THE ECOLOGY OF THE BAR BELLIED SEA SNAKE (*HYDROPHIS ELEGANS*) IN SHARK BAY, WESTERN AUSTRALIA

by

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ABSTRACT

This thesis examines factors underlying habitat use of the sea snake *Hydrophis elegans* and nearshore fish in Shark Bay, Western Australia. Differences in morphology, life history and diet between *H. elegans* and a sympatric sea snake, *Disteria major*, may facilitate co-existence by reducing competition through inter-specific resource partitioning. Morphological differences between sexes of *H. elegans* may reduce intra-specific competition. Tidal state may cause changes in predation risk and prey availability. Field observations showed that at low tide *H. elegans* foraged over shallow sand flats, which are inaccessible to the predatory tiger shark (*Galeocerdo cuvier).* At high tide, snakes and their potential prey (small fish) moved to deeper seagrass habitats, suggesting that these habitats grant snakes increased safety from predation, as well as access to potential prey. This is more likely true for *D. major*, because *H. elegans* appears to specialize on snake-eels (Family Ophichthidae), which occur mainly in sand habitats.

DEDICATION

This thesis is dedicated to my father, Reginald Glenn Kerford. His undying support and belief in my ability gave me the strength and determination to persevere and complete my Master's. Thank you.

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CHAPTER 1:

General Introduction

Many factors can affect habitat selection by a species, including predation risk, prey availability, or local competition. For example, Heithaus and Dill (2002), while studying the bottlenose dolphin (*Tursiops aduncus*) in Shark Bay, Western Australia, determined that food availability and predation risk by the tiger shark (*Galeocerdo cuvier*) were affecting dolphin habitat use. Further research showed that these factors were also affecting the habitat use of the pied cormorant (*Phalacrocorax carbo*) (M. Heithaus 2005) and dugongs (*Dugong dugon*) (A. Wirsing, pers. comm.). The bar bellied sea snake (*Hydrophis elegans*) is also a known prey of tiger sharks, comprising up to 50% of a small tiger shark's diet (Simpfendorfer et al. 2001). In addition, the bar bellied sea snake co-inhabits Shark Bay with two potential competitors, the olive headed (*Disteria major*) and Shark Bay sea snakes (*Aipysurus pooleorum)* (Storr and Harold 1978). The presence of a predator and potential competitors make sea snakes in Shark Bay a model system to study effects of these factors on habitat use.

The goal of my thesis was to examine the ecology of the bar bellied sea snake in Shark Bay. More specifically, I investigated the potential for resource partitioning within and among bar bellied and olive headed sea snakes by comparing morphology, life history and diet of these two species. I also attempted to determine whether tidal state, by influencing the local abundance of predators and prey, affects the habitat use of the bar bellied sea snake.

1.1 Study Site

Shark Bay is situated approximately 800 km north of Perth on the westernmost point of Western Australia (approx. 25° 45'S, 113° 45'E) (Figure 1.1a). This large, semi-enclosed body of water contains extensive areas of dense, species-rich seagrass beds, deep channels, and large shallow sand flats (Humphries 1990). Depths range from <2 m on the shallow sand flats and offshore seagrass banks, to 12-m in the deeper channels. The Bay's great species richness (including hundreds of species of fish, sharks, bottlenose dolphins, turtles, and sea snakes) contributed to Shark Bay's listing as a UNESCO World Heritage Area in 1991. The primary site for my study was the Eastern Gulf, offshore of Monkey Mia (Figure 1.1b).

1.2 The Study Species

My research focused primarily on the bar bellied sea snake, *H. elegans,* with some comparative data on *D. major* and their competitive relationship. *H. elegans* is a large hydrophiid snake, characterized by a greatly elongated body and relatively small head (Cogger 2000). They have 40-62 (personal observation) dark vertical bands contrasting with their pale bodies; in adults these bands are incomplete (i.e., they do not completely encircle the body). Juveniles differ from adults in having very distinct black heads and much paler bodies. Their bands are black and many are unbroken, making the contrast between the bands and their paler bodies much more pronounced than that of the adults. *H. elegans* is found throughout the waters surrounding Australia, stretching from

Brisbane on the east coast, across the northern coastline and down the West Coast, with Shark Bay being the most southern point of its distribution (Heatwole 1999). *D. major* is also a hydrophiid snake sharing a similar geographical range and coloration to that of *H. elegans*; however, *D. major* is generally shorter and has fewer bands (31-40, personal observation) and a larger head (Cogger 2000).

1.3 Chapter Summaries

During the Australian summer of 2003 and 2004, I used transect surveys to record the distribution and behaviour of *H. elegans* and *D. major* over sand and seagrass habitats at low and high tide. Because little is known about sea snake ecology or the potentially important role they may play in marine ecosystems, I begin in Chapter 2 by reporting all of the morphological, life history and diet data that I collected. I investigated how morphological differences between age, sex, and size classes, and between species, can help to reduce competition by facilitating resource partitioning within and between species, which allows the snakes' co-existence.

It has been shown that some sharks are unable to enter shallow habitats at low tide, suggesting that predation risk may fluctuate with the tide (Medved and Marshall 1983, Ackerman et al. 2000). In Chapter 3, I demonstrate how tidal state affects the habitat use of the bar bellied sea snake. Lastly, in Chapter 4, I address whether changes in tidal state also affect the habitat selection of potential prey (fish) of *H. elegans*.

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1.5 Figure

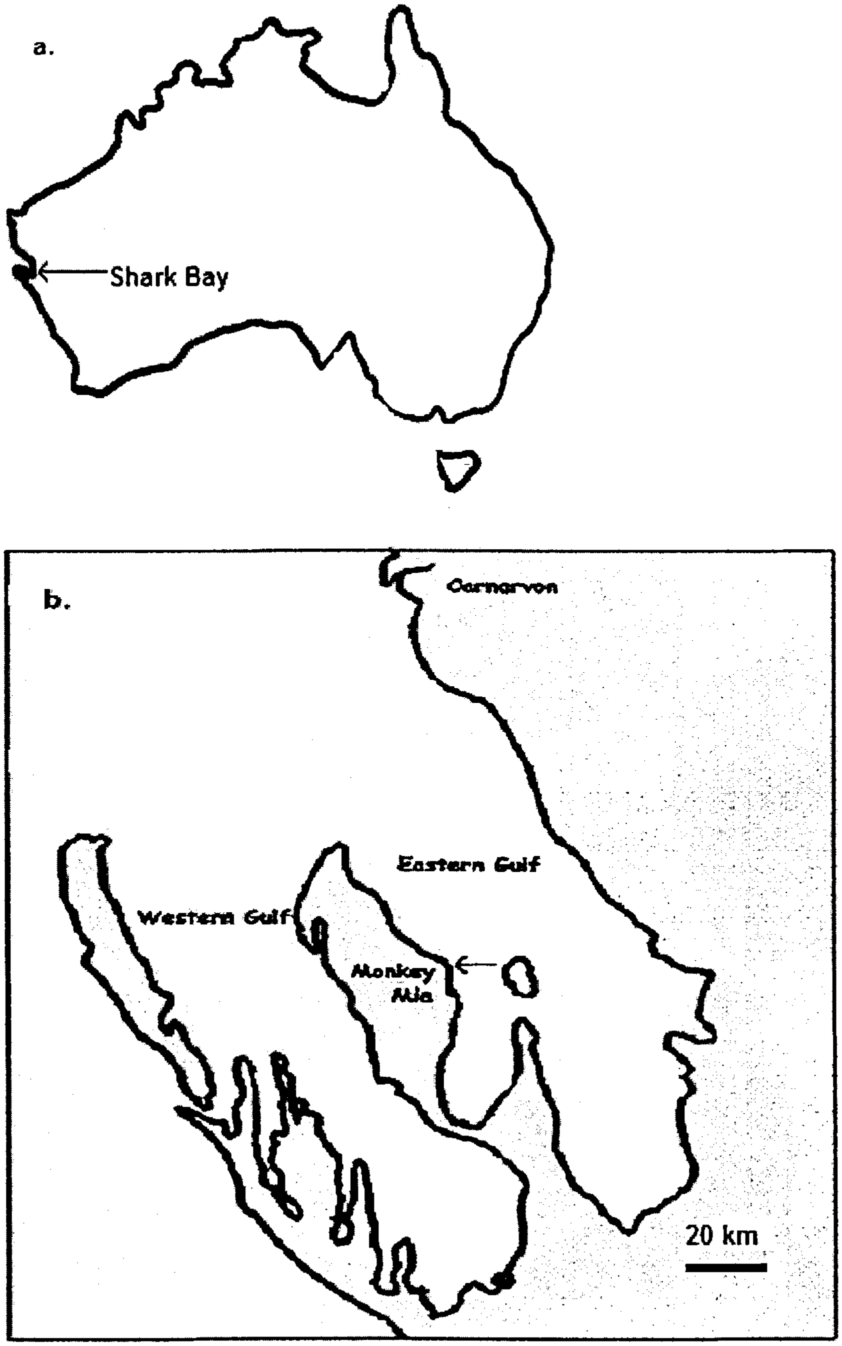

Figure 1.1 a. Shark Bay, Western Australia (indicated by arrow). b. The study area was located offshore from the Monkey Mia Dolphin Resort (indicated by arrows).

CHAPTER 2:

Morphological and life history traits of the sea snake *Hydrophis elegans* with notes on *Disteria major* and their competitive relationship

2.1 Abstract

Competition between and within species can be reduced by resource partitioning, and morphological differences between age, sex, and size classes, and between species, can help to facilitate this partitioning. This study examines intra- and inter- specific resource partitioning in two species of sea snakes (*Hydrophis elegans* and *Disteria major*) found on the West Coast of Australia, by investigating differences in their morphology and diet. The snakes were either collected directly from Shark Bay, Western Australia, or were part of a collection belonging to Western Australia Museum (Perth, WA). Measured morphological traits (weight, tail length, head width, head length, neck circumference and girth) for juvenile and adult female and male *H. elegans* grew allometrically with respect to snout-vent length, except for juvenile head width. Female *H. elegans* had significantly larger heads than their male counterparts. Females also consumed larger prey items than males, suggesting that the sexual dimorphism observed in *H. elegans* allows females access to larger prey than males, thus reducing competition. Only weight and head width of adult female and male *D. major* grew allometrically with respect to snout-vent length, and *D. major* had a significantly larger head than both sexes of *H. elegans*. This larger head size likely explains how *D. major* is able to consume much larger prey from a variety of fish taxa whereas sampled *H. elegans* consumed only prey belonging to the family Ophichthidae (snake eels). The difference in head size between *H. elegans* and *D. major* appears to facilitate co-existence through inter-specific resource partitioning.

2.2 Introduction

Species that share a habitat can reduce competition by utilizing different resources present within that habitat, i.e., by resource partitioning. Inter-specific resource partitioning is facilitated by morphological differences between similar species. These differences in morphology allow them to forage on different prey resources and thus reduce competition. Differences in prey use can also occur within a species, either between males and females as a result of sexual dimorphism, or between adults and juveniles through ontogenetic shifts in habitat or morphology (Werner and Gilliam 1984; Shine 1991; Pearson et al. 2002). Both inter- and intra-specific resource partitioning have been observed in a large array of terrestrial systems (Schoener 1974), as well as in freshwater and marine environments (Ross 1986). Despite the hundreds of studies on this topic, little is known about resource partitioning between, or within, species of sea snakes.

Recent advances have been made regarding sea snake ecology (Dunson 1975; Voris and Voris 1983; Heatwole 1999; Shetty and Shine 2002) however, there is still much to be learned about their behaviour and ecology. The waters off the West Coast of Australia provide an ideal system to address intra- and inter- specific resource partitioning in sea snakes as it is home to two species, the bar bellied sea snake (*Hydrophis elegans)* and the olive headed sea snake (*Disteria major)*, that share a similar geographical range (Heatwole 1999), and have a similar morphology.

