



Diel movement patterns in nominally nocturnal coral reef fishes (Haemulidae and Lutjanidae): Intra vs. Interspecific variation

William P. Collins¹ · David R. Bellwood¹ · Renato A. Morais^{1,2} · Nathan J. Waltham^{3,4} · Alexandre C. Siqueira^{1,5}

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Abstract Movement of animals, habitat connectivity, and nutrient transport are key elements in the ecological functioning of coral reef ecosystems. However, most studies have focused on the diurnal component of these aspects; nocturnal patterns are less known. Our study aims to address this knowledge gap by assessing diel movement patterns in ecologically and commercially important nocturnal coral reef fishes. We evaluate 122-days of acoustic telemetry data from 4 nocturnal species in 2 coral reef fish families (Haemulidae and Lutjanidae) on the Great Barrier Reef. For all species, we found a clear division between daytime resting areas on the reef and a move towards off-reef areas at night. This was highlighted in the low number of detections at night and the high average transitions between receivers at twilight. Over our study period, average nocturnal space use area (minimum convex polygon) of *Plectorhincus gibbosus* was

328,089 m², *Plectorhincus lineatus* 28,828 m², and *Lutjanus carponotatus* 20,369 m². However, results from a Principal Component Analysis revealed that space use, and movement, varied substantially within species; for 3 of the 4 species the main axis of variation correlated with individual-level behaviour. These large differences in individual space use patterns highlight the need for caution when using species averages when considering ecosystem functions. Overall, our preliminary observations provide a glimpse into the large spatial extent, potential habitat connectivity, and intra and interspecific variation in activity patterns among large nocturnal Indo-Pacific reef fishes. This highlights their potential importance in maintaining ecosystem links between coral reefs and adjacent habitats.

Keywords Diel patterns · Intraspecific variation · Behaviour · Space use · Function · Habitat

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✉ William P. Collins
william.collins@my.jcu.edu.au

¹ Research Hub for Coral Reef Ecosystem Functions, College of Science and Engineering, James Cook University, Townsville, QLD, Australia

² CRIOBE UAR3278, Université Paris Sciences et Lettres, Perpignan, France

³ Marine Data Technology Hub, College of Science and Engineering, James Cook University, Douglas, QLD, Australia

⁴ Centre for Tropical Water and Aquatic Ecosystem Research (TropWATER), College of Science and Engineering, James Cook University, Douglas, QLD, Australia

⁵ Centre for Marine Ecosystems Research, School of Science, Edith Cowan University, Perth, WA, Australia

Introduction

Habitat connectivity and the process of nutrient transport between adjacent habitats has long been an important avenue for ecological research (Sambrook et al. 2019). This topic has been particularly important in explaining the energy dynamics of coral reef ecosystems (Robinson et al. 2023), where the vast number of organisms on reefs can outweigh the energy and nutrients produced therein. Research has shown that coral reefs are highly reliant on off-reef resources, termed pelagic or spatial subsidies (Morais and Bellwood 2019; Benkwitt et al. 2021; Skinner et al. 2021; Robinson et al. 2023). These off-reef resources are usually derived from pelagic environments; plankton transported to coral reefs by water currents, where planktivorous reef associated organisms feed on them (Hobson and Chess

1978; Morais and Bellwood 2019; Skinner et al. 2021). But these external subsidies can also be delivered by organisms actively moving between reefs and nearby habitats (Sambrook et al. 2019; Benkwitt et al. 2021; Heidmann et al. 2021; Robinson et al. 2023). Functionally, fishes on coral reefs act as conduits between adjacent habitats, facilitating the important ecological function of nutrient/energy transfer. Some of the most likely participants in this process, because of their reliable daily migration between habitats, are nocturnal fishes (Heidmann et al. 2021; Collins et al. 2023).

The regular and repeated use of daytime reef resting sites by nocturnal fishes may represent an important nutrient subsidy for coral reefs (Francis and Côté 2018; Schiettekatte et al. 2023; Van Wert et al. 2023). Coral reefs support a large diversity of nocturnally active marine fishes. This includes the Apogonidae, Haemulidae, Holocentridae, Lutjanidae, Priacanthidae, and Pempheridae (Randall et al. 1998; Holzman et al. 2007; Schmitz and Wainwright 2011; Khan et al. 2017). Additionally, other families may also include facultative nocturnal species, e.g. Siganidae (Fox and Bellwood 2011). Although they form an integral part of the ecology of coral reefs, research into nocturnal fishes has been limited. To date, most published research on nocturnal coral reef fishes has focused on nocturnal larval behaviour (e.g. Stobutzki and Bellwood 1997; Fisher and Bellwood 2003; Simpson et al. 2008), visual morphology (e.g. Cortesi et al. 2020; de Busserolles et al. 2021; Fogg et al. 2022), abundance and distribution (e.g. Lecchini 2006; Holzman et al. 2007; Harvey et al. 2012; Collins et al. 2022, 2023), or diet (e.g. Marnane and Bellwood 2002; Cocheret de la Morinière et al. 2003; Holzman and Genin 2003). Movement is typically studied in diurnal coral reef fishes (Meyer et al. 2007; Heupel et al. 2010; Welsh and Bellwood 2012, 2014; Pittman et al. 2014; Meyer 2017; Scott et al. 2019). However, in nocturnal fishes, research on movement has primarily focused on the homing ability of apogonids after artificial displacement (e.g. Marnane 2000; Gardiner and Jones 2016; Rueger et al. 2016). Our understanding of the movement patterns of larger nocturnal species is very limited, and is largely restricted to the Caribbean (e.g. Nagelkerken et al. 2000, 2008; Appeldoorn et al. 2009; Hammerschlag-Peyer and Layman 2010). Given the key role of large nocturnal fishes in linking adjacent habitats and providing energetic/nutritional resources to reefs (e.g. Marnane and Bellwood 2002; Grober-Dunsmore et al. 2007; Pittman et al. 2014; Francis and Côté 2018; Collins et al. 2022), it is important to understand their movement and space use patterns.

