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Assessing fine-scale diel movement patterns of an exploited coral reef fish

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Abstract

Background: Understanding movement patterns of species requires that the spatial and temporal scales of experimental designs are appropriate to the proposed ecological questions. Previous research on large-scale movements of the exploited reef fish *Lethrinus miniatus* suggested that adult individuals may use coral reef slope habitat during the day, shifting to adjacent deeper sandy habitat at night. However, investigation of movement at a fine spatial and temporal scale is required to verify this diel activity pattern. Using a closely positioned acoustic telemetry system, movements of 11 *L. miniatus* were monitored among habitats from the reef crest, to reef slope and deeper adjacent sandy habitat over 3 months. Fine-scale movement patterns among these habitats were compared among four different 3 h periods of the day: dawn, day, dusk and night.

Results: Initial observations demonstrated significantly larger horizontal core areas and vertical areas of extent during crepuscular and night periods compared to during the day. Vertical space use (core area and extent) was consistently larger during dawn, dusk and night compared to during the day. Area of activity space extent within the water column and proportional overlap among areas used during different periods of the day varied among weeks, and displayed a pattern consistent with full moon periods.

Conclusions: Although previous evidence suggested that *L. miniatus* adults may shift to deeper habitats adjacent to the reef slope at night, greater space use across the shallow crest to deeper sand habitat was observed during dawn, dusk and night periods. Increased luminosity during dawn, dusk and night periods may cause *L. miniatus* to utilise a larger search area for foraging. While further research is required to confirm foraging during the hours of twilight and darkness, this fine-scale approach identified patterns in nocturnal activity for an important reef teleost. Knowledge of these temporal and spatial differences in *L. miniatus* behaviour and movement are important to understanding how this species coexists within ecological niches.

Keywords: Acoustic telemetry, Small-scale, Lethrinidae, Fisheries management

Background

Reef fishes move over multiple spatial and temporal scales. Understanding the movement ecology of particular species requires study on scales appropriate to the proposed ecological question [1]. Research conducted over large spatial scales (100 s of km) and periods of months to years can capture information on ontogenetic movement and spawning migrations of adult

populations, while studies encompassing small spatial scales (a few kilometres) and shorter time periods can effectively define activity space use of individuals. Spatial and temporal resolution of the sampling methodology varies with scale, thus, it is necessary to consider these elements in the context of intended research.

Home range or extent of activity space encompasses the majority of the area typically used by individuals during daily routine activities [2]. Daily space use can comprise movements between different habitats used for different functions, and these can be spatially and temporally separated. Reef fishes may traverse shallow reef crests, reef slopes and adjacent sandy habitats during

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different times of the day, and their activity is largely regulated by the diurnal (24 h) cycle of the sun rising and setting [3]. Use of different habitats during different times of day may help fulfil biological and ecological needs such as foraging, predator avoidance and resting [4]. These movement patterns are typical of Haemulids, which rest during the day among coral reefs and move along consistent routes to adjacent sandy habitats at night to forage [5]. Carangids also display a pattern of roaming the reef crest at night, using different foraging areas and displaying greater activity during daylight hours [6]. In contrast, diurnal scarids actively forage along the reef during daylight hours and rest inside mucous cocoons in crevices within these areas at night [7]. It appears that benefits are gained through use of different habitats at different times of the day for resting and feeding with movement between areas rich in specific resources (e.g., shelter, prey).

Recent tracking research on the space use of a tropical species, *Lethrinus miniatus*, hypothesised that lower detection frequency at night was due to movement away from the reef slope into the adjacent sandy habitat to forage [8]. This hypothesis is consistent with the documented ecology of *L. miniatus*, as a nocturnal predator of crustaceans and echinoderms [9]. Currey et al. [8] reached their hypothesis based on monitoring large-scale movement of adult individuals using a line of acoustic receivers parallel to the reef crest. Movement patterns of *L. miniatus* are not well understood and the resulting hypothesis of movement away from the reef crest at night could not be answered with the large-scale approach applied. This raises the questions: does space use of *L. miniatus* differ at different times of the day across habitats, and is use of these areas consistent through time? Individuals might utilise deeper areas off the reef crest for foraging during the night, while using shallower reef habitat during the day for resting. To test the Currey et al. [8] hypothesis, a fine-scale acoustic tracking approach that included reef crest, slope and adjacent sandy habitats was applied to the same population of *L. miniatus*.

The aim of this study was to determine whether diel differences in space use and distance from the reef crest were apparent in adult *L. miniatus*. Data were also used to identify whether the same areas and habitat types were used consistently over multiple months. Using an array of closely positioned acoustic receivers between reef crest and adjacent sand habitats, fine-scale horizontal and vertical space use was examined during different periods of the day and among weeks to identify the amount of overlap and reuse of these areas. Fine-scale data provided insight into diel activity to better define the variation in movement patterns observed for *L. miniatus* in other studies.

Results

Of the eleven *L. miniatus* fitted with acoustic transmitters, seven were detected over 93 days of monitoring between 22 March and 22 June 2014 (Table 1). The majority of these individuals (five) were detected consistently across the monitoring period and provided sufficient positions for inclusion in analyses. The other four individuals were excluded from the analysis because their detection profiles suggested they had perished. Detections varied among the four time periods of dawn, day, dusk and night, with more detections of individuals during daylight hours. Standardisation of detections based on sentinel tag data indicated that absence during crepuscular (dawn and dusk) and night periods was not an artefact of transmitter detectability.