I investigated the potential for resource partitioning within and among bar bellied and olive headed sea snakes by comparing morphology, life history and diet for these two species. I suggest that the differences in their head morphology alter their feeding ecology and therefore reduce competition between them, explaining how they can co-exist within the same habitat.

2.3 Materials and methods

2.3.1 Sampling location and capture methods

The specimens used for this paper were either collected from Shark Bay, or were from the collection of the Western Australia Museum (Perth, WA). Shark Bay is situated approximately 800 km north of Perth on the westernmost point of Western Australia (approx. 25° 45'S, 113° 45'E), and includes a series of peninsulas and islands. It is a large, semi-enclosed body of water that contains large areas of dense, species-rich seagrass beds, deep channels, and large shallow sand flats (Humphries 1991). Depths range from <2 m on the shallow sand flats and offshore seagrass banks, to 12 m in the deeper channels. Snakes (n=26) were collected in Shark Bay between 1 February and 31 April, 2004 using a 45-cm diameter dipnet when they surfaced to breathe. They were then euthanized by freezing.

The snakes (n=98) in the WA Museum collection had been caught by trawlers between 1959 and 2001 along the West Coast of Australia, ranging from 20°00 to 32°00'S, and 113°00 to 128°00'E. Seventy-nine out of the 98 museum snakes had been caught within Shark Bay and vicinity (24°50 to 25°80'S, and 113°10 to 113° 32'E).

2.3.2 Morphological and reproductive traits

Juveniles caught in Shark Bay were distinguished from adults based on differences in colour and size, and were not kept for dissection due to permit restrictions. No juveniles were present in the Museum collection. Adult specimens from Shark Bay and the Museum collection were weighed, and morphological traits measured. Snout-vent length (SVL) and tail length (TL) were measured from the tip of the snake's snout to the vent, and the vent to the tip of the tail, respectively, using a measuring tape (Fig. 2.1). Neck circumference was measured one hand width (approx. 10 cm) behind the parietal scales of the snake's head and abdominal circumference (girth) was measured at two thirds of the SVL. Maximum head length was measured from the tip of the snakes' snout to the anterior portion of the two parietal head scales, and maximum head width was measured directly behind the snakes' eyes. Both were measured using Vernier calipers (Fig. 2.1). Total body length was not considered for the analyses as it is strongly dependent upon TL, which can be damaged and thereby shortened. Therefore, SVL was used as the measure of body size.

A mid-ventral incision was made so that the snakes could be sexed and gut contents removed. The snakes were then classified as either pre-reproductive (sexually immature) or post-reproductive (sexually mature). The two factors that were used in determining male reproductive state were the length of the right and left testes, measured using Vernier calipers, and the state of the vas deferens (non-turgid=pre-reproductive, turgid or semi-turgid=post-reproductive). Females were considered pre-reproductive if they had yet to produce a clutch (unstretched oviducts) and post-reproductive if they had had a previous clutch (stretched oviducts), or were carrying a clutch (D. Pearson, WA

Museum, pers. comm.). Oviducal eggs were counted, measured and weighed. Eggs that were substantially smaller than other eggs in the same oviduct were considered non-viable and were not included (Ward, 2001).

2.3.3 Age

Age was determined from snout-vent length for *H. elegans* using the von Bertalanffy equation:

$$L_t = L_\infty(1 - e^{-K(t-t_0)})$$

L_t represents the mean length at age t, L_∞ represents the asymptotic mean length, K represents the growth coefficient and t_0 is the (nominal) age which the mean length is zero. Ward (2001) had previously determined all unknown parameters separately for male and female *H. elegans* in another population. Snakes that were larger than Ward's asymptotic mean lengths were not included in the age class results.

2.3.4 Gut content analyses

Gut contents (fish) were removed, weighed using a Sartorius balance, total length and head width measured using a measuring tape or Vernier calipers, respectively, and identified to the lowest taxonomic level possible, generally family.

2.3.5 Statistical analysis

Statistical analyses were performed using JMP (Sall et al. 2001). To meet assumptions of the statistical tests, morphological data were transformed to natural logarithms for all analyses. A general linear regression was used to test whether morphological traits of the three classes (juvenile, male, and female) of *H. elegans* increase allometrically with respect to SVL. The slope and intercept of the relationships for all morphological traits for each class were determined. Slope was then used as an indicator of the relative rate of growth for a given morphological trait, i.e., relative to snout-vent length. ANCOVAS were run to test whether the relative rates of growth of the morphological traits differed between the classes, with the natural log of each morphological trait as the dependent variable, and the natural log of SVL and snake class as the covariates. When a difference among the relative rates of growth was identified, the ANCOVAS were re-run between two classes at a time to determine which were responsible for the difference detected. The data were analysed in the same way for *D. major* except there were only two classes: male and female.

Differences between the relative rate of growth of each morphological trait were also compared between the two species. This was accomplished by running ANCOVAS with species and natural log of SVL as the covariates. "Species" represented 4 classes: male and female *H. elegans,* and male and female *D.major*. Again, when a difference was detected among the relative rates of growth, the ANCOVAs were run between all pairs of classes to determine which were responsible for the difference detected. T-tests were used to compare head size and prey size between adult *H. elegans* and *D. major,* and within each species the correlation between these variables was assessed.

A logistic regression model was derived using the graphing program SigmaPlot 5.0 (SPSS Inc.) to determine the body size at which male and female *H. elegans* become reproductive. This analysis could not be performed for *D. major* because the sample size was too small.

2.4 Results

2.4.1 Body size

The morphological traits of 123 *H. elegans* were measured. Seventeen snakes were classified as juveniles. These juveniles had all been caught in Shark Bay, along with 5 adult males and 2 adult females (Fig. 2.2a). Of the 106 adult snakes, 46 were males, and 60 were females. The majority of males were between 120 and 160 cm SVL with a mean SVL of 140.3 cm ±3.1 SE. The majority of females were between 140 and 180 cm SVL with a mean SVL of 157.7 cm ±2.7 SE (Fig. 2.2b).

Snout-vent length data were obtained for 52 *D. major* (n=26 from Shark Bay, n=26 from the Museum). However, the sex of only the 26 adult (no juvenile specimens present) Museum specimens could be determined due to permit restrictions. The majority of males and females fell between 80 and 120 cm (Fig. 2.3). The mean length was 89.7 cm ±5.5 SE for males (n=7), and 97.7 cm ±2.6 SE for females (n=19).

2.4.2 Morphological and reproductive traits

Morphological traits (weight, tail length, head width, head length, neck circumference, and girth) for juvenile, male and female *H. elegans* increased significantly with SVL (Table 2.1). The relative rates of growth of female and male weight (Fig 2.4a) and girth (Fig. 2.4b) differed significantly. Males and females also differed with regard to head length (Fig 2.4c) and neck circumference (Fig 2.4d) growth rates, with juveniles growing at a similar rate to that of males. The relative rate of growth of tail length (Fig 2. 4e) did not differ among the three classes. The relative rates of growth for female and male head width did not differ, but both increased significantly faster than that for juveniles (Table 2.2, Fig. 2.4f). All juveniles were from Shark Bay, while only a proportion of the adults were, so discontinuities apparent in Fig. 2.4 may partially reflect population differences.

The weight and head width of female and male *D. major* increased significantly with SVL. However, the neck circumference and girth of the females and head length and TL of the males did not (Table 2.3). The relative rates at which all morphological traits grew did not differ for male and female *D. major* (all P>0.1).

The ANCOVA results indicate that the relative rates of growth for all morphological traits differed significantly between species (where "species" represented 4 classes: male and female *H. elegans,* and male and female *D.major)* except tail length and head width (Table 2.4). The relative growth rates of weight (Fig. 2.5a), head width (Fig. 2.5b), and girth (Fig 2.5c) for female *H. elegans* were significantly greater than those for male and female *D. major.* The relative rate of growth of female *H. elegans* head length (Fig 2.5d) was significantly greater than that of male *D. major*, but not different from that of females (Table 2.4).

The logistic regression model indicates that female and male *H. elegans* attain sexual maturity at average sizes of 152.3 cm ±0.09 SE and 128.7 cm ±0.09 SE, respectively (Fig. 2.6). The largest pre-reproductive female was 162.6 cm and the smallest post-reproductive was 149.2 cm. For males these values were 133.7 cm and 123.1 cm, respectively. There were 8 pregnant *H. elegans,* all from the Museum's collection, and 4 pregnant *D. major*, 2 of which were collected from Shark Bay on 26th March and 23rd April, 2005. The smallest snakes with oviducal eggs were 149.2 cm and 97.3 cm for *H. elegans* and *D. major,* respectively. Larger females tended to have larger clutch sizes (Fig. 2.7).

2.4.3 Age

The juvenile *H. elegans* (n=17) were all estimated to be less than 2 years of age (Fig. 2.8). Males ranged from 2.3 to 15.4 years of age and females from 2.9 to 10.9 years. Based on the logistic regression results, males reach reproductive maturity at 3 years of age whereas female do not do so until 4 years of age. Based on the maximum ages calculated, males may live longer than the females, but the most abundant age class for males was 2-4 years, whereas it was 4-6 years for the females. There are no published age length relationships for *D. major.*

2.4.4 Gut content analysis

Forty-six gut content samples were retrieved from *H. elegans*, with 24 of these obtained in Shark Bay. Only 25 of the gut content samples were identifiable and all belonged to the family Ophichthidae (snake eels). Forty two percent of the adult females (25 of 60) had prey in their stomachs, compared to 46% of males (21 of 46). Female *H. elegans* have larger heads than males (mean lengths = 26.23 ± 0.53 SE and 23.39 ± 0.43 respectively; t=4.18, 104 df, P<<0.0001; mean widths = 18.03 ± 0.45 and 15.93 ± 0.42 respectively; t=3.43, 103 df, P=0.0004; see Fig. 2.4 also) and consume larger prey than their male counterparts (t=1.95, 22df, P=0.032; Fig. 2.9).

Only 7 gut contents were retrieved from *D. major.* The fishes identified belonged to 4 different taxa (2 Anguilliformes, 1 Perciformes, 3 Scorpaenidae, 1 Scaridae). *D. major* have significantly larger heads than *H. elegans* (mean lengths= 29.10 ± 0.54 and 24.81 ± 0.48 respectively; t=1.8, 53 df, P=0.04; mean widths= 20.17 ± 0.73 and 16.98 ± 0.44 respectively; t=3.9, 36 df, P<0.0001; see Fig. 2.5 also), despite the fact that their average SVL is significantly shorter. *D. major* ate significantly larger prey than *H. elegans* (t=-3.7, 15 df, P=0.001) (Fig. 2.9).

2.5 Discussion

2.5.1 Inter-specific resource partitioning

Although *H. elegans* grow longer, *D. major* is a larger snake with respect to head size and girth. It has been suggested that the head size of a snake is strongly correlated with its prey size (Shine 1991, Arnold 1993). Snakes with larger heads tend to forage on larger prey (Voris and Voris 1983), which is in accord with this study. The diet data collected for *H. elegans* suggest they forage only on long, slender snake-eels found over the sand (McCosker and Rosenblatt 1993), whereas *D. major* eat an assortment of fish species. The difference in the head morphology of the two snakes likely enables them to partition the available prey based on size, and thus reduce competition. *D. major* has a larger head width/girth ratio than *H. elegans* (0.19 and 0.14, respectively; t=-5.91, 33 df, P<0.0001), and this likely affects the choice of prey and thus affects the habitat in which the snakes' forage. *H. elegans* require a small head to tunnel into snake eel burrows, whereas *D. major* do not. Previous diet analyses for *H. elegans* (n=5; Voris and Voris 1983) did not show the extreme specialization reported here, although they were reported to have eaten very slender prey.