Compared to other nocturnal reef fish families, the diel movement patterns of the large-bodied Lutjanidae and Haemulidae have received most attention. However, despite both families being commercially important and widely distributed (in all tropical/subtropical oceans; Froese and Pauly 2023), most of the research has focused on Atlantic

species (e.g. Nagelkerken et al. 2000, 2008; Appeldoorn et al. 2009; Hammerschlag-Peyer and Layman 2010; Heidmann et al. 2021). In the Caribbean, these fishes generally reside in reef or mangrove habitats during the day, migrating at sunset to separate foraging locations, often in seagrass meadows (Nagelkerken et al. 2000; Appeldoorn et al. 2009; Hammerschlag-Peyer and Layman 2010; Currey et al. 2015). Understanding these patterns of movement and space use is essential for answering important questions related to species' ecosystem functions, energy/nutrient transfer between systems (Bellwood et al. 2019; Streit et al. 2019) and their response to anthropogenic stressors (e.g. fishing, habitat degradation, and the separation of habitats by barriers) (e.g. Grémillet and Boulinier 2009; Allen and Singh 2016).

Despite the suggested functional importance of nocturnal coral reef fishes, we still lack an understanding of the movement patterns of large nocturnal coral reef fishes in the Indo-Pacific. Do Haemulidae and Lutjanidae species make similar movements to their Caribbean counterparts? To answer this question, and to have a better grasp on the potential functional roles of these fishes, we describe the diel movement patterns of 4 commercially important, possibly nocturnal, reef fish species on the Great Barrier Reef (GBR). We analysed a 4-month acoustic telemetry dataset of Haemulidae and Lutjanidae species, breaking it down into the different periods of the day (day, twilight, night). Using this dataset, we were able to determine the magnitude of the area potentially used by these species, which is likely to include their cumulative foraging area (i.e. ecological footprint—the area over which an individual exerts an ecological effect, including feeding impacts). The results of our study provide a picture of where and when large-bodied fishes are utilising reef space, with important implications for our understanding of the extent to which these fishes may connect coral reefs with adjacent habitats.

Methods

Study location and acoustic telemetry array design

This study was originally conducted to assess the diurnal shelter use of large, site attached, fishes on the GBR (see Khan et al. 2017). This field survey was conducted from the 9th of September 2015 to the 27th of January 2016 at Lizard Island in the northern GBR (Fig. 1A) (see Khan et al. 2017). We studied the movement of individual fishes in the lagoon using acoustic transmitters and an array of passive acoustic telemetry receivers (Fig. 1). The array consisted of 16 passive acoustic receivers (Vemco VR2 W, 16 kHz) that were deployed for 5 months on the sand immediately adjacent to reefs at a depth of 1–4 m. The reef locations were chosen because most of the target species

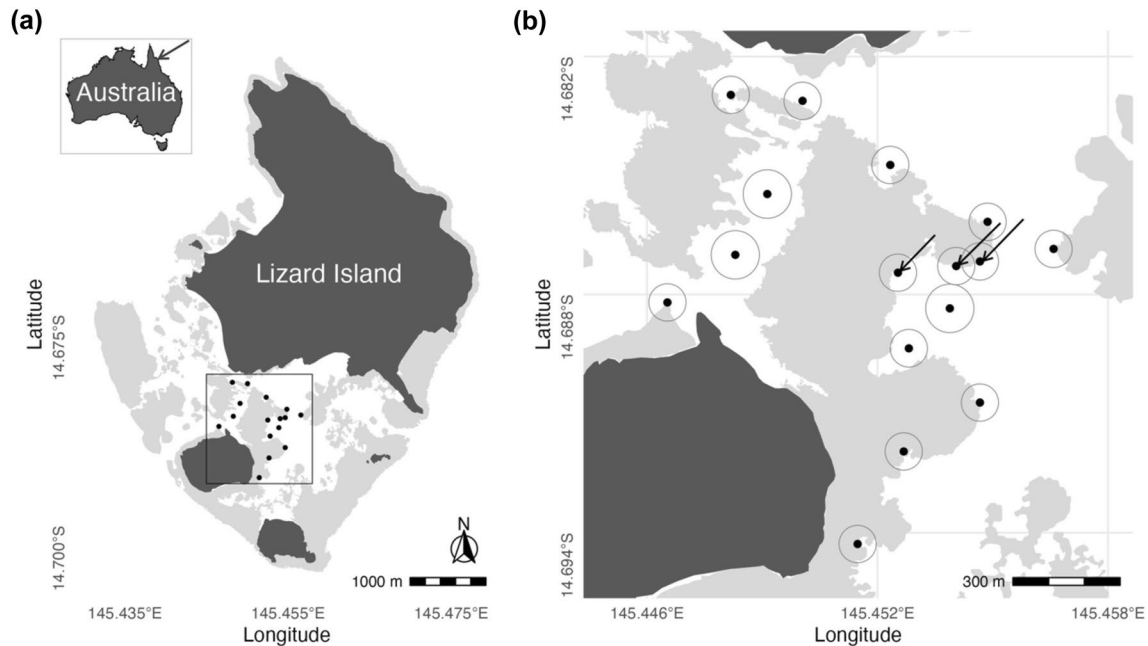


Fig. 1 **A** Location of Lizard Island in relation to Australia (black arrow; top-left) and the study site in the lagoon. Light grey shading shows the locations of coral reefs. The box with the solid line shows the location of the receiver array and the black dots represent the location of each acoustic receiver. **B** A focused view of the study

site with acoustic receiver locations (black dots), and their “working detection range” (the circle that surrounds each receiver, radius of 67.6 m for receivers on sand and 52.1 m for receivers on reef). Black arrows indicate the capture and release locations

