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EXAMINING THE MOVEMENT OF THE COMMON SPIDER CONCH *LAMBIS LAMBIS* IN SHALLOW WATER OF A NORTHEASTERN INDIAN OCEAN ATOLL USING PASSIVE ACOUSTIC TRACKING

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ABSTRACT Despite the commercial and cultural values of conch (family: Strombidae), there is a paucity of biological and ecological information to assist with the management of many conch fisheries. The common spider conch *Lambis lambis*, harvested throughout the Indo-Pacific for its meat and shell, is an example of such a data-deficient conch species. This study used passive acoustic tracking to estimate the spatial requirement and broad movement patterns of *L. lambis* over a 13-mo period in an extremely shallow (depth < 2 m) lagoonal environment of the Cocos (Keeling) Islands (CKI). The mean kernel utilization density home range for *L. lambis* during the study period was estimated at 18,059 ± 3,298 m^2 ($n = 14$). The mean home range was also estimated monthly and was found to be significantly larger in January (austral summer) than in the preceding October and November, likely a function of the reproductive cycle of *L. lambis* at CKI. Estimated home range size and animal size were not found to be correlated, and there were no observed differences between the sexes. The results show that, in an environment of preferable habitat with adequate resources, *L. lambis* have a home range that is relatively small when compared with studies of the Caribbean queen conch *Lobatus gigas*. The information on the spatial requirement and movement ecology for *L. lambis* at CKI from this study will assist with informing management techniques, not only for this fishery but also for other small conch fisheries worldwide.

KEY WORDS: *Lambis lambis*, Cocos (Keeling) Islands, Strombidae, telemetry, home range, mollusc, gastropod

INTRODUCTION

Conchs (family: Strombidae) are of high economic and cultural importance throughout their distribution but are also known to be vulnerable to overexploitation (Berthou et al. 2009, Cob et al. 2012, Stoner et al. 2018). Large declines in the most economically significant and widely studied conch species, the queen conch *Lobatus gigas* (Linnaeus, 1758), are well documented and have resulted in the complete closure of fisheries for this species in a number of countries (Theile 2005, Acosta 2006, Stoner et al. 2018). In some instances, overfished *L. gigas* populations have not recovered decades after the introduction of diverse management strategies (Stoner & Ray-Culp 2000, Tewfik & Guzman 2003, Stoner et al. 2012). With less scientific data and often less management, there is ongoing concern for the sustainability of the smaller conch fisheries (Anderson et al. 2011, Fröcklin et al. 2014). Management and trade regulations have been introduced for some conch fisheries (Jagadis et al. 2012, Annamary & Mohanraj 2014); however, there are many that would benefit from increased management attention (Allen & McKenna 2001, Mazo et al. 2013, Wagey et al. 2017). The data-poor nature of these fisheries and the paucity of knowledge surrounding the biology and ecology of the target species make determination of the most effective fishery management techniques problematic (Pilling et al. 2009, Bellchambers et al. 2011).

The common spider conch *Lambis lambis* (Linnaeus, 1758) is distributed throughout the shallow reefs and intertidal waters of the Indo-Pacific (Poutiers 1998). A recreational fishery for *L. lambis* occurs at the Australian Indian Ocean External Territory of the Cocos (Keeling) Islands (CKI) and is an example of a data-limited conch resource that has been shown to have concerns for sustainability (Hourston 2010, Evans et al. 2016). At CKI, *L. lambis* are found in the shallow waters of the southern atoll lagoon where they are highly associated with areas of macro-algae and coral outcrops (Bellchambers et al. 2011). Fishing occurs by hand while wading or snorkeling and is thought to have become popular in the 1970s (Lincoln-Smith et al. 1993). Anecdotal evidence suggests that the typical catch of *L. lambis* is between 200 and 1,000 individuals each fishing trip and that several thousand can be harvested for community events multiple times per year (Bellchambers et al. 2011). Relative abundance assessments of *L. lambis* at CKI have shown a general declining trend since the first recorded assessment in 1992 (Lincoln-Smith et al. 1993, Konzewitsch & Evans 2019).

Although the distribution and general morphology of *Lambis lambis* have been reported, there is relatively little information on the biology, ecology, or fisheries for this species (Bellchambers & Evans 2013). The movement of conch such as *L. lambis*, and marine gastropods in general, is poorly understood (Leiva & Castilla 2002, Dujon et al. 2019). Understanding the movement behavior of a species is fundamental to selecting fishery management techniques, especially for species that have characteristics that may make them particularly vulnerable to overfishing or do not benefit from common management techniques (Kramer & Chapman 1999, Newman et al. 2002, Grüss et al. 2011).