2.5.2 Intra-specific resource partitioning

Adult female *H. elegans* grow larger than their male counterparts, whereas this is not the case for *D. major*, which show much less sexual dimorphism with regards to morphology. Shine (1994) suggested that sexual dimorphism in snakes should favour larger females if the snake species is viviparous, clutch size increases with body size, and there is no male combat. Because *H. elegans* meets at least the first two of these criteria, it is probable that the females grow larger to increase the number of young they can produce in a single clutch. Sexual size dimorphism has also been observed in other species of water snakes (Arafura file snake, *Acrochordus arafurae,* Houston and Shine 1993; olive sea snake, *Aipysuris laevis,* Burns and Heatwole 2000; yellow-lipped sea krait, *Laticauda colubrine,* Shetty and Shine 2002). Dimorphism may also enhance resource partitioning between male and female sea snakes of the same species if it contributes to differences in their diet and habitat use. This appears to be the case for *H. elegans.* Although they are very specialized feeders regardless of their sex, prey size increases with head size, and females have significantly larger heads than the males. The resulting intra-specific resource partitioning would reduce competition between the sexes.

D. major displayed little sexual dimorphism. Their diet was varied but the sample size was too small to determine if both sexes are generalist feeders, or if they forage for different prey. The gut samples that were retrieved belonged to fish species with a range of head sizes, suggesting that a snake with a larger head may have a broader foraging niche. A larger sample size of *D. major* will be required to address these possibilities further.

In many species of sea snake, tail length differs between the sexes and can be used to differentiate between them (Heatwole 1999; Shine and Shetty 2001). This appears to be the case for *H. elegans*: for any given body length males have a longer tail than do females (see Fig. 2.4e). Male and female *D. major* did not differ significantly in tail length; however, this is likely a result once again of the small sample size.

2.5.3 Ontogenetic shifts

All juvenile *H. elegans* were caught in Shark Bay, in less than 2 m of water, while the water depth of the snakes caught by trawlers would have exceeded 15 m. This could suggest an ontogenetic habitat shift whereby juveniles are found in shallower water than their adult conspecifics. Juveniles may be confined to shallower waters because of food availability, because snake head size limits the size of prey they can consume (Mushinsky et al. 1982; Savitsky 1983; Houston and Shine 1993; Shine et al. 2003), and previous research has shown that smaller juvenile fish species are found in shallower water (Edgar and Shackley 1995). An alternate hypothesis may be that because juvenile snakes have a higher surface area to volume ratio than their adult conspecifics (Peters 1983; Shine et al. 2003), and sea snakes are ectotherms that rely on the external temperature to regulate their metabolism, they remain in the safer shallows (see Chap. 3), basking at the surface to maximize their rate of digestion and growth. This could also account for the differences in their colour as juveniles are much darker than adults, with very distinct black bands, which could increase the rate of thermal exchange (Peterson et al. 1993). As interesting as such a habitat shift would be, an alternate explanation for the lack of juveniles caught by trawlers is simply that the mesh of the nets is too large to retain the smaller snakes.

Previous research suggests that female and male *H. elegans* generally attain sexual maturity at 2 years of age (Ward 2001). The results of the present investigation suggest that male and female *H. elegans* attain sexual maturity at 3 and 4 years of age, respectively. The difference between the two studies could be attributed to the asymptotic mean length value used in the von Bertalanffy growth curve. The asymptotic mean length value had been determined for a population of *H. elegans* trawled on the northern Australian continental shelf (Ward 2001). Mean male and female SVL lengths of my study population were larger than those of Ward's population, suggesting that *H. elegans* on the West Coast grow larger. In that case, the age estimates could be inaccurate as Ward's parameters would not apply to my population.

The data from this study strongly suggest that although *H. elegans* and *D. major* share a similar geographical range and a comparable overall morphology, the differences in their head size have significantly altered their feeding ecology, and may facilitate their co-existence through resource partitioning. The difference in prey size between male and female *H. elegans* also suggests that sexual size dimorphism facilitates intra-specific resource partitioning. Future studies should address the foraging behaviour and habitat use of both of these species as these data would help explain the dietary differences between them.

2.6 Acknowledgments

I thank my assistants Trevor Bujas and Nadine Maynard, for all of their efforts in the field, and Larry Dill of Simon Fraser University without whose moral and financial support this project would not have been possible. Thanks to all of the members of the Dillery for their advice and editing throughout this entire process. I am also very grateful to the Western Australia Museum for allowing me the use of their sea snake collection as well as providing me with a wonderful work space. Thank you to fellow herpetologists Dave Pearson and Harold Voris for all of their advice and encouragement along the way. I would like to thank John McCosker for sharing his expertise on snake-eels and their general ecology. Lastly, a very special thank you to the crew at W.A.M., Brad Maryan, Paul Doughty and Glenn Moore, for giving more support and help than any one biologist could ever hope to receive. This work was conducted under the authorities of the Department of Conservation and Land Management permits SF004410 and CE000532, and Simon Fraser University Animal Care permit #659B-03. Financial support was provided by NSERC Canada (grant A6869 to L.M Dill).

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2.8 Figure Legends

Figure 2.1. Schematic diagram of morphological measurements (modified from Heatwole 1999 and Cogger 2000). SVL and TL were measured on straightened snakes.

Figure 2.2. Body size distribution *Hydrophis elegans* caught in Shark Bay (juveniles n=17, males n=5, females n=2), and WA Museum specimens captured off the West Coast of Australia (males n=46, females n=60).

Figure 2.3. Body size distribution of *Disteria major* (males n=7, females n=19) caught off the West Coast of Australia.

Figure 2.4. Morphological traits of female (n=60), male (n=46) and juvenile (n=17) *H. elegans* collected from the West Coast of Australia. (a) Scattergram of ln(weight) against ln(snout-vent length); (b) Scattergram of ln(girth) against ln(snout-vent length); (c) Scattergram of ln(head length) against ln(snout-vent length); (d) Scattergram of ln(neck circumference) against ln(snout-vent length); (e) Scatergram of ln(tail length) vs ln(snout-vent length); (f) Scattergram of ln(head width) vs ln(snout-vent length), with linear regression lines shown.

Figure 2.5. Comparison of morphological traits of female (n=60) and male (n=46) *H. elegans* and female (n=19) and male (n=7) *D. major* collected from the West Coast of Australia. (a) Scattergram of ln(weight) against ln(snout-vent length); (b) Scattergram of ln(head width) against ln(snout-vent length); (c) Scattergram of ln(girth) against ln(snout-vent length); (d) Scattergram of ln(head length) against ln(snout-vent length), with linear regression lines shown.

Figure 2.6. The relationship between snout-vent length (cm) and the reproductive state of female and male *H. elegans*. The point where the logistic regression line crosses y= 0.5 (represented by a circle) is the best estimate of the SVL at sexual maturity.

Figure 2.7. The relationship between snout-vent length (cm) and the number of eggs within a clutch for *D. major* and *H. elegans* ($y=0.70 + 0.035x$, $r^2=0.20$, $P=0.554$, and $y=-36.70 + 0.26x$, $r^2=0.68$, $P=0.012$, respectively).

Figure 2.8. Age distribution of *Hydrophis elegans* caught along the West Coast of Australia, based on the von Bertalanffy growth curve previously determined by Ward (2001).

Figure2.9. The head width of *H. elegans* males (n=13), females (n=12) and *D. major* (n=7) vs the width of the prey items found in their guts ($r^2=0.44$, $y=-5.32 + 1.13x$).

2.9 Tables

Table 2.1. Results of linear regressions examining the effects of ln snout-vent length on the ln values of other morphological traits (weight, tail length, head width, head length, neck circumference and girth) for three classes (male, female, and juvenile) of *H. elegans*.

Trait	Sex/Age	r^2	Slope	Intercept	F	P-value
Weight	**J**	0.839	2.350	-5.251	318.402	**<0.0001**
	M	0.421	1.885	-2.890	31.983	**<0.0001**
	F	0.810	3.250	-9.840	247.289	**<0.0001**
Tail Length	**J**	0.541	0.727	-1.152	17.698	**0.0008**
	M	0.174	0.407	0.596	9.240	**0.004**
	F	0.272	0.776	-1.362	21.633	**<0.0001**
H. Width	**J**	0.002	0.035	1.963	0.029	0.868
	M	0.322	0.756	-1.055	20.898	**<0.0001**
	F	0.511	1.078	-.2.663	60.713	**<0.0001**
H. Length	**J**	0.291	0.352	1.196	6.168	**0.025**
	M	0.206	0.464	0.807	11.414	**0.002**
	F	0.666	1.015	-1.959	115.652	**<0.0001**
Neck	**J**	0.253	0.540	-1.144	5.082	**0.040**
	M	0.320	0.612	-1.297	20.717	**<0.0001**
	F	0.692	1.128	-3.886	130.431	**<0.0001**
Girth	**J**	0.686	1.053	-2.827	32.7816	**<0.0001**
	M	0.222	0.616	-0.707	12.591	**0.001**
	F	0.690	1.137	-4.570	129.328	**<0.0001**

Note: Significant P-values are in bold.

Table 2.2. The results of ANCOVAS examining the effects of snout-vent length and class (male, female, and juvenile) on morphological traits (weight, tail length, head width, head length, neck circumference and girth) of *H. elegans*. Multiple pairwise comparisons were performed for each trait to determine which classes' traits grew at different rates, relative to SVL. Classes represented by different letters grew at a significantly different rate for that particular morphological trait, whereas classes with the same letter did not.

Trait	**P-value**	**J**	**F**	**M**
Weight	**0.0027**	AB	A	B
Tail length	0.15	-	-	-
Head width	**0.0006**	A	B	B
Head length	**0.0002**	A	B	A
Neck circumference	**0.0024**	A	B	A
Girth	**0.002**	AB	A	B

Note: Significant P-values are in bold.

Table 2.3. Results of linear regressions examining the effects of ln SVL on the ln values of other morphological traits (weight, tail length, head width, head length, neck circumference and girth) for two classes (male and female) of *D. major*.

Trait	Sex	r^2	Slope	Intercept	F	P-value
Weight	M	0.711	1.164	-1.198	12.292	**0.017**
	F	0.739	2.254	-3.968	48.108	**<0.0001**
Tail Length	M	0.092	0.128	-1.856	0.508	0.508
	F	0.433	0.834	-1.413	12.959	**0.002**
H. Width	M	0.633	0.777	-0.612	8.638	**0.032**
	F	0.320	0.752	-0.407	8.008	**0.012**
H. Length	M	0.202	0.156	2.475	1.268	0.311
	F	0.447	0.691	0.099	13.741	**0.002**
Neck	M	0.705	0.562	-0.567	11.929	**0.018**
	F	0.111	0.290	0.649	2.123	0.163
Girth	M	0.613	0.759	-1.081	7.933	**0.037**
	F	0.092	0.299	0.998	1.727	0.206

Note: Significant P-values are in bold.

Table 2.4. The results of ANCOVAS examining the effects of snout-vent length and "species" on morphological traits (weight, tail length, head width, head length, neck circumference and girth) of *H. elegans* and *D. major.* Multiple pairwise comparisons were performed for each trait to determine which "species'" traits grew at different rates, relative to SVL. "Species" represented by different letters grew at a significantly different rate for that particular morphological trait, whereas "species" denoted by the same letter did not.