are found along the reef edge (Kerry and Bellwood 2017; Khan et al. 2017). These locations also avoided receivers being exposed at low tides (which could happen in on-reef placements). A standard range-testing protocol was implemented in situ to assess the detection distances in the various habitat types in the array (Welsh et al. 2012). Further information about the testing protocol is provided in Supplementary material S1. The working ranges of the receivers were also tested and defined as the distance at which 50% of signal transmissions are successfully recorded. For receivers on the sand this was a mean radius of 67.6 m and for receivers on the reef 52.1 m. To understand movement and habitat use patterns of nocturnal fishes, we focused on 18 individuals from 4 focal species in 2 families (Haemulidae and Lutjanidae). Specifically, we tracked the movements of 8 individuals of *Plectorhinchus lineatus* (Total Length [TL] 370–504 mm, see Table S2), one *Plectorhinchus chaetodonoides* (TL 570 mm), 4 *Plectorhinchus gibbosus* (TL 425–500 mm), and 5 *Lutjanus carponatus* (TL 250–340 mm). These fishes were caught from 3 specific resting sites (see Fig. 1) by divers using barrier nets. These resting sites had been identified by divers prior to capture and were the most frequently used shelter sites in the study area. These locations also held the largest density of mixed-species aggregations of large reef fishes (Kerry and Bellwood 2016, 2017; Khan et al. 2017).

Acoustic transmitters and surgical procedure

After capture, fishes were transported to the Lizard Island Research Station and kept in 3600 L holding tanks. Individuals were then anaesthetised using MS-222 (tricaine methanesulfonate; 0.12 g L^{-1}), and an acoustic transmitter (Vemco V7-4x, random delay interval 190–290 s, power output 146 dB re $1 \mu\text{Pa}$ at 1 m) inserted into their peritoneal cavity through a small incision. The incision was closed with a single surgeon stitch using absorbable sutures and treated with povidone iodine antiseptic. Tagged fish were held for at least 12 h prior to release to ensure they were fully recovered. All fish were released at their capture location. Further specifics of the surgical procedure and methodology for the acoustic telemetry for this study can be found in Khan et al. (2017). All surgical procedures were conducted under ethics number #A2086. As these data were originally collected for a different project, the fish that were tagged for this study were released in February of 2015 and, for this study, the acoustic tracking began in September 2015.

Data analysis

Telemetry data were first inspected in the VUE software (Vemco, Halifax, Canada) and any spurious or false detections were removed prior to analysis following

Simpfendorfer et al. (2015). This method saw the initial removal of 2 individuals (one *L. carponotatus* and one *P. chaetodonoides*). We also removed any detections which occurred from the same individual, at 2 separate receivers within the same minute to ensure that double detections are not possible. Any individuals detected for less than 40 days (i.e. the duration between first and last detection, see Supplementary Table S2) were also removed from the study to avoid small detection durations. This caused the removal of *Lutjanus carponotatus* individual number 6 and *Plectorhinchus lineatus* individual number 6. All data processing and analysis after initial data clean-up was carried out in the R statistical software (R Core Team 2021). In order to assign each detection into a time of day (i.e. day, twilight, or night), we utilized the “getSunlightTimes” function from the “suncalc” package (Thieurmel and Elmarhraoui 2022) which uses astronomical calculations to delineate the position of the sun and other planets. We then assigned each detection to a period based on the time it occurred (for further detail see Supplementary Text S1).

The data extracted from the receivers allowed us to quantify, at an individual level, (a) the number of detections at each receiver and (b) the number of transitions between receivers. For (a), the detections were quantified as an average number of detections per hour at each receiver. For (b) Transitions represent the movement of an individual fish from one receiver to another, and were identified as consecutive detections of an individual fish between any 2 receivers. Transitions were assigned to a time period based off their destination detection. This metric provided information on the location and frequency of transitions. These metrics were then used as a proxy for movement patterns and relative space use across the receiver array.

To account for variation in the detections across time, we spilt the data into 30-day intervals (days 1–30, 31–60, 61–90, 91–120). We calculated the mean and Standard Error (SE) for detections and transitions for each individual over each period (day, twilight and night). This provided an average over 30 days and also a measure of uncertainty for each individual over the survey period. “Mean Movement Distance” was calculated by first determining the distance of each transition (conservatively assumed to be the linear distance between 2 receivers). We then grouped the data per period over the same 30-day interval and calculated mean and standard errors of the distances of transitions. This provided an average minimum movement distance and a measure of uncertainty for each individual movement distance over the course of the study. The total number of receivers visited was calculated as the number of unique receivers that an individual visited over the 122-day survey period. This metric provides an indication of how much of our survey area each individual utilized over

the survey period. Hence, individuals that utilize more of the survey area will be detected at a higher number of unique receivers than individuals that used a smaller part of the survey area. Occupancy extent was calculated for each individual over each diel period (day, twilight, and night) over the full 122-day survey period. The occupancy extent provides a proxy for how much area, within the array, an individual occupied. To do this, we calculated a minimum convex polygon (MCP) around all the receivers that an individual visited (Kraft et al. 2023) by using the “st_convex_hull” function from the sf package (Edzer Pebesma 2018). Despite only having one individual of *P. chaetodonoides*, we kept it in this analysis for comparison with the other species. The rationale for using MCP’s rather than other methods is addressed in supplemental material S1. To statistically compare the occupancy extent between species we ran a generalized linear model (GLM) using the “glmmTMB” function from the “glmmTMB” package (Brooks et al. 2017). We modelled the occupancy area (response) as a function of species and time of day (explanatory variables). The GLM used a tweedy distribution and log link function. Model suitability was tested using quantile–quantile and residual vs fitted plots. It must also be mentioned that there are specific limitations to these data. Notably, the use of these metrics does not reflect the exact movements or occupancy areas of these animals. As with all Minimum Convex Polygon (MCP) calculations, we estimate the known area that a fish could occupy; however, the exact occupancy area could be smaller or considerably larger than our estimate. This is a preliminary study that will hopefully provide a first minimum estimate and a basis for future studies to track the movement of these fishes in much greater detail.