Recent developments in passive acoustic telemetry allow the accurate measurement of marine animal movements and can provide relocation data at a high temporal resolution from multiple individuals over extended periods (Heupel et al. 2006, Simpfendorfer et al. 2008, Espinoza et al. 2011). Individual relocation data collected over appropriate temporal scales can be

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used to estimate the spatial requirements of marine species by estimating "home range," which is described as the area to which an animal confines its normal activity (Burt 1943). Recent work using acoustic techniques have provided estimates of home range for *Lobatus gigas* at various locations and environment types (e.g., Delgado & Glazer 2007, Bissada-Gooding & Oxenford 2010, Phillips et al. 2011, Stieglitz & Dujon 2017). There is still, however, a lack of similar studies for other conch species such as *Lambis lambis*, which vary considerably to *L. gigas* in morphology and potentially in spatial requirement.

This study used passive acoustic telemetry to investigate the movement patterns of *Lambis lambis* over a 13-mo period. The spatial requirements of a subpopulation of *L. lambis* are described by using two common methods to estimate home range and investigate temporal and biological (sex, length, and lip thickness) influences on home range. The difficulties of using passive acoustic telemetry to track a partly cryptic benthic species in an extremely shallow environment are also discussed. Quantifying the spatial requirement for this species will inform future management decisions and provide a platform for further studies of the movement ecology of this species and other Strombidae.

MATERIALS AND METHODS

Study Site

Located in the northeastern Indian Ocean, CKI are an Australian Indian Ocean External Territory comprising 27 islands over two separate coral atolls (Fig. 1A). This study focused on the shallow eastern side of the CKI southern atoll lagoon (12° 08″ S, 96° 53″ E) which is the main fishing area for *Lambis lambis* (Fig. 1B). The primary study site was approximately 75,000 m^2 (~250 × 300 m) and mostly shallow (<2 m) although the depth ranged to approximately 10 m (Fig. 1C). The site contained a high abundance of *L. lambis* and a mix of preferred benthic habitats (see Bellchambers et al. 2011) including macro-algae (e.g., *Caulerpa* spp.), coral rubble, and isolated outcrops of scleractinian coral and sand. The site was bounded by nonfavorable *L. lambis* habitat to the east (intertidal sand flats) and west (coral dominated blue hole mosaic), and remained open to fishing for the entire study period.

Acoustic Range Test

An *in situ* acoustic range test was conducted over a 5-day period (February 2–7, 2017) before commencement of the study. The range test used 10 acoustic receivers (VR2W; VEMCO Ltd., Bedford, NS, Canada) deployed in a 200-m straight line at 0, 10, 20, 40, 60, 80, 100, 125, 150, and 200 m. The receivers were downward facing, attached to a rope held taut by a 20-kg benthic weight and an 8-inch float, and positioned as high in the water column as possible to maximize acoustic coverage. A VEMCO V16 transmitter was attached to the rope below each receiver and a VEMCO V9 transmitter was attached to a weight at the 0-m mark at the approximate height it would be on a tagged *Lambis lambis*. The range test revealed that detections of the V9 transmitter reduced from greater than 80% of transmissions at 20 m to approximately 50% at 40 m, approximately 10% at 80 m, and no significant detections past 100 m. From these results, and *in lieu* of data from prior movement studies on the species, a receiver spacing of 75 m was selected to strike a balance between a primary study site large enough to record movement over 13 mo while also providing acoustic overlap to allow for an assessment of *L. lambis* movement patterns.

Acoustic Tracking and Tagging

Eighteen acoustic receivers (VR2W) were spaced 75 m apart to form a VEMCO Positioning System (VPS) grid array within the primary study area (Fig. 1C). The receivers in the array were deployed using the same method described in the range test. A V16 sync transmitter was fastened on the rope below each receiver, and a HOBO Pendant temperature logger was installed

