

Fish movements within community-managed fishery reserve networks: an acoustic survey of *Lethrinus harak* in Vanuatu

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ABSTRACT: Acoustic telemetry has been increasingly used for monitoring fish movements at different spatial and temporal scales. In this study, passive telemetry and fine-scale habitat data were integrated for the first time to investigate the relevance of community fishery reserves (CFRs) for managing reef fish resources. In Efaté Island (Vanuatu), 38 thumbprint emperors *Lethrinus harak* (Lethrinidae) were tagged at 7 sites and tracked between April 2011 and February 2012 using an acoustic array of 16 receivers. The survey area extended over 11.3 km² of fringing reef in 3 coastal community tenures that included 3 small CFRs. Habitats were mapped using very high resolution satellite imagery and ground-truthing. Thirty fish were detected for up to 229 d (median = 153 d). Six geographical groups were identified among 21 resident fish. These groups showed strong fidelity to small sites (116 to 763 m) that were located in reserves and fished areas, across community tenures, and across 12 habitat types. Overall, 42 excursions were detected at several hundreds to thousands of meters from the fidelity sites along contiguous fringing reefs, across habitat types, and across boundaries of CFRs and community tenures. The estimated home range size of *L. harak* ranged from 116 to 3979 m (median: 763 m) and was highly varied within fish groups. We concluded that home range size and behavioral plasticity of *L. harak* limit the effectiveness of small individual CFRs for protecting this species. Networks of CFRs would be more effective but require management arrangements between neighbor communities.

KEY WORDS: Acoustic telemetry · Fish movement · Community-managed area · Fishery reserve · *Lethrinus harak* · Vanuatu · Coral reef

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INTRODUCTION

In small Pacific countries, culture-based sociopolitical organization, remoteness of coastal populations, land dispersion, and limited human and financial governmental capacities have favored community-based initiatives for regulating reef fishing practices (Ruddle et al. 1992, Ostrom et al. 1999, Johannes 2002). Taboos have traditionally enforced local, village-specific, harvest restrictions (e.g. species and gear bans) and area closures within marine tenures.

The latter raise very specific issues compared to westernized, permanent no-take zones and are used by communities as fishery management tools (Sale et al. 2005). First, closed areas are usually used as marine fallow areas: they are temporarily opened and harvested periodically to address communities' or fishers' socioeconomic needs rather than long-term ecosystem conservation objectives (Cohen & Foale 2013, Cinner et al. 2006). Net biomass exports from such community fishery reserves (CFRs) therefore occur through larval dispersion and spillover of juve-

niles and adults as well as through direct, occasional outputs by fishers during openings. Second, CFRs are necessarily embedded in marine tenures, thus limiting in effect their potential size which is typically 1 to 2 orders of magnitude smaller than that of westernized no-take zones (Foale & Manele 2004). Size of CFRs is particularly critical for managing mobile species threatened by fishing because closures efficiently protect those fish that spend most of their time within the reserve boundaries (Kramer & Chapman 1999).

Positive effects of CFR on the abundance of exploited reef finfish and invertebrates have been documented both directly and indirectly within these reserves, through underwater observations of resource density (e.g. Léopold et al. 2009, Dumas et al. 2010) and through catch and fishing yield monitoring during the reserve openings (e.g. Jupiter et al. 2012, Cohen & Alexander 2013), respectively. These positive ecological effects and short-term fishing benefits explain the general acceptability of CFRs among fishers and coastal communities (Johannes 1998, Bartlett et al. 2009) and, consequently, the upsurge of conservation programs in the Pacific since the 1990s. During the last decade, hundreds of small CFRs (<0.1 to 1 km²) have been established in the South Pacific, most often with the support of local and national governments and/or international organizations (Alcala & Russ 2006, Govan 2009). These small CFRs are better enforced locally and last longer than other community-based fishing restrictions, particularly for reef finfish (Léopold et al. 2013).

Surprisingly, despite the enthusiasm that they have generated locally and regionally in the Pacific, little field information is available on the ecological mechanisms that determine the effects of CFRs on reef resources (but see Waldie et al. 2016). This knowledge would be extremely valuable for promoting effective reserve designs and also for providing sensitive explanations and avoiding the disillusionment of local communities in case of reserve failure. Conversely, the literature on westernized, permanent no-take zones is informative despite the knowledge gaps on the interactions between CFRs and reef resource space uses. A large number of acoustic surveys have shown that differential mobility of adult reef fish very likely impacted no-take zone effectiveness because of the spillover effect (e.g. Meyer et al. 2007, 2010, Chateau & Wantiez 2008, Marshall et al. 2011). Acoustic telemetry has been increasingly used in the last decade for assessing site fidelity behaviors among reef fish, daily and migratory movements, home range size and shape, and habitat uses patterns (e.g.

Zeller & Russ 1998, Marshall et al. 2011, Bijoux et al. 2013, Currey et al. 2014, Garcia et al. 2014, Matley et al. 2015). Several authors have also documented the effects of habitat structure and diversity on fish movements and discussed the expected outcomes of no-take zones (Hitt et al. 2011, Pittman et al. 2014). Whether or not these findings could be extrapolated to CFRs in the Pacific context needs to be investigated due to their specific characteristics.

Following other acoustic studies concerning the connectivity between no-take zones and neighbor areas, this paper presents one of the first acoustic surveys conducted in community-managed marine areas in the Pacific. This survey was part of an action research program aimed at improving coral reef fishery management in Vanuatu (southwest Pacific). Specifically, both passive telemetry and fine-scale habitat data were jointly used to empirically investigate the relevance of CFRs for managing reef fish resources. In Vanuatu, current national fishing regulations target high-value commercial species such as invertebrates (i.e. lobsters, trochus, and sea cucumbers) and are less concerned with reef finfish species that are used for local consumption and local markets. The implementation of small CFRs has therefore been widely promoted by the Fisheries Department since the 1990s as a way to protect and stockpile reef resources for the benefits of local communities (Hickey & Johannes 2002). In this study, we acoustically monitored the movements of the thumbprint emperor *Lethrinus harak* (Lethrinidae), a species targeted by near-shore fishers throughout Vanuatu (Amos 2007). Fish response to a reefscape mosaic, closed areas, and community tenures was investigated. The results allowed us to make recommendations on the size and location of CFRs within communities' marine tenures. Management perspectives based on home range analysis are discussed for designing effective individual CFRs and CFR networks according to space-use patterns of *L. harak* and marine tenure.