Principle component analysis

A principal component analysis (PCA) was used to assess the relationships between each time period, species, and individual against various independent variables: the mean number and standard error (SE) of detections, the mean number and SE of transitions, mean and SE of movement distance, total number of receivers visited, and total occupancy extent. These independent variables were selected for this study as all were readily measurable for each species and were useful indicators of space use. The single *P. chaetodonoides* individual was also included in the PCA for comparison with other species. The PCA was performed on a Euclidian distance correlation matrix, and all independent variables were scaled and centred. This was conducted using the ‘rda’ function from the ‘vegan’ package (Oksanen et al. 2022).

Detection density

To test whether individuals were leaving the array at night, we compared the number of detections per receiver, per hour, at night, with a null expectation based on detections during the day. This expectation assumes that the studied species are nocturnal, are being detected by our receiver sites during the day, and move around the 2 km² study area (the area encompassing all receivers, Fig. 1B inset) at night. The null expectation of the detection density across the 2 km² area was calculated by first dividing the total day-time detections by the number of daylight hours each day, to get the detections per hour. This number was then divided by 2,000,000 m², to calculate the hourly detections per meter, which was then multiplied by the average working range of a single receiver. This resulted in the number of expected detections per hour, per receiver. The average area covered by receivers was conservatively estimated by using the working distance (where 50% of detections were recorded during the range testing, a radius of 67.6 m for the 3 receivers on sand and a radius of 52.1 m for the 13 receivers on reef). We then calculated the observed detections per receiver, per hour, at night as the total night detections divided by the number hours in each night, and then divided by the number of receivers. If the number of expected detections per receiver was equivalent or lower than the observed detections per receiver, then these fish are likely to have stayed in the 2 km² area. Contrarily, if our expected detections exceeded the observed detections, individuals were likely moving over a larger area than anticipated, beyond the receiver array. To test this statistically we used a generalised linear model (GLM) from the “stats” package from R Core Team (2021) to compare the actual and expected detections per hour (response) as a function of time and day (day vs night; explanatory variables). The GLM was fit with a Gamma and log link function. Model suitability was also tested using quantile–quantile and residual vs fitted plots. Our goal was to get a preliminary indication of the potential size of nocturnal movements, given the constraints of an array designed for other purposes. It is our hope that these results will be further evaluated using a more extensive acoustic array.

Results

Our preliminary data suggest that the number of detections across the array differ between day, twilight, and nocturnal periods, especially in the central receivers (Fig. 2A). The average number of detections was highest during the day (90.4 per hour), followed by the twilight (35.56. per hour), and night (6.5 per hour). However, there was a common pattern across diel periods, with most detections occurring

in the centre of the array and less detections occurring at the outer receivers. We found a similar trend when assessing the transitions between receivers (Fig. 2B). The highest number of transitions were found in the central receivers for all time periods. However, the transitions in the periphery of the array were rare during the day but much more common during the twilight and night. Unlike the detections, transitions were more common in the twilight period (2.19 per hour), followed by the day period (1.34 per hour) and then the night period (1.45 per hour).

Results from the GLM on detection density showed that if tagged individuals were homogeneously spread across the receiver array area (2 km²) at night, we would expect to see an average of 0.44 detections per receiver, per hour. This was not significantly different (p -value > 0.05) to our actual findings of 0.41 mean detections per receiver, per hour, at night.

To delve into the extent of transitions further, we plotted movements on an individual basis, and found high intra-specific variability over the 122-day survey period (Fig. 3; Fig. S1). For *L. carponotatus*, *P. gibbosus*, and *P. lineatus*, there were marked differences in individual movement patterns. Some individuals utilised only a small part of the array, while other individuals had extensive movement across most of the array. Interestingly, these movement and space use patterns were highly consistent within individuals, a pattern they retained over time (the 122 days) and between times of the day (day, twilight and night) (Fig. 3). It appears, visually, that the number of days that an individual was detected had little effect on the movement patterns. Some individuals were detected over a high number of days but still utilised a smaller amount of the array (e.g. *P. lineatus* #4) compared to other individuals of the same species (e.g. *P. lineatus* #9) which utilized a larger proportion of the array (Fig. 3, Fig. S2, Table S2).

By looking at the diel movement patterns in multidimensional space (PCA), we found a clear distinction between the day and twilight/night periods (with the twilight period sitting within the night period; Fig. 4A). The large day/night differences are driven mainly by the day period having a high mean number of detections, a high standard error in detections, and a low occupancy extent and number of receivers visited. On the other hand, for the night period, we found fewer mean detections but a larger occupancy area.

It is important to highlight, however, that the day/night difference is mostly represented on PC2, which explains 26% of total variance. PC1, with 51% explained variance, is mainly driven by intraspecific and, to a lesser extent, interspecific variation. Among species, *Lutjanus carponotatus* is restricted to low negative values in PC1 (Fig. 4B). *Plectorhinchus lineatus* sits mostly at the negative values of PC2 and spans the widest range in PC1 (Fig. 4B). In comparison, *Plectorhinchus gibbosus* sits mainly on the positive side of PC2 and presents a lower variation along PC1.