Horizontal space use

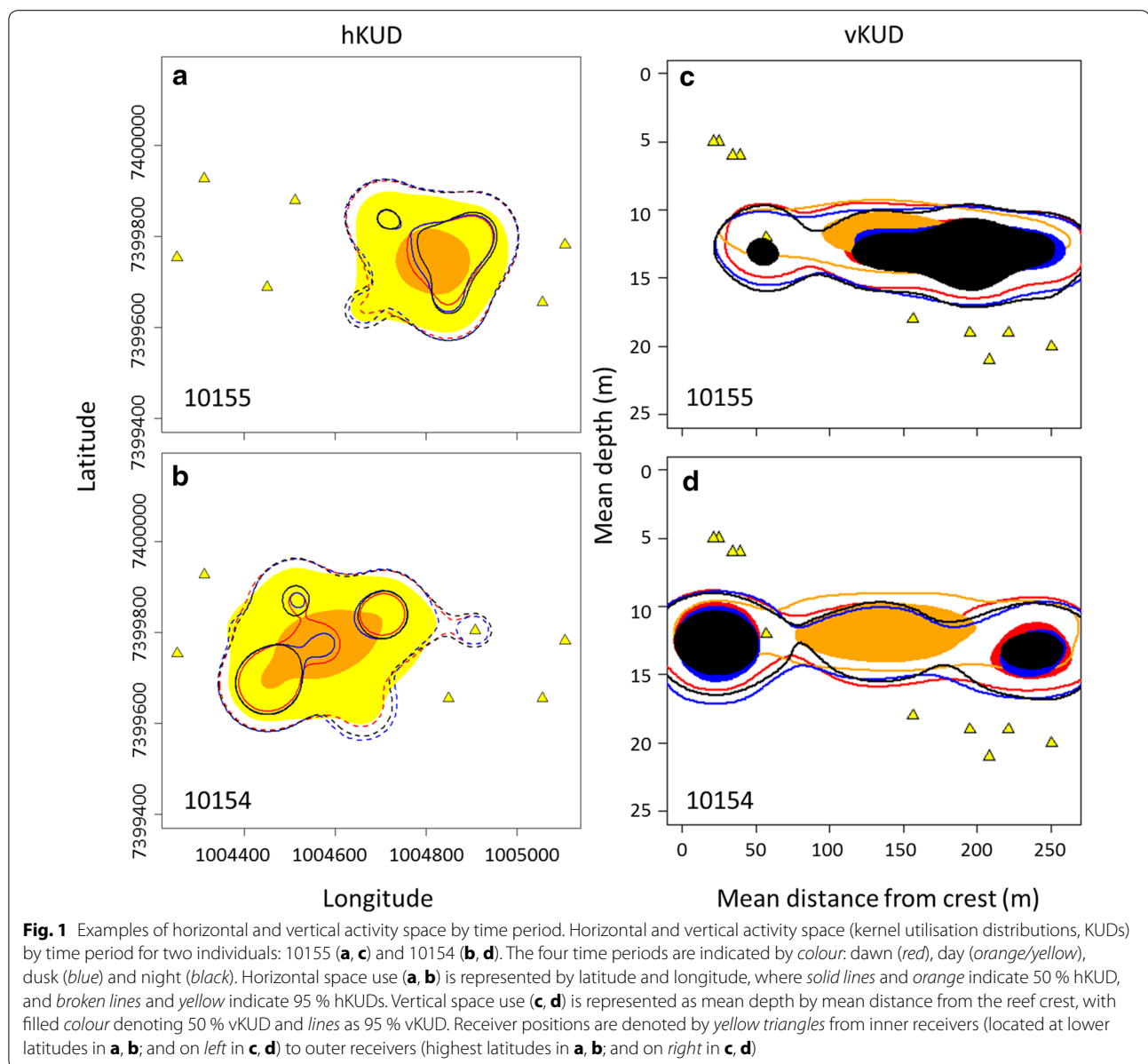
Tagged individuals occupied horizontal space across a number of receivers, including stations located on both inner and outer receiver lines (Fig. 1) indicating use of reef crest, slope and sandy habitats. In general, the location of daytime horizontal kernel utilisation distributions (hKUDs) were different to hKUDs for dawn, dusk and night periods. Specifically, core use areas (50 % hKUDs) were significantly larger for dawn, dusk and night periods than the core use areas during day periods (Table 2; Fig. 2a). Dawn, dusk and night core use areas were also more broadly distributed between inner and outer receivers compared to day periods (e.g. Fig. 1a, b). Mixed effects models illustrated an overall trend in lower mean activity space for day periods, despite variation in 50 and 95 % hKUD size estimates (Fig. 2a, b). Fish size was not a significant factor in horizontal space use (Table 2).

Activity space extent (95 % hKUDs) during dawn, dusk and night periods was not significantly greater compared to during the day (Table 2; Fig. 2b). Greater variability was observed in 95 % hKUD for individual 10168

Table 1 Details of *Lethrinus miniatus* monitored at Heron Island Reef

Individual	FL	Date released	Last detection	COAs
10154	435	23/03/2014	22/06/2014	7994
10155	464	22/03/2014	22/06/2014	10,056
10158	421	23/03/2014	3/05/2014	115
10162	410	23/03/2014	22/06/2014	9964
10164	388	22/03/2014	26/03/2014	171
10168	376	23/03/2014	22/06/2014	1634
10170	415	22/03/2014	22/06/2014	9471

Individual *L. miniatus* were monitored from 22 March 2014 to 22 June 2014. FL refers to the size of the individual (fork length), and COAs are the number of centre of activity estimates obtained during the monitoring period



(and lower 50 % hKUD) which was likely due to the home range of this individual straddling the boundary of the monitored area, meaning space use would have been underestimated.

Vertical space use

Patterns in vertical space use were similar among individuals. Similar to hKUDs, vertical kernel utilisation distributions (vKUDs) illustrated clear differences between periods, with day contrasting dawn, dusk and night periods. Core space use during the day was concentrated among the middle of the reef slope, compared to dawn, dusk and night core areas which were spread among all

receivers (e.g., Fig. 1c, d). Vertical core area was not significantly different among periods (Table 2; Fig. 2c). Core depth use was often shallower during the day, however, depth use overall was consistent among individuals (c. 10–15 m). In contrast, activity space extent was significantly larger during dawn, dusk and night periods than during the day (Table 2; Fig. 2d), illustrating the nocturnal habits of this species.

Overlap in daytime vertical space use with dawn, dusk and night periods revealed significant differences for core (50 % vKUD) estimates (mixed effects model, $F = 11.029$, $df = 5$, $p < 0.001$), but not for extent of movement (95 % vKUD) estimates (mixed effects model, $F = 2.628$,

Table 2 Model results for activity space among time periods

	50 % hKUD	95 % hKUD	50 % vKUD	95 % vKUD
Day vs dawn	<i>0.006</i>	0.085	0.064	<i><0.001</i>
Day vs dusk	<i>0.001</i>	0.493	0.092	<i><0.001</i>
Day vs night	<i>0.002</i>	0.565	0.190	<i>0.001</i>
Dawn vs dusk	0.410	0.263	0.842	0.692
Dawn vs night	0.496	0.222	0.529	0.411
Dusk vs night	0.882	0.910	0.665	0.232
FL	0.131	0.922	0.141	0.217

Mixed effects model results (*p* values, significant values indicated in italics) for horizontal and vertical kernel utilisation distributions (KUDs), comparing among time periods (dawn, day, dusk and night) and individual size (fork length, FL). All models included individual as a random effects term

$df = 5, p = 0.067$). Overlap was lowest for day periods, and average core areas comprised 37 % of the area used at dawn, 29 % at dusk and 30 % at night areas. An overlap of 72 % of the core areas was observed between dawn and dusk and dawn and night, and 28 % overlap of dusk and night areas. High overlap was observed across periods for movement extent (77–91 %). In general, this highlights the greater spread of vertical core areas used during dawn, dusk and night periods.