Trait	P-value	*H. elegans*		*D. major*	
		F	M	F	M
Weight	**0.0017**	A	B	B	B
Tail length	0.1798	-	-	-	-
Head width	0.5974	-	-	-	-
Head length	**0.002**	A	B	AB	B
Neck circumference	**0.0009**	A	B	B	B
Girth	**0.0002**	A	B	B	B

Note: Significant P-values are in bold.

2.10 Figures

Figure 2.1

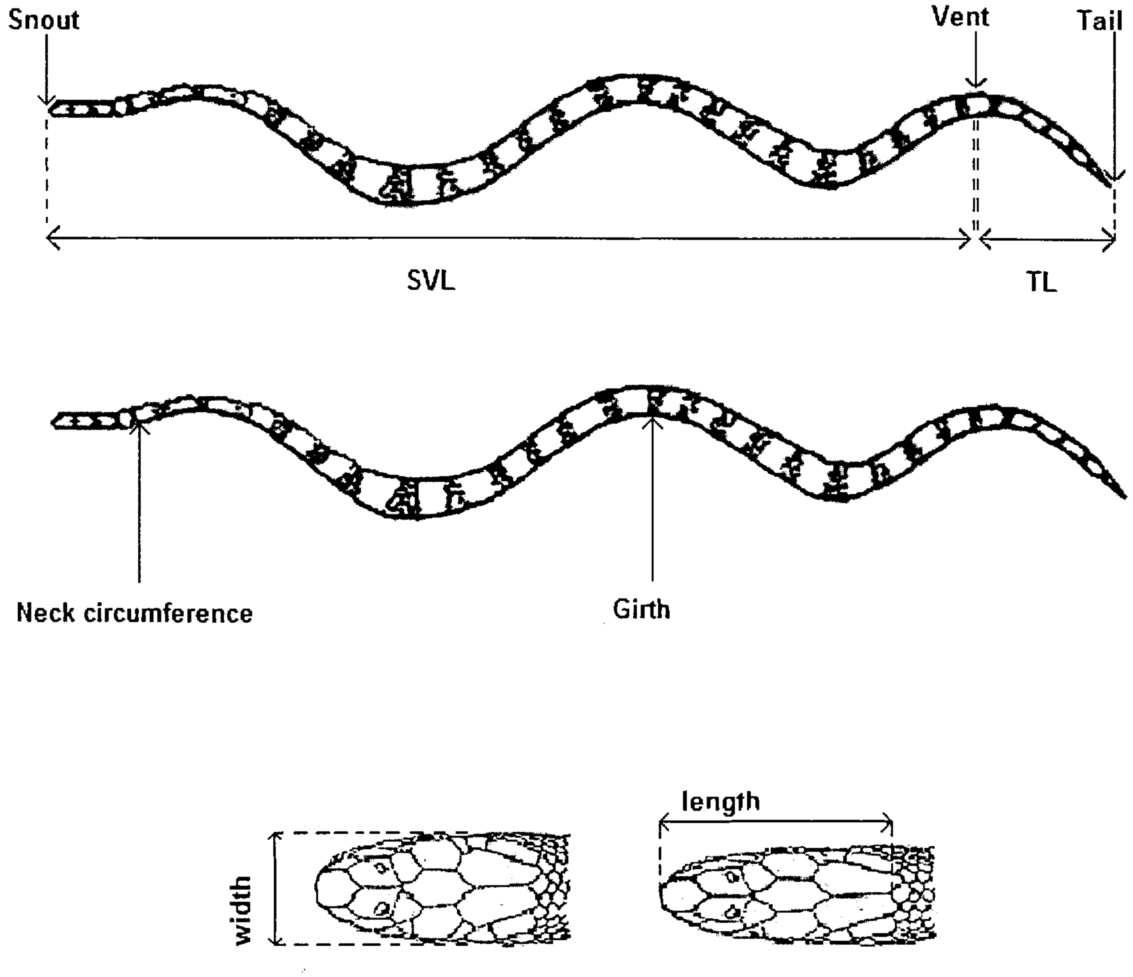


Figure 2.2

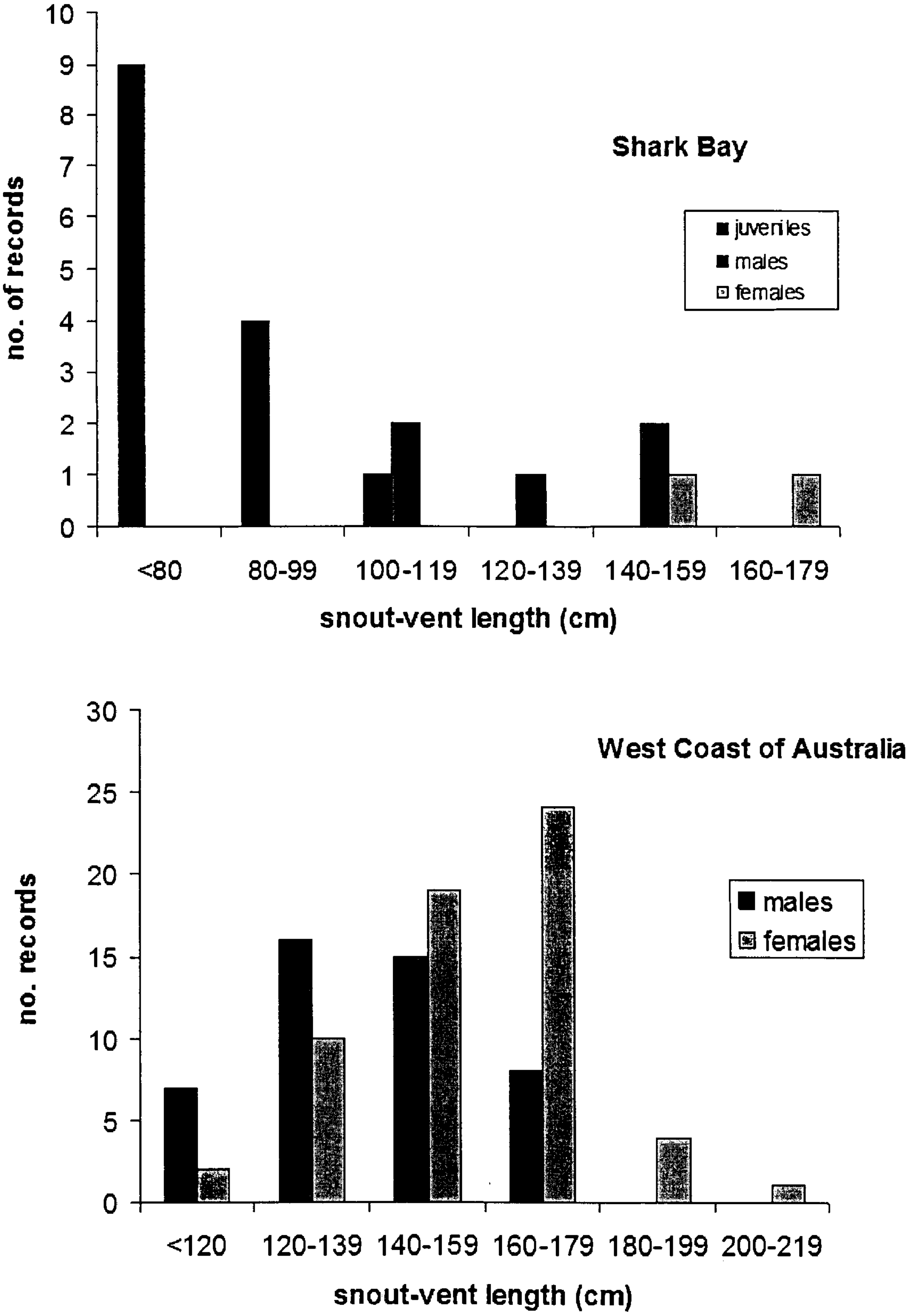

Shark Bay
■ juveniles
■ males
▨ females
no. of records
10
9
8
7
6
5
4
3
2
1
0
<80
80-99
100-119
120-139
140-159
160-179
snout-vent length (cm)
West Coast of Australia
■ males
▨ females
no. records
30
25
20
15
10
5
0
<120
120-139
140-159
160-179
180-199
200-219
snout-vent length (cm)

