

Exploring habitat selection in sea snakes using passive acoustic monitoring and Bayesian hierarchical models

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ABSTRACT: Resource selection studies often use analytical techniques that provide information at either a population or an individual level. We applied a Bayesian hierarchical model that simultaneously estimates population- and individual-level habitat selection to explore how varying levels of dietary specialisation affect resource requirements of 2 species of sea snakes that occupy the same coastal environment. We used passive acoustic telemetry to monitor the movements of the 2 species — a dietary generalist, *Hydrophis (Lapemis) curtus*, and a dietary specialist, *H. elegans* — and investigated how individuals select habitats based on habitat type, depth and proximity to sources of freshwater within a nearshore environment. Composition of diets in both species was also assessed using regurgitated material from captured individuals. Selection of habitats by the 2 species differed, with *H. elegans* displaying an affinity for mudflat and seagrass habitats <4 km from sources of freshwater and depths <3 m. *H. curtus* selected for slightly deeper seagrass habitats (1–4 m) further from freshwater sources (2–5 km). Data from regurgitated material showed that the diet of *H. curtus* comprised at least 4 families of fish and displayed some level of intraspecific predation, whereas *H. elegans* preyed solely on eels. Both species predominantly selected seagrass areas, indicating that these habitats provide key resources for sea snakes within nearshore environments. The results illustrated the utility of Bayesian hierarchical models when analysing passive acoustic monitoring data to provide population-level habitat selection metrics and incorporate individual-level variability in selection, both of which are necessary to inform targeted management and conservation practices.

KEY WORDS: Acoustic telemetry · Coastal habitat · *Hydrophis (Lapemis) curtus* · *Hydrophis elegans* · Resource selection · Dietary specialisation

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INTRODUCTION

Understanding the habitat selection patterns of animals is important when identifying long-term resource requirements, assessing impacts of habitat change or examining resource partitioning between competing species within an ecosystem (Thomas & Taylor 1990, Alldredge & Griswold 2006, Johnson et al. 2008). How individuals select habitats is often

measured by comparing the relative use of habitats to their overall availability (e.g. selection ratios, chi-squared statistic), and when habitats are used disproportionately to their availability, individuals are said to be selective (Rogers & White 2007). How individuals use particular habitats is often quantified in several different ways, e.g. using presence/absence within categorical habitat types (e.g. Liu et al. 2012, Davy et al. 2015), measuring the amount of time indi-

viduals spend within habitats (e.g. Benhamou 2011, Benhamou & Riotte-Lambert 2012), or overlapping metrics of home range with habitat coverage (e.g. Bond et al. 2002, Millspaugh et al. 2006). The relative use of a particular habitat is most often measured by observing the movements of several individuals of a population using various methods (e.g. mark-recapture, trapping, radio-telemetry, GPS tracking). In aquatic systems, the use of passive acoustic telemetry has proven an effective method to monitor long-term movement patterns of aquatic animals and has been used as the basis for habitat selection studies (Cooke et al. 2004, Donaldson et al. 2014).

Habitat selection study designs can vary depending on several factors. These factors include whether habitat use data is collected on individual animals or at a population level, the scale at which such selection is assessed and how habitat use and availability is defined and measured (Thomas & Taylor 1990, 2006, Erickson et al. 2001). Thomas & Taylor (1990) categorised 3 study designs from a review of past habitat selection studies which were based on how attributes of habitat use, availability and scale were measured. Design 1 studies calculate habitat selection by measuring habitat use on a population level, where individual animals are not identified and individual-level selection is not possible (e.g. aerial surveys). In this design, habitat availability is also measured over the study area at a population level. Design 2 studies measure habitat use by individual animals; however, the availability of habitat is measured only at the population level. This design is the most commonly used in telemetry-based studies, including passive acoustic monitoring work (Manly et al. 2007), where habitat use of individual animals is monitored and habitat availability is defined over the scale of the study site. Design 3 studies measure both habitat use and habitat availability for each individual in the study. This design often assesses habitat availability by only including habitat types present within individuals' home ranges (i.e. defined by minimum convex polygons or kernel utilisation distributions).

In addition to the 3 categories of habitat selection studies, Erickson et al. (2001) proposed a 4th design in which habitat use is measured multiple times, and habitat availability is measured for each use location. Typically, habitat availability in these studies is measured within a defined moving window around each animal location and requires semi-continuous movement tracks of individuals (e.g. Apps et al. 2001). Habitat availability in this study design is also often defined based on *a priori* knowledge of habitat use characteristics of the studied species (Thomas

& Taylor 2006). The design of habitat use studies affects the statistical analyses used to assess habitat selection and the associated error in the final estimates (see Thomas & Taylor 2006, Manly et al. 2007). The choice of design also affects the cost of the habitat selection study, where studies that use Design 1 are often relatively cheaper than designs that involve the capture and monitoring of individuals using labour-intensive techniques or expensive monitoring equipment and infrastructure (e.g. GPS tracking, acoustic telemetry). However, increased individual-level data can provide habitat selection information at a higher resolution which can be used to compare between species or over long temporal scales (Rogers & White 2007).

The present study adapts Bayesian analytical techniques developed by Thomas et al. (2006) for Design 2 type studies using GPS monitoring data and applies this to passive acoustic monitoring data to scale habitat selection from the individual to the population level using 2 species of true sea snakes as case studies. True sea snakes are marine elapid snakes (Elapidae, Hydrophiinae) commonly found in shallow tropical and subtropical habitats throughout the Indo-West Pacific region (Heatwole 1999). They are frequently encountered in nearshore habitats, with previous reports indicating that coastal and estuarine areas act as important habitats for feeding (Ineich & Laboute 2002), shelter (Bonnet et al. 2009, Liu et al. 2012), predator avoidance (Kerford et al. 2008, Wirsing & Heithaus 2009) and as potential mating and nursery grounds (Voris & Jayne 1979, Stuebing & Voris 1990). Different species of sea snakes have varying levels of dietary specialisation and are often associated with specific habitat types (Glodek & Voris 1982).