Vertical activity space by period and week

Weekly analysis of space use revealed that the significant differences between daytime areas of activity compared with dawn, dusk and night periods were

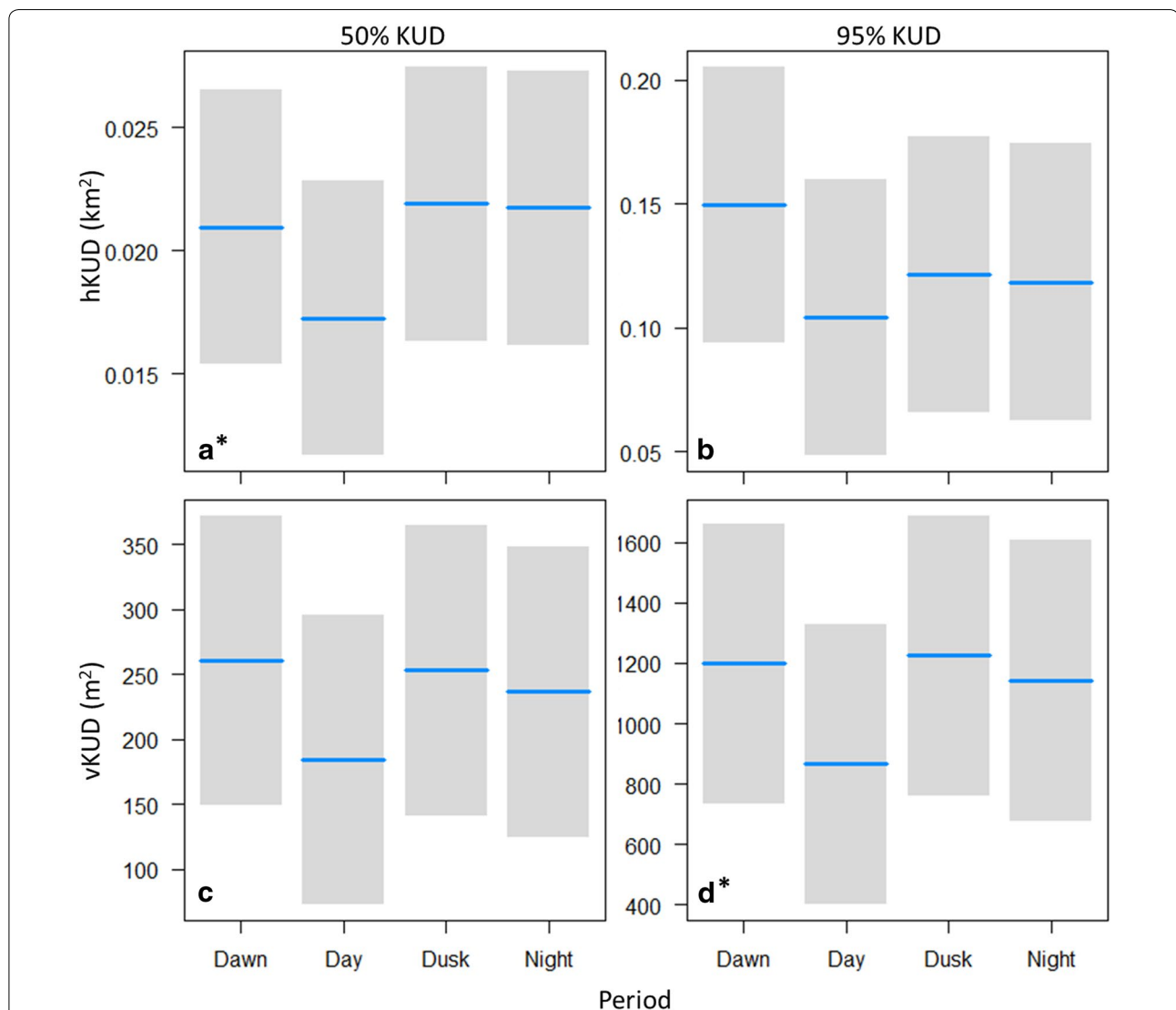


Fig. 2 Model plots of horizontal and vertical activity space by time period. Results from mixed effects models illustrating 50 % (a) and 95 % (b) horizontal kernel utilisation distribution (KUD) area and 50 % (c) and 95 % (d) vertical KUD area by time period (dawn, day, dusk and night). Lines indicate mean KUD, grey shading is the 95 % confident intervals, and asterisks signify significant differences among periods

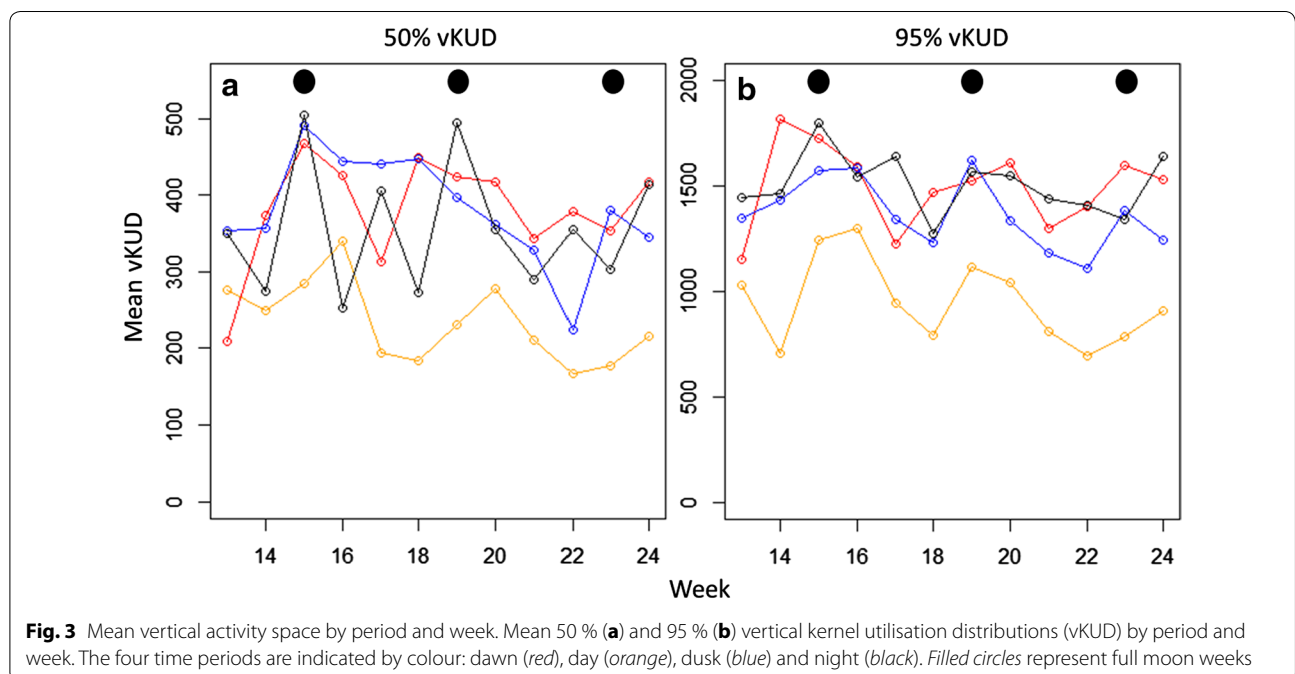
consistent through time (Table 3; Figs. 3, 4). Statistically, 95 % vKUDs were dissimilar among dusk and night periods, but overall vertical space use patterns among periods were similar for both 50 and 95 % vKUDs. Extent of activity space was also significantly related to week through the monitoring period (Table 3; Fig. 4c). Activity space extent was significantly influenced by week and the model predicted larger areas within the water column used around weeks 15–16 (14–27 April), 19–20 (12–28 May) and week 24 (23 June; Fig. 4c). Full moon occurred on 15 April (week 15), 15 May (week 19) and 13 June (week 23) during the monitoring period (denoted on Fig. 3).