MATERIALS AND METHODS

Fishing and management context in Efaté Island, Vanuatu

In Vanuatu, most of the population lives in rural coastal areas and engages in small-scale fishing activities (VNSO 2007). Strong geographical variations in fishing pressure are observed throughout the archipelago according to natural conditions (e.g. reef

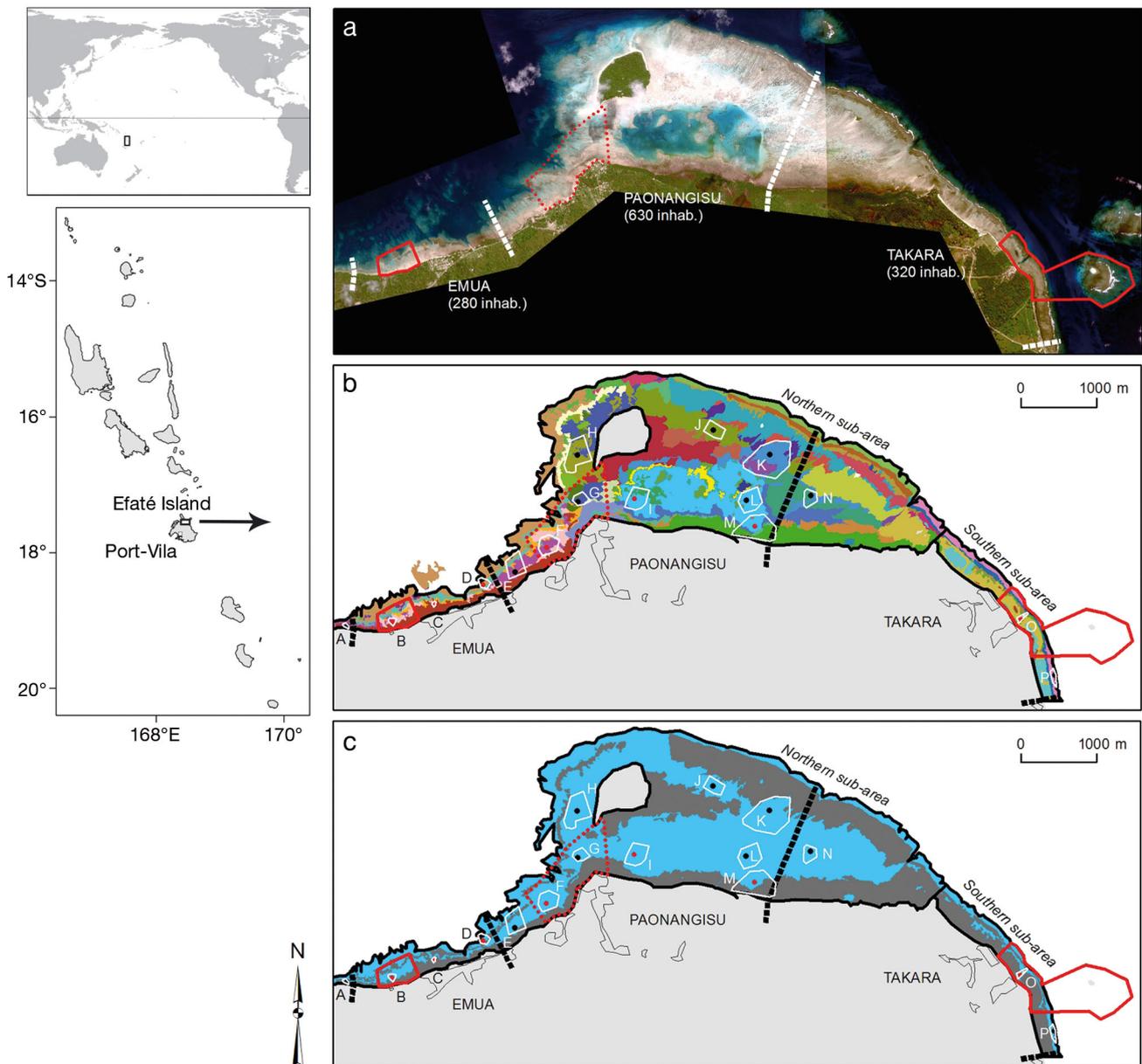


Fig. 1. Location of the study area off the northern coast of Efate island, Vanuatu. (a) Worldview 2 satellite images, (b) habitat map, and (c) intertidal areas of the reef system. White polygons (b,c) represent the detection range of each acoustic receiver ($n = 16$, A to P). Coloured areas in (b) represent the marine habitats. Grey and blue areas in (c) represent the intertidal zone and deeper areas, respectively. The location of the 7 fishing and releasing sites of tagged fish (b,c) are indicated by red spots (receivers B, C, D, F, I, M, and O). The thick dotted lines represent the marine tenure boundary of each of the 3 villages. The thick solid polygon lines represent the boundary of both study sub-areas. The red solid and dotted polygon lines represent the boundary of the existing and planned community fishery reserves, respectively

geomorphology or habitat diversity) and socioeconomic factors (e.g. transport infrastructures, commercial networks, urban demand for fish, and demographic pressure) (Cillaurren et al. 2001). Owing to the proximity of Port-Vila, Vanuatu's capital, near-shore finfish resources are exposed to greater sustainability issues on Efate Island than in the rest of the country.

The survey was conducted on Efate Island over a relatively large reef area (11.3 km^2) that encompassed 3 villages' tenures, namely Emua, Paonangisu, and Takara, totaling ~ 1200 inhabitants (Fig. 1a). Environmental conditions, fishing status and management regimes differed among villages (Léopold et al. 2013; Table 1). Paonangisu village was characterized by the largest reef fishing grounds, population level,

Table 1. Characteristics of the 3 villages in this study (Efaté Island, Vanuatu): population size, reef fishing grounds (coastal length, surface, and marine habitats), fishing capacities (number of gillnets, spearguns, and wooden canoes), and marine fishery reserves (date of creation, coastal length, and surface). Gillnet: 25 m long, 1.5 to 6 m high, 15 to 50 mm square mesh size. Note: Paonangisu's fishery reserve was planned and not in force at the time of survey

Population	Reef fishing grounds		Main habitats (% area)	Habitat types (n)	Fishing capacities			Fishery reserve		
	Linear extent (km)	Area (km ²)			Gill- net	Spear- gun	Canoe	Date of creation	Linear extent (km)	Area (km ²)
Emua 280	2.1	1.4	Fringing reef (70%) Outer reef (30%)	7	32	9	2	2005	0.55	0.2
Paonangisu 630	4.1	7.6	Fringing reef (54%) Outer reef (23%) Lagoon (12%) Seagrass bed (11%)	44	66	15	10	Planned	1.14	0.7
Takara 320	4.9	3.6	Fringing reef (87%) Outer reef (13%)	11	19	9	7	2008	0.94	0.8

and subsistence and commercial fishing pressure, which yielded higher socioeconomic needs and fishery dependence than the other villages. No community-based fishery management rule was enforced in this village due to sociopolitical conflicts that undermined local governance efficiency. However, fishers perceived a decline in reef resources early on and proposed the implementation of a shoreline-bounded CFR. The planned CFR is adjacent to the most populated area of the village to facilitate permanent visual surveillance and discourage poaching (Fig. 1a). Community reliance on reef fishing for their livelihoods was higher in Paonangisu village than in Emua and Takara villages. The 2 latter communities had established a well-enforced shoreline-bounded CFR for several years and some other temporary local fishing restrictions were effective at the time of this study (Fig. 1a). Although fishers mentioned that fish abundance within both CFRs had increased they questioned the adequacy of its dimension and location.

The 3 communities were strongly involved in, and supportive of, the acoustic survey because it was expected that the results would provide crucial information to support local decisions related to the use of CFR for the management of coral reef fisheries within their respective marine tenure.

Fine-scale habitat mapping

The marine area was composed of 1 to 6 m deep lagoons (1 km²), 0.5 to 2 m deep fringing reefs (8.3 km²), and a 0.5 to 10 m deep outer slope (2 km²) representing the main coral reef geomorphologic

units of the island. The limit of the intertidal area was mapped using GPS. It includes 4.9 km² of reef crest and near-shore seagrass beds and reef flats and accounted for 43% of the study area (Fig. 1c).

