

Diel patterns in three-dimensional use of space by sea snakes

Udyawer *et al.*

TELEMETRY CASE REPORT

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Diel patterns in three-dimensional use of space by sea snakes

Vinay Udyawer^{1*}, Colin A Simpfendorfer¹ and Michelle R Heupel^{1,2}

Abstract

Background: The study of animal movement and use of space have traditionally focused on horizontal and vertical movements separately. However, this may limit the interpretation of results of such behaviours in a three-dimensional environment. Here we use passive acoustic telemetry to visualise and define the three-dimensional use of space by two species of sea snake [*Hydrophis (Lapemis) curtus*; and *Hydrophis elegans*] within a coastal embayment and identify changes in how they use space over a diel cycle.

Results: Monitored snakes exhibited a clear diel pattern in their use of space, with individuals displaying restricted movements at greater depths during the day, and larger movements on the surface at night. *Hydrophis curtus* generally occupied space in deep water within the bay, while *H. elegans* were restricted to mud flats in inundated inter-tidal habitats. The overlap in space used between day and night showed that individuals used different core areas; however, the extent of areas used was similar.

Conclusions: This study demonstrates that by incorporating the capacity to dive in analyses of space use by sea snakes, changes over a diel cycle can be identified. Three-dimensional use of space by sea snakes can identify spatial or temporal overlaps with anthropogenic threats (e.g. trawling, dredging) and help develop targeted management policies that mitigate any adverse effects to ensure healthy populations of sea snakes.

Keywords: *Hydrophis (Lapemis) curtus*, *Hydrophis elegans*, Kernel utilisation distribution (KUD), 3D

Background

The identification of patterns in the movements of individuals, and their relationship to ecological phenomena, have been a critical aspect in studies of terrestrial, avian, and marine organisms [1]. Traditionally, studies on the movement and use of space by animals have been represented in two dimensions (e.g. Latitude–Longitude or Easting–Northing); this, however, may not fully represent the reality of the environment that most animals occupy. Recent advances in technology and analytical techniques have allowed integration of the vertical axis into studies examining the use of space to a high degree of spatial resolution. These advances have improved our

understanding of the spatial ecology of a range of terrestrial, avian, and marine organisms [2–5].

Since aquatic animals live in a three-dimensional environment and have the ability to move in all three dimensions, their use of space is most accurately represented in the same number of dimensions. Sea snakes are a group of marine elapid snakes that spend their entire lifecycle in the marine environment and are found in a range of habitats, including coral reefs, open oceans, and coastal embayments [6]. Past studies have used mark-recapture and genetic studies to infer broad-scale movements and population connectivity between patchy reef environments over large temporal scales [7, 8].

A few attempts to understand movement and use of space by reef-associated olive sea snakes [*Aipysurus laevis*; 9, 10] and pelagic yellow-bellied sea snakes [*Hydrophis (Pelamis) platura*; 11, 12] have contributed the majority of what is currently known about these taxa. Rubinoff and colleagues [11, 12] studied the short-term