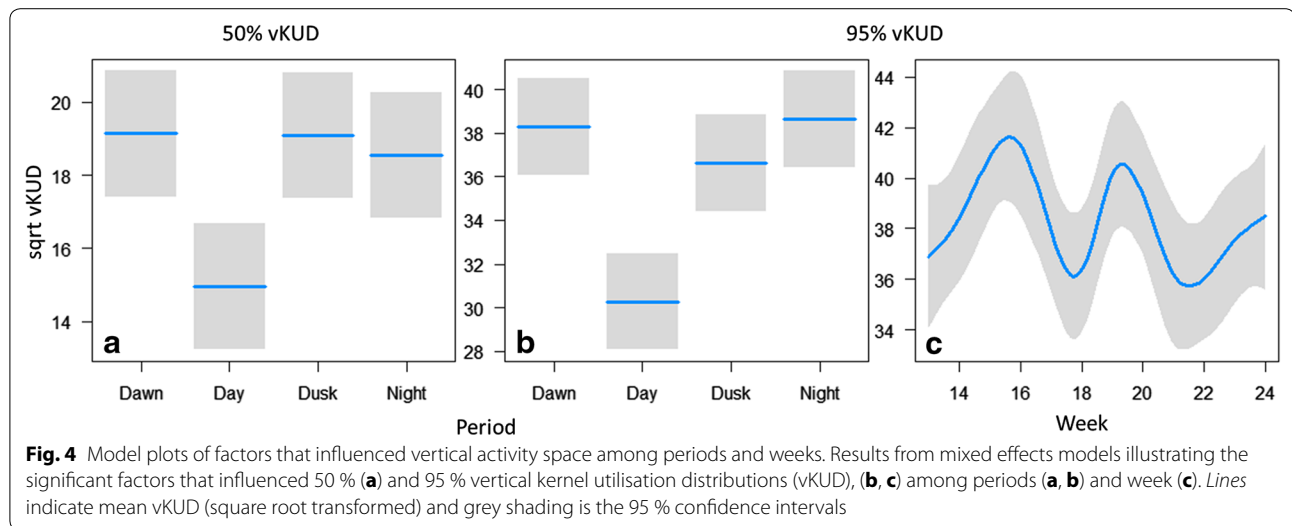
Percent overlap of activity space was calculated to determine whether activity space included consistent re-use of space across weeks. Estimates of 50 and 95 % vKUD were calculated for each time period (dawn, day, dusk and night) and compared among monitoring weeks. Variation was observed in the overlap of core space use among periods over time, with significant differences in overlap only observed between dusk and night periods (Table 3; Fig. 5a, b). Significant differences were detected among weeks for core and extent of space use (Table 3; Fig. 6a, b). Dawn and day periods followed the same trend with a peak in core space use at week 19, while overlap fluctuated among weeks for dusk and night, with

Table 3 Model results for vertical activity space among time periods by week

	Activity space		Percentage overlap		Cumulative area	
	50 % vKUD*	95 % vKUD*	50 % vKUD ^x	95 % vKUD ^x	50 % vKUD	95 % vKUD
Day vs dawn	<0.001	<0.001	0.967	0.056	<0.001	<0.001
Day vs dusk	<0.001	<0.001	0.702	0.171	<0.001	<0.001
Day vs night	<0.001	<0.001	0.053	0.183	<0.001	<0.001
Dawn vs dusk	0.953	0.079	0.733	0.586	0.770	0.564
Dawn vs night	0.403	0.725	0.048	0.862	0.001	0.084
Dusk vs night	0.438	0.036	<0.001	0.711	0.002	0.248
Week	0.066	<0.001	<0.001	<0.001	0.482	<0.001

Results of mixed effects models (*p* values, significant values indicated in italics) examining vertical activity space use (kernel utilisation distributions, KUDs) of *Lethrinus miniatus* by period and monitoring week. Area, percentage overlap and cumulative area by week were calculated for core (50 %) and extent (95 %) of activity space. Week was fitted as a natural spline with varying degrees of freedom (models with *df* = 3 provided best fits to the data for all estimates except 95 % vKUD and 95 % overlap estimates, where *df* = 7). Transformations of vKUD are indicated as asterisks (square root transformed) and crosses (arcsine square root transformed)



