,975	0.106	0.748
LH-12	*L. harak*	230	November 19, 2009	277	26,744	0.257	2.085
LO-1	*L. obsoletus*	214	November 19, 2009	85	10,479	0.381	2.162
LO-2	*L. obsoletus*	184	November 19, 2009	85	19,310	–	–
LO-3	*L. obsoletus*	194	November 19, 2009	85	14,648	0.009	0.071
LO-4	*L. obsoletus*	287	November 19, 2009	85	26,549	0.009	0.084
LO-5	*L. obsoletus*	202	November 19, 2009	85	26,838	0.004	0.040
LO-6	*L. obsoletus*	175	November 19, 2009	71	2,885	0.246	1.731

Parentheses surrounding KUD values for LH-8 indicate erroneous home range estimates due to a detection span of only 5 d

receiver at the opening of the main channel to the outer reef (receiver 12, Fig. 1). The receiver remained in place after completion of the 4-month home range study to record the incidence of fish movement along a recurring migratory pathway, presumably to a spawning site, and was far outside the range of normal daily movements for any individual. The link between spawning activity and migrations was based on island-wide collections of *L. harak*; gonadosomatic index values $\left(\mathrm{GSI} = \frac{\text{ovary weight}}{\text{Gutted body weight}} \times 100\right)$ of mature, active females were plotted by lunar day.

Data analysis

We calculated center of activity (COA) locations by using the mean position algorithm of Simpfendorfer et al. (2002), based on weighted arithmetic mean latitude and longitude of detections within sequential 2-h periods. Receiver locations were recorded in WGS84 geographic coordinates, and an Albers equal-area projection was used for subsequent spatial analysis.

The size of home ranges of individual *L. harak* and *L. obsoletus* was estimated using kernel utilization distributions (KUDs) based on COA locations. The KUD is a probability density estimation approach that measures intensity of area use on a two-dimensional plane over time (Worton 1989). It is a bivariate function that returns the probability density that an individual is found at a geographic location. We define an individual's home range as where it spends 95 % of its daily activity (95 % KUD). This estimate incorporates broader areas including range limits and corridors between more heavily frequented locations, whereas the 50 % KUD represents the core home range. The 50 and 95 % KUDs, along with associated isopleths, were estimated for a 1,000 by 1,000 cell grid using the *kernelUD* function in the *adehabitat* package for the R statistical computing language (Calenge 2006). The default *ad hoc* method was used to estimate the appropriate smoothing parameter. The relationship between body size and area usage (home range estimates) was examined for each species using linear regression. This analysis included only those individuals with a detection span greater than 1 month. Diurnal movement patterns of individuals were explored by plotting individual detections, visually coded by receiver location, against time of day across the entire detection span. Natural log-transformed home range size was compared between species using analysis of variance.

Results

Acoustic tagging and tracking

Tagged individuals ranged from 195 to 316 mm FL for *L. harak* and from 175 to 287 mm FL for *L. obsoletus* (Table 1). These size ranges encompass virtually the entire

reproductive size range for both species (Taylor and McIlwain 2010). Further, there was no tagging-induced mortality for any individual immediately following implantation. For *L. harak*, individuals were released in three batches: nine individuals were released on October 17, two individuals were released on November 3, and one individual was released on November 19, 2009.

Individuals of both species were monitored using the full array of receivers until February 10, 2010. Additional monitoring for spawning migrations lasted until the final tags exhausted their battery power (August 21, 2010). Total detection spans ranged from 5 to 277 d (mean = 155.5 d, SD = 103.7 d) for *L. harak* and from 12 to 84 d for *L. obsoletus* (mean = 72.0, SD = 29.4; Table 1). During the full receiver deployment (release until February 10, 2010), each fish in the study was detected on 100 % of the days until the end of its detection span, with the exception of LO-1 (69 %) which disappeared from January 4 to January 15. Mean daily detections for individuals ranged from 137 to 957 (mean = 483) for *L. harak* and from 176 to 325 (mean = 250) for *L. obsoletus*. The mean number of daily detections was not related to fork length for *L. harak* ($F_{1,11} = 0.143$, $r^2 = 0.014$, $p = 0.713$) or *L. obsoletus* ($F_{1,5} = 1.056$, $r^2 = 0.209$, $p = 0.362$), and differences in daily detections between species were not statistically significant (t test, $t_{16} = 1.976$, $p = 0.066$).