The present study focused on 2 species of sea snake that are abundant within coastal environments: spine-bellied sea snakes *Hydrophis curtus* (previously *Lapemis curtus*) and elegant sea snakes *H. elegans*. *H. curtus* are generalist feeders that are known to feed on a wide range of fish species in coastal and pelagic environments (Voris & Voris 1983, Lobo et al. 2005), whereas *H. elegans* are eel specialists that target prey in shallow, mudflat environments (Voris & Voris 1983, Kerford 2005). We hypothesised that since these 2 species have varying levels of dietary specialisation and target prey in different habitats within coastal environments, their habitat requirements and selection would be different, on both an individual and a population level. The present study used passive acoustic telemetry to monitor the movements of the 2 species in a tropical

embayment and aimed to explore how sea snakes select habitats within this system based on type of habitat, depth of habitat and proximity to sources of freshwater. These factors were chosen to explore how differential dietary specialisation may influence selection of habitats based on availability of prey, physiological constraints to diving and osmoregulation. Dietary composition was also examined using opportunistically collected regurgitated material from captured individuals to confirm the degree of dietary specialisation in both species within the study area. Findings of the study were also considered in the context of the potential of this analytical methodology to inform future management policy of sea snakes in nearshore environments.

MATERIALS AND METHODS

Study site

This study was conducted in Cleveland Bay (19.20° S, 146.92° E), on the northeast coast of Queensland, Australia (Fig. 1). Cleveland Bay is a shallow coastal

bay (<10 m deep), which covers an area of approximately 225 km² and consists of multiple habitat types including extensive seagrass meadows, small patches of coral reef, sand and mud flats. Several sources of freshwater enter the bay from the southern end and provide the majority of freshwater input. An array of 63 VR2 and VR2W acoustic receivers ('station'; Vemco) was used to passively monitor movements of tagged sea snakes. Sentinel-tag range testing indicated that stations had a maximum detection range of 525 m with no overlap between stations (M. R. Heupel unpubl. data). Receivers were suspended mid-water column and anchored at fixed locations within the study site (Fig. 1). The acoustic array covered the eastern and western sections of the bay that corresponded to Conservation Park zones within the Great Barrier Reef Marine Park (Fig. 1). The area between the 2 monitored sections was part of the Townsville Port, which is exposed to heavy boat traffic, seasonal trawling and dredging; therefore, placing receivers in that area was not possible. However, monitored individuals have been detected on either side of the Townsville port area (Udyawer et al. 2015a,b).

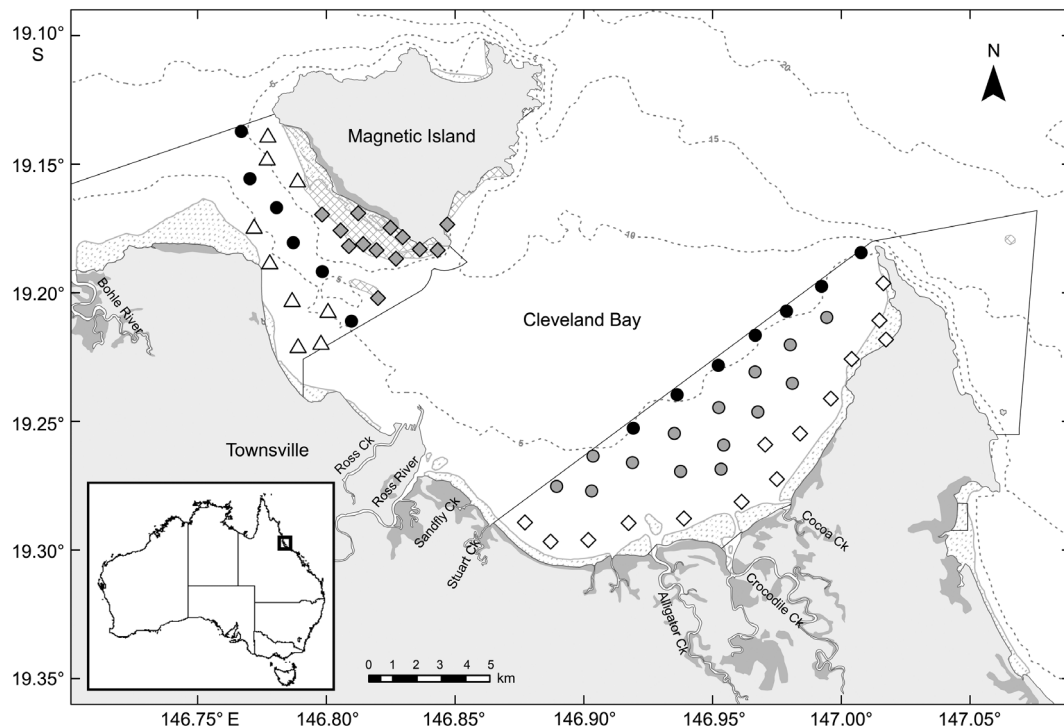


Fig. 1. Cleveland Bay (inset: Australia, with study area marked by □). Points represent locations of acoustic receiver stations deployed on the east and western side of Cleveland Bay divided by a port area. The major habitat types are represented at each station: deep mud substrate (HT1, ●), intertidal mudflat (HT2, ◆), fringing reef (HT3, ◇), inshore sandy substrate (HT4, △) and seagrass meadows (HT5, ○). Broken grey lines indicate bathymetry and solid lines are boundaries of Conservation Park zones. Cross-hatching indicates fringing reefs, grey stippled areas indicate intertidal mudflats and dark grey areas along the coast indicate mangrove habitats. Note rivers serving as sources of freshwater in the southeast of the bay. Ck = creek

Field methods

Two species of sea snake (spine-bellied sea snake *Hydrophis curtus* and elegant sea snake *H. elegans*) were targeted for this study. Sea snakes were located after dark and captured off the surface using dip nets. Once captured, the snout–vent length (SVL) and mass were recorded and each individual was fitted with a passive integrated transponder (PIT) tag for future identification. Individuals in good body condition and with an appropriate weight (>300 g) were surgically implanted with depth-sensitive acoustic transmitters (V9P-2H, Vemco). Transmitters were small (diameter: 9 mm, length: 29 mm, weight: 2.9 g) and <1% of the body weight of the individuals tracked (mean \pm SE, $0.91 \pm 0.11\%$) to avoid any deleterious effects of transmitter implantation. The method of implanting tags was similar to that used by Pratt et al. (2010). In summary, a local anaesthetic (Xylocaine[®], lignocaine) was administered at the site of implantation. A small ventro-lateral incision (ca. 2 cm) was made approximately 2–3 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 on board before being released in good condition at the 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 d.