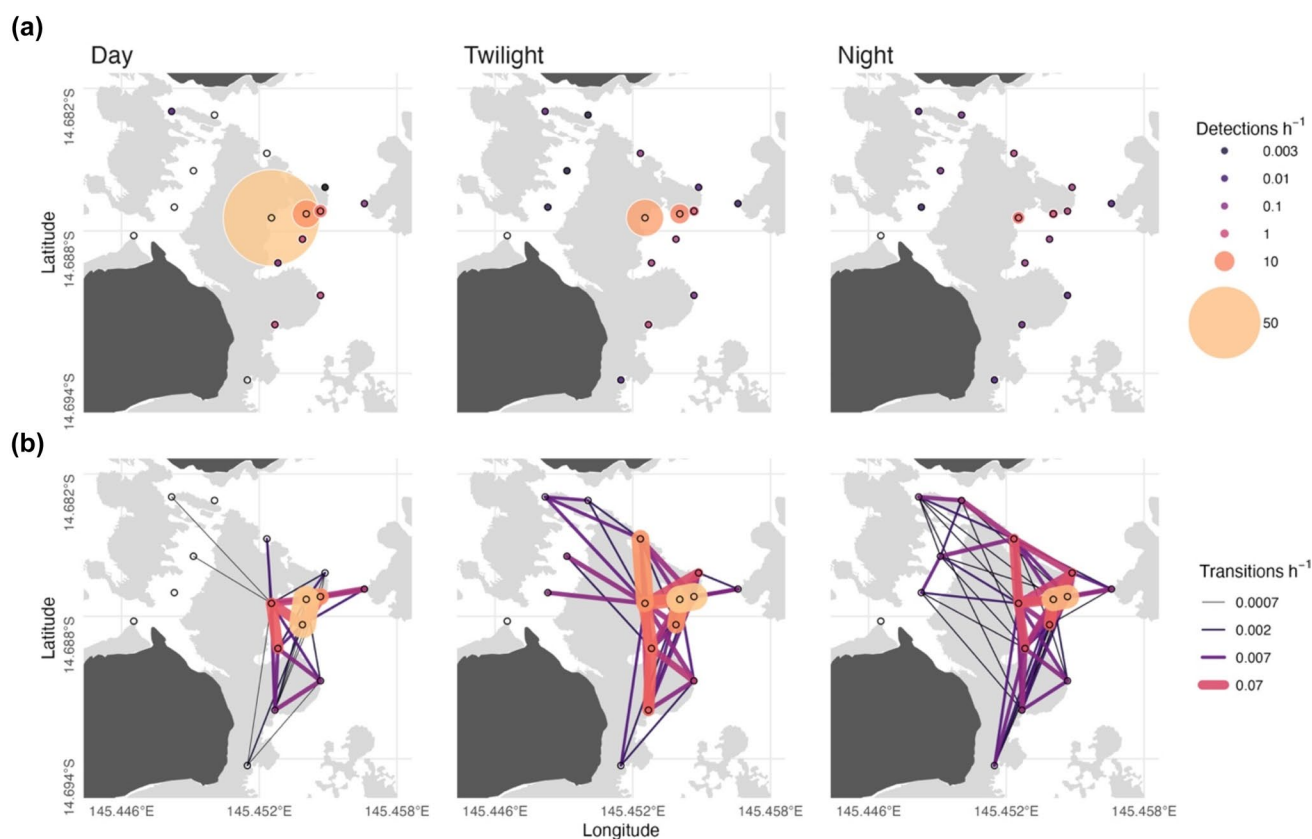


Fig. 2 Acoustic detections and transitions over the 122-day survey period, split into day, twilight and night periods. Similarly to Fig. 1, dark grey polygons indicate land and light grey polygons show the reef locations. **A** Average number of detections per hour for each acoustic receiver over the 122-day survey period. Dots represent the location of each receiver, the size and colour of the dots represent the

mean number of detections per hour. Unfilled dots represent receivers which had zero detections. **B** Average number of transitions between receivers per hour. The colour and thickness each line represent are proportional to the number of transitions. This figure includes data from *P. chaetodonoides*

Plectorhinchus chaetodonoides sits relatively central and varies mostly along PC2. Separating the different individuals within species shows that the variation along PC1 and PC2 (Fig. 4C) is driven largely by intraspecific differences. All individuals show some level of day/night difference along PC2, indicated by the shape of each triangular polygon, with lower vertices being twilight/night points and higher vertices being the day points. However, the main variation along PC1 is driven by individuals and their relationship with the mean number of transitions, the mean distance of combined transitions, and the standard error in both variables. In summary, all individuals have day-night transitions, but within-species (individual) variation in the area occupied, especially at night, can be large. This is especially notable in *P. lineatus* which drives most variation along PC1.

The interspecific variation in the PCA is also reflected in the total space use among species (Fig. 5). *Lutjanus carponotatus* used the smallest areas over the study period, occupying an area of 9418 m² (95CI: 2571–34,491 m²) during the day and 20,369 m² (95CI: 7180–57,783 m²)

during the night. This was then followed by *Plectorhinchus lineatus* which occupied a mean area of 51,887 m² (95CI: 27,578–97,623 m²) during the day and 28,828 m² (95CI: 13,660–60,838 m²) during the night. Finally, *Plectorhinchus gibbosus* had the highest occupancy areas over the 122-days, occupying an average area of 149,789 m² (95CI: 77,308–290,225 m²) during the day and 328,089 m² (95CI: 193,236–557,051 m²) during the night. However, we did not find a statistically significant difference (p -value > 0.05) between the size of day vs night occupancy areas. The only significant finding was the difference in the size of occupancy areas between species during the day.

Discussion

Utilising passive acoustic telemetry, we provide a preliminary evaluation of movement patterns of large nocturnal fishes over a 122-day study period. Average number of detections within the array per hour appear to differ between