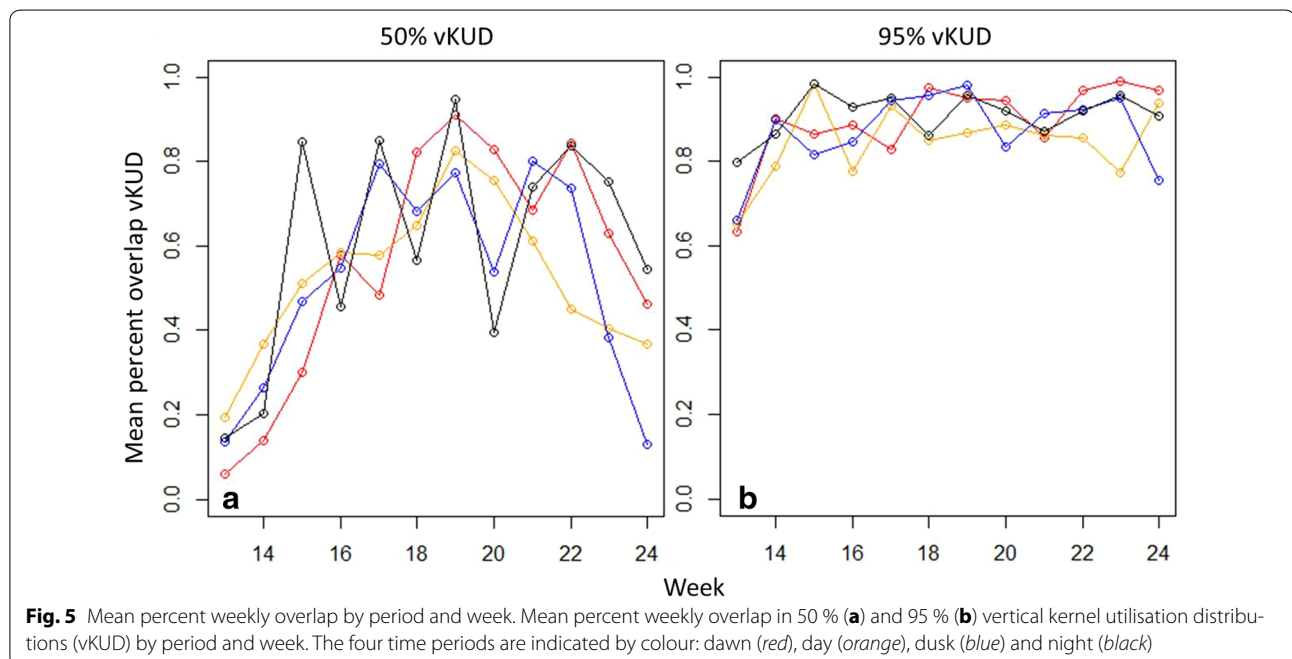


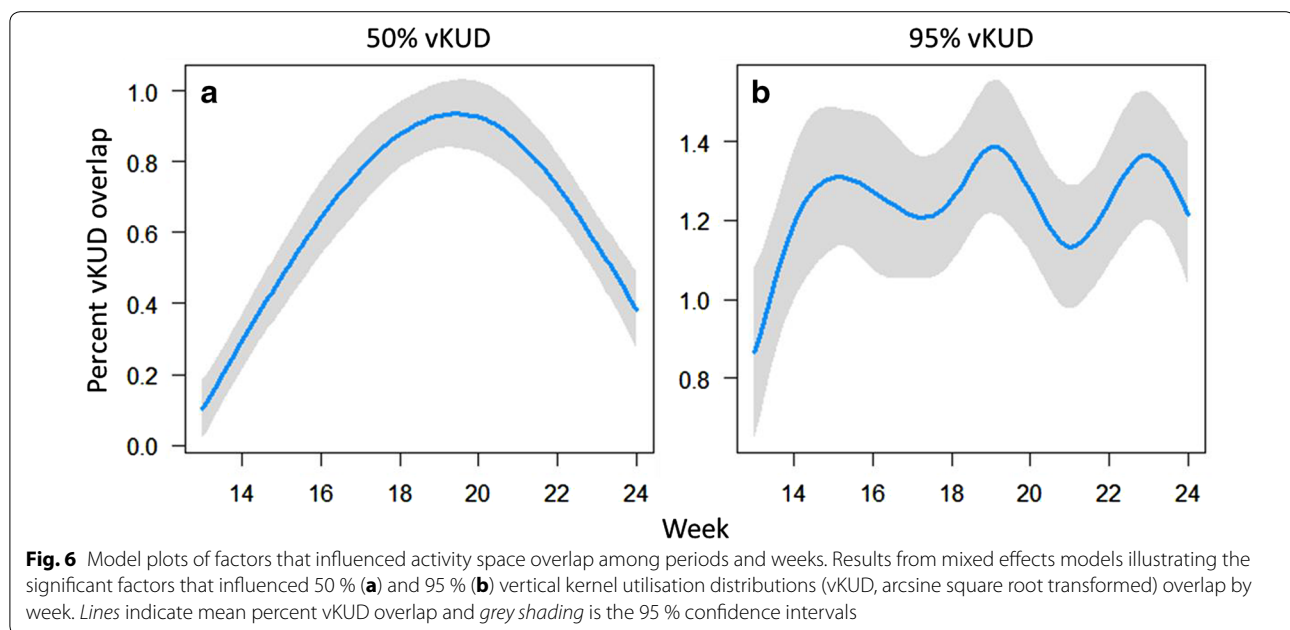
night overlap ranging between 50 and 90 % between successive weeks (Fig. 5a). Following week 22 (8 June), overlap decreased for all periods, signifying core activity shifted to using different areas for the final two weeks of monitoring (Fig. 5a). An n-shaped pattern was observed for percent overlap of core areas by model results, with a peak in overlap between weeks 18–20 (28 April–25 May) decreasing thereafter (Fig. 6a).

Overlap of home range extent was consistently high through time and ranged between 80 and 100 % from week to week for each period (Fig. 5b). Model results

(best-fitting model included week fitted as a natural spline with $df = 7$) indicated the overlap of mean space use extent fluctuated among weeks, with greater overlap around weeks 15, 19 and 23, corresponding to full moon periods (Fig. 6b).

While percent overlap provided an estimate of the area used among weeks, extrapolating as to whether the area of space use increased with time was achieved by calculating the cumulative 50 and 95 % vertical KUDs. Patterns in space use were similar (non-significant) among crepuscular periods (dawn and dusk) for core and extent





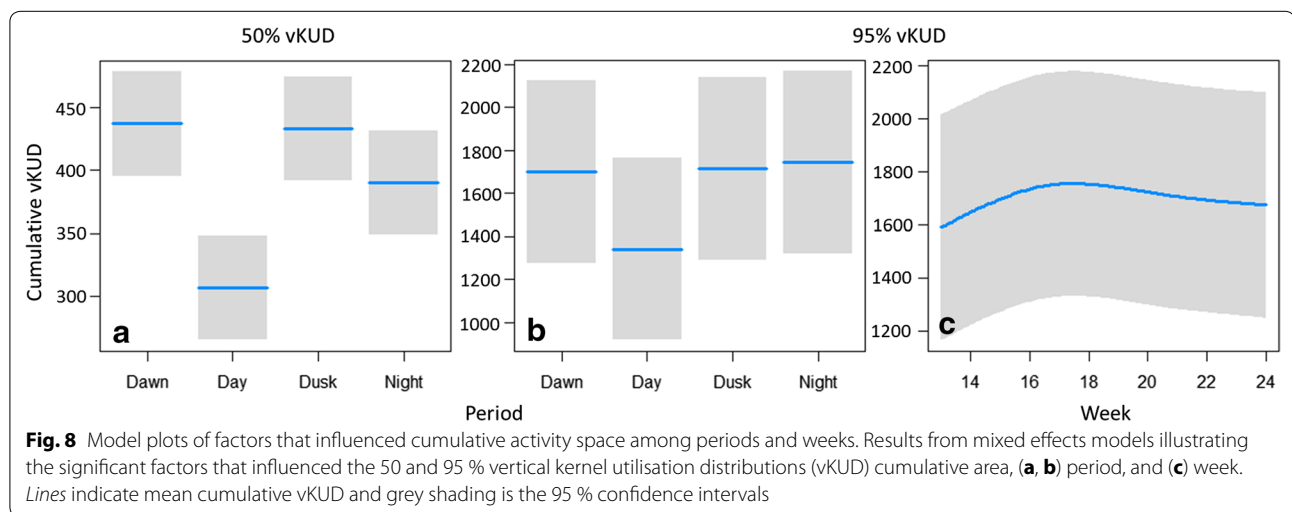
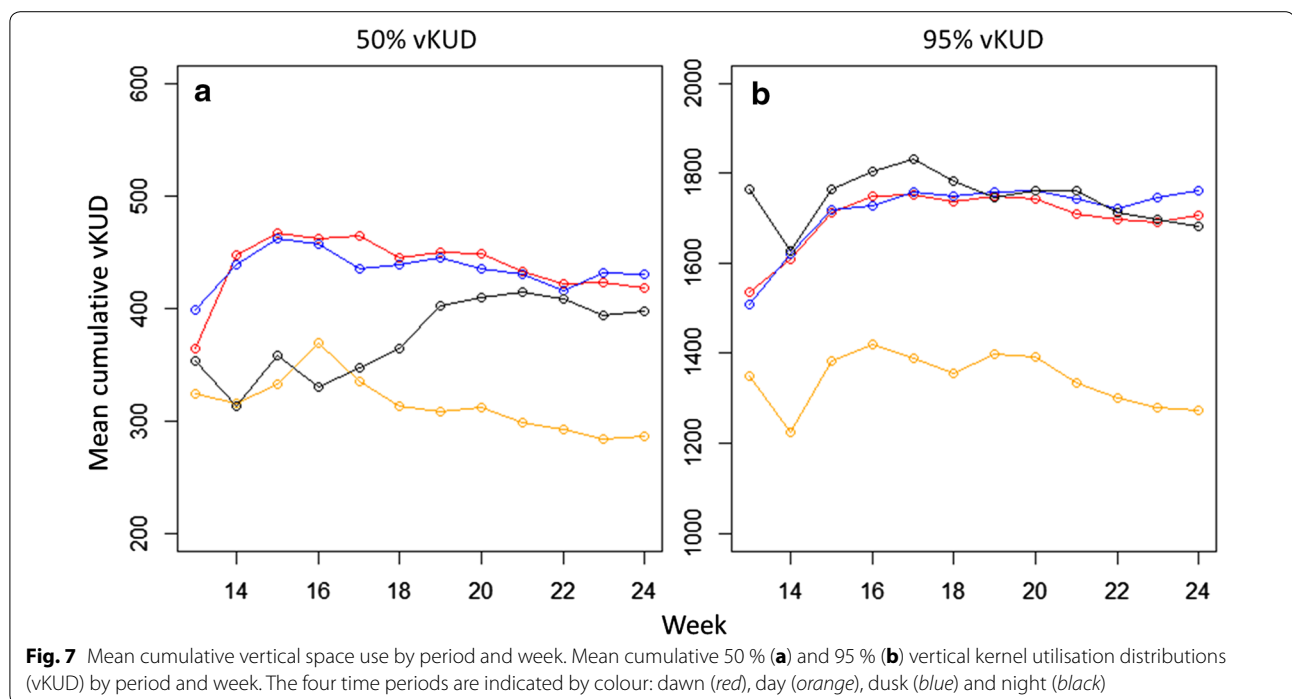
areas, becoming relatively stable after the third week of monitoring (week 16; Fig. 7a, b; Table 3). Night time core space use of individuals showed an overall increasing trend with time, while the extent of movement peaked later than day time and crepuscular periods. Cumulative space use during the day was consistently lower than all other periods. Significant differences were revealed among weeks for 95 % vKUDs (Table 3; Fig. 8c), however confidence bands were broad, indicating variation in the data. Separation between daytime and crepuscular/night periods, were further highlighted by 95 % vKUDs (Figs. 7b, 8b). Core areas were not only larger in cumulative area for crepuscular and night periods compared to day, but there was also greater area used during crepuscular periods overall (Fig. 7a; Table 3).