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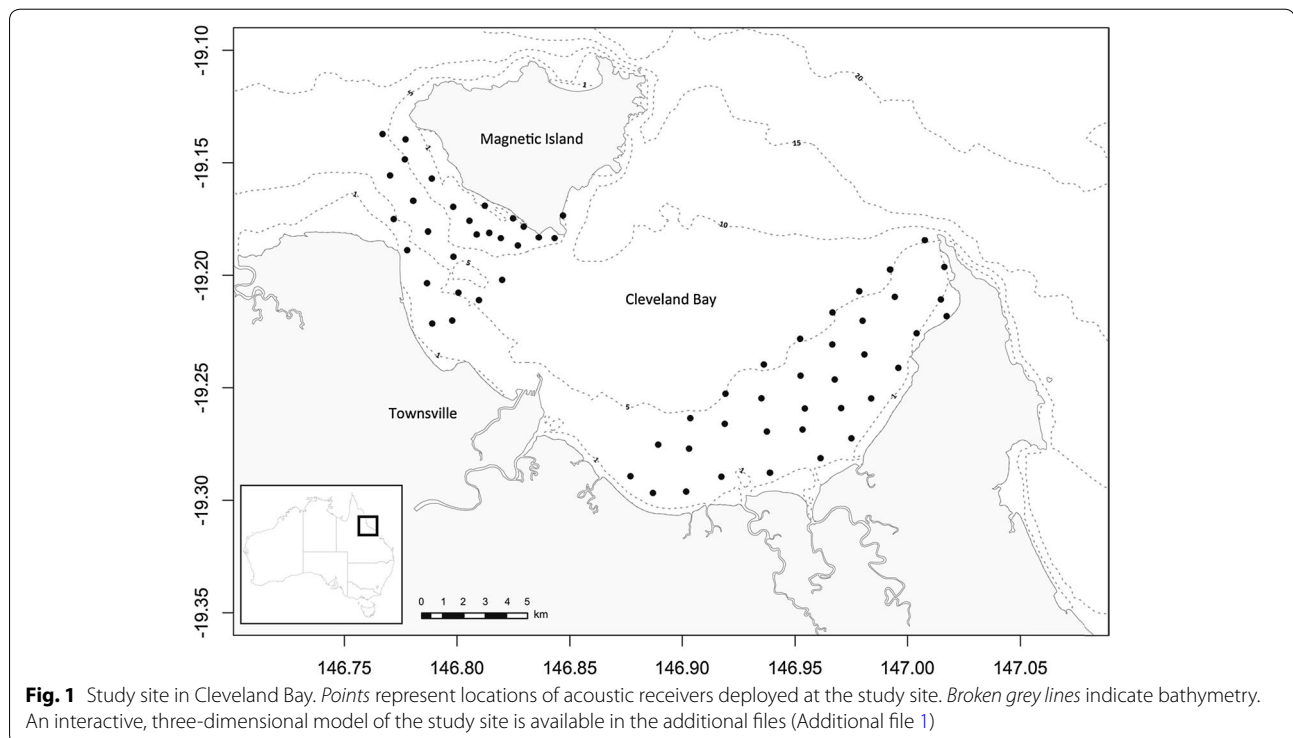
movements (3.8–31.2 h monitored) of fifteen *H. platura* tagged with depth-sensing ultrasonic tags and examined vertical and horizontal patterns of movement separately, publishing their results in two articles. The first, examined the movements of tagged snakes in the vertical axis, looking at the depths and durations of dives [11] followed by the second that focused on the horizontal movements of tagged individuals [12]. They found that despite *H. platura* being considered a surface-dwelling pelagic sea snake, tagged individuals spent the majority of the monitoring period (87%) underwater and dove as deep as 50 m. Burns and Heatwole [9] found that *A. laevis* displayed restricted movements around their home reef with small home ranges (1,500–1,800 m²) and that home ranges of all snakes ($n = 11$) overlapped with two or more individuals. Estimates of space used and overlap between monitored individuals, however, did not consider their use of depth. Studies of eel movements by Simpfendorfer et al. [2] revealed that failure to consider vertical movement can result in an overestimation of home range overlap if individuals are using the same two-dimensional location but different depths.

Currently, very little is known about how sea snake species that occupy coastal and inshore waters use space, with the majority of past studies in these habitats often focusing on abundance and diversity based on incidental capture in trawl fisheries [13, 14]. To provide information

on the movement patterns of sea snakes in a coastal system, we tracked two species of sea snake in Cleveland Bay, Queensland Australia (Fig. 1, Additional file 1, <https://dl.dropboxusercontent.com/u/31456301/3DSS/SM1/index.html>) to define three-dimensional movement patterns. The aims of this study were to: (a) use passive telemetry to understand and visualise how sea snakes use space within the water column, and (b) examine any diel patterns in the use of three-dimensional space by tagged sea snakes. Patterns in the three-dimensional use of space were also considered in the context of their potential to inform on the susceptibility of sea snakes to anthropogenic threats (e.g. trawling, dredging).

Results

Twenty-five individuals from two species of sea snake, spine-bellied sea snake (*Hydrophis curtus* previously *Lapemis curtus*: $n = 19$) and elegant sea snake (*Hydrophis elegans*: $n = 6$), were tagged within the study site and monitored between January and November 2013. The majority of monitored individuals were juvenile, which were difficult to sex using external morphological feature. Only two adult female *H. curtus* and a single adult male *H. elegans* were monitored; therefore, to avoid inaccurate conclusions related to the small sample size of reproductively mature individuals in this study, sex was excluded as a covariate in further analyses.