Habitat selection

Selection of different habitats within the acoustic array by both sea snake species was examined using an adapted version of the Bayesian random-effects discrete-choice model previously formulated by Thomas et al. (2006). The model examined how tagged individuals selected habitats based on relocations from passive acoustic telemetry on a population level and individual level, incorporating individual as a random effect.

Raw detection data from each station in the array was first standardised to hourly detections for each individual to account for temporal variation in detections and for individuals that had a tendency to be detected at the same station. The monitoring period was divided into hourly time periods, and an individual was considered present at the station with the highest proportion of detections for that hour. The model used hourly presence of individuals alongside attributes of habitat at each station (Fig. 1) to investi-

gate habitat selection at a population as well as individual level. Three habitat attributes of each station were considered: (1) proximity to the closest source of freshwater (creeks or rivers; pFW); (2) depth standardised to highest astronomical tide (depths at king high tide; hDep); and (3) 5 categorical habitat types determined from their location in the bay and the habitat at the point of anchorage of each station—deep mud substrate (deep, HT1), intertidal mudflat (mudflat, HT2), fringing reef (reef, HT3), inshore sandy substrate (sand, HT4) and seagrass meadows (seagrass, HT5; Fig. 1).

The model contained 3 components, a data (likelihood) model, a parameter model and a hyperparameter model. The data model calculated the probability (p) of use of each station (s) by individual (i) and was assessed using a model formulated by Thomas et al. (2006) and similar to McDonald et al. (2006) and Thomas et al. (2004):

$$P_i(s) = \frac{e^{x(s)\beta_i} a_i(s)}{\sum_{r \in S} e^{x(r)\beta_i} a_i(s)} \quad (1)$$

where s (1, 2, 3, ..., 63) is a station, $x(s)$ is a k -dimensional vector of attributes for each station s (e.g. pFW, hDep, HT1–5), $a_i(s)$ is the relative availability of station s to individual i , and β_i ($\beta_{i1}, \beta_{i2}, \dots, \beta_{ik}$) is a k -dimensional vector of parameters for individual i . In the present study, individuals moved freely between both sides of the monitored area, and all stations were equally available to all tagged sea snakes; therefore $a_i(s) = 1/63$, which reduced the model to a discrete-choice model:

$$P_i(s) = \frac{e^{x(s)\beta_i}}{\sum_{r \in S} e^{x(r)\beta_i}} \quad (2)$$

Variation in habitat use was explored both within populations and between individuals using these models. For this, subsets of tagged individuals were chosen using a selection model that was included within the parameter model. The parameter model was formulated as:

$$\beta_{il} \sim \text{Normal}(\beta_l^*, \sigma_l^2) \quad (3)$$

where $l = 1, 2, \dots, k$ using hyperparameters of β_l^* and σ_l^2 . Fitted models yielded estimated posterior distributions and Bayes estimates (means of posterior distributions) for population-level habitat selection (β_l^*), individual selection parameters (β_{il}) and the variability in habitat selection among tagged individuals for each covariate (σ_l^2 ; Thomas et al. 2006). The discrete-choice model allowed modelling of the probability of use for each station s characterised by associated habitat attributes (i.e. pFW, hDep, HT1–5) by each

tagged individual i and allowed exploration of the variability in habitat selection among individuals.

Uninformative prior distributions were chosen for the hyperparameters characterising the limited information available about the values of these parameters and were formulated as:

$$\beta_i^* \sim \text{Normal}(0,0.01) \quad (4a)$$

$$\sigma_i^2 \sim 1/\text{Gamma}(0.01,0.01) \quad (4b)$$

Model construction and selection

Bayesian models were fitted using JAGS (version 3.4.0; Plummer 2003) within the R statistical environment (R Development Core Team 2014) using the R2jags package (Su & Yajima 2014). Posterior distributions were built using 3 Markov chains with 10 000 iterations per chain, with the first 1000 used as a burn-in for parameter convergence, and a thinning interval of 10. The R2jags package was also used for model selection, determining the values of deviance information criterion (DIC), a Bayesian equivalent to the Akaike information criterion (see Burnham & Anderson 2002). Models with the smallest DIC values were considered to be the best fitting.

Model selection was conducted similarly to Thomas et al. (2006), on 2 levels. The first was to determine if population level, individual level, a combination of both, or neither (random habitat selection) contributed most to explaining the variation in the detection data. These were determined by fitting 4 global models with all measured covariates formulated as:

Global model 1 (full model). A model with population-level effects and individual random effects with covariates [$x(s)$] pFW, hDep and the 5 habitat type covariates (HT1–5). This model is appropriate if individual selection occurs and common population-level selection occurs across all individuals.

Global model 2. A model with individual random effects but no common population-level effects. This model was fitted by setting all population-level effects to zero ($\beta_i^* = 0$). This model is appropriate when individual selection occurs but there is no common population-level selection across individuals.

Global model 3. A model with population-level effects but no individual random effects. This model is appropriate when population-level selection occurs but individuals do not vary in their selection of habitat attributes. This model was fitted by setting $\beta_{ii} = \beta_i^*$ for all individuals (i) and $\sigma_i^2 = 0$.

Global model 4 (no-selection model). A model with neither population-level effects nor individual random effects. This model was fitted by setting all population-level and individual random effects to zero ($\beta_{ii} = 0$; $\beta_i^* = 0$). Thus, the probability of use of every station is the same as its availability. For this model, there are no parameters to estimate, with $p_i(s) = 1/63$.

The second level of model selection assessed the combination of covariates (i.e. pFW, hDep, HT1–5) that produced the model best explaining the variance in the data using the most parsimonious global model selected above. This level of model selection also used DIC to assess model performance. Models with different combinations of covariates were also compared against the no-selection model (Global model 4) to assess if individuals selected habitats significantly more or less than random.

Depth preferences and proximity to freshwater sources

The Bayesian modeling approach used above provides good information on the influence habitat depth (hDep) and proximity to freshwater (pFW) had on habitat selection by tagged individuals. To determine which depths and distances from freshwater sources (hDep and pFW) individuals selected for detection data within habitats were compared to those available within the study site using Chesson's α (Chesson 1978):

$$\alpha = \frac{(R_n/P_n)}{\Sigma(R_n/P_n)} \quad (5)$$

where R_n is the proportion of detections within a habitat depth (hDep) or distance (pFW) n , and P_n is the proportion of hDep or pFW of n available in the study site. The available hDep values in the study site and the hDep used by each individual were binned into 0.5 m intervals and the values of pFW were binned into 0.5 km intervals. Values of α ranged from 0 to 1, with values $>1/(\text{number of intervals})$ indicating electivity for, and values $<1/(\text{number of intervals})$ indicating avoidance of the habitat attribute. To highlight this, electivity values were standardised by subtracting $1/(\text{number of intervals})$, with the resulting deviations >0 indicating electivity and deviations <0 indicating avoidance.