Discussion

Fine-scale telemetry data illustrated differences in space use of *L. miniatus* during different periods of the day. Fewer detections of this species on the reef slope at night documented by Currey et al. [8] was hypothesised to reflect dispersal away from daytime areas on the reef slope to deeper sandy areas at night. Application of an expanded fine-scale telemetry array revealed that horizontal core use areas and vertical extent of activity space were significantly smaller during the day compared to dawn, dusk and night periods, with the latter likely comprising space beyond the outer sandy area detection range. When examined on a weekly basis, this diel pattern was stronger for vertical space use, corresponding with a lifestyle of nocturnal mobility and foraging

behaviour [10]. Individual core areas varied in size, and re-use through time, while overlap differed through time. Day time extent of activity space was also smaller in area compared to other times of the day and, over time, appeared to be linked to lunar phase. Fine-scale analysis of movement patterns revealed more detail about the habitats exploited by this species and the consistency of their use through time, increasing our understanding of the movement ecology of *L. miniatus*.

Diel patterns in activity are common for many coral reef fishes [11–13]. With most fishes being either diurnal or nocturnal, a complex sequence of events occurs on coral reefs during dusk and dawn transition periods [3]. Patterns in daily activity influence how species persist in their environment and adapt to different niches [14]. For nocturnal species, foraging typically occurs during crepuscular and night periods while daylight hours are spent resting or patrolling [3, 15]. Diurnally active species typically leave night time refuges at dawn to forage, returning to rest at sunset (e.g. [16, 17]). Crepuscular periods in particular can be advantageous hours for foraging, since low light levels can provide predators with an advantage [18]. Feeding on crustaceans, echinoderms, molluscs and small fish, *L. miniatus* is known as a nocturnal predator that forages in sandy habitats adjacent to coral reefs, reported to only feed opportunistically during day [9]. This is consistent with recent research that revealed low presence of this species on a reef slope during night hours (1800–0600 h), and a suggested shift to deeper sandy habitats at night [8]. Although the dawn and dusk periods selected in this study comprised portions of



day and night hours, the strong patterns observed likely relate to nocturnal habits.

Horizontal and vertical space use for dawn, dusk and night periods was significantly larger than day periods, indicating larger areas are used, potentially as part of their foraging strategy. Although greater mobility and a larger night time space use could be expected for *L. miniatus* as a nocturnal predator, movements were not restricted to sandy habitat, as proposed by Currey et al. [8]. Instead, crepuscular and night hKUDs were spread across the monitored area, encompassing reef crest, slope and sandy

regions. Patrolling large areas across habitat types could provide greater foraging opportunity among patches of sand between areas of coral cover in depths of greater than 7 m. Analysis of paths of movement and tortuosity (e.g., [14]) would assist in elucidating evidence of feeding activity. Interestingly, individuals displayed relatively consistent depth use within the water column between reef crest and outer sand habitat, particularly for individuals with the most data (i.e. individuals 10155, 10162, 10170, 10154). For these benthic foragers [19], the lack of detections near deep sandy sediment (i.e., at 20 m+) suggests

this area may not have been used for foraging since individuals did not appear to be spending time near the benthos. Since this species occurs to depths >100 m [20] and long-distance movements have been reported, the home range of these individuals likely extends further away from the reef crest than the monitored area. Thus, foraging areas may be located in deeper habitats further offshore and the observed midwater space use at the edge of the array may represent a midwater transit corridor. Shifts between daytime reef habitat for resting to sand habitat for foraging at night are common for haemulids [5, 21, 22], and like acanthurids that use landmarks, it is plausible that *L. miniatus* could visually follow bottom contours to deeper foraging areas nearby [23]. However, individuals used the monitored area during all periods of the day (including night). Therefore, movements to any habitats outside the acoustic array were interspersed with substantial time spent on and close to the reef.