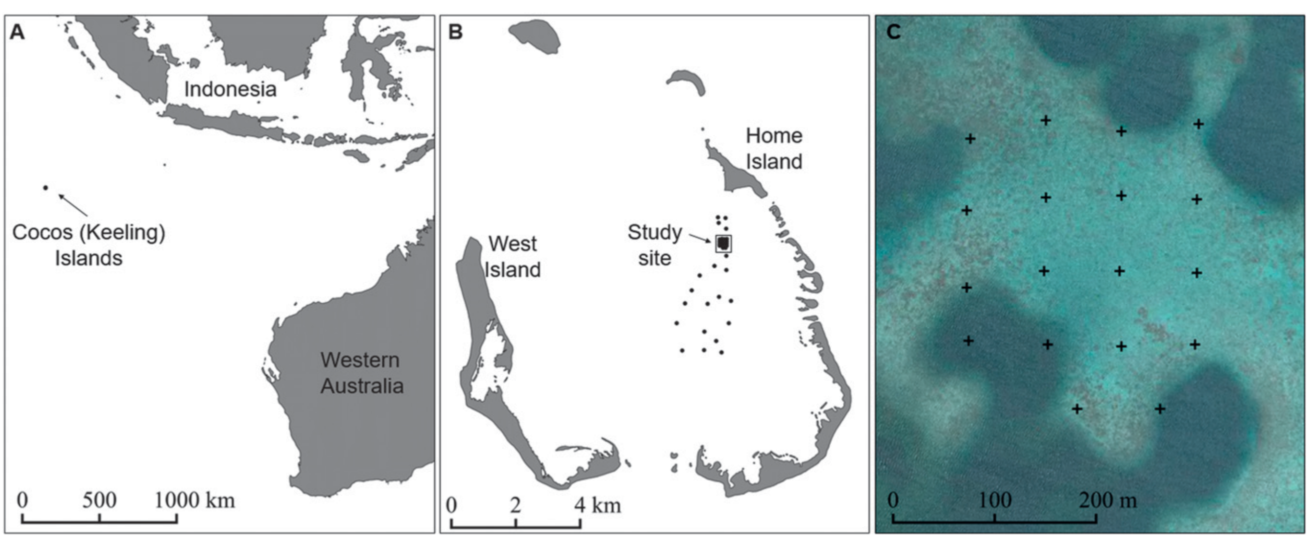

Figure 1. Location of (A) CKI within the Indian Ocean, (B) the study site within the southern atoll showing all acoustic receiver locations (black dots), and (C) the primary study site with acoustic receiver locations (+) overlaid on satellite imagery.

in the center of the VPS array to provide water temperature data every 20 min. An additional 22 VR2W receivers were placed in a nonoverlapping linear array on shallow corridors between deeper "blue holes" to the north and south of the primary study site (Fig. 1B). The combination of a VPS grid and a linear array was used to record movement within the primary study area and also capture the timing and direction of any broad scale movement away from this area if it occurred (Heupel et al. 2006). The receivers were cleaned of fouling material twice (April and July 2017) during the study period.

Twenty *Lambis lambis* (10 males and 10 females) were collected at five locations within the primary study area. Measurements of total length and lip thickness were recorded. An area near the shoulder on the ventral side of each *L. lambis* was scrubbed with a wire brush and dried before a V9 transmitter was adhered to the shell using a super glue gel and epoxy putty. The weight of a V9 tag in water (2.0 g) was considered a negligible addition to the overall weight of the animal. The tagging process took less than 5 min, and each animal was released at the point of capture.

Data Analysis

Only 79 VPS position estimates could be calculated for the 20 tagged *Lambis lambis* over the 13-mo period. Therefore, further analysis using this method was not possible. Position estimation was still possible using the mean-position estimate (MPE) algorithm to calculate a center of activity as described in Simpfendorfer et al. (2002). The MPE algorithm estimates the position of a transmitter using an XY coordinate system by calculating the mean of the receiver locations, weighted by the number of detections recorded on each receiver. Preliminary analysis of the movement data indicated that calculating the MPE algorithm over a 24-h period was appropriate. The tracking duration for each tagged animal was calculated as the number of days between first and last detections. Mean daily detections of the 18 fixed V16 transmitters from all 18 VPS array receivers in the primary study area were calculated and used as an index of acoustic range. Data were tested for normality (Shapiro–Wilk), and a Spearman's rank correlation was applied to calculate the effect of wind speed (Cocos Islands Airport: Bureau of Meteorology 2018) and water temperature on the acoustic range. ANOVA was used to compare the mean daily V16 tag detections between seasons: "Tradewinds" (May–October) and "Doldrums" (November–April).

Home range was estimated using two common methods: minimum convex polygon (MCP) (Mohr 1947) and utilization distribution probability function using the kernel method (KUD) (Van Winkle 1975, Worton 1989). Home range estimates using MCP were calculated with 5% of the most extreme relocations excluded. The KUD estimations used bivariate normal kernel density estimate with a reference bandwidth smoothing parameter for 95% KUD (home range) and also for 50% KUD, which is considered the "core area" of space use for an organism (Worton 1989, Vander Wal & Rodgers 2012). To investigate temporal variation, monthly home range (95% KUD) was also estimated when sufficient data collection allowed. An overall mean monthly home range was calculated by pooling the monthly home range estimates for each tagged animal between March 1, 2017 and February 28, 2018. The mean estimated home range was also calculated by averaging the individual home ranges for each month to show monthly home range trends throughout the study period. ANOVA was used to compare the differences in home range between months and between sex. Correlation between home range and morphological data was tested using the appropriate correlation test (Pearson or Spearman's rank) after testing for normality. All statistical analyses were performed in R (v3.5.0, R Development Core Team 2018). Home range calculations were performed using the "adehabitat" package for R (Calenge 2006). Visualization of the results was performed in QGIS (v3.10.1 Coruña, QGIS Development Team 2019).