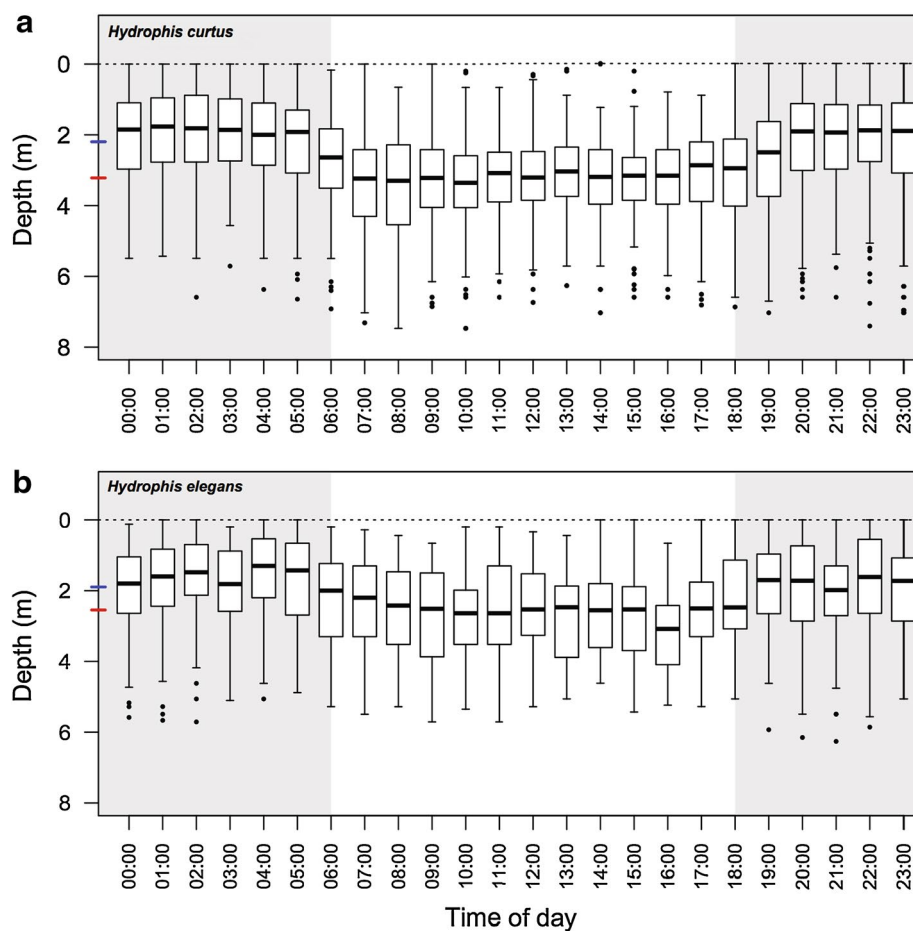
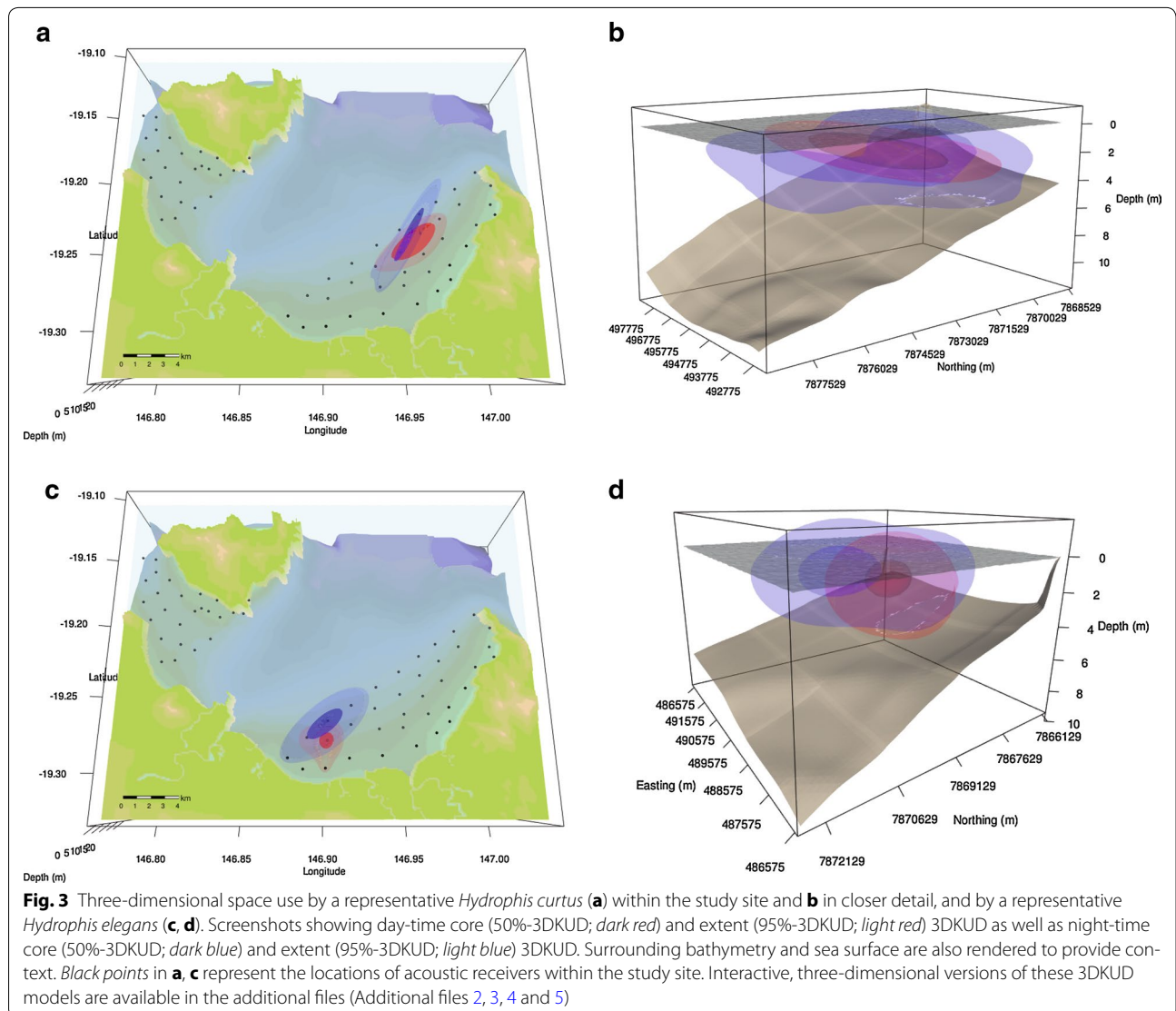