During daylight hours, monitored *L. miniatus* spent most time along the reef slope to crest. This space use is consistent with that reported by Currey et al. [8]. These core areas along the reef were smaller in size than for hours of twilight or darkness, which corresponds with other studies in which less movement occurred during the day than in other periods, e.g., mullids, haemulids, and lutjanids [14, 24, 25]. Daytime horizontal core areas for *L. miniatus* were generally located within the areas used during other periods, like that for *Kyphosus sectatrix* [26]. Thus, horizontal core areas used during dawn, dusk and night periods were spatially separated from areas used during the day, which was more restricted along the reef. Vertical core areas were similar and only marginally shallower during the day than in other periods, and represented 29–37 % of dawn, dusk and night areas by overlap. Coral reef fishes including mullids, scarids and acanthurids often display some degree of diel spatial separation in habitat use [16, 24, 27], and a greater amount of time spent over a smaller area by *L. miniatus* signifies the lifestyle of this species may incorporate resting during the day. The complexity of coral structure interspersed with sand on the Heron Island reef slope could be used for opportunistic foraging, or may also assist in daytime predator avoidance for *L. miniatus*, as has been observed for haemulids and lutjanids in the Caribbean [14]. For activity space extent, horizontal areas were similar in size along the reef during daytime, with significantly larger vertical areas used during crepuscular and night periods. However, like *Plectropomus leopardus* [28], movement within the water column substantially overlapped among periods, which may be an effect of the estimates incorporating movements across the monitoring period of >3 months, including potential temporal variability.

By examining vertical space use at a weekly temporal scale, stronger trends were observed through the monitoring period. Vertical space use extent fluctuated from the start of monitoring in March and peaked during the middle to end of each month (April, May and June) until the cessation of monitoring in towards the end of June. The amount of overlap in the extent of space use among weeks also displayed this trend, while core area overlap increased from March, peaked during the beginning of May, and decreased in size thereafter. Strong seasonal trends have been observed for other reef-associated fishes such as carangids, where shifts in core areas to spawning grounds occur during June to September [29]. While the proportion of mature *L. miniatus* females begins to increase in May within the region of the study site [30], spawning occurs on the Great Barrier Reef (GBR) between July and October, rendering this possibility as a cause for the observed pattern unlikely. High variability was evident in area and overlap among weeks, periods and individuals, which signifies that trends with time are unrelated to spawning or environmental drivers related to season. Alternatively, a strong correlation was observed between the monthly trend for increased home range extent and the weeks in which full moons occurred. Three expansions in vKUD area were demonstrated among all periods coinciding with moon illumination, and increased size of overall search areas during these phases may be necessary since higher luminosity may alter prey behaviour, making prey capture more difficult [31]. If larger home ranges during this moon phase are linked to a need to increase search area, this would explain the high degree of overlap in space use among periods. Although the relationship between lunar cycle and activity has not been investigated for reef fish, increased catch-per-unit-effort of pelagic fishes has been observed during full moon periods, indicating increased foraging activity during times of prey availability [32, 33]. The underlying relationship between activity space and moon luminosity has been observed for terrestrial carnivores [34] and presents a possible explanation for the temporal variation observed. Further research is required to link moon luminosity to space use and foraging behaviours in reef fishes.

Like the model results for space use overlap, cumulative vertical space use, or re-use of area, was variable with time. Cumulative core area was consistently high during crepuscular periods, suggesting that individuals reused the same large areas during dawn and dusk hours. Similarly, the smaller core daytime areas were revisited, and overall movement extent for all periods was relatively stable after the first few weeks of monitoring. Night areas in which individuals spent most time (core areas) appeared to increase in size through time, but it was the

weekly difference in space extent which was significant, which implies increased travel to new areas and variability through time.

Fine-scale data revealed diel activity space use of *L. miniatus* which reflects a nocturnal lifestyle. Testing the hypothesis proposed by Currey et al. [8], it appears that monitored individuals occupied smaller areas on the reef slope during the day. Rather than simply shifting to deeper adjacent sandy areas during night, larger horizontal and vertical areas were used during crepuscular and night periods. While these patterns reflect a limited number of individuals, these trends were persistent and clear, particularly when incorporating temporal variation by examining vertical space use at a finer weekly scale. Understanding how animal behaviour and movements change temporally and spatially (among habitats) is important to understanding how species coexist within ecological niches [35, 36]. Insight into diel activity potentially related to foraging, predator avoidance or intraspecific competition can be gained through analysis at a finer-scale and enhanced resolution, which provided a better understanding of the ecology of this exploited species.

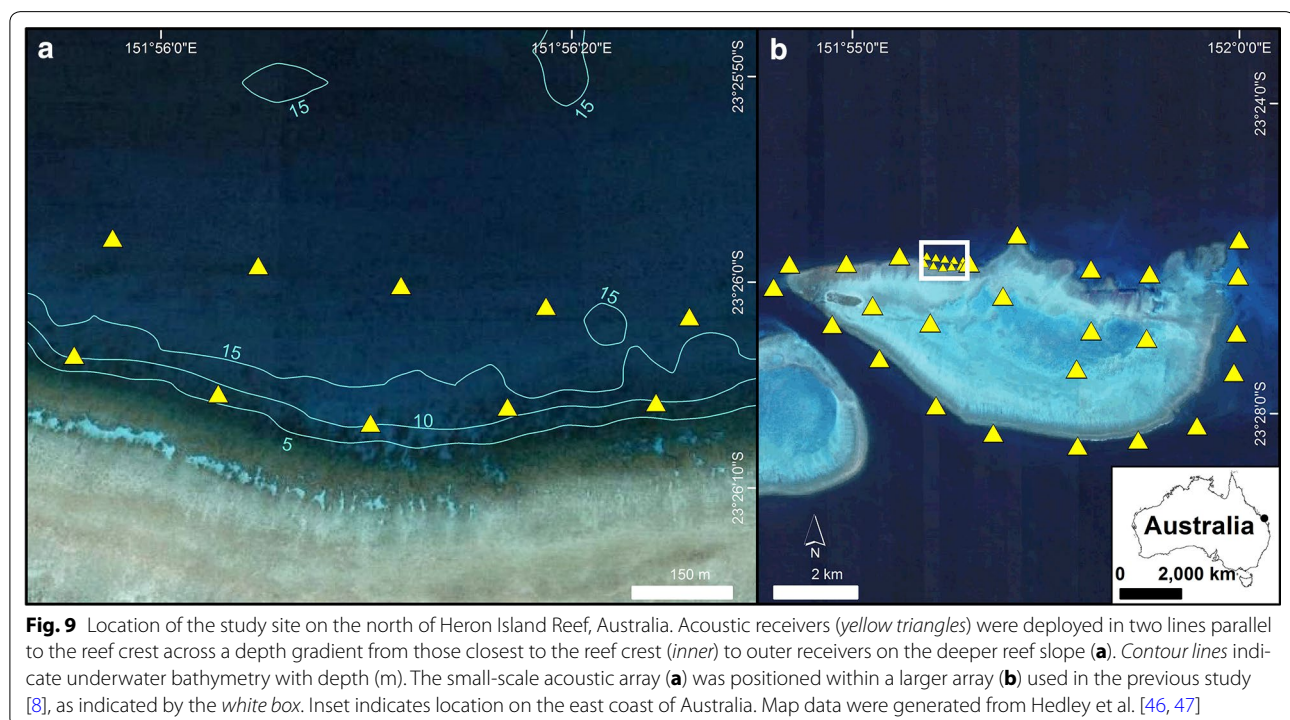
Methods

Study site and sampling

An array of Vemco VR2W[®] acoustic receivers deployed on the northern reef slope of Heron Island Reef

(23.4500°S, 151.9167°E), Capricorn-Bunker region of the GBR was utilised to monitor *L. miniatus* movements (Fig. 9). The study site included reef crest habitat, complex coral cover and coral bommies with sand patches on the reef slope, descending into sandy habitat, reaching approximately 40 m in depth in the northern channel. Ten receivers were deployed 22/3/2014–23/3/2014 on star pickets embedded in the substrate in two lines parallel to the reef crest, <200 m in distance apart. Inner receivers were positioned close to the reef crest (5–12 m in depth) and outer receivers were positioned in sand habitats (18–21 m in depth).