Home range estimation

Estimates of home ranges using 50 and 95 % KUDs varied within and between species (Table 1; Fig. 2). Values of 95 % KUD estimates ranged from 0.259 to 8.222 ha for *L. harak* (excluding LH-8, which was only tracked for 5 d) and from 0.040 to 2.162 ha for *L. obsoletus*. Mean home range sizes (95 % KUD) were 2.6 (±2.9 SD) and 0.8 (±1.0 SD) ha for *L. harak* and *L. obsoletus*, respectively, and these values differed statistically ($F_{1,14} = 5.3$, $p = 0.037$). Both species spent the vast majority of their time in shallow-water backreef habitats. Despite a high number of detections, isopleths were not generated for LO-2 because the algorithm results failed to converge after several thousand iterations.

A high degree of overlap in home range areas of individuals was observed within and between species (Fig. 2). Home range size, however, increased significantly with individual FL for *L. harak* (Fig. 3), but not for *L. obsoletus* ($r^2 = 0.099$, $p = 0.606$). Daily movement patterns for individual LH-8 suggest it was eaten by a predator on the fifth day, which resulted in erroneously high home range estimates.

Movement patterns

Daily detection plots demonstrated several patterns common to both species (Fig. 4). These included strong diurnal patterns and higher daytime activity. Diurnal patterns included crepuscular shifts between daytime and nighttime locations (shown by LH-1, LH-3, LH-5, and LO-1; Fig. 4a–c, e). Several individuals appeared to have disjunct daytime and nighttime home ranges (Fig. 4b, e). For example, LH-3 (Fig. 4b) spent the vast majority of time during the day near receivers 3, 4, and 7 and relocated to receiver 5 at night. Activity (movement between receivers) was greater during the daytime for LH-3 and LO-1. The other individuals generally remained within the range of a single receiver.

There were also species-specific characteristics in daily movements. For *L. harak*, nighttime locations for some individuals shifted between shallower and deeper receivers at approximately 2-week intervals (Fig. 4a, c), indicating tide-induced movements where extremely shallow water during nighttime neap tides forced individuals to seek refuge in deeper water. Lunar cycle migrations are also evident for LH-12 (Fig. 4d) and are highlighted in the following section. For most *L. obsoletus* individuals, detection rates decreased significantly at night (Fig. 4f) likely because of poor signal reception within high rugosity habitats.

Spawning movement and periodicity

Four months of detection data from the receiver array identified clear migration patterns for every *L. harak*. These migrations began several days before full moon and occurred nightly, lasting until third-quarter moon. Migratory pathways were consistent for each individual and led from the core home range area (50 % KUD) to the deeper sand channels (receivers 9 and 11) and eventually onto the fore reef via receiver 12 (Fig. 2). Individuals then disappeared from the receiver array for an average duration of 4.13 h (SD = 1.52 h) and were not recorded by any other outer-reef receiver to either side of receiver 12. Continued tracking of these migrations for 11 lunar cycles (after which battery life of all tags was exhausted) using a single receiver at station 12 suggested that these migrations occur each lunar cycle throughout the year.

These migrations presumably occurred for the purpose of forming a spawning aggregation, and spawning activity was confirmed through GSI data (Fig. 5). A significant increase in mean GSI occurred prior to the migratory period and peaked at the beginning. The subsequent decrease suggests *L. harak* spawn during these lunar migrations, most likely at a fixed aggregation site in the outer reef beyond the channel opening. Examination of migration times (where the beginning and ending of a migration were denoted by the exit from and return to the channel at receiver 12) indicated that the duration of presumed spawning was correlated with strong outgoing tides.