A habitat map of the study area was created from 2 very high spatial resolution (2 m) multispectral Worldview 2 images acquired on 11/07/2010 and 21/08/2010. Images were processed and photo-interpreted according to the user's flow chart described by Andréfouët (2008) to ensure high accuracy and a high number of classes, including a sun-glint correction following Hochberg et al. (2003). Ground-truthing was conducted in November 2010 and May 2012 on 77 stations distributed across the study area. Stations were selected using the satellite image to cover the range of color and texture visible on the image. Vertical photographs were used to measure percentage of cover of algae, seagrass, live coral, dead coral, broken branching coral, sand, rubble, and rock (old eroded coral substrate). The habitat map was vectorized and imported into a geographical information system (GIS). The habitat polygons were then used to document the movements of fish between habitat patches.

The habitat map included 64 habitats (surface area in the range 0.01 to 0.26 km²) defined according to categories and relative size of cover, geomorphology, and exposure to wave action (Fig. 1b). The composition and spatial distribution of the habitat patches rendered the reef heterogeneity and habitat patchiness. The survey area was composed of 2 sub-areas characterized by different environmental conditions. The northern sub-area (93.5% of the survey area) showed high complexity and low-to-medium expo-

sure to wave action. The southern sub-area (6.5% of the survey area) was composed of an elongated, shallow reef flat highly exposed to wave action and broken by a 1 to 6 m deep and 50 m long channel (Fig. 1a,b). Sub-areas were separated by a narrow 120 m long reef flat exposed to strong tidal currents and swell.

Receiver array

Passive acoustic telemetry was used to monitor fish movements. A discontinuous array of 16 omnidirectional receivers (Vemco VR2W, 69 kHz) was deployed in strategic locations in the survey area, 14 in the northern and 2 in the southern sub-areas, at distances exceeding 300 m in most cases (Fig. 1b,c). The deployment of receivers between sub-areas was proportional to the surface of each sub-area. As compared with the only other passive acoustic survey of *Lethrinus harak* (Taylor & Mills 2013), the array design allowed for detecting medium-distance and long-distance fish movements, whereas most short-distance movements (<300 m) remained undetected. Receivers were moored at 0.5 to 5 m depth, facing upwards.

The detection range of each receiver was empirically tested in similar meteorological and tidal conditions to account for spatial variability in acoustic signal transmission due to marine habitat structure (Marshall et al. 2011, Welsh et al. 2012). Starting at each receiver, a coded V8-4L Vemco (69 kHz, 1 s delay) transmitter was towed along 5 to 8 transects at a constant speed of 1 m s⁻¹ in the water column at a height of ~1 m above the sea bottom to mirror the behavior of *L. harak*. The transmitter position was monitored every second by a handheld GPS unit. The position of the last transmitter detection logged by the hydrophone on each radial was used to estimate the detection range of the hydrophone on this radial. A detection polygon was then created for each receiver by joining the most distant detection points in a GIS. Very high variation in detection range was observed (18 to 370 m) among radials and among hydrophones according to reef habitats and depth. Detection zones varied by 2 orders of magnitude among hydrophones, ranging from 2630 m² to 219 230 m² (median: 3580 m²; Fig. 1b,c). The overall coverage of the acoustic array represented 8.6% of the marine survey area (i.e. 17.6% of the area submerged at very low tide). Because range tests were done only once and control tags were not used, we did not assess potential change in the shape and/or surface of the estimated detection zones in relation to

temporally variable environmental conditions (e.g. tidal current, wave action, weather conditions).

Individual detection zones were overlaid on the habitat map in a GIS. The receiver deployment strategy aimed to maximize the diversity of the dominant habitat types covered in the southern and northern sub-areas, given the available number of receivers and their site-specific detection range (Table 2). The detection range of all acoustic receivers covered 21 different habitat types that altogether represented 72% of the study area. Individual detection zones included 1 to 4 habitat types (≥10% cover) (Table 2, Fig. 1b). We assumed that detection zones covered similar habitat types when these habitat types covered >50% of the surface of the detection polygons.

Fish tagging

Lethrinus harak (Lethrinidae) was selected based on ecological and fishing criteria. This ubiquitous species commonly visits a wide diversity of coral reef habitats over coastal reefs, lagoons, mangroves, channels, and seagrass inshore areas (Carpenter & Allen 1989, Laroche et al. 1997, Unsworth et al. 2009, Kimirei et al. 2011). Personal underwater observations conducted prior to the acoustic survey confirmed that *L. harak* was present over the whole survey area. Moreover, *L. harak* was regularly caught by the entire local fishing community regardless of age, gender, and gear (i.e. gillnet, seine, castnet, handline, and speargun). This commonly targeted species provided an excellent opportunity to involve local communities and to maximize the chance of local appropriation of the results.

Fish (n = 38) were tagged with acoustic transmitters between May and August 2011. Fish were caught, tagged, and released in small groups (3 to 7 fish) at 7 sites corresponding to different habitat types and fishing contexts (Fig. 1b,c). These sites were close to receivers to increase detection probability given the anticipated site fidelity behavior of *L. harak* (Ebisawa & Osawa 2009, Taylor & Mills 2013). Fish were caught using harmless techniques (i.e. barbless hooks or non-entangling nets) during daylight hours and stored for 1 to 2 h in an aerated 100 l container. Then they were anesthetized in a 20 l container filled with a 0.2 ml l⁻¹ sea water solution of clove oil. Fish were removed after 30 to 120 s according to opercula and fin movements. A 1 cm incision was made anterior of the anus to insert a V8-4L Vemco transmitter (69 kHz, 210 d battery life, 90 ± 40 s delay for the first 60 d, 240 ± 70 s delay afterwards in order to prolong

Table 2. Habitat types covered by the receiver array as derived from very high spatial resolution (2 m) multispectral Worldview 2 imagery and underwater ground-truthing. Geomorphology, exposure to wave action and dominant substrate cover are indicated. Habitat cover (>10%) is indicated in brackets for individual receivers (A to P; see Fig. 1)