Dietary composition

Since individuals captured in the present study were tagged and released in healthy condition, com-

plete gut contents of individuals by dissection or forced regurgitation were not conducted. However, on multiple occasions, individuals regurgitated the contents of their stomach on board minutes after capture. Regurgitated material were at different stages of digestion, but in most cases, prey were fresh. Regurgitated samples from individuals were collected and identified where possible to provide information on the diet of the 2 species. The prey composition in the samples were compared to data from previous studies. Prey selectivity metrics (e.g. Ivlev's selectivity index) for dietary specialisation were not calculated, as prey availability within the study site was not measured and opportunistic sampling may not fully represent the diet of species. Therefore, dietary composition of the 2 species was noted and compared between the 2 species on the basis of prey species composition present in regurgitated materials.

RESULTS

Sampling and tagging

Movements of 19 *Hydrophis curtus* and 6 *H. elegans* were monitored within Cleveland Bay, Queensland, Australia, between January 2013 and March 2014. Animals were captured, tagged (tag life: ~215 d) and released in January 2013 and April 2013 to ensure that multiple animals of both species were tracked simultaneously while still maximising the monitoring period. Initial tagging trips focused within the full extent of the bay; however, no sea snakes were captured in the western section, and therefore, tagging effort was concentrated within the eastern section of the bay. All snakes were caught and tagged in the eastern section of the bay and detection data showed that individuals of both species were mainly detected in this area. However, some individuals were detected on the western side revealing short excursions to fringing reef near Magnetic Island (Fig. 1) before returning to the eastern

side of Cleveland Bay. Tagged *H. curtus* were predominantly detected at stations within seagrass habitat (12 430 detections, 86 %) followed by deeper mud habitats (1494 detections, 10.3%; Table 1). *H. curtus* were detected in all but 1 habitat type (inshore sandy substrate, HT4) and only detected twice within fringing reef habitat (HT3; Table 1). In contrast, *H. elegans* were detected in all habitat types, predominantly in seagrass (HT5; 3820 detections, 79.5 %) and intertidal mudflat habitats (HT2; 902 detections, 18.1%; Table 1).

Habitat selection model

Analysis of habitat selection using Bayesian random-effects discrete-choice models revealed the full global model (including both population-level and individual random effects) was most parsimonious for both species (Table 2). The best-fitting model was also ranked higher than the no-selection model (Global model 4; Table 2), which indicated that selection of habitat types at both the population and individual level were non-random. The contribution of covariates within the best global model also showed the full model (including all covariates; pFW, hDep, HT1–5) best explained the variation in the data and was significantly better than the no-selection model in both species (Table 3).

The best-fitting models showed that population-level parameter estimates closely matched those of individual-level estimates for both species (Fig. 2). The influence of covariates on overall habitat selection (at both population and individual levels) can be interpreted by assessing the value of the Bayes estimates (means of posterior distributions) and if the 95 % credibility intervals include zero. Covariates that did not include zero within the credibility intervals were considered to significantly contribute to habitat selection. Bayes estimates that were positive were interpreted as covariates positively selected for, and vice versa. For population-level selection, proximity to freshwater (pFW) and habitat

Table 1. Number of detections (and percentages) of sea snakes *Hydrophis curtus* and *H. elegans* in the 5 representative habitat types within Cleveland Bay, Queensland, Australia, during the monitored period (January 2013 to March 2014)

	Deep mud substrate HT1	Intertidal mudflat HT2	Fringing reef HT3	Inshore sandy substrate HT4	Seagrass meadows HT5
<i>H. curtus</i>	1494 (10.3%)	514 (3.6%)	2 (<0.1%)	0 (0%)	12430 (86.1%)
<i>H. elegans</i>	229 (4.6%)	902 (18.1%)	34 (0.7%)	6 (0.1%)	3820 (76.5%)

Table 2. Model selection to evaluate the best global model that explains the variability in the data. Models included all covariates and were constructed to examine all possible combinations of population-level and individual-level parameters. Model performance was assessed using calculated deviance information criterion values (DIC)

Global model	<i>H. curtus</i>			<i>H. elegans</i>		
	DIC	Δ DIC	Rank	DIC	Δ DIC	Rank
(1) Full model: population and individual random effects (all covariates)	79007.1	0	1	17943.3	0	1
(2) Individual random effects only, no population effects	79022.5	15.4	2	17966.5	23.2	2
(3) Population effects only (all covariates), no random effects	88071.2	9064.1	3	22469.0	4525.7	3
(4) No population effects, no random effects (no-selection model)	137212.3	58205.2	4	38580.9	20637.6	4

Table 3. Model selection to estimate the contribution of covariates in population effects for the most parsimonious global model (see Table 2). Individual random effects (*) were included in all candidate models except the no-selection model. Model performance was assessed using calculated deviance information criterion values (DIC). (See Fig. 2 for abbreviations)

Model	<i>H. curtus</i>			<i>H. elegans</i>		
	DIC	Δ DIC	Rank	DIC	Δ DIC	Rank
pFW, HDep, HT1–HT5* (full model)	79007.1	0	1	17943.3	0	1
No covariates* (only individual random effects)	79022.5	15.4	2	17966.5	23.2	2
pFW, HDep*	87666.1	8659.0	3	27424.6	9481.3	3
pFW, HT1–HT5*	89301.0	10293.9	4	27513.5	9570.2	4
HDep, HT1–HT5*	100716.2	21709.1	5	34179.5	16236.2	5
HT1–HT5*	102994.7	23797.6	6	34662.2	16718.9	6
pFW*	123556.0	44548.9	7	37192.5	19249.2	7
HDep*	131479.5	52472.4	8	43839.3	25896.0	9
No-selection model (no population effects, no individual random effects)	137212.3	58205.2	9	38580.9	20637.6	8

depth (hDep) were significant covariates to habitat selection for both species (Fig. 2A,C). Deep mud substrate (HT1) and seagrass meadows (HT5) were positively selected for by both species, with seagrass selected significantly more than random in both cases. In both species, intertidal mudflat habitats (HT2) were avoided; however, variability in the population-level parameter estimates resulted in a pattern not significantly different from random. Fringing reef (HT3) and inshore sandy substrate (HT4) habitats were selected against by both species, with significant avoidance by *H. curtus* (Fig. 2A). Individual-level parameters followed the same patterns, with selection for deep (HT1) and seagrass (HT5) habitats and avoidance of reef (HT3) and sandy (HT4) habitats.