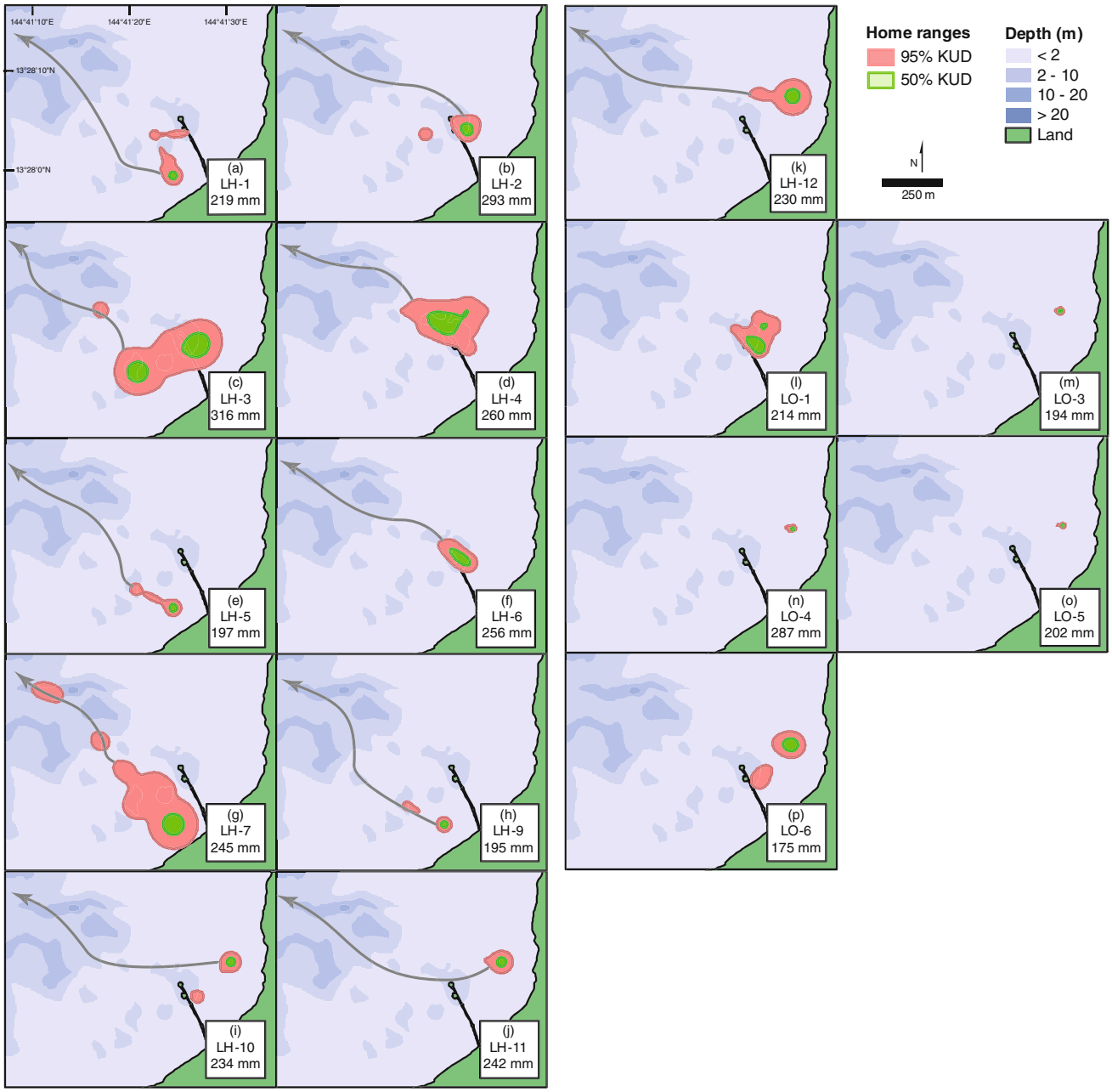

Fig. 2 Individual home range estimates (95 and 50 % kernel utilization distributions) of *L. harak* (**a**–**k**) and *L. obsoletus* (**l**–**p**). *Arrows* represent reoccurring monthly migratory pathways for each individual. Depth profiles explained in the key