Figure 2.3

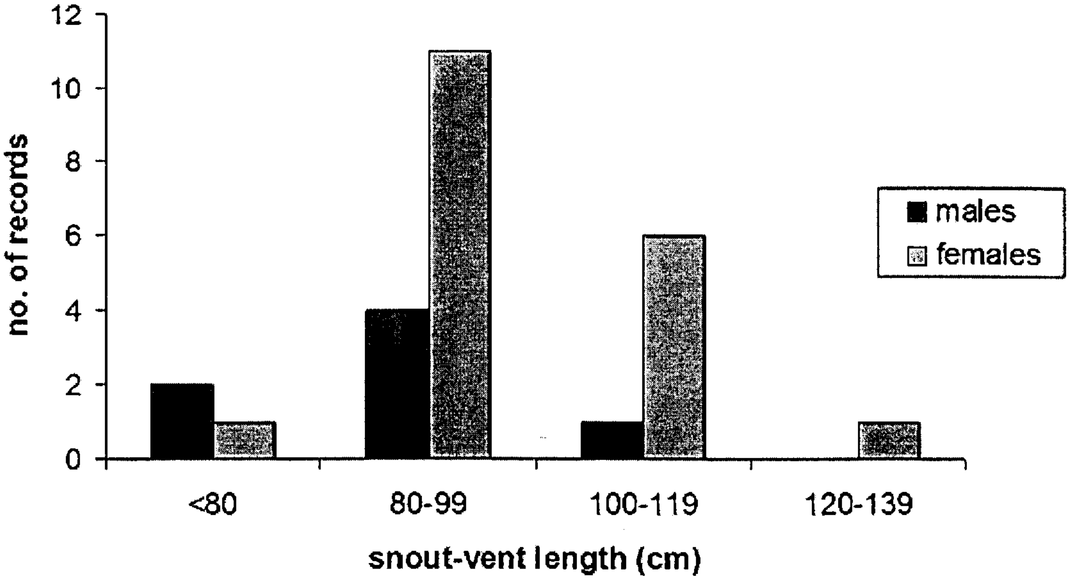
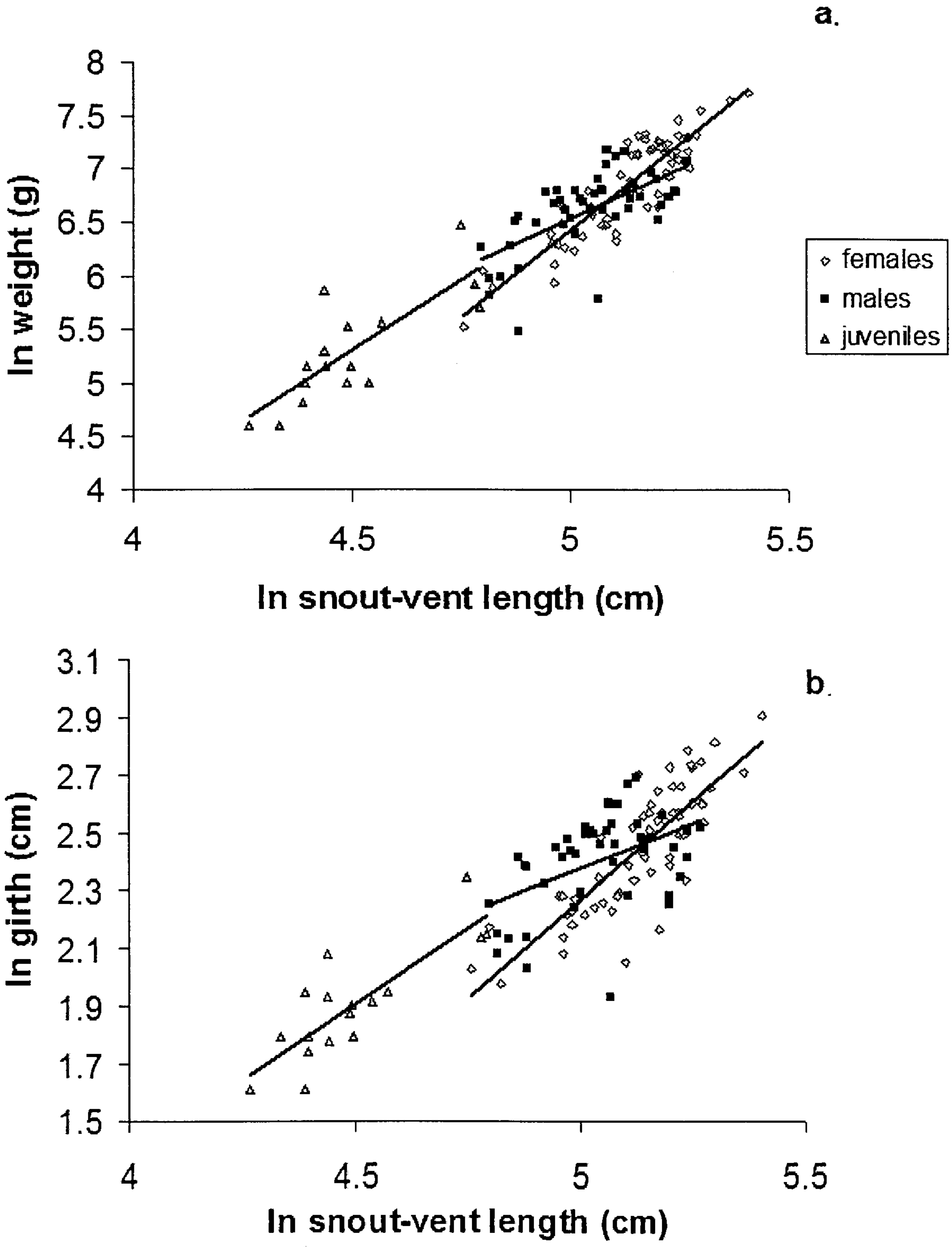
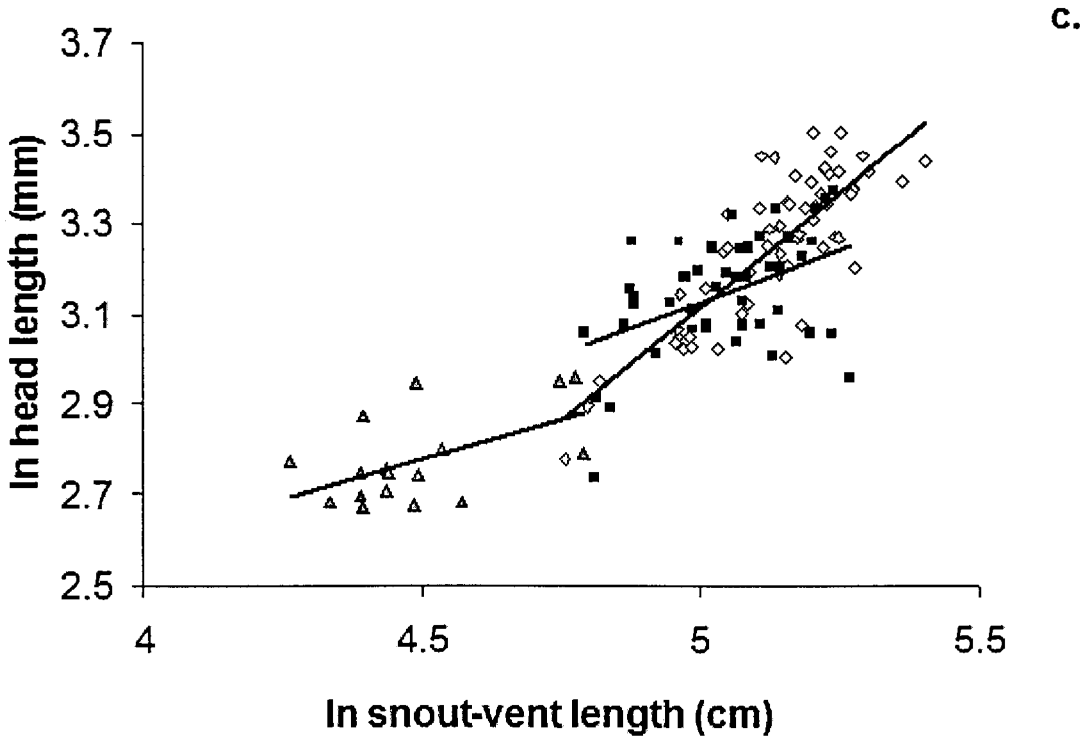
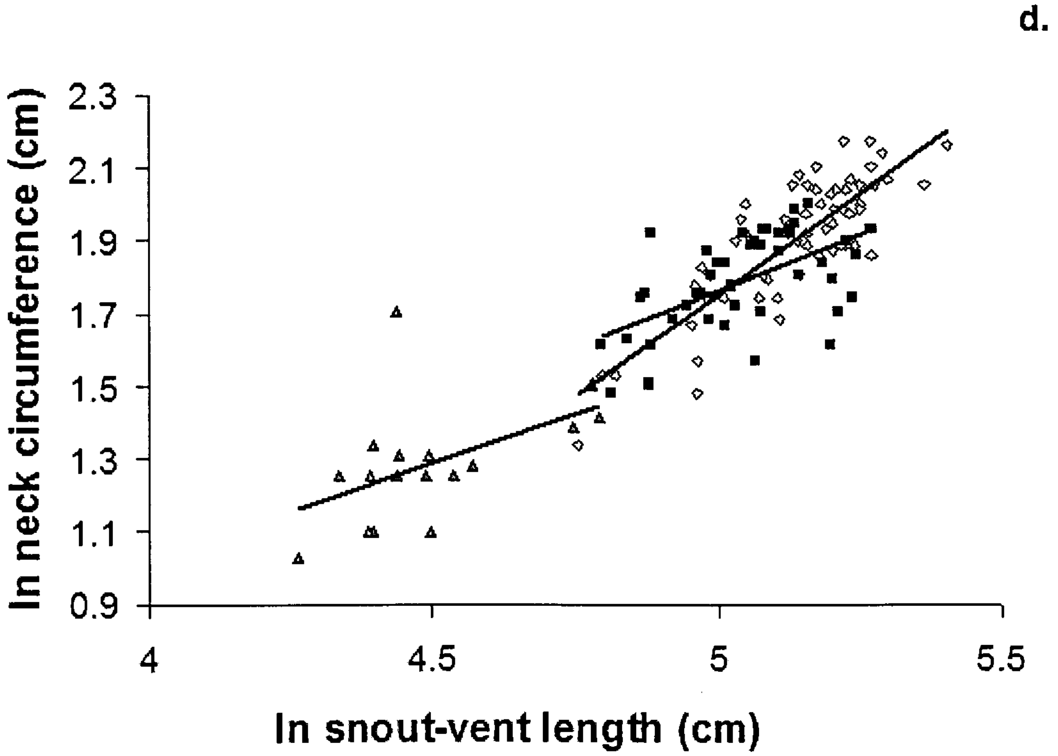
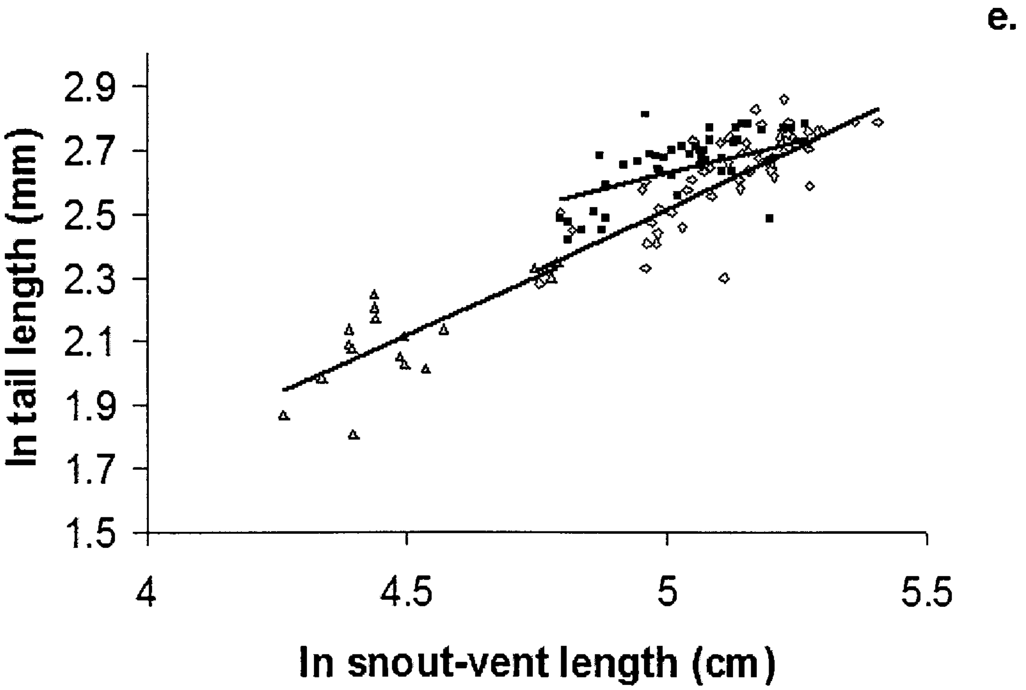

12
10
8
6
4
2
0
no. of records
males
females
<80
80-99
100-119
120-139
snout-vent length (cm)

Figure 2.4


a.
8
7.5
7
6.5
6
5.5
5
4.5
4
ln weight (g)
4
4.5
5
5.5
ln snout-vent length (cm)
◇ females
■ males
▲ juveniles
b.
3.1
2.9
2.7
2.5
2.3
2.1
1.9
1.7
1.5
ln girth (cm)
4
4.5
5
5.5
ln snout-vent length (cm)


c.
3.7
3.5
3.3
3.1
2.9
2.7
2.5
ln head length (mm)
4
4.5
5
5.5
ln snout-vent length (cm)


d.
2.3
2.1
1.9
1.7
1.5
1.3
1.1
0.9
ln neck circumference (cm)
4
4.5
5
5.5
ln snout-vent length (cm)


e.
2.9
2.7
2.5
2.3
2.1
1.9
1.7
1.5
ln tail length (mm)
4
4.5
5
5.5
ln snout-vent length (cm)