ID	Geomorphology		Habitat types		Surface (m ²)	Inter-tidal zone (%)	Coverage of receivers	
	Large scale	Local scale	Ex-posure	Dominant cover			Total (%)	Receiver ID (% detection zone)
Southern sub-area								
1	Oceanic-exposed fringing	Reef flat	High	Pavement, rubble	18 536	72	7	O(15)
2	Oceanic-exposed fringing	Reef flat	High	Hard bottom, algae	42 936	–	2	O(11)
3	Oceanic-exposed fringing	Reef flat	High	Hard bottom, coral	29 148	–	7	O(24)
4	Oceanic-exposed fringing	Forereef sand pool and channels	High	Sand, rubble	179 856	–	2	O(34)
5	Oceanic-exposed fringing	Upper forereef	High	Hard bottom, pavement, coral	323 552	–	4	P(99)
Northern sub-area								
6	Lagoon-exposed fringing	Terrace	Low	Sand, seagrass	612 924	98	11	M(47)
7	Lagoon-exposed fringing and lagoon edge	Reef flat	Low	Hard bottom, coral cover (<5%)	300 264	–	6	M(11)
8	Enclosed lagoon	Lagoon floor	Low	Sand, rubble, algae (<10%)	65 492	–	24	I(24)
9	Enclosed lagoon	Lagoon floor	Low	Sand, rubble	892 452	–	18	I(72), L(94), M(33)
10	Oceanic-exposed fringing	Terrace	Medium	Sand with small coral colony, algae (<15%)	468 796	–	9	J(100)
11	Oceanic-exposed fringing	Terrace	Medium	Sand, rubble, scattered coral colony, algae & seagrass (<15%)	423 088	–	36	K(64), N(44)
12	Oceanic-exposed fringing	Terrace	Medium	Sand, rubble, hard bottom, scattered coral colony, algae & seagrass	361 952	–	7	N(56)
13	Oceanic-exposed fringing	Terrace	Medium	Sand, algae (<50%)	59 212	–	91	K(25)
14	Oceanic-exposed fringing	Terrace	Medium	Sand, rubble, algae (<20%)	236 652	–	33	H(73)
15	Oceanic-exposed fringing	Reef flat	Medium	Rubble, hard bottom, sand, algae (<20%)	316 928	–	11	G(76), H(16)
16	Oceanic-exposed fringing	Reef flat	Medium	Hard bottom, rubble, algae (<60%), scattered corals	61 196	–	13	G(18)
17	Oceanic-exposed fringing	Reef flat	Medium	Rubble, sand, seagrass & algae (<50%)	467 048	97	2	A(43), C(44)
18	Oceanic-exposed fringing	Reef flat	Medium	Rubble, sand, algae (<50%)	221 484	–	33	A(56), B(89), F(60)
19	Oceanic-exposed fringing	Reef flat	Medium	Rock, rubble, algae (<20%)	153 332	–	12	C(56), F(26)
20	Oceanic-exposed fringing	Escarpment	Medium	Rock, algae & corals (<5%)	346 284	99	4	D(24), E(16)
21	Oceanic-exposed fringing	Forereef, low relief	Low	Rock (70%), rubble, dead coral (10%), corals (<5%)	2 564 988	–	1	D(67), E(17)

battery life), sterilized in ethanol absolute, into the peritoneal cavity. The incision was then sutured. Once the harmless surgical procedure was completed (5 to 9 min), the fish were measured, gently transferred into a recovery cage at sea for 2 h to check for post-operative mortality, and then released at fishing sites if normal swimming behavior returned (Thorsteinsson 2002). Overall post-operative survival rate was 95%.

The receivers logged the presence of individual fish (i.e. transmitter code, date, and time) passing within their detection zone from May 2011 to June 2012. Acoustic data were downloaded on a monthly basis.

Data analysis

Detection data obtained for each individual fish were analyzed to characterize the temporal and spatial mobility, home range, and overall reef use patterns of *L. harak*. Detection data during the first 24 h following tagging were excluded from analysis given that tagged fish may exhibit aberrant movements immediately after release (Zeller 1997, Chateau & Wantiez 2008, Marshall et al. 2011). Individual detections were regrouped in hourly bins corresponding to each hour of the day. We assumed that a fish whose presence was logged by a receiver during any hourly

bin spent that hour in the detection zone of this receiver. Since the preliminary analysis of detection data revealed that the difference in signal delay across the survey period did not affect fish detection rate, all detection data during both time periods (i.e. during the first 60 d and afterward) were pooled.

To assess the similarity of movement patterns among fish, each individual fish was characterized by its presence (in hourly bins) on each receiver. A non-linear multidimensional scaling ordination (n-MDS) and hierarchical cluster analysis was then performed in PRIMER-E© to identify potential geographical groups of *L. harak* in the area. A geographical group included those fish that displayed similar detection patterns within the acoustic array. The presence of geographical groups on each receiver was mapped as a proportion of their total presence using bubble plots to display the overall distribution of movements of each group. Non-detection periods were not considered in this analysis.

To investigate fish response to the reefscape mosaic, presence of marine reserves, and community tenures, a series of variables was estimated from acoustic data for individual fish and geographical fish groups. These variables are described here below.

The total detection span of each fish was defined as the difference in date between its release and its last detection logged by the receiver array. A residency index was estimated by the number of days a fish was detected within the acoustic array relative to its total detection span. This index was used for identifying resident and non-resident fish within the acoustic array.

Movement patterns and home range were then described for the resident fish. The home range of a fish was defined as the area in which it spends the majority of its time and engages in most of its routine activities, including foraging and resting (Kramer & Chapman 1999, Botsford et al. 2009). Home range is typically composed of a fidelity site (i.e. core area) and excursion site(s) that are visited occasionally (Chateau & Wantiez 2007, 2008).

In this study, site fidelity was measured by the number of hours a fish was detected in the proximity of a receiver as a proportion of the total number of hours this fish was detected within the array (i.e. non-detection periods were not considered). A high value of this index (i.e. close to 1) was indicative of a fish exhibiting site fidelity. Excursions from fidelity sites included travel to, and residency at, destination sites (Chateau 2008). The number, monthly rate, distance, duration, and swimming speed of excursions were calculated for each fish living within a home

range. Although it is unlikely that a fish swims in a straight line without stopping, swimming speed was used to detect peculiar (e.g. fast) movements.

Linear measurements of home range and fidelity sites were also provided to characterize fish movements. Maximum linear fidelity site size was estimated as the maximum dimension of the corresponding receiver detection zone. Maximum linear home range size was defined as the longest distance moved by resident fish within the array during their total detection span. It was estimated as the maximum linear dimension of the fidelity site for fish detected by a single receiver and as the minimum linear distance between the 2 most distant receivers' detection zones for fish detected on multiple receivers (Chateau & Wantiez 2007, 2008, Meyer et al. 2010). The effect of fish size on home range size and swimming speed was investigated using the Spearman rank coefficient test. Differences in residency, home range size, and excursion distance of individual fish among geographical fish groups were investigated using the non-parametric Kruskal-Wallis (KW) test. Reef habitat utilization by individual fish and geographical groups was examined in terms of diversity of potentially-used habitat types and the number of habitat patches in their home range.

Diurnal and nocturnal movements of *L. harak* were investigated by plotting individual detections against time of the day across the whole detection period.

Finally cross-boundary movements through community fishery reserves and marine tenures were characterized (i.e. distance traveled, frequency, and duration) for all individual fish and geographical groups.

RESULTS

Tagged fish size ranged from 162 mm to 320 mm FL (Table 3), encompassing the maturity size of *Lepturinus harak* (210 to 220 mm FL; Kulmiye et al. 2002, Ebisawa 2006). Overall, 30 fish (79% of tagged fish) were detected within the acoustic array. Their size ranged from 170 to 322 mm. The total detection span ranged between 1 and 229 d (median: 153 d) (Tables 3 & 4).