The model also assessed the spatial elements of habitat use within the bay (Fig. 3). Parameter estimates for each station showed that in both species, habitats on the southeastern side of Cleveland Bay were selected preferentially. Overall habitat selec-

tion in *H. curtus* indicated deep water and habitats close to freshwater sources in the southeast of the bay were used significantly more than random, with detections restricted to the eastern side of the bay (Fig. 3A). However, *H. elegans* displayed more extensive movements and were detected on reef and sandy habitats near Magnetic Island (Fig. 3B). Habitat selection in *H. elegans* also showed that despite extensive movement within the bay, only habitats in close proximity to freshwater sources were selected more than random (Fig. 3B). As the proximity to freshwater sources was used as a proxy for the influence of freshwater input from creeks, the results showed that sea snakes preferred habitats close to the mouths of Ross River and secondary creeks in the southeast section of the bay (Fig. 3). Both species displayed higher detection frequencies in habitats closer to the mouth of Ross River than the smaller secondary creeks in the southeast of the bay, which is likely due to the increased flow rate and volume of freshwater input into Cleveland Bay.

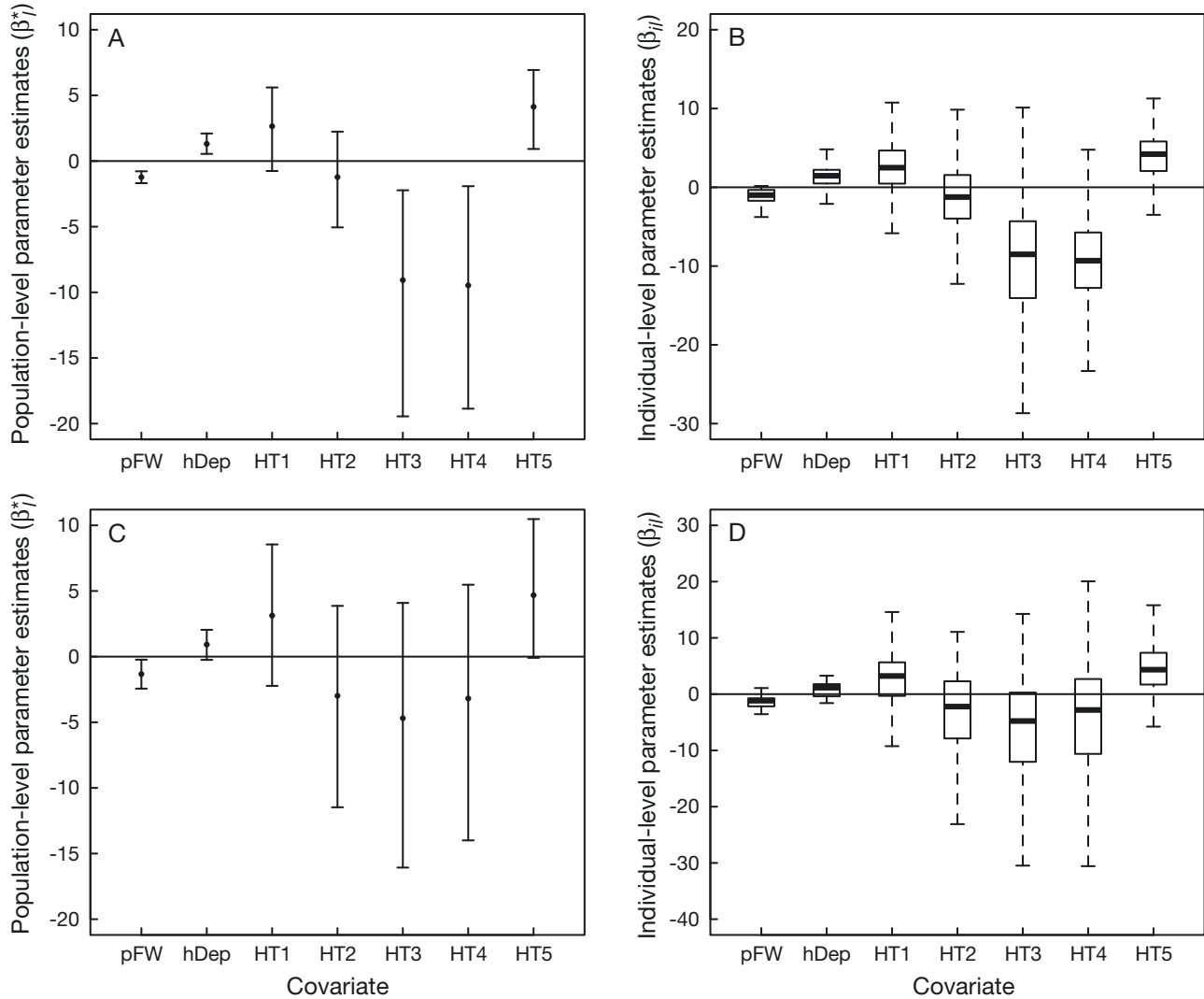


Fig. 2. Posterior distribution parameters from the most parsimonious Bayesian model (see Table 3) for (A,B) *Hydrophis curtus* and (C,D) *H. elegans*. (A,C) Population-level Bayes estimates (β_j^*) with bounds representing 95% credible intervals. (B,D) Box-plots of distribution of individual-level parameter estimates (β_{ij}) for each covariate in the fitted model with boxes displaying the first and third quartiles around the median and outer bounds extending to ± 1.5 times the interquartile range of the quartiles. pFW: proximity to freshwater sources; hDep: habitat depth; habitat type covariates: HT1, deep mud habitat; HT2, intertidal mudflat habitat; HT3, fringing reef habitat; HT4, inshore sandy habitat; HT5, seagrass habitat

Depth preferences and proximity to freshwater sources

Results of habitat selection models showed that pFW and hDep significantly influenced habitat selection (Fig. 4). Monitored individuals of both species were detected more often at stations close to freshwater sources (Fig. 4A) and at shallow depths (Fig. 4B). Individual *H. elegans* displayed an affinity to habitats <4 km from sources of freshwater in habitats <3 m in depth, while *H. curtus* selected for slightly deeper habitats (1–4 m) further from freshwater sources (2–5 km; Fig. 4C,D). There was an

inherent correlation with depth increasing with distance from freshwater sources; however, in this case, the difference in depth and habitat preferences between species was clear.