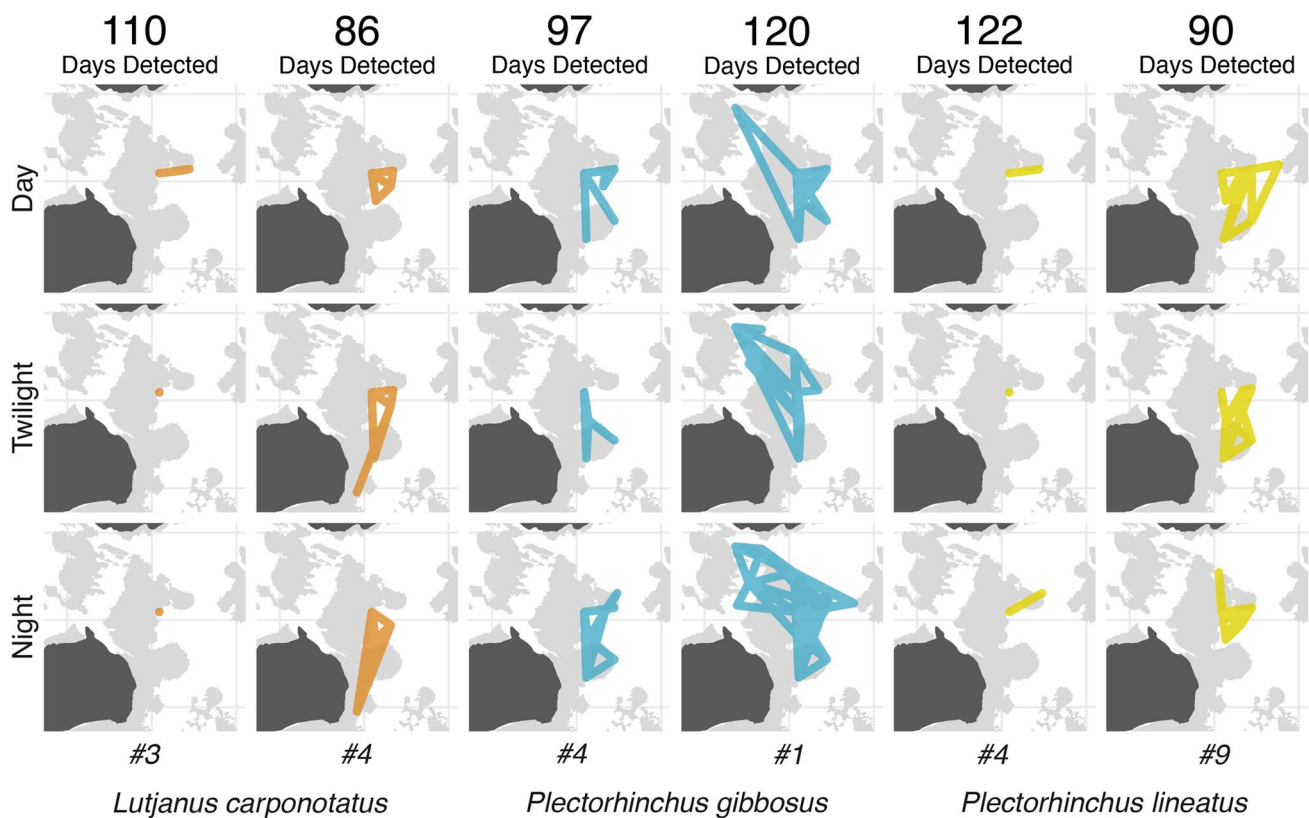


Fig. 3 Transitions between receivers for selected individual fishes across the 122-day survey period. The lines represent the transitions between acoustic receivers, dark grey polygons indicate land and light grey polygons show the reef locations. This figure displays the

2 individuals from each species that have the most contrasting movement patterns (see Fig. S1 for all individuals). The numbers above the maps show survey days that each individual was detected over the course of the study (data for all individuals are included in Table S2)

day, twilight, and night periods, with the highest detections during the day and lowest at night. However, we found more transitions between receivers at night. When looking at the movement of individuals over the 122-days, we found that there was a high level of both intra, and, especially, interspecific variation in movement patterns. For individuals, this variation in movement patterns was conserved across the diel cycle and through time: individuals that utilised a higher amount of the array area were mobile in the day and night, and remained so throughout the 122-day period.

Day, twilight, and night

Our results support previous observations (Khan et al. 2017) on the movement of the focal species tracked in this study. These fishes maintain an on-reef resting site during the day, characterised by a high number of detections on the reef, and a low number of receiver visits. They then move away from resting sites during the night, probably to forage (Nagelkerken et al. 2000, 2008; Appeldoorn et al. 2009). This is characterised in our data by the number of detections dropping substantially at night, especially in the central ‘resting

areas’ (the receivers with the highest daytime detections, as seen in Fig. 2). We also saw the highest total number of transitions per hour during twilight period and the individuals surveyed also visit a higher number of receivers at night. These results suggest movement away from resting sites, behaviour that aligns with movement patterns recorded in Lutjanidae and Haemulidae from the Caribbean (Nagelkerken et al. 2000; Beets et al. 2003; Appeldoorn et al. 2009; Currey et al. 2015; Khan et al. 2017).

The locations where individuals may be going to at night, however, remain uncertain. Previous studies from the Caribbean have reported that Lutjanidae and Haemulidae species utilise a large number of nocturnal habitats, mainly shallow seagrass beds, sandy substrata, mangroves, reef crest locations and gorgonian habits (Appeldoorn et al. 2009; Hammerschlag-Peyer and Layman 2010). Of these potential habitats, it is hard to say which ones our study individuals are utilising. The detection density results suggest that the detections per receiver, per hour, at night were not significantly different from what would be expected if the fishes that were detected during the day were moving randomly around the adjacent 2 km² array area. However, if individuals