Behavior types

Two behavior types were identified. The first behavior type related to 9 fish (170 to 280 mm FL) that did not exhibit site fidelity. For these fish, residency

Table 3. Summary of detection data and movement characteristics of non-resident *Lethrinus harak* tagged in Efate Island, Vanuatu. Minimum, maximum and median (in brackets) values are indicated for individual fish detected in each village. See Fig. 1 for receiver ID and Table 2 for habitat type ID

	Emua village	Paonangisu village	Takara village	All
Number of tagged fish	1	7	1	9
Fork length (mm)	245	170–280	240	170–280 (241)
Total detection span (d)	227	2–205	1	1–227 (61)
Total presence (hourly bins)	69	1–46	3	1–69 (15)
Movement patterns				
Maximum linear dimension (m)	1205	386–1988	182	182–1988
Receiver ID	D E F	E G H I J K M	O	D E G H I J K M O
Habitat types (ID)	19–21	6–11, 13–16, 20, 21	1–4	1–4, 6–11, 13–16, 19–21
Between-receiver movements	0	4	1	5
Cross-boundary movements				
Fishery reserve	0	2	0	0–2
Village's tenure	1	0	0	0–1

was low, and detection was occasional within the array (≤ 69 hourly bins detected), which indicated that they were probably not resident within the monitored area thus precluding a detailed analysis of their movements (Table 3). Four of these fish undertook between-receiver movements (1 to 2 per fish) over 160 to 1200 m distances across multiple habitat types, whereas the presence of the 5 other fish was sporadically localized by 1 single receiver. The maximum linear dimension of the spatial domain used by

each individual non-resident fish ranged from 182 to 1988 m (median: 390 m).

The second behavior type related to the remaining 21 detected fish (170 to 320 mm FL) that displayed restricted movements within a home range. Total detection span and residency index within the acoustic array ranged between 24 and 229 d (median: 163 d) and between 0.27 and 0.99 (median: 0.73) among these fish except for 1 fish (0.07). Their presence exceeded 80 hourly bins except for

Table 4. Summary of detection data and movement characteristics of resident *Lethrinus harak* tagged in Efate Island, Vanuatu. Minimum, maximum and median (in brackets) values are indicated for each geographical fish group. See Fig. 1 for receiver ID and Table 2 for habitat type ID

	Emua village	Paonangisu village			Takara village	
	EM1	PA1	PA2	PA3	PA4	TA1
Number of tagged fish	5	5	1	2	3	5
Fork length (mm)	182–280 (250)	170–322 (265)	260	280–321 (300)	272–298 (292)	221–262 (250)
Total detection span (d)	91–218 (187)	108–210 (163)	225	178–211 (195)	42–169 (138)	24–229 (113)
Total presence (hourly bins)	241–3383 (779)	24–343 (112)	258	635–1130 (883)	101–285 (262)	91–1284 (224)
Residency index	0.42–1 (0.99)	0.07–0.61 (0.37)	0.53	0.73–0.88 (0.80)	0.40–0.88 (0.41)	0.34–0.96 (0.80)
Home range						
Maximum linear dimension (m)	116–3979 (3258)	307–3011 (1068)	513	386–1173 (780)	763–2702 (1343)	182
Fidelity site (receiver ID)	B	F	G	I	L & M	O
Habitat types (ID)	14–21	8–10, 15, 16, 18, 19	14–16	8, 9, 14, 15	6, 7, 9, 11–13	1–4
Site fidelity index	0.94–1	0.9–1	0.99	0.99–1	0.95–0.99	1
Fidelity site linear dimension (m)	116	307	227	386	763	182
Number of excursions	0–13	0–2	1	0–1	0–3	0
Excursion distance (m)	521–3398	534–1008	286	787	157–562	0
Excursion duration (h)	7–263	24–124	81	92	18–48	0
Maximum swimming speed (m min ⁻¹)	2.3–28.0	1.1–2.6	0.1	1.8	5.4–13.0	
Non-detection periods						
Number	119–718	15–236	169	250–324	65–160	50–379
Mean duration (h)	2–44	21–263	31	10–17	15–24	5–53
Cross-boundary movements						
Fishery reserve	0–11	0–1	1	1	0	0
Village's tenure	0–11	0	0	0	0–1	0

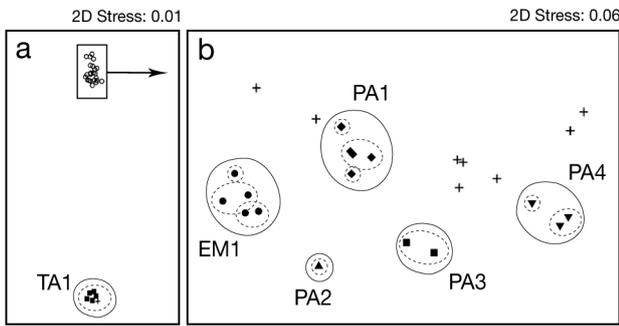


Fig. 2. Non-metric multidimensional scaling ordination of space use by *Lethrinus harak* in (a) the whole study area and (b) the northern sub-area. Two behavior types corresponding to non-resident fish (crosses) and resident fish (squares) were observed. Geographical fish groups derived from hierarchical cluster analysis are indicated (EM1, PA1, PA2, PA3, PA4, and TA1). Solid and dotted lines represent envelopes of 30% and 60% similarity clusters, respectively

1 fish (24 h) (Table 4). These fish were considered resident within the survey area, even though 4239 non-detection periods (lasting up to 45 d, median: 4.3 h) were observed overall. Home range size and reef use patterns were then further analyzed for these fish.

Home range and movement patterns of resident fish

Resident fish were categorized into 6 geographical groups (Fig. 2). Residency was broadly similar among geographical groups (KW test, $p = 0.11$) although the statistical power of the test was reduced by the small group sizes (1 to 5 individuals).

The home range of *L. harak* comprised a fidelity site and usually 1 or several excursion sites. We present fidelity site characteristics first. In each group, site fidelity of individual fish ranked above 0.89, showing a marked site fidelity behavior to a single receiver ($n = 20$) or 2 receivers located at a 370 m distance ($n = 1$) (Table 4). Fidelity sites extended over 116 to 386 m (except for 1 fish: 763 m; median: 227 m) and did not overlap among fish geographical groups. They were located in different environmental, fishing, and management contexts over the entire survey area. Specifically, fidelity sites were observed in the 3 community tenures, in marine reserves and fished areas, and in 12 habitat types (Fig. 3, Tables 2 & 4). Most fish were caught for tagging at their fidelity site. However, for 3 fish belonging to 3 different groups, fidelity sites were located at a 60 to 800 m distance from the catching sites, suggesting that they had been caught and tagged during excursions.