Fig. 2 Patterns in diel use of different depths by tagged **a** *Hydrophis curtus* ($n = 19$) and **b** *Hydrophis elegans* ($n = 6$) over the monitoring period. Mean depths recorded by day (red) and night (blue) are represented as ticks on the y-axis

Data from depth sensors showed that individuals from both species displayed a strong diel pattern in use of the water column (Fig. 2). Snakes were found at significantly greater depths during the day (06:00–18:00 h) and were active on the surface at night (t test, *H. curtus*: $t = 26.37$, $p < 0.05$, *H. elegans*: $t = 9.51$, $p < 0.05$). *Hydrophis curtus* displayed a more varied dive profile, diving to an average depth of 3.2 m (SE: ± 0.03 m; max depth = 7.5 m) during the day and 2.1 m (SE: ± 0.03 m; max depth = 7.4 m) at night. While, *H. elegans* generally used comparatively shallower water and dived to an average of 2.5 m (SE: ± 0.05 m; max depth = 5.7 m) during the day and 1.8 m (SE: ± 0.04 m; max depth = 6.2 m) at night. Individuals of *H. curtus* were generally present in deep water on the eastern side of Cleveland Bay (Fig. 3a, Additional file 2, <https://dl.dropboxusercontent.com/u/31456301/3DSS/SM2/index.html>), whereas *H. elegans* were restricted to shallow water directly adjacent to the southern shore (Fig. 3c, Additional file 3, <https://dl.dropboxusercontent.com/u/31456301/3DSS/SM4/index.html>).

The integration of depth data into analysis of space use showed a difference in the three-dimensional kernel utilisation distributions (3DKUD) for individuals of both species during day and night (Fig. 3b, d; Additional files 4, 5; <https://dl.dropboxusercontent.com/u/31456301/3DSS/SM3/index.html>, <https://dl.dropboxusercontent.com/u/31456301/3DSS/SM5/index.html>). Sufficient data from 12 of the 19 tagged *H. curtus*, and 5 of the 6 *H. elegans* were available to calculate reliable 3DKUDs to compare diurnal and nocturnal use of space. Despite the difference in depths occupied by individuals, generalised linear mixed models (GLMM) showed that volumes of core (50%-3DKUD) and extent (95%-3DKUD) of space used by *H. curtus* were not significantly different between day and night (50%-3DKUD: $F_{1,11} = 0.44$, $p = 0.52$; 95%-3DKUD: $F_{1,11} = 0.20$, $p = 0.66$; Fig. 4a). Similarly, the volume of 50%-3DKUD used by *H. elegans* was not significantly different between day and night ($F_{1,4} = 5.58$, $p = 0.07$); however, *H. elegans* displayed significantly



larger 95%-3DKUD volumes at night compared to the day ($F_{1,4} = 18.79, p = 0.01$; Fig. 4b).