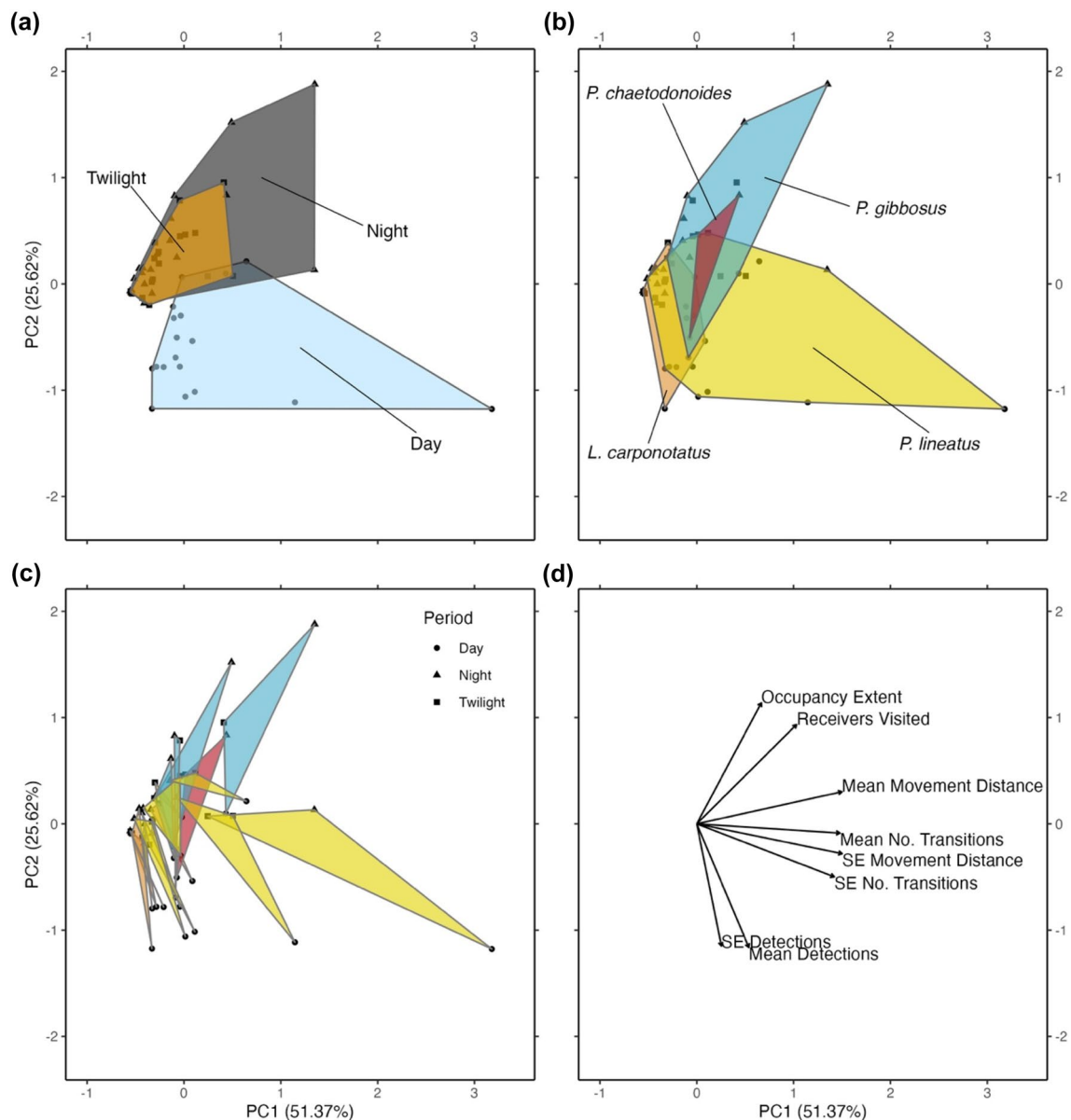


Fig. 4 Principal component analysis (PCA) calculated using multiple movement and space-use metrics from the acoustic telemetry data. The PCA and correspondent vector loadings are the same for all plots, however, the convex hulls differ to highlight various groupings.

A Hulls represent the results from each period (day, twilight, and night). **B** Hulls are grouped by each species. **C** Hulls are grouped by each individual and are coloured by species. **D** Vector loadings

were moving close to the reefs, we would have detected a higher proportion based purely on our spatial study design, where most receivers followed the reef contour. Although our expected detection per receiver hypothesis is a simplified representation (fish movement/distribution is likely to be much more patchy than a simple random distribution; Fox and Bellwood 2011; Welsh and Bellwood 2012), it is still hard to tell where these individuals could be spending most of their time during the night. Furthermore, the Lizard Island lagoonal system lacks extensive shallow water seagrass habitats or mangrove areas similar to those described

in the Caribbean (Proske and Haberle 2012; Saunders et al. 2015; York et al. 2018). The detection density results suggested that the Haemulidae and Lutjanidae individuals in the Lizard Island lagoon appear to be feeding in locations within the study area and inside the lagoon at night. Despite this, we cannot discount the potential for these fishes to be migrating out of the lagoon to feed, potentially on deeper sandy habitats or deeper seagrass/algae habitats away from the Lizard Island reef complex. It is also important to note that the prevalence of shallow intertidal areas within our array may also be influencing the movement of these fishes.

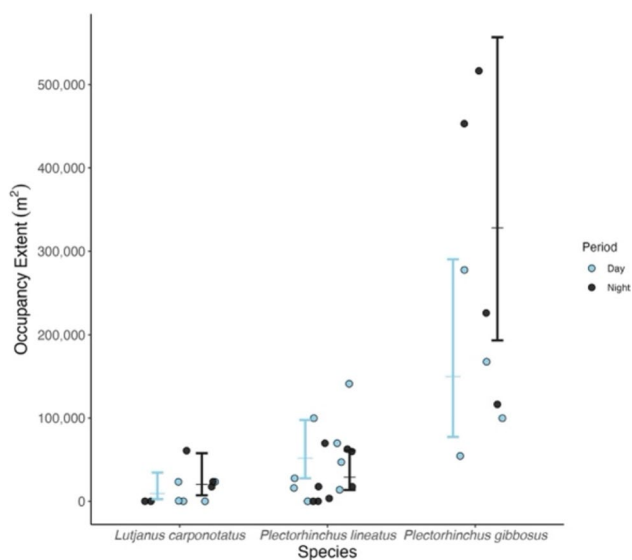


Fig. 5 Individual occupancy extent during each period, indicated by dots (day/light blue, night/dark grey), over the 122-day survey period. The error bars represent the species average and the 95% confidence intervals. These species-level error bars are presented for the day (blue), and night (black)

Although we did not have the necessary data to assess this, tidal fluctuations may reduce access to some shallow locations of the study site. In future studies, the influence of tidal variation on the movement of nocturnal fishes may be a promising avenue.