RESULTS

No transmitter detections were recorded on the 22 linear array receivers placed to the north and south of the primary study site over the 13-mo period. A total of 399,596 transmitter detections were recorded within the primary study area. Six animals were omitted from analysis as they were either not detected for more than four days after release or were suspected to be detached transmitters or animal deaths because of an extremely high proportion of detections at a single receiver. Position estimates were therefore calculated for 14 tagged *Lambis lambis* (nine males and five females; total detections = 275,774; Table 1). The proportion of tagged *L. lambis* detected within the primary study site each day ranged from 0.21 to 1.0 (mean = 0.63 ± 0.01). Time-series data showed a below average proportion of animals detected between March and August 2017 and also between January and February 2018 (Fig. 2). The number of days where position estimates were able to be calculated for an animal ranged from 33 days to 398 days, which was the full study period (mean = 250 ± 27 days) (Table 1). The number of detections within a 24-h period that were used for the position estimation of an animal ranged from 1 to 555 (mean = 78.6 ± 1.9 detections). The mean tracking duration (days between first and last detections of an animal) was 369 ± 15 days, which represents 92.8% of the study period (Table. 1). The median tracking duration was 397 days (99.7% of the study period).

The mean daily detections from the 18 fixed V16 transmitters displayed a very strong negative correlation to the mean daily wind speed over the study period (r_s = –0.86, $P < 0.001$) (Fig. 3). ANOVA indicated that a significant ($P < 0.001$) decline in detections was observed throughout the windier (mean speed > 12 knots) "Tradewind" season. A strong positive correlation between mean daily V16 transmitter detections and water temperature was also observed ($r = 0.64$, $P < 0.001$).

The mean estimated home range (95% KUD) for *Lambis lambis* over the study period was 18,059.0 ± 3,298.1 m^2. Home range varied markedly among tagged animals, with estimates ranging from 4,509.1 m^2 (M4) to 43,310.57 m^2 (M9) (Table 1, Fig. 4). The mean core area (50% KUD) was 3,207.8 ± 671.8 m^2, and the mean MCP home range was 9,641.6 ± 1,823.9 m^2 (Table 1). An ANOVA test did not indicate a difference in the estimated home ranges between the sexes ($P > 0.95$). Total length (r_s = –0.18, P = 0.54) and lip thickness (r_s = 0.28, P = 0.32) of *L. lambis* both displayed weak correlation to estimated home range (KUD 95%).

The mean of the monthly home ranges across the study period was 6,684.6 ± 748.5 m^2 (n = 70) and individually ranged from 11.7 m^2 (F4: February 2018) to 24,491.8 m^2 (M5: January

TABLE 1.

Data summary for each acoustically tagged *Lambis lambis*.

ID	Length (mm)	Total no. of detections	Duration (day)	Position estimates (day)	95% KUD (m^2)	50% KUD (m^2)	95% MCP (m^2)
F1	145	5,354	363	203	28,246	6,092	12,344
F2	150	15,309	398	303	8,919	953	4,873
F3	140	1,998	397	161	29,531	6,917	11,880
F4	170	21,332	398	298	17,562	2,308	10,857
F5	148	1,608	288	33	7,390	1,094	1,300
M1	140	2,775	203	143	4,727	245	3,298
M2	140	61,113	398	311	25,257	3,832	15,942
M3	135	14,747	351	264	14,387	1,550	5,504
M4	145	31,020	398	322	4,509	346	2,398
M5	155	52,456	398	398	27,421	4,341	23,681
M6	135	6,454	396	215	28,794	6,355	11,241
M7	113	22,268	397	364	8,261	701	6,212
M8	135	33,324	388	326	4,511	368	5,000
M9	114	6,016	398	169	43,311	6,697	20,452
Mean ± SE	140.4 ± 3.9	19,698.1 ± 5,054.9	369.4 ± 15.2	250.7 ± 26.9	18,059.0 ± 3,298.1	3,207.6 ± 671.8	9,641.6 ± 1,823.9

Duration is the number of days between first and last detections. Study period = 398 days.