Discussion

This study has provided a comprehensive and detailed description of several aspects of emperorfish movement. This was facilitated by total numbers of detections, daily detection rates, and detection spans for individuals that are among the highest recorded in the reef fish telemetry literature. Further, home range sizes and movement patterns identified here suggest that even small marine reserves can provide adequate protection for these and other species with limited, defined home ranges and predictable movement patterns.

An increasing number of studies have shown clear use of defined home ranges and strong site fidelity in a variety of coral-reef fishes (Ehrlich 1975; Sale 1978; Zeller 1997; Kramer and Chapman 1999; Eristhee and Oxenford 2001; Welsh and Bellwood 2011; Marshell et al. 2011). The present study has demonstrated this for *L. harak* and *L. obsoletus*, both of which have home range sizes less than ten hectares. This has important implications for spatial

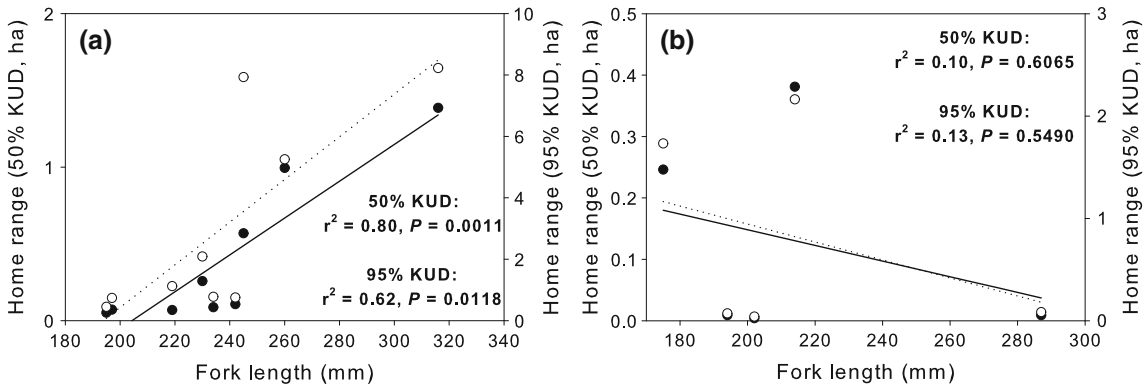

Fig. 3 The linear relationship between fork length (mm) and home range size (ha) for **a** *L. harak* and **b** *L. obsoletus* using both 50 % (*filled circles*; *solid line*) and 95 % (*open circles*; *dotted lines*) KUD estimates