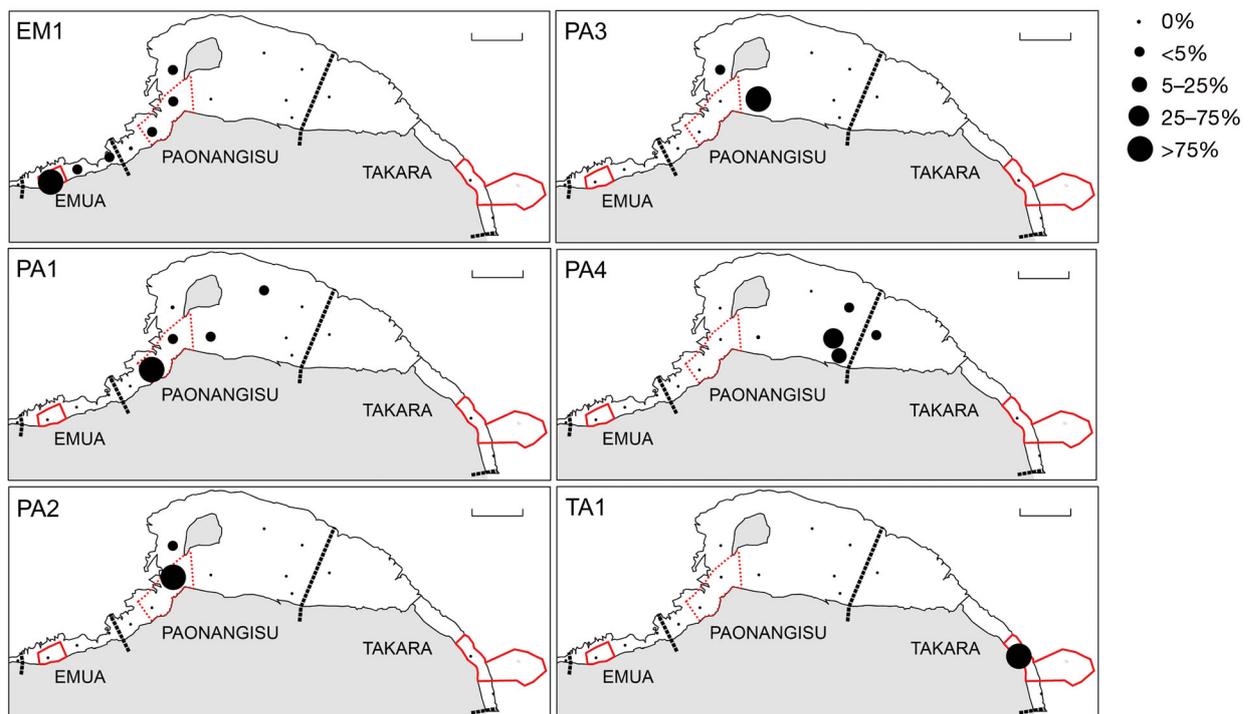


Fig. 3. Spatial distribution patterns (bubble plots of hourly detection bins) of each geographical group of *Lethrinus harak* in the study area. The thick dotted lines represent the marine tenure boundary of each village. The red solid and dotted polygon lines represent the boundary of the existing and planned community fishery reserves, respectively. Percentages are the proportion of hourly detection bins of each group within the receiver array. Scale bar = 1 km

Home range of neighbor or widely-distant geographical groups partly overlapped due to fish excursions from fidelity sites, except TA1 group (Fig. 3). Maximum linear home range size ranged from 116 to 3979 m (median: 763 m) among tagged fish. Most of them ($n = 14$, 67%) resided in ≤ 1340 m wide areas while one-third of the fish ($n = 7$, 33%) resided in areas ≥ 1780 m (Table 4). However, within geographical fish groups, the estimated home range size varied by 1 order of magnitude among individual fish. This suggested that space use patterns were highly variable even in the same reef area. Maximum linear home range size was not significantly different among geographical groups (KW test, $p = 0.07$) and not correlated to fish size (Spearman rank test, $p = 0.23$). However, these tests were possibly insufficiently powered to detect true effects of group and/or size due to small sample size.

Habitat-use patterns did not reveal significant habitat preferences for *L. harak*. Tagged fish were detected in 16 and 4 habitat types in the northern and southern study sub-areas, respectively, including hard and soft bottoms, seagrass beds, and areas partly covered with rubble, algae, and/or corals (Table 4). These habitat types represented 66% and 28% of the surface of each sub-area, respectively. Visited habitat types were partly specific to geographical groups (Table 4) and varied among fish within these groups, except in the PA2 and TA1 groups.

In each fish group except TA1, between 1 and 4 fish ($n = 10$ in total, 63%) occasionally moved out of fidelity sites (i.e. 1 to 5 times per month), totaling 42 detected excursions. Although detection data did not allow for statistical analysis of the spatial and temporal characteristics of excursions, marked differences in fish movements were observed. Travel distance and excursion duration ranged from 160 m to 3400 m (median: 2130 m) and from 7 h to 11 d (median: 18 h). Tagged fish moved to, or undoubtedly crossed, several different habitat types during 71% and 29% of detected excursions, respectively. They visited up to 7 different habitat types per excursion including hard and soft bottoms, seagrass beds, and areas partly covered with rubble, algae, and/or corals. Excursions were unidirectional in 3 geographical groups, producing elongated activity spaces that followed reef geomorphology outlines, and multidirectional in other groups (Fig. 3). No excursions were detected between the northern and southern sub-areas, suggesting a limited degree of connectivity between these reef areas.

Swimming speed ranged between 0.1 and 28 m min^{-1} (median: 2.6 m min^{-1}) among 134 between-

receiver movements, suggesting that most of these movements were not linear. Interestingly, long-distance (2130 to 3400 m), fast-swimming (18 to 28 m min^{-1}) excursions of 3 mature fish (23 to 28 cm FL) from the same geographical group were repeatedly observed by the same receivers. These specific movements occurred around new and/or full moon over 3 to 5 lunar cycles between August and December 2011.

Diurnal and nocturnal detection patterns of *L. harak* within home range showed that 24 h activity patterns were widely variable among resident fish (Fig. 4). These patterns were not clearly associated with any particular receiver or geographical group, suggesting that their cause was multifactorial.

Cross-boundary movements

Four geographical fish groups (EM1, PA1, PA2, and TA1) were strongly resident within a single CFR of the survey area (Fig. 3, Tables 3 & 4). The linear extent of Emua, Paonangisu, and Takara villages' CFRs was 0.5-, 1.6-, and 1.3-fold larger than the median home range size of *L. harak* as estimated by this survey, respectively.

Despite the observed fidelity behavior, fish movements suggested some degree of connectivity of *L. harak* population between CFRs and between villages' tenures in the survey area. On one hand, a total of 34 outward, eastward excursions (6 to 13 per fish) were recorded for 4 of 5 fish of EM1 group during the survey period. During 21 of these unidirectional excursions, fish would have undoubtedly crossed Emua village's boundary that was located 1500 m from their fidelity site. They were detected both within (15 excursions lasting 8 to 58 h each) and beyond (6 excursions lasting 9 to 21 h each) the Paonangisu village's proposed CFR. No inward movement of other tagged fish was observed into Emua village's reserve.

On the other hand, 2 of 6 fish in PA1 and PA2 groups were detected outside the Paonangisu village's proposed CFR and during a single excursion each. These excursions lasted 82 h and 120 h and were recorded on the same receiver located 220 m northward of the reserve's boundary. A fish belonging to PA3 group was also detected on this receiver during a single excursion that very likely crossed the proposed CFR.