The overlap between areas used by individuals during the day and at night showed that 50%-3DKUDs of both species had a low proportion of overlap (Fig. 4c), suggesting that despite similar volumes, there was little overlap in the core areas used. The mean proportion of overlap in 50%-3DKUDs between day and night was significantly lower than that of a random pattern for both species (t test, *H. curtus*: $t = -2.47, p = 0.02$; *H. elegans*: $t = -3.93, p = 0.02$). In contrast, 95%-3DKUDs showed a high degree of overlap between day and night (Fig. 4d). The mean proportion of overlap in 95%-3DKUD between day and night for both species was not significantly different from random (t test, *H. curtus*: $t = 1.52, p = 0.15$; *H. elegans*: $t = 0.07, p = 0.94$).

Discussion

The representation of space used by sea snakes in their natural environment requires the integration of their diving capabilities. Here we show that the use of new techniques in three-dimensional spatial analyses is appropriate when considering how sea snakes use space and facilitate detection of diel changes in movement. Previous attempts at understanding sea snake movements and their use of space by Rubinoff et al. [11, 12] and Burns and Heatwole [9] utilised ultrasonic transmitters to reveal short-term movements of the pelagic yellow-bellied sea snake, *Hydrophis (Pelamis) platura*, and the reef-associated olive sea snake, *Aipysurus laevis*, respectively. These studies were very useful in defining movement; however, as the vertical and horizontal