Dietary composition

Regurgitated material from captured individuals showed significantly different prey species composition between the 2 species of sea snakes (Figs. S1 & S2 in the Supplement at www.int-res.com/articles/suppl/m546p249_supp.pdf). *H. curtus* regurgitated at least 4

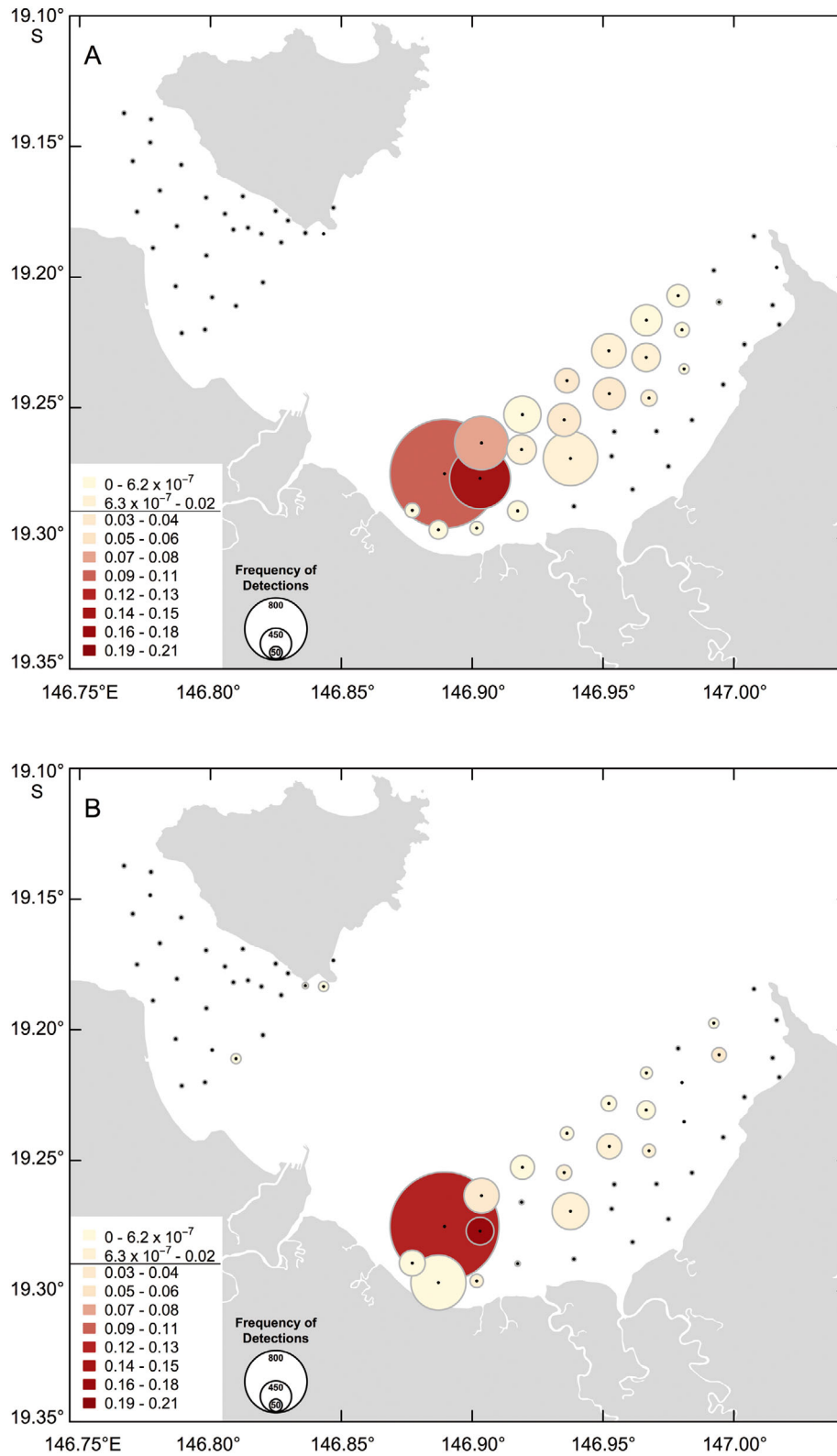


Fig. 3. Frequency of detections and predicted mean probability of habitat use at each station ($p_i(s)$; see Eq. 2) by (A) *Hydrophis curtus* and (B) *H. elegans*. Size of circle represents the frequency of detections at each station. Colour of circles represents if individuals selected habitats significantly more/less than random, with darker red circles representing higher estimated probability of selection. Horizontal line in the colour key indicates random habitat selection probability