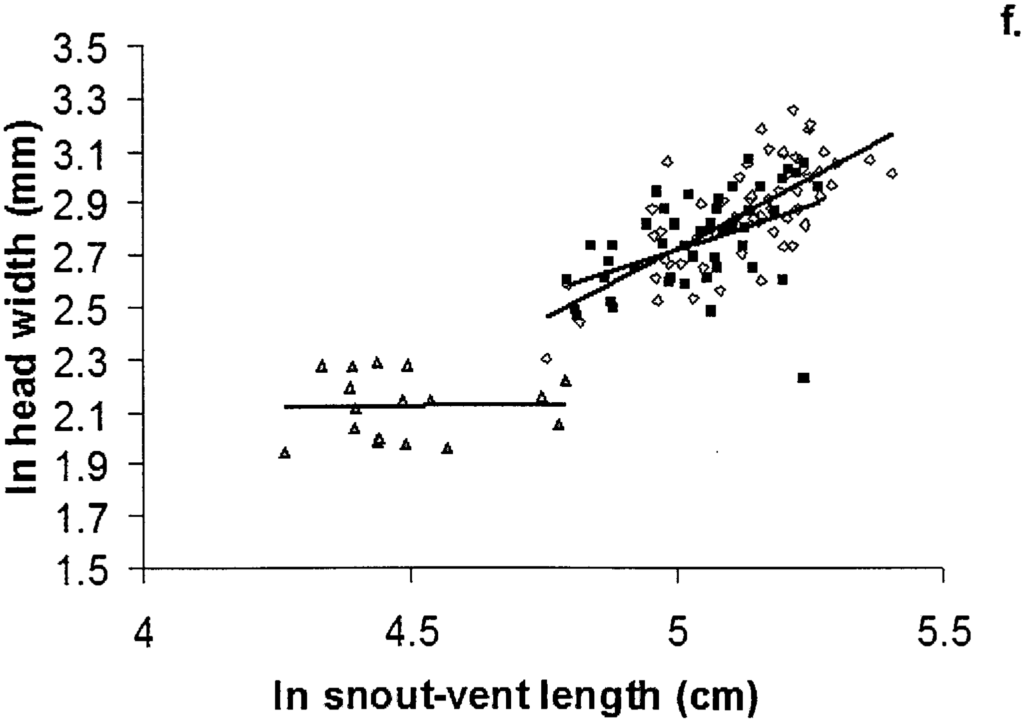
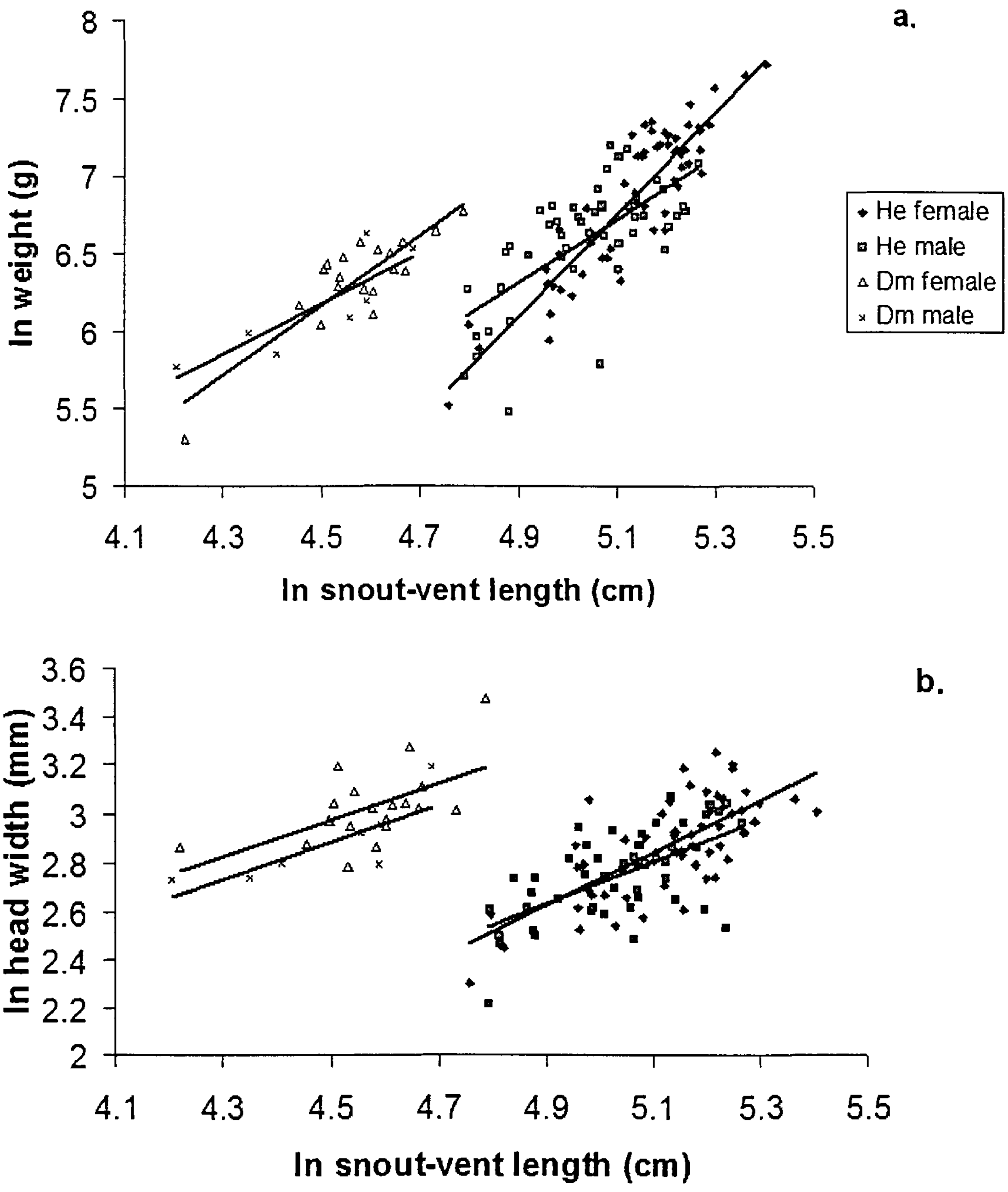
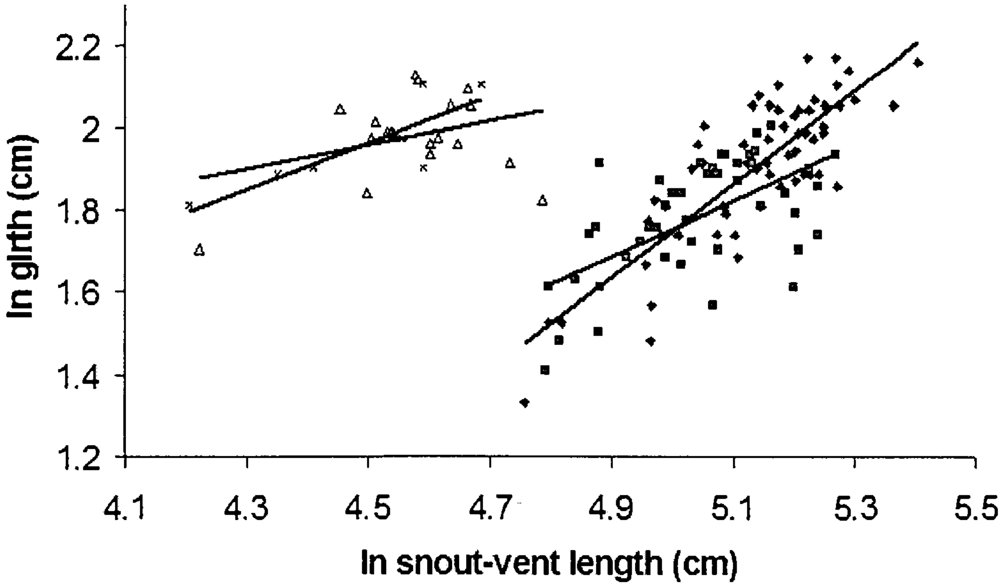

f.
3.5
3.3
3.1
2.9
2.7
2.5
2.3
2.1
1.9
1.7
1.5
ln head width (mm)
4
4.5
5
5.5
ln snout-vent length (cm)

Figure 2.5


a.
8
7.5
7
6.5
6
5.5
5
ln weight (g)
4.1
4.3
4.5
4.7
4.9
5.1
5.3
5.5
ln snout-vent length (cm)
◆ He female
▫ He male
△ Dm female
× Dm male
b.
3.6
3.4
3.2
3
2.8
2.6
2.4
2.2
2
ln head width (mm)
4.1
4.3
4.5
4.7
4.9
5.1
5.3
5.5
ln snout-vent length (cm)

c.


2.2
2
1.8
1.6
1.4
1.2
ln girth (cm)
4.1
4.3
4.5
4.7
4.9
5.1
5.3
5.5
ln snout-vent length (cm)

d.

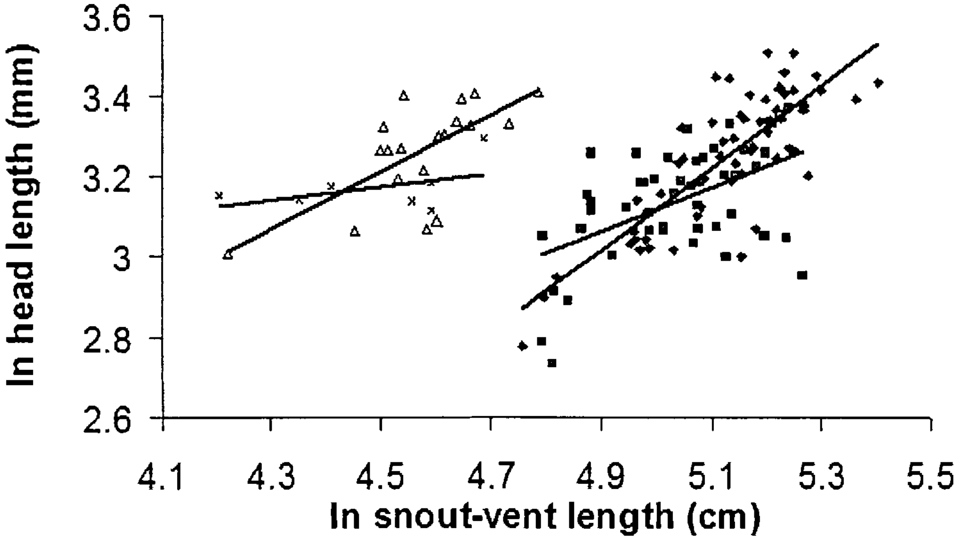
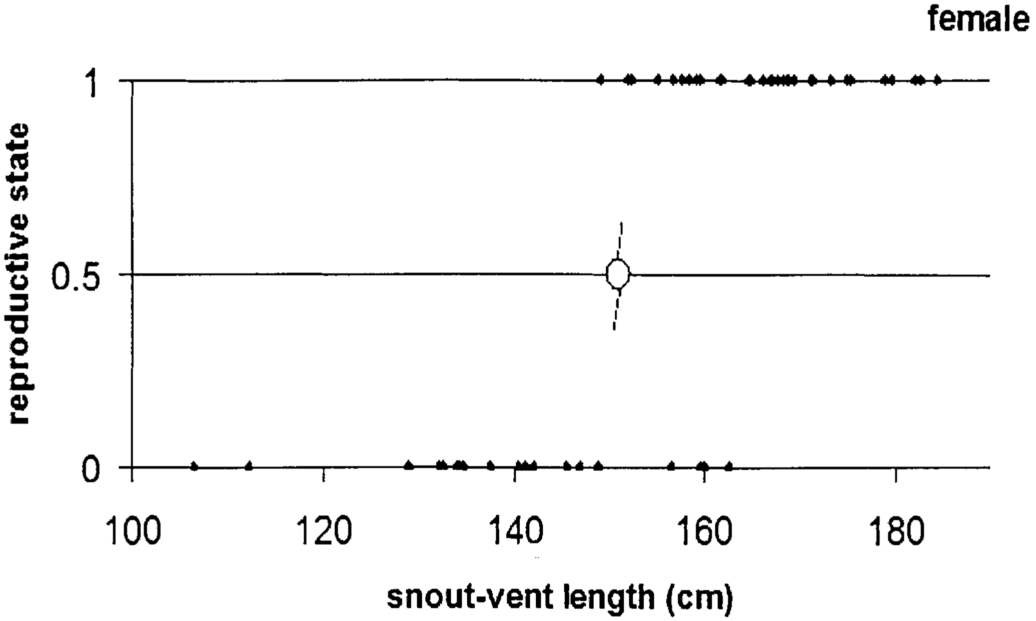