2018). The month with the lowest estimated mean home range of the 12 mo with full datasets (i.e., March 1, 2017–February 28, 2018) was October 2017 (2,924.2 ± 982.8 m^2; $n = 8$) and the highest was in January 2018 (12,217.2 ± 2,966.0 m^2, $n = 9$) (Fig. 5). An ANOVA test indicated a significant difference in home ranges between months ($F_{(8,59)} = 3.08$, $P < 0.01$), and the Tukey HSD test found that January 2018 had a significantly higher mean home range than October 2017 ($P = 0.022$) and November 2017 ($P = 0.023$) (Fig. 5). Insufficient movement data were collected between May and July 2017 to enable the calculation or comparison of mean monthly home range (95% KUD) for these months. Visualization of the monthly movement of the animal with the most temporally consistent movement data (M2) showed spatial variance between months despite the estimated home range never extending further than approximately 150 m away from the release location (Fig. 6).

DISCUSSION

The mean estimated home range (18,059 m^2) calculated by KUD for *Lambis lambis* was markedly less than those reported for *Lobatus gigas* in acoustic tracking studies that were performed over a comparable time frame (e.g., Glazer et al. 2003: 59,800 m^2; Delgado & Glazer 2007: 27,705 m^2). The mean estimated home range calculated by the MCP method (9,642 m^2) is comparable to MCP estimations for *L. gigas* (e.g., Bissada-Gooding & Oxenford 2010: 11,031 m^2; Phillips et al. 2011: 8,595 m^2); however, these studies were over much shorter time periods (<12 wk). Considering the larger size and presumably greater nutritional requirement of *L. gigas* relative to *L. lambis*, these results are in line with the suggestion that home range generally increases with body size (Kramer & Chapman 1999). A recent acoustic tracking study of *L. gigas* by Stieglitz and Dujon (2017) identified two distinct types of movement

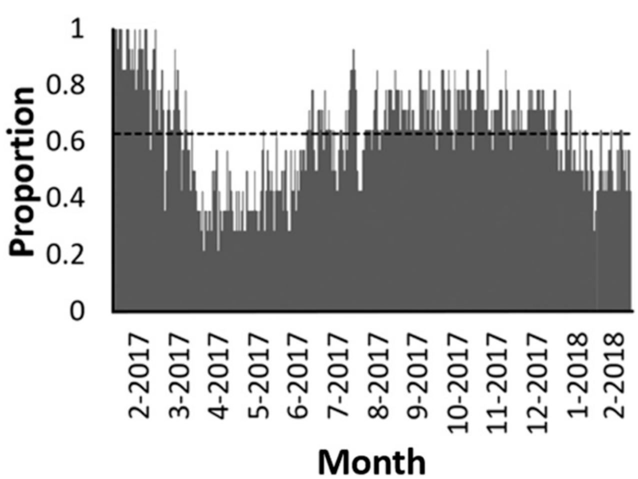

Figure 2. Time-series bar graph of the proportion of tagged *Lambis lambis* detected daily throughout the study period. Dashed line indicates the mean (0.63).

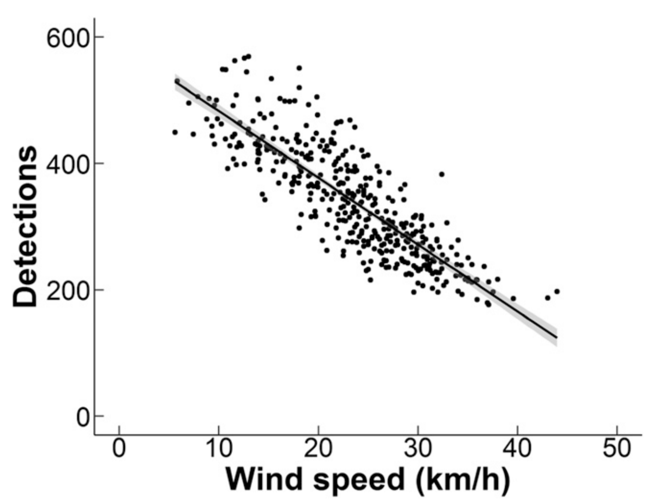

Figure 3. Mean daily V16 tag detections by mean daily wind speed (km/h) with linear regression line and 95% confidence interval (shading).