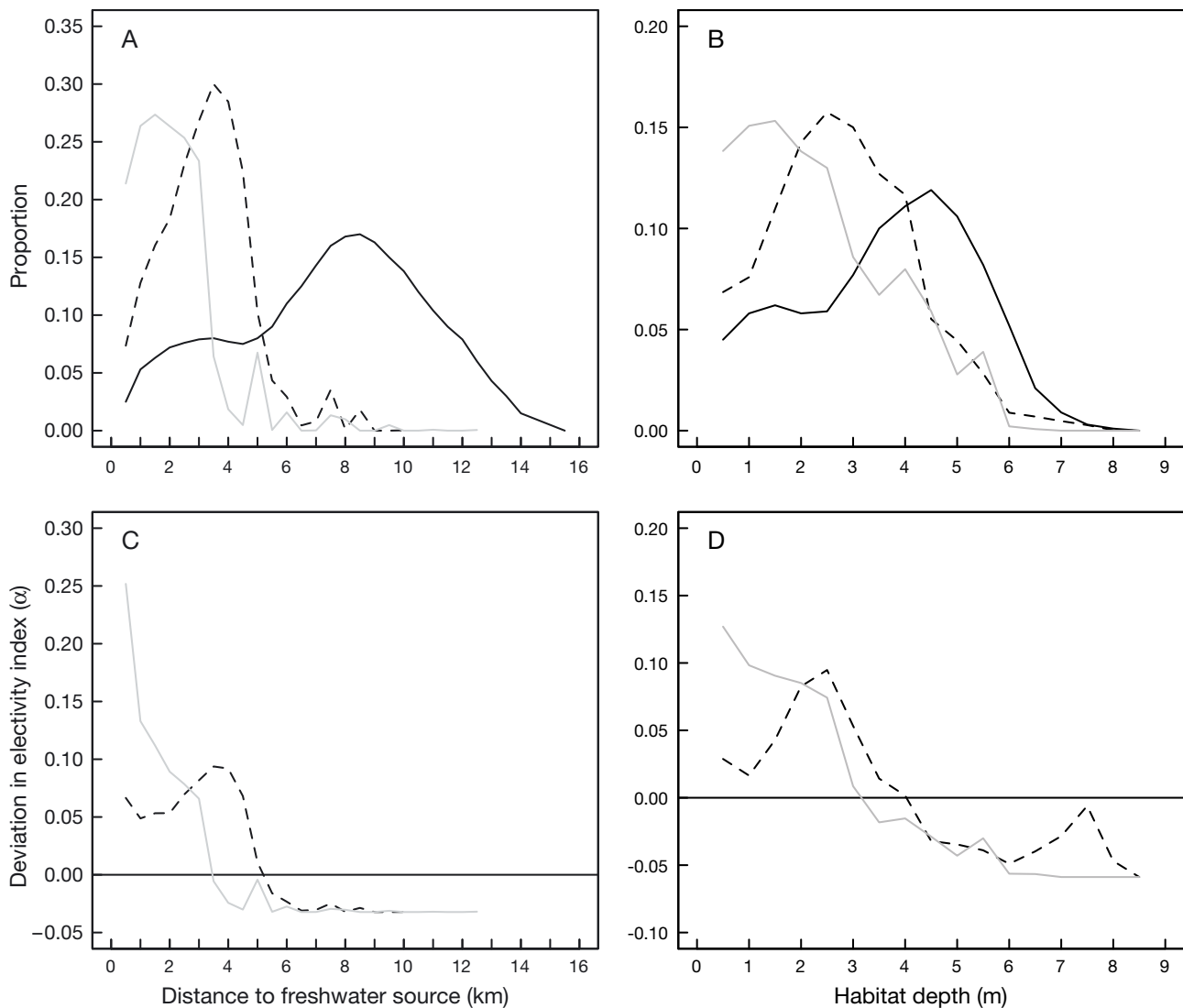


Fig. 4. Use of habitats in relation to proximity to freshwater and depth. Proportion of (A) available distances to freshwater sources and (B) habitat depths available in Cleveland Bay (solid black lines) and the proportion of detections within the respective habitat attributes by *Hydrophis curtus* (dashed black line) and *H. elegans* (solid grey line). Selection for (C) freshwater and (D) depth in *H. curtus* (dashed black line) and *H. elegans* (solid grey line), with values >0 indicating affinity

families of juvenile coastal fishes (Carangidae: *Caranx ignobilis*, *Parastromateus niger*, *Gnathanodon speciosus*; Triacanthidae: *Tripodichthys* sp.; Leiognathidae: *Leiognathus* sp.; Gobiidae: *Amblygobius* sp.; Fig. S1B), whereas samples from *H. elegans* solely comprised snake eels (Ophichthidae; Fig. S2B). A juvenile *H. curtus* (SVL: 640.4 mm) regurgitated a juvenile conspecific (Fig. S1C), suggesting that in coastal habitats with large numbers of juveniles, *H. curtus* display some level of cannibalism. Several *H. curtus* were also caught with recreational fishing gear (circle hooks, lures and bait) in their stomachs (Fig. S1D), suggesting an opportunistic generalist approach.

DISCUSSION

Results of the present study support the proposed hypothesis that sea snakes select habitats differently based on their degree of dietary specialisation. The generalist feeder *Hydrophis curtus* uses a wide range of habitats including deeper waters within the bay, whereas the eel specialist *H. elegans* selects shallower mudflat habitats where prey abundances are greater. The present study also shows the utility of Bayesian hierarchical models to analyse passive acoustic telemetry data. The use of random effects in the models accounts for individual-level variation in

the data model, while population-level inferences were still possible using the parameter models that provided metrics based on Bayes estimates (means of individual-level posterior distributions). This technique shared information between the data model and parameter models where individual-level estimates contributed to population-level estimates, which in turn influenced individual-level estimates through the parameter model (Thomas et al. 2006). This feedback loop allowed each individual to be equally represented in the overall model even if some individuals displayed low numbers of relocations. Often in passive telemetry studies, individuals with low numbers of relocations are removed from population-level inferences (e.g. activity space, movement metrics, etc.) to allow for more robust estimates; however, this drastically reduces the sample size and inflates the error associated with each estimate. Here the use of Bayesian techniques with passive acoustic data provided reliable individual- and population-level estimates and associated error estimates in the form of credible intervals to explore habitat use in sea snakes.

In this study, passive monitoring of the 2 species of sea snake in Cleveland Bay showed that individuals used the area based on the type of habitat, depth and proximity to sources of freshwater. Individuals of both species were detected at receiver stations on both sides of the bay, but detection rates may have been biased toward the eastern section of the bay due to capture location. Nevertheless, high use of seagrass and deep habitats by *H. curtus*, and seagrass and mudflat habitats by *H. elegans*, as well as differences in diet, suggest that sea snakes use these areas differently. Previous studies of sea snake populations have revealed similar tidal-based patterns in activity and short-term presence, with the probability of presence in shallower habitats increasing with increased tidal reach (Dunson 1975, Kerford et al. 2008, Udyawer et al. 2015a). Kerford et al. (2008) and Wirsing & Heithaus (2009) found similar patterns for *H. elegans* and *H. (Disteira) major* respectively in Shark Bay, Western Australia, where individuals were observed refuging in shallow seagrass habitats during high tides and foraging in adjacent sandflat habitats during low tides. A similar combination of effects (i.e. predator avoidance and increased prey abundance) likely governs the selection of seagrass habitats by the individuals examined in the present study. Increased data on prey availability and predator abundance may highlight this difference.