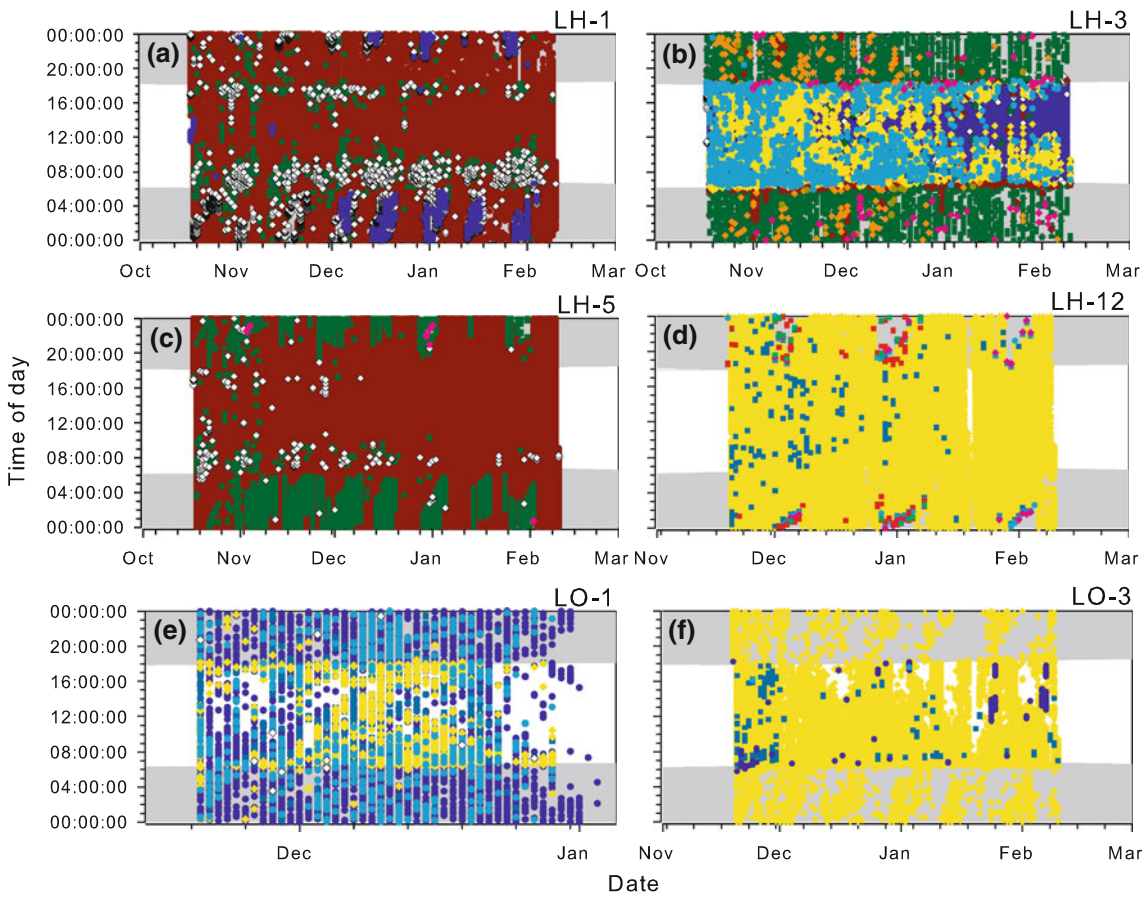

Fig. 4 Daily detections of *L. harak* (**a**–**d**) and *L. obsoletus* (**e**–**f**). *Unshaded regions* represent the period between sunrise and sunset. Detections are *color*- and *shape*-coded to correspond with numbered receivers in Fig. 1

management. Home ranges, migration routes, and spawning sites identified in this study and in Marshell et al. (2011) demonstrate that small marine reserves on Guam offer adequate protection for several high-value medium-bodied reef fishes. Many reviews and meta-analyses have demonstrated that reserve size does not affect the magnitude of biological responses for exploited fishes (Cote et al. 2001; Halpern 2003; Micheli et al. 2004; Lester et al. 2009; but see Claudet et al. 2008), suggesting that small reserves can be highly effective. Prime examples are Apo and Sumilon in the Philippines (Russ and Alcala 1996), where density and biomass of exploited species have shown strong responses to protection. Naturally, reserve size should at least match or exceed the range of movements for valued species (Gell and