Lastly, a non-resident fish and 2 resident fish from PA4 group moved across villages' boundaries on a single occasion, i.e. 2 from Emua village's tenure to

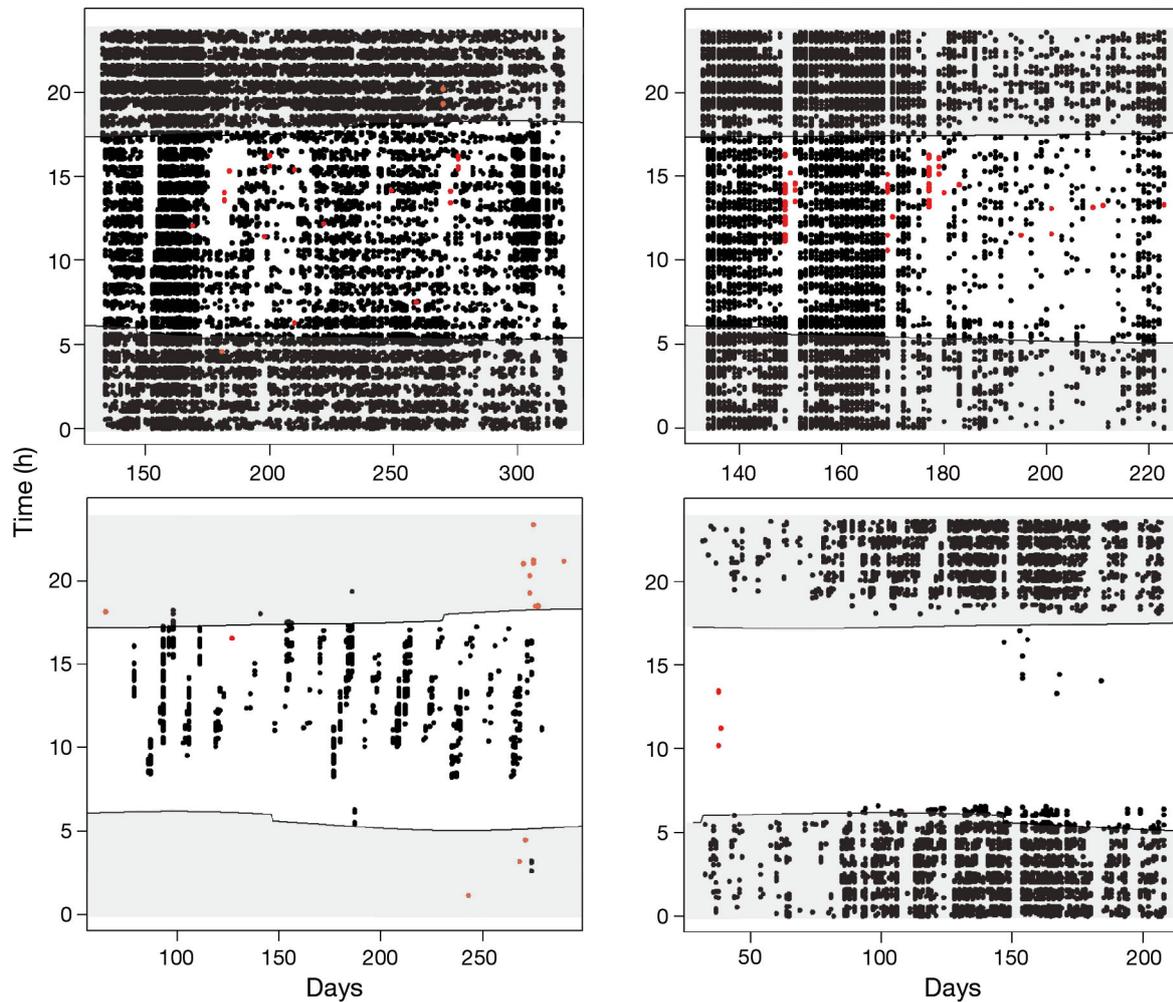


Fig. 4. Detection patterns of 4 individual fish of *Lethrinus harak* from (a,b,c) EM1 and (d) PA3 geographical groups during daytime and nighttime (in grey shading) periods. Black and red dots represent detections on fidelity sites and during excursions, respectively

Paonangisu village's tenure and one from the latter to Takara village's tenure.

DISCUSSION

Non-detection periods and uncertainty of home range estimates

Non-detection periods are inherent to passive acoustic telemetry of marine fishes as a result of receiver-to-receiver gaps, receiver detection range, and transmitter delay. Accurate monitoring of home-range utilization requires continuous acoustic coverage by receiver arrays with the appropriate spacing and scale (often over distances of several kilometers). In practice, however, an ideal design is difficult to

achieve because of inherent trade-offs between spatial extent, resolution, and number of available receivers in passive telemetry surveys (Sale 1998). These trade-offs may lead to underestimating fish home range (e.g. Meyer et al. 2010, Bijoux et al. 2013, Currey et al. 2014, Pittman et al. 2014) since most movements outside the array remain unknown. For example, our results indicate that short-distance (<160 m) and short-time (<7 h) excursions of *Lethrinus harak* were not captured during this survey because the receivers were positioned too far apart.

Non-detection periods may be attributed to temporally variable environmental factors obstructing acoustic signal transmission within the array, and to fish movements into non-detection zones. For instance, excursions from the fidelity site by TA1 group's fish were not detected, possibly due to the

low mobility of these fish and/or the low coverage of the acoustic array in the southern study sub-area. Similarly, the non-resident fish might live within home ranges whose core areas could be located within non-detection areas. This hypothesis is supported by detection data showing that the movement scale of non-resident fish was of the same order of magnitude of that of resident fish. If one assumes that the 4239 non-detection periods recorded for resident fish in this survey correspond to movements into non-detection areas, this would imply that only 2% of their true excursions were effectively detected. Given that swimming speed estimates indicated that *L. harak* may operate 1.1 to 1.7 km-long movements within 1 h, resident fish would have been able to move over several kilometers during most non-detection periods. Our estimates of home range dimension should therefore be interpreted conservatively because they were based only on presence data within a discontinuous receiver array.

Excursions and home range size

This study confirmed that, in Vanuatu, *L. harak* lives within a home range, as has been previously shown in Japan (Nanami & Yamada 2009) and Guam (Taylor & Mills 2013). Site fidelity behavior and excursion movements have been documented among a wide variety of reef fish species using passive telemetry. Results consistently emphasize non-uniform space use over short (i.e. hours) to medium (i.e. days and weeks) time frames (Holland et al. 1996, Zeller 1997, Bellquist et al. 2008, Chateau 2008, Mason & Lowe 2010, Marshall et al. 2011).

Our results also highlighted the high variability of home range dimension among conspecifics inhabiting the same reef areas (i.e. 116 to 3980 m), as already reported for other fish species (Chapman et al. 2012) and commonly observed in taxonomically diverse natural populations (Sloan Wilson et al. 1994). However, the spatial, temporal, and individual drivers of mobility patterns of *L. harak* remain difficult to explain. Excursions over hundreds to thousands of meters have commonly been documented among coral reef fishes in response to exploratory, circadian, and spawning factors, among others (Lindholm et al. 2006, Chateau & Wantiez 2008, Meyer et al. 2010, Currey et al. 2014, Matley et al. 2015). In this study, the periodically detected long-distance (>2 km), fast-swimming movements for 3 tagged fish (EM1 geographical group) based upon the detection patterns were consistent with

those previously described during monthly spawning migrations of *L. harak* (Carpenter & Allen 1989, Taylor & Mills 2013). This suggests that transient spawners undertook regular spawning trips in the survey area at the beginning of the summer season, probably within small groups and spread over several sites since large aggregations of *L. harak* were not reported by local fishers. Spawning migrations from fidelity sites have also been documented for *L. miniatus* (Currey et al. 2014) and a large variety of reef fish species (e.g. Chapman et al. 2012, Claydon et al. 2012, Nanami et al. 2014).