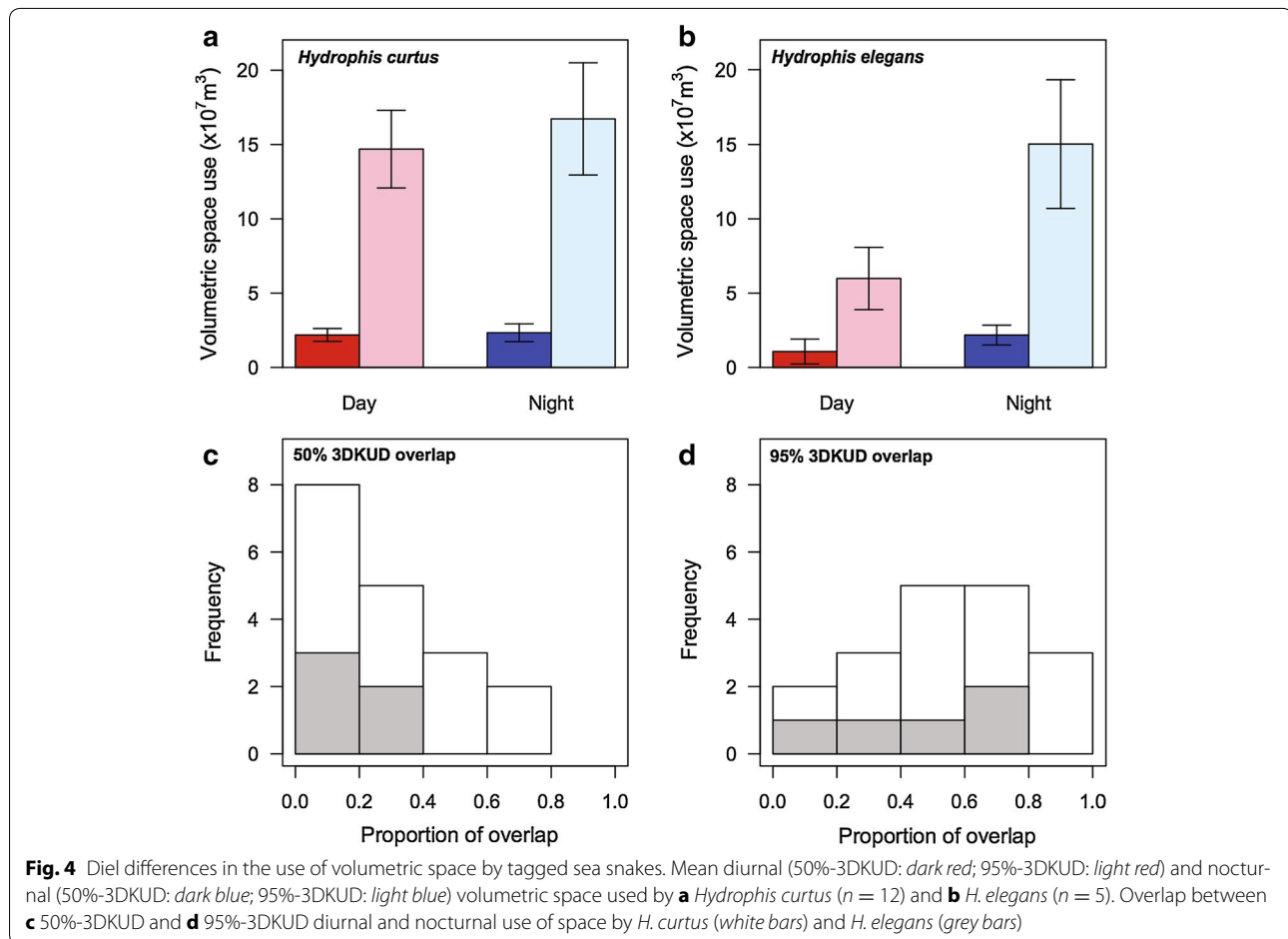


Fig. 4 Diel differences in the use of volumetric space by tagged sea snakes. Mean diurnal (50%-3DKUD: dark red; 95%-3DKUD: light red) and nocturnal (50%-3DKUD: dark blue; 95%-3DKUD: light blue) volumetric space used by **a** *Hydrophis curtus* ($n = 12$) and **b** *H. elegans* ($n = 5$). Overlap between **c** 50%-3DKUD and **d** 95%-3DKUD diurnal and nocturnal use of space by *H. curtus* (white bars) and *H. elegans* (grey bars)

patterns of movement were examined separately [e.g. 11, 12], the interpretation of the movements and use of space of these species was limited. The present study demonstrates that with the current advances in statistical analyses, the integration of vertical and horizontal axes will allow for a more accurate interpretation of the patterns of movement and of the use of space in sea snakes.

The results in the present study indicate a clear diel change in diving patterns, use of space and habitat by both species of sea snakes within Cleveland Bay. The drivers of change are potentially numerous, but one factor that most likely has an important influence on diurnal and nocturnal behaviour is the abundance and activity of prey. *Hydrophis elegans* almost exclusively prey on snake eels (Family Ophichthidae) [15, 16], which are abundant within the shallow mud-flat benthos of Cleveland Bay. This may not only restrict the use of space by *H. elegans* to mud flats close to the mouths of creeks within Cleveland Bay, but might also drive some of their movements at night. The movements and activity patterns of eels within coastal habitats are closely related to diel patterns, with greater activity and movement at night [17, 18].

Increased activity of prey species at night may explain the greater use of space by *H. elegans* at night and the low proportion of overlap between core areas between day and night. On the other hand, the diet of *H. curtus* is varied and includes a wide range of prey species [16] suggesting *H. curtus* are not restricted to a particular habitat within the bay. This may explain the larger volumes and increased overlap between spaces used between day and night. The results also indicate that different species of sea snakes likely display different patterns in diel movements and, therefore, susceptibility to natural and anthropogenic threats will vary.

One aspect of the present study that needs to be considered is that the majority of individuals that were monitored were juvenile. The few adults that were monitored displayed similar patterns of diel movements to juvenile conspecifics; however, previous studies have shown that movement patterns in adult sea snakes can vary seasonally, with increased movements displayed by males during breeding season related to mate-searching behaviours [6, 19]. This is an additional factor that needs to be considered when exploring diving and movement patterns

of sea snakes over multiple seasons. In the present study, low numbers of tagged adults and limitations in tag life restricted the ability to explore such seasonal changes in three-dimensional movement patterns related to breeding cycles. Additionally, ontogenic shifts in habitat use and diets in sea snakes during different life stages may also alter movement patterns. Presently, very little information is available on ontogenic changes in diet or habitat use in sea snakes. Further long-term studies are required to investigate if dietary preference and use of habitat changes with life stages in sea snakes, which can potentially influence how individuals move within the environment and use space.

Globally, the primary anthropogenic threat to marine reptiles is capture in coastal trawl fisheries [20]. Trawl fisheries target a range of commercially valuable species (e.g. *Penaeus esculentus*, *Penaeus longistylus*, *Amusium ballotti*) that are fished during different times of the year and at different times of the day [21]. The diel patterns observed in the present study, with increased space used in the water column at night suggest that these species of sea snakes have an elevated susceptibility to nocturnal trawling activity; however, this may vary for other species and differ among life stages. In Australia, bycatch in the trawl fishery is effectively managed by mandatory use of bycatch-reduction devices (BRD) as well as spatial and temporal restrictions to fishing. The combination of BRDs and fishing restrictions has been shown to be effective in reducing landings of sea snakes in Australia [22]. These management practices, however, may not be practical or enforceable in other parts of the world where coastal fisheries overlap with sea snake populations. Monitoring the movements of sea snakes and understanding how they use space within heavily trawled areas can help identify areas of spatial or temporal overlap that can be more effectively mitigated using targeted management policy.