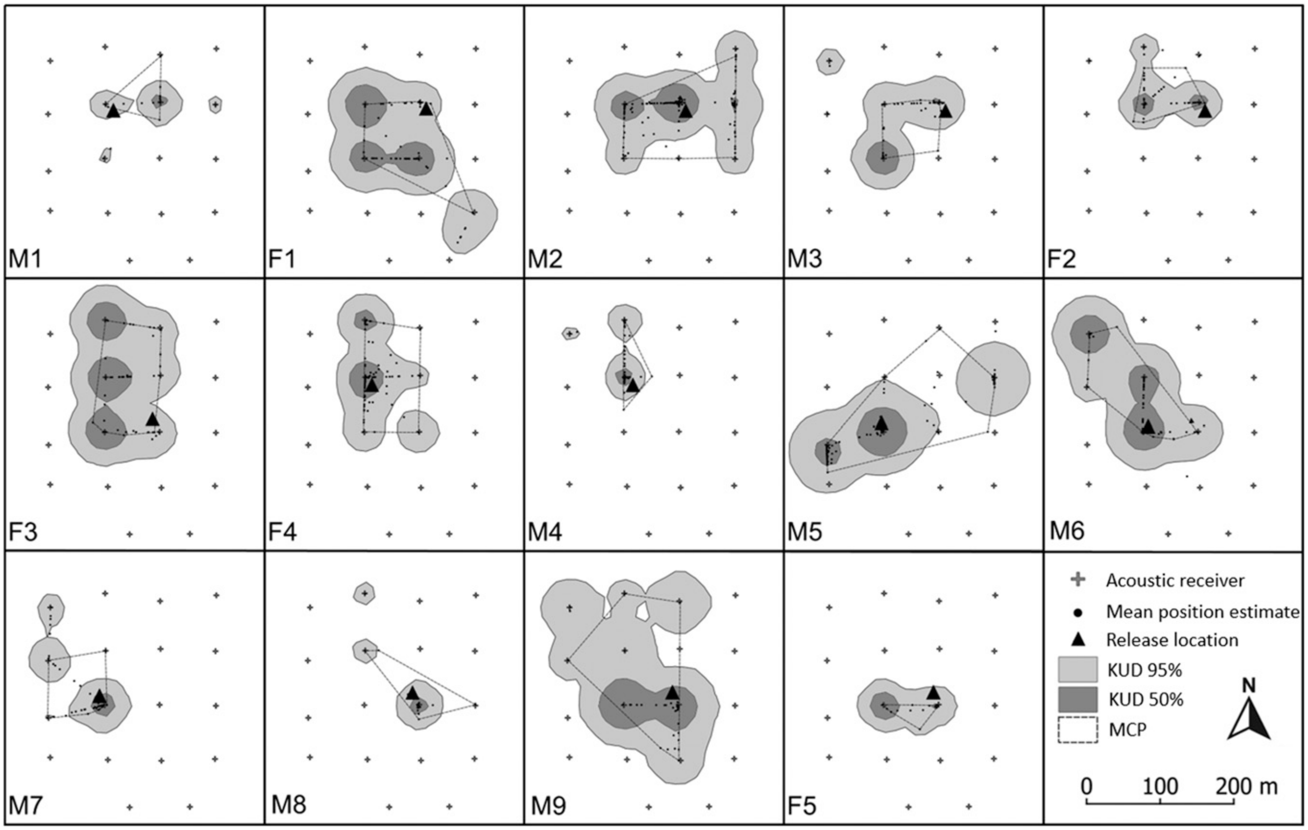

Figure 4. Minimum convex polygon, KUD 95%, and KUD 50% for each of the 14 tagged *Lambis lambis* over the entire study period.

behavior: Type 1 was characterized by a highly localized distribution, and Type 2 displayed two or more heavily used areas connected by large (~1 km) movements. Although large movements similar to Type 2 behavior cannot be excluded, these appear unlikely for the *L. lambis* tracked in this study as no transmissions were detected on the extended linear array receivers. The Type 1 behavior displayed by *L. lambis* in this study is consistent with that observed when resources are not limited, and the home range estimations in this study should be interpreted in this context (McLoughlin & Ferguson 2000, Stieglitz & Dujon 2017). It is expected that the home range of *L. lambis* in an area of limited resources would be higher than those observed in this study.

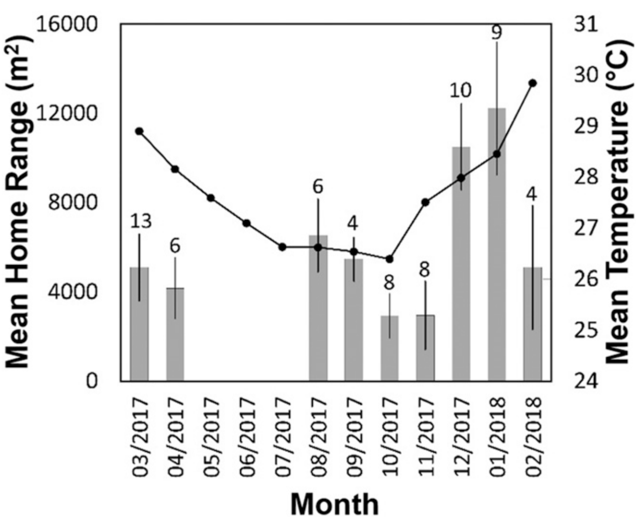

Figure 5. Bar chart of mean home range (95% KUD ± SE) and line graph of mean temperature for each full month of tracking within the study period. The number of home ranges used for the calculation of mean home range is displayed above the error bar. There were insufficient relocation data between May and July 2017 for the mean monthly home range calculation.