Occupancy extent and nutrient transfer

Nash et al. (2015) conducted a review examining the relationship between home range and body size in coral reef fishes, focusing exclusively on studies that calculated home ranges using minimum convex polygons. This makes their study particularly relevant for contextualizing our results. For *P. gibbosus*, the average night occupancy area (over 122 nights) was 328,089 m². This value places the average *P. gibbosus* from our study outside the 95% highest posterior density, positioning it at the upper limit of the home range to body size relationships observed in reef fishes (Nash et al. 2015; Collins et al. 2023). However, it must be noted that our array was not able to capture the true extent that these individuals were occupying at night, since these individuals could have been moving to areas outside of our receiver array. If this is the case, these results would provide a striking parallel to results recently published on nocturnal apogonids at Lizard Island which showed that apogonids were able to move distances roughly 430 times larger than expected based on their body size (Collins et al. 2023). These findings suggest that what we know about the relationship between space use and body size in coral reef fishes is likely to be

inherently biased to the diurnal way of life. There is a high likelihood that the relationship between size and space use in nocturnal fishes is completely different from their diurnal counterparts.

The repeated use of off-reef nocturnal feeding locations and on-reef diurnal resting sites are likely to be an important conduit for nutrient transfer in coral reef ecosystems on the GBR. The large body sizes and extensive ranges make this a particularly interesting areas for further study. Whilst this link has been well studied in the Caribbean, it is yet to be defined in detail for the Indo-Pacific, including the GBR (Sambrook et al. 2019).

Intraspecific variation

Our PCA emphasised the predominance of intraspecific variation in the number of transitions and the total length of transitions. Unfortunately, most studies limit exploration of individual variation by using species averages. However, it has been shown that intraspecific effects may be as important as species effects for shaping ecological processes (Des Roches et al. 2018). For fishes in particular, within-species variation is very common, especially in behaviour (Quinn and Brodeur 1991; Hammerschlag-Peyer and Layman 2010; Fox and Bellwood 2011; Winberg and Sneddon 2022; Guerra et al. 2023). Indeed, previous work from the Caribbean correlates strongly with our results. Most of these studies look at the movement distance away from the resting site and show large variation in the distances travelled by individuals (Ogden and Ehrlich 1977; Tulevech and Recksiek 1994; Beets et al. 2003; Hammerschlag-Peyer and Layman 2010). For example, one study reported *Haemulon sciurus* individuals travelling less than 20 m (15.3 times lower than the species average) while other individuals travelled up to 767 m (2.51 times higher than the species average) (Beets et al. 2003).

One individual in our study illustrates the point about differential behaviour very well. Although we could not run formal statistical analyses due to a lack of replication of individuals, compared to other individuals of the same species, *Plectorhinchus gibbosus* #1 had a much more extensive use of space (Fig. 3; Fig S1), especially around the periphery of the receiver array. Individual *P. gibbosus* #1 had a night-time area of 517,000 m², 1.57 times the species average from our study, while *P. gibbosus* #4 had a night-time area of just 116,000 m² or 2.82 times smaller than our species average. Results for *P. lineatus* were similar, but with a larger magnitude, with *P. lineatus* #9 occupying an area 5.5 times our species average and *P. lineatus* #7 occupying 7.2 times smaller areas than the species average. Similar patterns of extreme intraspecific variation in movement and space use of smaller, diurnal, coral reef fishes are also reported. For example, Streit et al (2021) found a high variability in the

weekly use of core areas of small, coral-associated damselfishes; one individual of *Chromis viridis* occupying a “maximum core area” that was double their recorded species average, and a “maximum extent” nearly triple the species average.

Management implications

Various studies have discussed the ecological importance of intraspecific variation in behaviour and movement, most commonly highlighting the importance of this mechanism for driving the colonisation of new areas, gene flow between populations, ecosystem functioning and exploiting separate resources (Des Roches et al. 2018, 2021; Shaw 2020; Winberg and Sneddon 2022). On top of these commonly discussed ecological factors, our results also highlight potential implications for fisheries management (Allen and Singh 2016; Lea et al. 2016; Mignucci et al. 2023). Fisheries management is inherently depended on space use. The permission or exclusion of fishing activities from determined areas is the most common approach (Tundi Agardy 1994; Laffoley et al. 2019). However, in our study species (families Lutjanidae and Haemulidae), daytime reef resting sites mean that we associate these fishes with reef habitats despite having very little understanding of their nocturnal foraging sites. Large foraging areas, combined with extensive intraspecific variation in space use means we may lack the information required to effectively conserve or manage these species (Grüss et al. 2011; Green et al. 2015; Weeks et al. 2017; Chung et al. 2019). Large-scale studies of within-species and cross-habitat connectivity are urgently needed to adequately assess the importance of near reef habitats. This would provide a more holistic understanding of reef functioning and allow for informed conservation and fisheries management and planning into the future.

Conclusions

Our preliminary results suggest that the nocturnal fishes *Plectorhincus gibbosus*, *Plectorhincus lineatus*, and *Lutjanus carponotatus* leave their on-reef resting locations at night, exploring large areas of the lagoon. As a result, these species likely provide an important energy and nutrient link between reef and off-reef habitats. However, the total extent of this nocturnally used area, or the locations/habitats utilised, are still unknown. We also found evidence of extensive inter- and intra-specific variability in the movement and space use patterns of these fishes. Finally, we posit that nocturnal fish movements are much larger than expected based on body size alone and that, compared to their diurnal counterparts, nocturnal fishes have very different patterns of movement and space use.

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Data Availability Data and code required to reproduce all the analyses and results will be made available in “Research Data JCU”, a public data repository hosted by James Cook University upon acceptance.

Declarations

Conflict of interest The authors declare no competing interests.

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