Selection of habitat by tagged sea snakes showed that both species were associated with shallow depths.

Previous reports of sea snake assemblages have noted the importance of shallow coastal and estuarine habitats during vulnerable periods of their life (Voris & Jayne 1979, Voris 1985, 2015, Stuebing & Voris 1990, Wassenberg et al. 1994, Bonnet et al. 2014). These habitats may provide a combination of increased resources (e.g. prey, freshwater) and reduced predation risk to maximise survival. Wassenberg et al. (1994) suggested that sea snakes might choose shallow habitats during vulnerable life stages (i.e. juveniles and gravid females) to reduce energy expenditure when surfacing for air or capturing prey. Previous work in Cleveland Bay has shown that the most frequently encountered age classes were juveniles, with adults encountered in summer months during parturition periods (V. Udyawer unpubl. data). The non-random selection of habitats has also been observed in sea snakes that occupy coral reef habitats, with individuals of *Emydocephalus annulatus* actively selecting shallow habitats associated with increased food sources (i.e. damselfish eggs; Shine et al. 2003). Association with shallow depths in the present study was also related to sources of freshwater, with individuals detected less frequently in other available habitats (e.g. HT4 or HT3 habitats). Therefore, there is likely a combination of factors that drive habitat selection.

Reduced salinity in coastal regions limits the seaward movements and distribution of most marine snakes (Lillywhite & Ellis 1994, Lillywhite et al. 2008, Lillywhite & Tu 2011, Brischoux et al. 2012, Liu et al. 2012). In Cleveland Bay, access to freshwater is available throughout the year and this may play an important role in sea snakes' use of these habitats. Selecting habitats close to freshwater sources may help snakes maintain internal water balance and remain hydrated. Liu et al. (2012) found similar patterns exhibited by closely related amphibious sea kraits (*Laticauda semifasciata*, *L. laticaudata* and *L. colubrina*), where access to sources of freshwater was an important factor influencing selection of habitats within a coastal environment. Changes in habitat selection by individuals between the wet and dry seasons may improve our understanding of the importance of seasonally variable freshwater runoff for sea snake populations (Lillywhite et al. 2014). Unfortunately in the present study, the battery life of tags (215 d) was not long enough to encompass multiple seasons to explore such differences.

Habitats close to freshwater sources may also be important foraging areas for sea snakes. The distribution of prey species may drive the selection of seagrass and deeper outer bay habitats by *H. curtus* as

they feed on a range of small pelagic and benthic fish species found in such habitats (Voris & Voris 1983, Lobo et al. 2005). The predominant selection of intertidal mudflat and seagrass habitats may reflect the eel-specialised diets of *H. elegans* (Voris & Voris 1983, Kerford 2005). Stomach contents of individuals were not directly collected for this study, but regurgitated items from both species closely matched diets described in previous studies, suggesting that dietary niche separation may allow the 2 species of sea snake to overlap in similar habitats with reduced competition.

Previous literature on the diet of *H. curtus* is extensive, as this species is encountered globally as trawl and fishing bycatch. In all previous observations, *H. curtus* were considered generalists with the most diverse gut contents, including 5–31 families of fishes as well as other invertebrates (Glodek & Voris 1982, Voris & Voris 1983, Fry et al. 2001, Marcos & Lanyon 2004, Lobo et al. 2005). Observations of *H. curtus* with fishing gear in the alimentary tract reflect anecdotal evidence from local recreational fishermen and previous research activity that this species opportunistically consumes bait (S. Moore pers. comm.). Scavenging behaviour by generalist feeders is common in the marine environment (Kaiser & Spencer 1994); however, this has not been recorded previously in sea snakes. In nearshore areas with increased fishing activity, *H. curtus* may consume bait or discarded fish that could affect foraging behaviours, ultimately increasing their susceptibility to capture in fishing gear and increasing mortality rates as a result.

An interesting finding in the present study was the regurgitation of a conspecific by a juvenile *H. curtus*. Predation on conspecifics is often viewed as a strategy to increase survival of an individual by reducing intraspecific competition and can act as a selective force in ontogenic distributions or habitat selection (Keren-Rotem et al. 2006). Cannibalism in reptiles is often a by-product of opportunistic predatory behaviours, especially in environments with a high density of conspecifics (Polis & Myers 1985). The high abundance of juvenile *H. curtus* within Cleveland Bay coupled with a generalist diet may explain the observed incident of cannibalism in the present study.

Management implications

Patterns in habitat selection can be useful in assessing resource requirements of target species populations and can also provide information on the biological importance of particular habitats (All-

dredge & Griswold 2006). These patterns in resource requirements are most useful to managers at the population level to address management concerns and develop targeted management policy (Manly et al. 2007). However, in many cases these metrics are often averaged among a subset of individuals in the population, which often does not provide the complete information required to make such management decisions (Thomas et al. 2006). The present study demonstrates the use of hierarchical models to provide both individual- and population-level habitat selection metrics incorporating individual variability to allow for a more accurate understanding of resource requirements. This study also indicates that the selection of habitats by sea snakes within nearshore environments is strongly influenced by the availability of the preferred habitat type as well as the depth and proximity of the habitat from sources of freshwater.

Coastal and nearshore environments are under increasing pressure, with natural and anthropogenic changes causing degradation and loss of habitats (Turner et al. 1999, Pratchett et al. 2011). Seagrass meadows are important habitats that provide sea snakes critical resources (e.g. shelter, prey); therefore, any degradation or loss in the availability of this habitat may have dire consequences for the health of local sea snake populations. The degree of specialisation in diets or habitats may affect the ability of species to cope with any changes in habitat availability (Munday 2004, Munroe et al. 2014). Species like *H. elegans*, with highly specialised diets, may not be able to adapt to the degradation or loss of preferred habitats compared to generalist species like *H. curtus* that have the ability to adapt to a wide variety of prey species and may successfully adapt to other habitat types. The Bayesian approach to exploring habitat selection used here has highlighted habitat selection at both a population and individual level, which provides a holistic picture of resource requirements of sea snake populations needed for designing management and conservation policy (Thomas et al. 2006). Understanding the habitat requirements of sea snakes is not only important to further our understanding of these poorly studied taxa, but is essential when developing conservation and management strategies in light of increasing natural and anthropogenic disturbances in coastal and nearshore environments (Elfes et al. 2013).

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