In general, the estimated home ranges for *Lambis lambis* were much smaller over shorter time frames (i.e., month *versus* year), which indicates that the tagged animals moved between areas within the primary study site throughout the year. This trend is also apparent in the visualization of the monthly estimated home range for individual *L. lambis* which displayed spatial variance while maintaining fidelity to the release site over the study period (Fig. 6). The mean estimated home range in January 2018 was found to be significantly ($P < 0.05$) larger than that in October 2017 and November 2017, and, although not found to be significant because of the small sample size, the mean home range in December 2017 was markedly larger as well. This period of increased space use is possibly a function of the reproductive cycle of *L. lambis* at CKI. A histological study of specimens collected over the period of a year by Bellchambers and Evans (2013) found a high proportion of mature gonads in females during December and January. These months also coincided with increasing water temperatures (Fig. 5), which is a typical annual pattern observed at CKI (Konzewitsch & Evans 2019). Larger home ranges have been observed for *Lobatus*

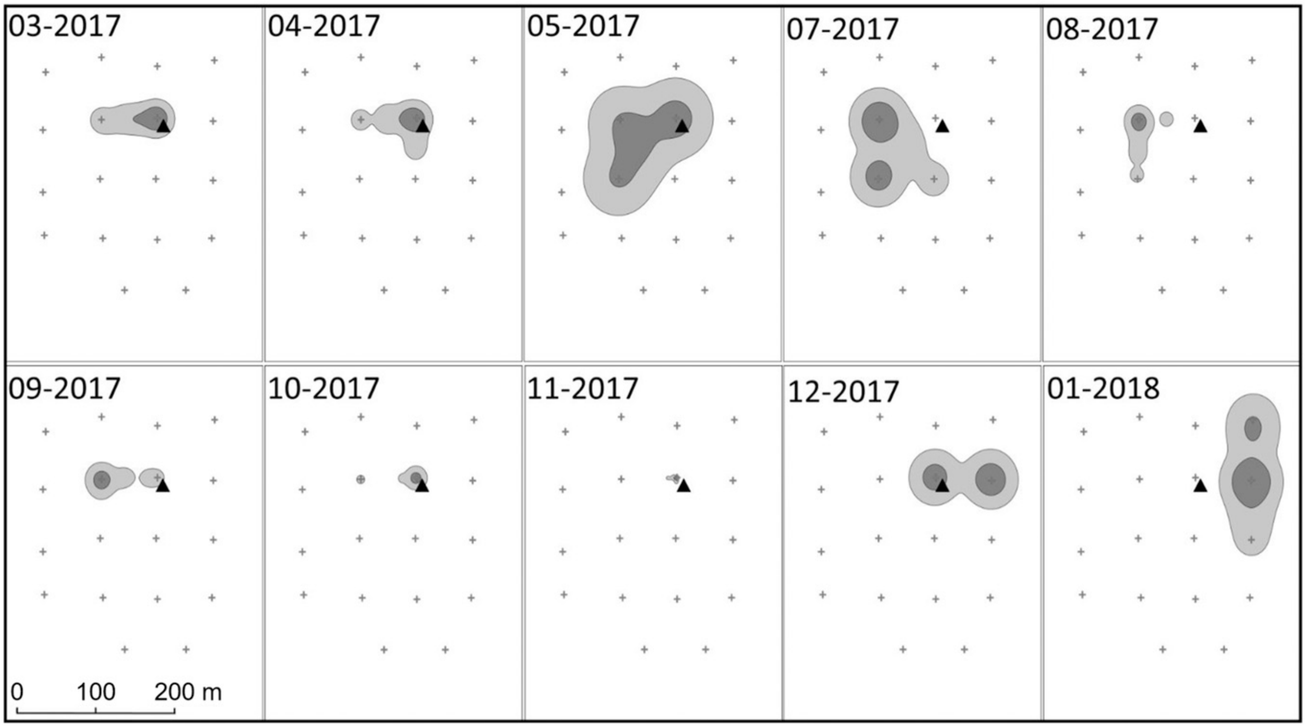

Figure 6. KUD 95% (light gray) and KUD 50% (dark gray) for a single tagged *L. lambis* (M2) calculated for each month of the study period (insufficient relocation data were collected in June 2017 and February 2018 for KUD estimation). Release location is marked with a triangle.

gigas during periods of warmer water, which also corresponds to increased reproductive activity (Stoner et al. 1992, Glazer et al. 2003). In addition to the influence of temperature on the metabolic rate, this increased spatial requirement may be due to males searching for mates and females moving to appropriate habitat to lay their egg masses (Glazer et al. 2003). It is likely that these factors are also directly or indirectly linked to *L. lambis* at CKI; however, further investigation is required to confirm this.