Conclusions

Here we applied three-dimensional kernel utilisation distribution analyses to understand how sea snakes use space in their natural environment. This study also demonstrated that such analyses allow examination of changes in how individuals move and behave over a diel timescale and identify potential drivers that cause these changes. Abundance and activity patterns in preferred prey of *H. curtus* and *H. elegans* may explain the differential diurnal and nocturnal use of space by these two species. Finally, understanding how sea snakes use space within their three-dimensional environment can also help identify spatial and temporal overlaps with anthropogenic threats (e.g. trawling, dredging) and allows managers to develop targeted policy designed to mitigate any

adverse effects to vulnerable populations of sea snakes. Inclusion of the vertical axis (i.e. depth, altitude, height) in the visualisation and analysis of spatial data clearly enhances our understanding of how animals occupy space and move, and may ultimately allow for more accurate assessment of their susceptibility to threats. Similar techniques can greatly benefit future studies on the spatial ecology of aquatic, aerial and arboreal animals in their natural habitat and refine their susceptibility to natural and anthropogenic threats that operate in the same three-dimensional environment.

Methods

Field methods

This study was conducted in Cleveland Bay (19.20°S, 146.92°E), on the northeastern coast of Queensland, Australia (Fig. 1). Cleveland Bay is a shallow coastal bay (<10 m deep) that covers an area of approximately 225 km² with the western and southern margins bounded by the mainland and Cape Cleveland, respectively, and a large continental island, Magnetic Island, to the north of the bay (Fig. 1). The majority of the bay has soft sediment substrates with extensive seagrass meadows, with the exception of a fringing reef system on the lee of Magnetic Island. Multiple tidal creeks with mud-flat and mangrove habitats line the southern shore and provide the majority of freshwater input.

Spine-bellied sea snakes (*Hydrophis curtus*; previously *Lapemis curtus*) and elegant sea snakes (*Hydrophis elegans*) were located at night and captured from the surface of the water using dip nets. Once captured, the maturity of each individual was recorded as either juvenile or adult, with the sex of adults determined using external morphological features (by investigating hemipenal bulges or exposing the hemipenes). The determination of sex in juvenile individuals was unreliable using external morphological features; therefore, the sex of juveniles was not considered in the present study. Snout-vent length (SVL) and mass of each captured snake were recorded, and each individual was fitted with a passive integrated transponder (PIT) tag for future identification. Individuals in good condition and exceeding the minimum weight (>300 g) to carry a transmitter were surgically implanted with acoustic transmitters with depth sensors (V9P-2H, Vemco Ltd.). Transmitters were small (diameter 9 mm, length 29 mm, weight 2.9 g) and less than 1% of the body weight of the individuals tagged (mean \pm SE; $0.91 \pm 0.11\%$) to avoid any deleterious effects. The methods of implanting tags were similar to those of Pratt et al. [23]. In general, a local anaesthetic (Xylocaine[®]; lignocaine) was administered at the site of implantation, a small ventro-lateral incision (ca. 2 cm) made approximately 4–5 cm anterior to the cloaca and

the transmitter inserted into the peritoneal cavity, after which the incision was closed using surgical sutures. Individuals were allowed 30–40 min to recover from the anaesthetic before being released at their location of capture. Transmitters were uniquely coded for each individual, transmitted measurements of depth at 69 kHz, and had a battery life of approximately 215 days. An array of 63 VR2W acoustic receivers (Vemco Ltd.) was used to passively monitor the movements of tagged sea snakes within Cleveland Bay (Fig. 1). Range tests using sentinel tags indicated receivers had a maximum detection range of 525 m (unpublished data, M. Heupel). Data from the acoustic receiver array were downloaded every 3–4 months.

Data analysis

Raw data were first standardised for temporal variation in detections through a position-averaging algorithm that computed an individual's centre of activity at 30-min intervals [24]. The volume of space used by tagged individuals was examined by calculating three-dimensional kernel utilisation distributions (3DKUD) for both species in the *R* environment [25] using the 'ks' package [26] and rendered using the 'rgl' and 'misc3d' packages [27, 28]. Calculations of 3DKUD and estimation of volume of core space (50% contour; 50%-3DKUD) and the extent of space (95% contour; 95%-3DKUD) used by tagged individuals were conducted using code adapted from Simpfendorfer et al. [2] and Cooper et al. [4]. Interactive plots of diel patterns in 3DKUD (Fig. 3) were rendered using the 'brainR' package in *R* and code adapted from Muschelli et al. [29]. The proportion of overlap in the space used between day and night was also calculated for 50%-3DKUD and 95%-3DKUD for both species using *R* code from Simpfendorfer et al. [2].