Eleven adult *L. miniatus* were captured by line fishing using rod and reel (13.6 kg line and 27.2 kg leader) with barbless 8/0 hooks baited with pilchard or squid on 22–23 March 2014. Excess gases from the swim bladder were released post-capture by venting, then individuals were anaesthetised with Aqui-S. A V13D[®] transmitter with pressure (depth) sensor (Vemco Ltd., Canada, 364 day battery life) was surgically implanted into the abdominal cavity via a small incision made longitudinally between the pectoral and ventral fins on the left side. The incision was closed by two simple interrupted stitches using absorbable sutures. Fish were released after a fork length (FL, in mm) measurement was recorded, a dart tag (PDS; Hallprint[®]) for identification fitted externally and after recovery in fresh sea water (total procedure <8 min).



Data analysis

Data from receivers were analysed in the R environment version 3.1.0 [37]. Detection data were examined to identify any spurious detections, e.g. data that represented fast, erratic movements (i.e., consistent with fish consumed by predator), or lacked vertical movement aside from a consistent tidal signature (i.e., individual perished). Fish with these detection characteristics were assumed to have perished and were removed from analyses. Detections during the first 48 h were removed for all individuals to remove any effect of handling on fish behaviour. To test for variability in transmitter detection with time of day, mean detections of *L. miniatus* were standardised to mean detections of sentinel tags (deployed in the array during the monitoring period) per hour, according to Payne et al. [38]. Transmitters were detected when within distances of approximately 270 m from the receivers, determined by range testing at Heron Island Reef during a previous study [8].

For individuals detected for >5 days by two or more receivers, average positions were calculated at 10 min intervals [39]. To estimate diel individual space use, four discrete 3-h periods were selected from the data to represent dawn, day, dusk and night. The 3-h duration was selected to enable sufficient data points for space use estimation and a balanced sampling design. The hours selected for dawn (0400–0659) and dusk (1700–1959) were based on timing of local sunrise, sunset and astro twilight calculated across the 3 months of monitoring. Since dawn and dusk behaviours typically occur over 1 hour of changing light [3], a portion of these 3 h periods would likely encompass day and night behaviours. Hours selected for day and night periods incorporated midnight and midday. Data for remaining hours were excluded as buffer periods.

Horizontal and vertical space use was estimated using kernel utilisation distributions (KUDs). Horizontal space use KUDs (hKUD; [40]) were calculated using the *ade-habitat* package in R [41]. Vertical KUDs (vKUD) were estimated using the *ks* package in R [42] in a linear two-dimensional space to determine the vertical use of the water column perpendicular to the reef crest. The perpendicular distance between each acoustic receiver to the closest point on the reef crest was calculated, and since receivers were positioned between the reef crest and the sand, average positions were represented as the mean distance to crest by mean depth (similar to [8, 43]). Both space use estimates were calculated for core use areas (50 % KUD) and extent of activity space (95 % KUD). Data were screened for normality and homogeneity of variances.

Mixed effects models were used to determine whether differences in horizontal and vertical KUDs existed

among time periods (dawn, day, dusk and night time periods) and individual fish size (FL). KUDs were treated as the response variable, period and FL were modelled as fixed factors and models were analysed using the *nlme* package in R [44]. Individual fish was treated as a random effects term to account for the lack of temporal and spatial independence among individuals and to reduce the effect of individuals with more detections. Mixed effects models were also used to determine whether there were differences in overlap of vertical KUDs among periods. Significance was assessed at the $p < 0.05$ level.

For each period (dawn, day, dusk, night), comparisons in the size of vertical areas (50 and 95 % vKUDs) through time were examined using mixed effects models. Response variables were square root transformed vKUD estimates (to satisfy assumptions of homogeneity of variance and normality), period and week were fixed factors, and individual fish ID was the random effects term. Week was fitted as a natural spline with varying degrees of freedom, with the best-fitting model compared using the Akaike Information Criterion corrected for small sample bias (AIC_c).

To ascertain whether the 50 and 95 % vKUDs covered the same locations for each time period through subsequent weeks, proportional overlap of areas from week to week were calculated. Overlap was represented as the proportion of the previous week's value, and values were arcsine transformed. Models were weighted by week using the *varIdent* variance structure to achieve homogeneous variances, since patterns in residual variance were found through time [45].

For each period (dawn, day, dusk and night), utilisation of new areas per week was examined using cumulative weekly activity space. Cumulative 50 and 95 % vKUDs for consecutive weeks were calculated with position data from that week, and added to the positions of all previous weeks in an iterative manner [43]. The difference between the current and previous week's vKUD as a function of the previous week's value was calculated to identify whether individuals were using new areas with time. Models were weighted by week for 50 % vKUD estimates only.

Authors' contributions

LMC developed the study, designed the fish sampling and data collection, carried out analyses, drafted and edited the manuscript. MRH provided project funding, designed the study, participated in fish sampling and commented on drafts of the manuscript. CAS assisted with fish sampling and analysis, and commented on drafts of the manuscript. AJW assisted with analysis and commented on drafts of the manuscript. All authors read and approved the final manuscript.

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Acknowledgements

We thank the staff and students of the Fishing and Fisheries Research Group for assisting with this project, particularly A Tobin, F de Faria, S Moore, E Lédée and P Yates. Infrastructure and field support provided by the Australian Animal Tagging and Monitoring System facility of the Integrated Marine Observing System and the Australian Institute of Marine Science was greatly appreciated. Maps were produced by E Lédée with data provided by R Beaman, the Commonwealth of Australia (Great Barrier Reef Marine Park Authority), Google™ earth and DigitalGlobe. Funding for this research was provided by the Australian Research Council awarded to MRH. Additional research funding was granted to LMC from James Cook University (JCU) School of Earth and Environmental Sciences (SEES). LMC was also supported by an AIMS@JCU Postgraduate Research Scholarship and stipend. All research activities were conducted under GBRMPA permit numbers G10/33754.1 and G10/33758.1 and Queensland Department of Agriculture, Fisheries and Forestry permit number 144482. Treatment of all animals was conducted under ethical guidelines approved by JCU animal ethics number A1566.

Compliance with ethical guidelines

Competing interests

The authors declare that they have no competing interests.

Received: 7 January 2015 Accepted: 11 September 2015

Published online: 29 September 2015

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