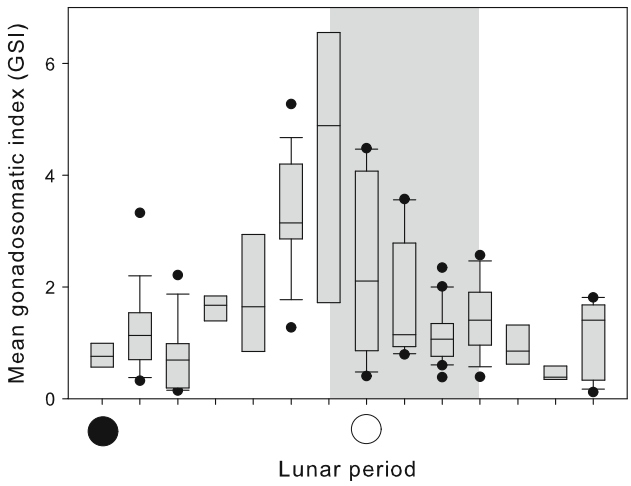

Fig. 5 Gonadosomatic index values for active, mature female *L. harak* plotted by lunar day (bin = 2 days). *Black and white circles* represent new and full moons, respectively. *Shaded region* indicates the period during which individuals were consistently recorded migrating outside their home range areas

Roberts 2003), but progressively more studies are showing that targeted reef fishes have small defined home ranges, especially on coral reefs. Further, increases in density and biomass of fishes is a desired outcome of marine reserve establishment, but ultimately population viability depends on reproductive success through time. Hence, migratory routes and spawning locations are also major factors affecting vulnerability to exploitation (Rhodes and Tupper 2008) and efficacy of marine reserves (Pillans et al. 2011).

Consecutive nightly migrations of *L. harak* occurred for eleven lunar cycles (until all transmitter batteries were exhausted), suggesting this species spawns throughout the year. Migrations likely end at a consistent spawning site (Domeier and Colin 1997) but the question remains whether this site is located within the marine reserve boundary. Our data strongly suggest that it does. Swimming speeds of individuals detected migrating ranged from 12 to 28 m min^{-1} (mean: 20 m min^{-1}). Assuming swim speeds remained consistent in the outer-reef zone and fishes spawn immediately on arrival, then individuals could migrate for a maximum of 2.5 km from the mouth of the channel. This would take them just outside of the marine reserve at either boundary, avoiding outer-reef receivers. However, it is very unlikely that individuals would travel so far because spawning would not be instantaneous. Given the time frame of disappearance, swim speeds of individuals, and lack of detections at outer-reef receivers in either direction of the channel, we presume that the aggregation site lies in the deeper outer reef in the vicinity of the channel opening. Depending on environmental conditions, the timing of aggregations would allow *L. harak* to use ebb tide currents flowing out of the channel to better disperse eggs, a common behavior in fishes that aggregate to spawn (Johannes 1981; Robertson 1983; Colin and Bell 1991; Domeier and Colin 1997; Colin 2010).

The presumed scale of spawning migrations suggests that small marine reserves can offer full protection to segments of the population, but many questions remain regarding spawning behavior in *L. harak* and *L. obsoletus*. Pillans et al. (2011) stressed improving knowledge of spawning behavior after finding that *Lethrinus nebulosus* left the Mangrove Bay Sanctuary in Western Australia during spawning periods. Little is known about spawning behavior in lethrinids (Domeier and Colin 1997), with most information derived from anecdotal accounts reported by fishermen (Johannes 1981; Hamilton 2005). Johannes (1981) provided a summary of spawning times and locations for lethrinids, based on extensive interviews with fishermen in Palau, Micronesia. There, all lethrinids form aggregations around the new moon and the days following, and spawning takes place at night. On Guam, migrations and GSI data suggest spawning activity occurs around full moon. It is unclear how spawning effort is distributed within and among lunar periods. GSI data suggest that spawning commences early in the migration period and may continue throughout. Further, it is unclear whether individuals from outside of Piti Marine Reserve are aggregating at the same site and if so from how far individuals are travelling. The nightly occurrence and time frame of migrations suggests that many small spawning aggregations occur around Guam rather than few large aggregations. We did not see evidence of spawning behavior in *L. obsoletus*, and this species clearly does not make significant migrations between November and February.