Estimations of volume of 50%-3DKUD and 95%-3DKUD were log-transformed prior to statistical analyses. The differences in the volume of space used between day and night were compared using generalised linear mixed models (GLMM) with individuals' ID treated as a random factor within each model ($\sim 1|ID$) to account for variability between individuals and the repeated measures nature of the data. Additionally, *t* tests ($\alpha = 0.05$) were conducted to examine whether the mean proportion of overlap between areas used during the day and at night (both 50%-3DKUD and 95%-3DKUD) varied from that expected if there were no pattern in proportions of overlap (i.e. mean proportion = 0.5). The data for proportional overlap of the occupied space were arcsine-transformed prior to analysis. All statistical analyses and plotting were conducted in the *R* statistical environment [25].

Additional files

Additional file 1: Three-dimensional model of study site in Cleveland Bay (Fig. 1). Black points represent locations of acoustic receivers. Depth has been exaggerated for ease of viewing bathymetry. Sea surface represented at highest astronomical tide at Townsville Port. For the interactive version of this data please visit <https://dl.dropboxusercontent.com/u/31456301/3DSS/SM1/index.html>

Additional file 2: Three-dimensional space use by a representative *Hydrophis curtus* within the study site (Fig. 3a). Day-time core (50%-3DKUD; dark red) and extent (95%-3DKUD; light red) 3DKUD as well as night-time core (50%-3DKUD; dark blue) and extent (95%-3DKUD; light blue) 3DKUD are represented. Surrounding bathymetry and sea surface are also rendered to provide context. Black points represent the locations of acoustic receivers within the study site. For the interactive version of this data please visit <https://dl.dropboxusercontent.com/u/31456301/3DSS/SM2/index.html>. Close up version of this model is available in Additional file 4.

Additional file 3: Three-dimensional space use by a representative *Hydrophis elegans* within the study site (Fig. 3c). Day-time core (50%-3DKUD; dark red) and extent (95%-3DKUD; light red) 3DKUD as well as night-time core (50%-3DKUD; dark blue) and extent (95%-3DKUD; light blue) 3DKUD are represented. Surrounding bathymetry and sea surface are also rendered to provide context. Black points represent the locations of acoustic receivers within the study site. For the interactive version of this data please visit <https://dl.dropboxusercontent.com/u/31456301/3DSS/SM4/index.html>. Close up version of this model is available in Additional file 5.

Additional file 4: Close up three-dimensional model of diel pattern in space use of a representative *Hydrophis curtus* within Cleveland Bay (Fig. 3b). Day-time core (50%-3DKUD; dark red) and extent (95%-3DKUD; light red) 3DKUD as well as night-time core (50%-3DKUD; dark blue) and extent (95%-3DKUD; light blue) 3DKUD are represented. Depth has been exaggerated for ease of viewing bathymetry. Sea surface represented at highest astronomical tide at Townsville Port. For the interactive version of this data please visit <https://dl.dropboxusercontent.com/u/31456301/3DSS/SM3/index.html>. Overall version of this model is available in Additional file 2.

Additional file 5: Close up three-dimensional model of diel pattern in space use of a representative *Hydrophis elegans* within Cleveland Bay (Fig. 3d). Day-time core (50%-3DKUD; dark red) and extent (95%-3DKUD; light red) 3DKUD as well as night-time core (50%-3DKUD; dark blue) and extent (95%-3DKUD; light blue) 3DKUD are represented. Depth has been exaggerated for ease of viewing bathymetry. Sea surface represented at highest astronomical tide at Townsville Port. For the interactive version of this data please visit <https://dl.dropboxusercontent.com/u/31456301/3DSS/SM5/index.html>. Overall version of this model is available in Additional file 4.

Abbreviations

3DKUD: three-dimensional kernel utilisation distribution; 50%-3DKUD: the core three-dimensional home range, 50% contour of the three-dimensional kernel utilisation distribution; 95%-3DKUD: the extent of the three-dimensional home range, 95% contour of the three-dimensional kernel utilisation distribution; GLMM: generalised linear mixed models.

Authors' contributions

VU: designed the study, conducted fieldwork, analysed data, drafted the manuscript and created the figures and graphics; CAS: designed the study, provided materials and field resources, assisted in analyses and drafting of the manuscript; MRH: designed the study, provided materials and field resources, assisted in analyses and drafting of the manuscript. All authors read and approved the final manuscript.

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Compliance with ethical guidelines**Competing interests**

The authors declare that they have no competing interests.

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