3.6
3.4
3.2
3
2.8
2.6
ln head length (mm)
4.1
4.3
4.5
4.7
4.9
5.1
5.3
5.5
ln snout-vent length (cm)

Figure 2.6


female
1
0.5
0
reproductive state
100
120
140
160
180
snout-vent length (cm)

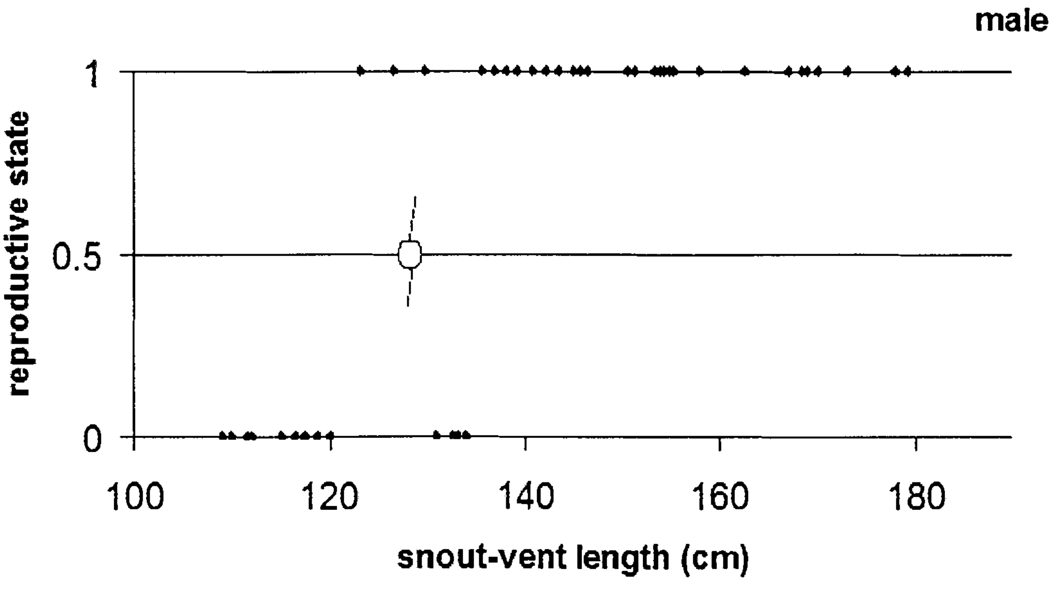
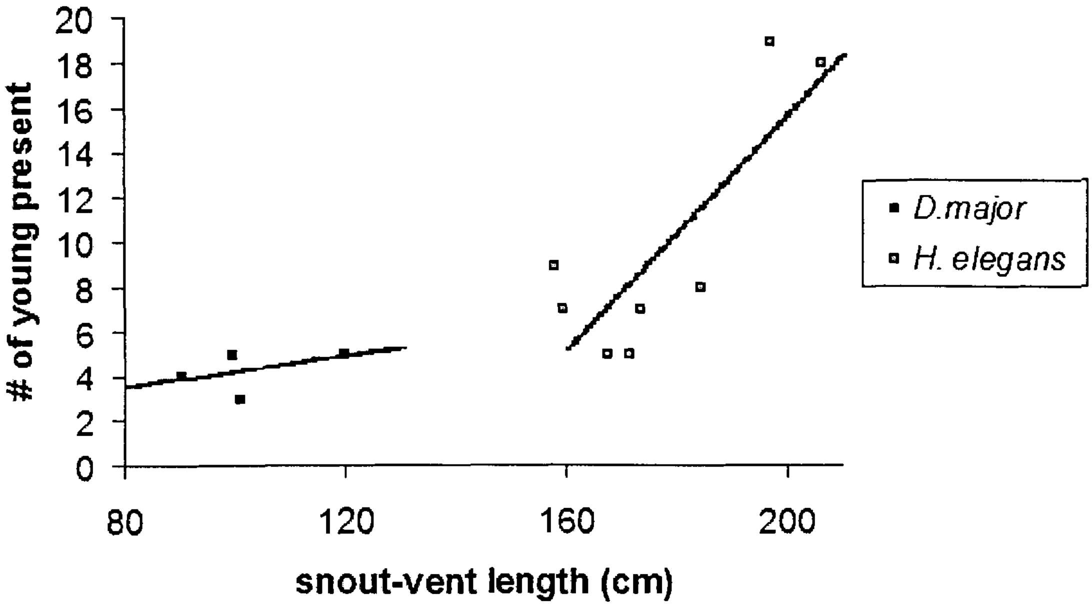
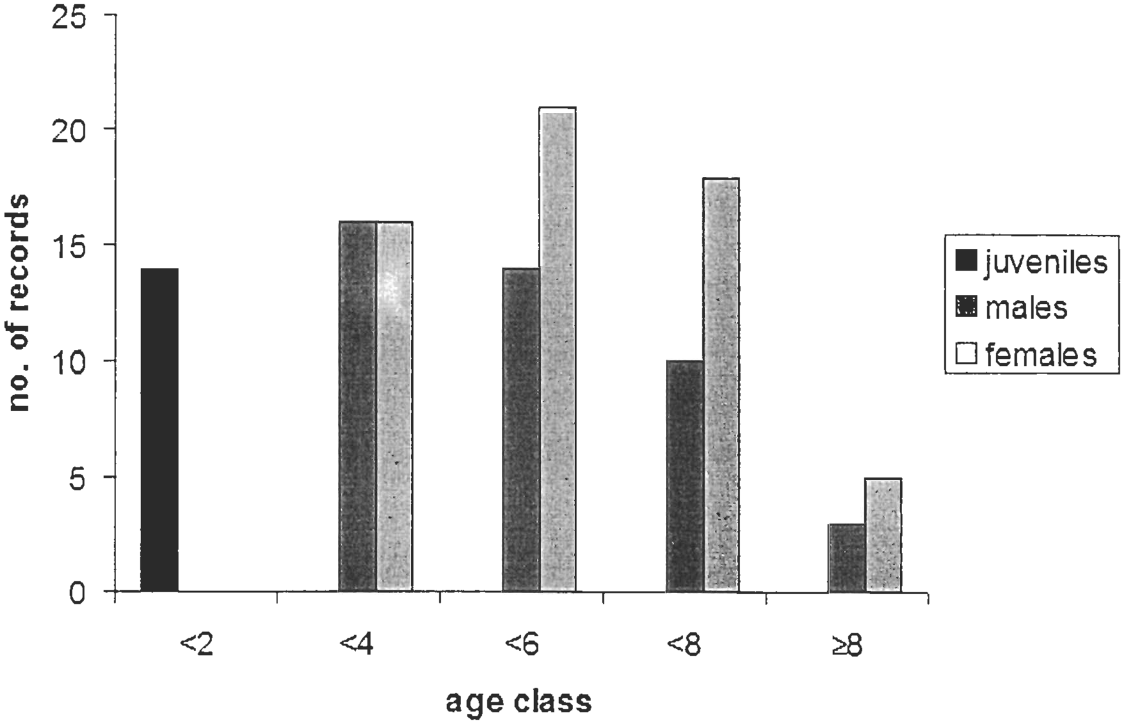

male
1
0.5
0
reproductive state
100
120
140
160
180
snout-vent length (cm)

Figure 2.7



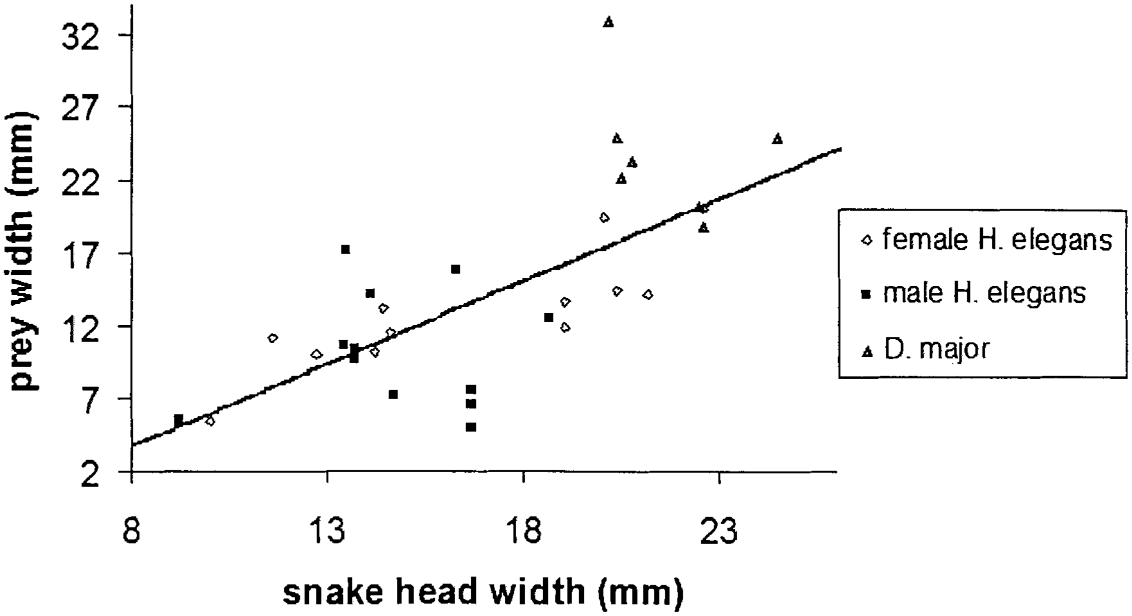
20
18
16
14
12
10
8
6
4
2
0
# of young present
80
120
160
200
snout-vent length (cm)
■ D.major
□ H. elegans

Figure 2.8



25
20
15
10
5
0
no. of records
<2
<4
<6
<8
≥8
age class
juveniles
males
females

Figure 2.9


32
27
22
17
12
7
2
prey width (mm)
8
13
18
23
snake head width (mm)
◇ female H. elegans
■ male H. elegans
▲ D. major

CHAPTER 3:

Habitat use of the bar bellied sea snake (*Hydrophis elegans)* in Shark Bay, Western Australia

3.1 Abstract

Habitat use often varies with changes in prey availability and/or predation risk. In marine environments, both prey availability and predation risk may be influenced by abiotic factors including tidal state. I used belt transects to investigate the effect of tidal state on the habitat use of the bar bellied sea snake (*Hydrophis elegans*). Snake prey are primarily found over sand habitats, suggesting that snakes should forage preferentially in these habitats if prey availability were the major determinant of their habitat use. However, snake habitat use varied with tidal cycle. At low tide, more snakes were found over sand, whereas at high tide, snakes used primarily seagrass habitats. The shift in habitat use with tidal state is likely due to an avoidance of predators during high tide, because tiger sharks (*Galeocerdo cuvier*), a major predator of sea snakes in Shark Bay, are likely able to enter shallow sand habitats only at this time. In support of this hypothesis, snakes were found foraging (a risky behaviour which exposes their hind end) over sand at low tide but not at high tide.

3.2 Introduction

Two primary characteristics of habitats that determine their suitability to a forager are food availability and predation risk (Lima and Dill 1990, Pratt and Fox 2001, Sapir et al. 2004). However, animals usually must make decisions based on both of these factors simultaneously because habitats often differ with regard to both. Habitats that have the highest availability of food often are also the most dangerous and animals must trade-off energy intake (food availability) and predation risk (Dill 1986). For example, baboons, *Papio cynocephalus ursinus*, trade-off foraging profitability for a lower predation risk by spending more time foraging in low risk, poor food quality habitat (Cowlishaw 1997). Juvenile black surfperch, *Embiotoca jacksoni* (Holbrook and Schmitt 1988), pink and chum salmon, *Oncorhynchus gorbuscha,* and *O. keta*, respectively (Magnhagen 1988), and bluegill sunfish, *Lepomis macrochirus* (Gotceitas and Colgan 1990) all make similar decisions, opting to forage in dangerous habitats only when foraging rewards are high relative to those available in safer habitats.