Home ranges of *L. harak* were considerably larger than those of *L. obsoletus*. Species-specific behaviors may explain this; *L. obsoletus* tends to be dependent on rugose coral-associated habitat (B. Taylor pers. obs.) while *L. harak* is common in a variety of backreef habitats (Taylor et al. 2012). Home range size and shape for many reef fishes varies in response to habitat pattern and availability (Kramer and Chapman 1999). Thus, habitat distribution coupled with frequent use of rugose shelter may limit the range of movements in *L. obsoletus*. Maximum home range size for *L. harak* was an order of magnitude greater than that of conspecifics in Japan (Nanami and Yamada 2009). Strong diurnal patterns identified in the present study account for these differences because estimates from Nanami and Yamada (2009) excluded nighttime and crepuscular movements. However, while differing methodologies make regional comparisons tenuous, both studies identified ontogenetic expansions in home ranges. Such expansions have been documented for other reef fish (Marshell et al. 2011) and are typically interactively driven

by changes in habitat preference (Dahlgren and Eggleston 2000; Lecchini and Galzin 2005) and diet (Nakamura et al. 2003). Size distributions of *L. harak* in Piti Marine Reserve demonstrate that juveniles prefer sea grass but expand to other habitats as they grow larger (Taylor et al. 2012). Accordingly, the smallest individuals here had tiny home ranges confined primarily to sea grass (e.g., LH-1, LH-5, and LH-9), whereas larger individuals occupied several habitats over a broad range (e.g., LH-3 and LH-4).

Both species of lethrinids showed strong diurnal patterns of movement. On average, daytime activity levels were greater than those at night. We observed both species resting in or against coral or rock refuges during the night, and telemetry data suggest that individuals retire to the same general areas each night. Some individuals were found to occupy one area or habitat type during the day and another at night, making daily crepuscular migrations between them. This "commuting" behavior is known from several small- to medium-bodied reef fish species that live in complex and variable habitats (Holland et al. 1993; Meyer and Holland 2005; Claisse et al. 2011; Marshell et al. 2011). Because of the high spatial resolution required, it can be difficult to determine whether all individuals make daily commutes (Claisse et al. 2011). Here, this behavior was very clear for individuals with home ranges exceeding the ranges of individual receivers (e.g., LH-3), but shorter commutes may have been interpreted as remaining in one core location at all times.

Within Piti Marine Reserve, some individuals frequently visited the area where fish feeding by divers is common, but feeding did not appear to affect the overall distribution of fishes in the vicinity. Chateau and Wantiez (2008) inferred slightly higher presence of three *Lethrinus nebulosus* in a New Caledonian marine protected area during times of peak human activity, suggesting altered behavioral patterns resulting from potential human feeding activity. High densities of *L. harak* and *L. obsoletus* were observed at the feeding area in Piti, but home ranges of many nearby individuals in this study did not overlap with it at all. Few studies have evaluated the effects of humans feeding wildlife in the marine environment, but those that have generally find that any effects are highly localized and difficult to tease apart from underlying habitat variability (Cole 1994; Hawkins et al. 1999; Milazzo et al. 2005). Our data suggest some individuals migrate to or reside at the feeding site, but most nearby individuals have distinct diurnal movement patterns that do not include the feeding site. Higher densities where fish are fed by divers are likely driven in part by increased carrying capacity resulting from increased food availability. Densities within habitats throughout the rest of the marine reserve are comparable to those in other marine reserves on Guam (Taylor et al. 2012).

Previous work on Guam has revealed significant demographic differences, which suggest marine reserves have positively affected lethrinid populations within protected boundaries (Taylor and McIlwain 2010; Taylor et al. 2012). Vast differences in spawning potential between sites that are open and closed to fishing have important implications for fishery management, but population sustainability still hinges on actual reproductive processes and linkages among sites. The identification of a protected spawning site in the present study provides further evidence that marine reserves in Guam support a disproportionately high proportion of the total island-wide reproductive potential and demonstrate how small marine reserves can adequately protect individuals of exploited species throughout their life histories, including temporary migrations.

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