The median tracking duration (397 days) showed that most of the tagged *Lambis lambis* were located within the primary study area at the end of this study period, which suggests that the primary study area was at a suitable spatial scale. But the mean number of days on which a position estimate could be made (251 days) indicated that there were gaps in transmitter detections that spanned more than 24 h. Selecting the appropriate spatial scale is one of the inherent challenges of acoustic tracking study design and numerous environmental, geographical, and biological factors require consideration against logistical constraints (Heupel et al. 2006). In this study, the trade-off between acoustic overlap and the overall size of the primary study site was likely responsible for the gaps in detection rather than movement of *L. lambis* away from the site. This is reinforced by the observation of an increase in detection gaps between April and August (Fig. 2), which corresponds with the "Tradewind" season at CKI (Evans et al. 2016). Wind is known to negatively affect acoustic range (Gjelland & Hedger 2013, Huveneers et al. 2016) and was shown to be strongly negatively correlated with detection range in this study (Fig. 3). Other factors that may have negatively affected acoustic range include biological fouling of equipment and the cryptic behavior of *L. lambis* which is often found in aggregations under coral outcrops or dense *Caulerpa* mats (Bellchambers et al. 2011). These results underline the importance of increased focus on site-specific environmental factors within acoustic tracking study design and a baseline understanding of the spatial requirement of the target species (Heupel et al. 2006, Kessel et al. 2014, Reubens et al. 2019).

Despite the gaps in detection, there were still an average of 78.6 detections a day per transmitter from which to calculate center of activity using the MPE algorithm. The MPE algorithm has primarily been used to identify short-term (~30 mins) areas of activity for mobile marine species such as elasmobranchs (e.g., Heupel & Hueter 2002, Speed et al. 2011) and teleosts (e.g., March et al. 2010, Parsons et al. 2010), but there are a small number of examples of its use to successfully track benthic invertebrates such as decapods with time intervals up to 3 h (MacArthur et al. 2008, Bertelsen & Hornbeck 2009, Wiig et al. 2013). The results of this study show that the use of the MPE algorithm over a 24-h interval is suitable to broadly describe the spatial requirements of slow-moving benthic invertebrates over a large temporal scale. Moreover, this method is particularly suited to problematic marine environments where the use of more accurate triangulation methods, such as VPS, may require an array design that is not spatially or logistically feasible or cost-effective. The MPE algorithm, however, is known to bias toward higher home range calculations as the relocation data are often "pulled" toward receiver stations, which may exaggerate the actual movement of the animal (Wiig et al. 2013). For this reason, home range estimations within this study are likely to be biased high and probably overestimate the actual spatial requirement of *Lambis lambis*. Successful collection of fine-scale movement data through VPS would provide more accurate estimations of home range for *L. lambis* and may reveal short-term movement patterns for the species, especially in regard to habitat use.

The results of this study show that, in an area with adequate resources, mature *Lambis lambis* have a relatively small home range and display a degree of site fidelity. This behavioral trait, along with the tendency for *L. lambis* to aggregate in shallow water, makes this species particularly vulnerable to localized overfishing and environmental impacts such as habitat shifts or ecosystem perturbation. The maintenance of a healthy spawning stock that is able to replace itself through recruitment is critical to sustainable fishery management, and there is concern for the population of *L. lambis* at CKI (Evans et al. 2016, Konzewitsch & Evans 2019). The estimated home range within this study suggests that, for *L. lambis*, the protection of relatively small areas of breeding stock could be a viable management technique to ensure a minimum level of recruitment and combat Allee effect which has been identified as an issue with the recovery of *Lobatus gigas* populations (Stoner & Ray-Culp 2000).

This study provides a base from which to build the knowledge of movement ecology of the commercially and culturally important common spider conch *Lambis lambis*. Further study into the movement of this species at various life stages and the influence of environmental variables on movement and recruitment are important to informing decisions on the best management technique for *L. lambis* and other molluscan species that are susceptible to overexploitation.

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