Home range size of *L. harak* was consistent with that of other lethrinids (Kaunda-Arara & Rose 2004, Currey et al. 2014). However, it was larger than the home range size previously estimated for this species by Nanami & Yamada (2009) and Taylor & Mills (2013) using active tracking and passive telemetry, respectively. Additionally, unlike Taylor & Mills (2013), we did not find any positive correlation between fish size and home range estimate. Several authors also observed that fish size and home range dimension of lethrinids (Matley et al. 2015) and other reef fish species (e.g. Bellquist et al. 2008, Marshall et al. 2011) were not systematically correlated (but see Nash et al. 2015).

These different findings partly arose from the differences in home range estimation methods. In order to meet the correct conditions for using statistical home range estimation methods, the acoustic survey must be appropriately designed (Laver & Kelly 2008). Specifically, kernel density estimation has been extensively used in acoustic studies for estimating home range of reef fish such as *L. harak* (Taylor & Mills 2013) but was inappropriate in this study due to the strong spatial heterogeneity of detection patterns of tagged fish (Downs et al. 2012).

Instead, we considered all recorded excursions from fidelity sites to estimate the maximum linear dimension of the home range of *L. harak* (e.g. Meyer et al. 2010) including hypothetical spawning migrations to nearby areas, which might have resulted in overestimation of the home range size of this species. Indeed, regular, directed long movements of fish to transient spawning sites are usually considered to be migrations outside the home range of participating fish (e.g. Taylor & Mills 2013, Green et al. 2015). Nevertheless, we argue that our home range estimates are appropriate for quantifying the spatial scale of fish movements that is relevant for management (Pittman et al. 2014, Matley et al. 2015, Waldie et al. 2016), which was the main objective of this study.

Habitat-use patterns and management implications

Effectiveness of temporary closures

This study describes the response of a *L. harak* population to the habitat mosaic, in terms of (1) fish residency in habitat patches, (2) movements within and between habitats and (3) linear range of movements.

The results indicate that space-use patterns alter the potential effectiveness of small CFRs to act as refuges for this species. We observed that site fidelity behavior was consistent across geographical fish groups, reef habitats, and fishing status. The results suggest that small sub-populations of *L. harak* reside within non-exclusive home ranges commonly extending over <1.3 km. This study therefore suggests that this species could benefit from small spatial refuges (i.e. ~2 km wide), as already found by Taylor & Mills (2013). However, *L. harak* did not exhibit significant habitat preferences, although outer reefs were less frequently used than the reef flat area. The ability of fish to swim across multiple reef habitats increases travel distances, home range size, and habitat connectivity at the scale of one to several kilometers, which increases exposure to fishing. Fish mobility across many habitat types consequently undermines the potential ability of small individual CFRs to protect this species (Kramer & Chapman 1999).

CFRs that do not encompass the home range of target fish cannot significantly limit spillover, which compromises their effectiveness. As demonstrated by our survey, typical shoreline-bounded CFRs (i.e. hundreds of meters wide) in Vanuatu are expected to better protect the small contingent of the population that use very small, reserve-centered home ranges. Such small CFRs may therefore contribute to increase the abundance of these sedentary fish within their boundaries during closure, as commonly observed within small no-take zones (DeMartini 1993, Halpern 2003) and reported by local fishers during our program. However, this sedentary contingent of fish becomes temporarily vulnerable to fishing during periodic openings of CFRs, particularly as the harvest may be very intensive. Given that the rest of the fish residing within CFRs may be caught during outward excursions or spawning migrations, the entire fish population of CFRs may consequently become accessible to fishers at one time or another. Although this may be of short-term benefit with regard to the social acceptability of CFRs within communities, they raise serious resource sustainability

issues and question the use of CFRs as a management tool.

Unless harvesting conditions within CFRs are linked to fish reef uses, reserve size, and location issues, there may be unrealistic expectations about CFRs being able to sustain surrounding fisheries. To balance the trade-off between fishery yield and biomass buildup, it is suggested that only CFRs that encompass the home range size and suitable habitats of a significant part of the target fish population may be harvested during short and controlled openings (e.g. Takara and Paonangisu villages' existing and planned CFRs in this study). CFRs that do not meet this condition should be permanently closed in order to limit fishery outcome to spillover only, as in permanent no-take zones (e.g. Emua village's CFR in this study).

Despite our results being specific only to *L. harak*, communities may consider that large CFRs can protect a wider range of species and habitats than small ones, although reserves cannot be of optimum size for all target species in coral reef fisheries (Sale et al. 2005). The use of small no-take zones should also be considered in specific locations that are critical for the development of focal species (e.g. spawning and resting sites, juvenile nurseries). These ecological considerations should be integrated in the local decision-making process when setting CFR boundaries. This is not an easy task as it also necessitates taking into account other critical factors such as the local power relations, the cohesion of the community, ownership issues between communities, and the subsequent distribution of expected socioeconomic benefits (Cohen & Steenbergen 2015).

Encouraging networks of community fishery reserves

Large-scale networks of no-take zones are increasingly promoted for achieving both conservation and fisheries management objectives (Gaines et al. 2010). Our results further argue for creating networks of CFRs that account for fish movement patterns and local tenure, particularly in those areas where implementing sufficiently large CFRs is locally unacceptable (e.g. in small community marine areas) and/or unenforceable. In this study, we showed that the home range of *L. harak* population of Emua and Paonangisu villages' CFRs was influenced by reef habitats and geomorphology. Specifically, home ranges of sub-populations overlap along contiguous fringing reef, while the habitat break between the northern

and southern study sub-areas likely represented a natural barrier to *L. harak* movements. This barrier prevented connectivity between the northern sub-area and Takara village's CFR. Habitat breaks have been shown to limit reef fish movements (e.g. Meyer et al. 2010, Marshall et al. 2011) and should be considered when setting CFR networks in reef areas (Chateau & Wantiez 2008).

Although this study was limited to a single target species, our results provide 3 main arguments for establishing CFR networks in Vanuatu and other Pacific island countries. First, adult fish mobility across reserve and village boundaries allows for connecting neighbor CFRs that overlap with fish home range, hence increasing fish protection compared to individual CFRs. Second, the typically-small contiguous community tenures at island scale could decrease spacing between neighbor CFRs if the latter are widespread among coastal communities. A sufficiently large contingent of fish populations that live within a home range may consequently be capable of moving safely from a reserve to another, therefore increasing overall protection. For instance, the fidelity and spawning sites of *L. harak* may be protected by 2 CFRs located in Emua and Paonangisu villages, therefore reducing the probability of capturing those fish that exhibit long outward movements from Emua's CFR. Third, fish plasticity toward reef habitats and fidelity site locations may increase the choices that communities have regarding the designation of suitable areas to be protected from fishing whilst also taking into account local sociopolitical and socioeconomic factors.

The effectiveness of networks of small reserves that would be strategically located in areas where resident fish spend most of their time or undergo critical phases (i.e. spawning sites) is the subject of a growing debate (Grüss et al. 2011). Our results indicate that reserves must also be situated to allow for movement of adult fish of the focal species among protected habitats. This acoustic study is one of the first evidence-based contributions to reserve network design in the context of community-based management of coral reef ecosystems and fisheries. Although it needs to be extended to other community-managed areas and other target reef fish species to embrace the diversity of fishery contexts, our results encourage between-community governance relationships to improve CFRs' location, size and spacing. Further research is required to investigate how such CFR networks can provide effective long-term protection for a wide range of coral reef fish while sustaining fishery benefits.

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