In the studies mentioned above, animals made choices between safe and dangerous habitats that were stable through time. However, in some systems, prey availability and predation risk may fluctuate temporally over periods of hours to months because they are influenced by abiotic factors such as temperature, salinity, and tidal state. For example, food availability and predation risk from tiger sharks (*Galeocerdo cuvier*) influenced habitat use of bottlenose dolphins (*Tursiops aduncus*) in Shark Bay, Western Australia, but the effect was driven by seasonal changes in water temperature (Heithaus and Dill 2002). During the cold winter months, tiger sharks are virtually absent and the dolphins spend the majority of their time in the shallow, high prey density seagrass habitat, while during the summer months, when the tiger sharks are abundant, the dolphins select the deeper, lower prey density waters where tiger sharks are less abundant. Less clear is why tiger sharks do not make greater use of deep habitats, where dolphins are more available, but it may be due to tiger sharks targeting alternative prey (Heithaus et al. 2002, Dill et al. 2003).

Bar bellied sea snakes (*Hydrophis elegans)* are an important prey species for tiger sharks in Shark Bay (Simpfendorfer et al. 2001), and may help drive the spatial and temporal patterns of shark abundance (Heithaus 2001, Heithaus et al. 2002), so understanding their habitat use patterns and the factors affecting these patterns are important to understanding the Shark Bay community. Tiger sharks and sea snakes both appear to show a preference for shallow habitats in Shark Bay (Heithaus 2001, Heithaus et al. 2002). However, some shallow areas may be inaccessible to sharks at low tide, resulting in a fluctuating predation risk within these habitats. Therefore, tidal state could be important in determining snake habitat use. The objective of this study was to measure habitat use of *H. elegans* in Shark Bay, and to determine if variation in tidal state (and by inference, of predation risk) influences the snakes' use of habitat.

3.3 Materials and methods

3.3.1 Study site

Shark Bay is situated approximately 800 km north of Perth on the westernmost point of Western Australia (approx. 25° 45'S, 113° 45'E) (Fig. 3.1a) . This study was conducted in the Eastern Gulf, offshore of the Monkey Mia Dolphin Resort (Figure 3.1b). The study site contains large areas of dense, species-rich seagrass beds, deep channels, and large shallow sand flats (Humphries 1990). Depths range from <2 m on the shallow sand flats and offshore seagrass banks, to 12 m in the deeper channels. Shark Bay's great species richness (including hundreds of species of fish, sharks, bottlenose dolphins, turtles, and sea snakes) and lack of human disturbance contributed to its listing as a UNESCO World Heritage Area in 1991 and makes it an ideal location to study the habitat use of *H. elegans*.

3.3.2 Study species

H. elegans is large hydrophiid snake, characterized by a greatly elongated body and relatively small head (Cogger 2000). They have 40-62 (personal observation) dark vertical bands contrasting with their pale bodies; these bands are incomplete in adults (i.e., they do not go around). According to Heatwole (1999), *H. elegans* is confined to the waters off the northern coasts of Australia (and Southern New Guinea), with Shark Bay being the most southern point of its distribution.

3.3.3 Transect surveys and behavioural data

Five sites were identified within the study area and 2-km transects were positioned at each site: one in a sand habitat, one in a seagrass habitat (Figure 3.2). Two observers drove along these transects in a 4.5-m boat at 7 km/hour. Transects were haphazardly surveyed on non-consecutive days between February 21 and April 21, 2004, at low and high tide. All *H. elegans* sightings within 5 m of the transect were recorded. I recorded the behaviour (i.e., breathing, foraging, resting and travelling) of each snake sighted. Breathing snakes were those with their head above the water surface. Snakes swimming above the substrate were recorded as travelling and foraging was assumed when the snake was in contact with the bottom, repeatedly poking the substrate with its head, or its head was inserted into the substrate with its tail sticking straight up in the water column. Snakes were considered to be resting if they were lying motionless on the bottom.

Tidal state, water temperature, cloud cover and sea state data were recorded at the beginning of each transect. The snakes spend little time at the surface, but detecting them on bright days was relatively easy because the sun reflected off their bodies as they surfaced. However, cloud cover eliminated this reflection, making them extremely difficult to locate at the surface; hence, only data collected when cloud coverage was ≤ 20 % was used for subsequent analyse. Rough water conditions also made it difficult to detect snakes. Sea state was measured using the Beaufort scale, with 0 representing water with no wind rippling. It was virtually impossible to see snakes surfacing or swimming below the surface when wind conditions were $\geq$ Beaufort 2, and therefore only sightings recorded in Beaufort conditions ≤ 1 were included in the analyses. The total numbers of snakes sighted in each habitat (sand and seagrass) for both tidal states (low and high) were divided by the total number of km of that habitat surveyed in order to provide an index of relative abundance. The relationships between snake abundance and habitat, tide, and site number, as well as the habitat x tide interaction, were analyzed using an ANCOVA. *Post hoc* Tukey tests were performed to compare the four combinations of habitat and tide to determine whether tidal state influenced the habitat use of *H. elegans*.

Focal follows of individual *H. elegans* were conducted when environmental conditions permitted. Snake behaviour was recorded at 2-min intervals (scan samples), along with substrate type, tidal state and the general direction the snake was heading. If a breathing event occurred during that 2-min interval, that was considered to be the primary behaviour. Focal data were divided into four habitat categories: sand or seagrass, at either low or high tide. The data for follows within a habitat category were pooled because the snakes within a habitat category generally allocated the same proportion of time to each behaviour. Focal data were recorded as the proportion of scan samples during which the snake was engaged in a particular behaviour, and interpreted as the percentage of time allocated to each behaviour.

3.3.4 Decoy experiment

As depth increases, the ability to view the bottom decreases due to light reflectance on the water (Endler, 1990) and turbidity, and could potentially lower the detectability of submerged *H. elegans*. Therefore, I conducted a decoy experiment to evaluate whether sighting probability of *H. elegans* over sand varied between low and high tide. Five rubber snakes painted to resemble *H. elegans* were randomly dropped along a transect with a sand bottom and their locations marked with GPS. Transects (n=20 each for low and high tide) were driven at 7 km/hour (Beaufort Sea state = 0 or 1, cloud coverage $\leq$20%) and a volunteer who was not watching during decoy placement counted the decoys observed. The mean numbers observed over sand at low and high tide were then compared.

3.3.5 Habitat analysis

Habitat variables were characterized at each transect. Substrate was classified as either sand, rubble (consisting of broken shells, rocks, corals, algae), senesced seagrass, or live seagrass, either *Amphibolis antarcticus* or *Posidonia australis*. Percent coverage and composition of the substrate was recorded at 50-m intervals for each transect using a 1 m^2 quadrat, randomly positioned. Seagrass biomass was estimated as the total volume occupied (Mumby et al. 1997) by multiplying seagrass height in a quadrat by the percent coverage.

3.4 Results

3.4.1 Decoy experiment

The mean water depth varied by 0.7 m between low and high tide (1.2 m and 1.9 m, respectively). Depths varied between 1.1 m to 1.2 m, and 1.8 m to 2.1 m for low and high tide, respectively. The mean numbers of snake decoys sighted over sand at low (3.2 ± 1.105 SD) and high tides (3.2± 0.894 SD) were identical, suggesting that detectability of *H. elegans* over sand does not vary with tidal state (Figure 3.3).

3.4.2 Snake habitat use

I surveyed 213.1 km over sand habitat (94.5 km low tide, 118.6 km high tide) and 300.3 km over seagrass habitat (122.2 km low tide, 178.1 km high tide). Mean low and high tide water depth were 1.32 m (range 0.5-5 m) and 3.13 m (range 1.8-10.7 m), respectively. The ANCOVA determined that habitat (sand or seagrass), tide (low or high), site (1-5), and the interaction between tide and habitat were significant in determining where and when snakes were located (Table 3.1). There were significantly more snakes sighted over sand at low tide than at high tide, and than over seagrass at either low or high tide. However, significantly more snakes were sighted over seagrass than over sand at high tide (Figure 3.4). All sites had the greatest number of snake sightings/km over sand at low tide except site # 3 (Figure 3.5), where the most snakes were sighted over seagrass at high tide.

3.4.3 Snake behaviour

The only behaviour seen over seagrass at high tide was breathing. This observation is potentially due to a detection bias; however, another similarly coloured species of sea snake present within the bay (*Disteria major)* was frequently observed foraging and travelling over seagrass at high tide. Snakes were only documented foraging over the sand, significantly more so at low (0.25 ± 0.438 SD) than at high (0.033 ± 0.180 SD) tide (t= 3.5, 103df, P=0.0003) (Figure 3.6a). The limited focal follow data for sand at low tide suggested that each individual snake was allocating a similar amount of time to foraging and breathing (Table 3.2). The focal data also suggested that *H. elegans* forage over sand at low rather than high tide (t=10.8, 2df, P= 0.004) which concurs with the transect data (Figure 3.6b).

3.5 Discussion

Results from this study suggest that the bar bellied sea snake is shifting out of the sand habitat and into alternate habitats, perhaps including seagrass, at high tide. The results also suggest that the snakes forage primarily over sand habitat at low tide. The number of *H. elegans* in the seagrass habitat at either tide height is probably underestimated because the snakes may often be within the seagrass mat and more difficult to detect there. However, tidal state would not influence the detection of *H. elegans* that were not within the seagrass mat because *D. major* was frequently sighted foraging above the seagrass. Therefore it is probable that *H. elegans* is not using the seagrass habitat for foraging.

H. elegans are specialized feeders, foraging almost exclusively on snake eels (Ophichthidae) (Chapter 2). Snakes eels are found in most tropical waters and tend to occupy shallow, non-permanent sand burrows (McCosker and Rosenblatt 1993). My behavioural data suggest that *H. elegans* forage over sand at low tide by burrowing head first in the sand, leaving their tails waving and vulnerable to attack. This behaviour would be extremely risky to perform if predators were present. Many sharks are known to enter shallow habitats more frequently when tides are high because such areas are inaccessible to them at low water (sandbar shark, *Carcharhinus plumbeus*; Medved and Marshall 1983, leopard shark, *Triakis semifasciata*; Ackerman et al. 2000), and this is likely the case for tiger sharks in many of the shallow sand habitats I surveyed. At high tide, the tiger sharks are able to enter the sand habitat, increasing the risk there. Lima and Dill (1990) suggested that animals have the ability to assess predation risk and alter their behaviour accordingly, e.g., by shifting to another habitat (e.g., Sih 1983), and the results from this study support this belief.

Previous research focusing on predator-prey interactions in seagrass meadows has concentrated on habitat structure, and has not properly addressed the antipredatory responses displayed by prey species (Main, 1997). One common antipredatory response is for prey species to lower their activity levels when predation risk is elevated (e.g., Anssi et al. 1997, Brodin and Johansson 2002, Sih and McCarthy 2002). An ideal strategy for *H. elegans* would be to take refuge and rest under the seagrass canopy at high tide and spend all their time foraging at low tide. Although *H. elegans* were rarely observed sleeping/resting in this study, it is known that they do so (Heatwole 1999, Greer 1997). It has also been reported that *H. elegans* prefer to rest on soft substrate such as mud or sand (Redfield et al. 1978). Given that, one would expect to see them frequently resting over the sand, but this behaviour was not observed. The only other place they could be resting is within seagrass meadows, where the substrate would also be somewhat sandy and soft, and where they would be more difficult for predators to detect. This would explain why the snakes were mainly observed surfacing to breathe over seagrass at high tide, and suggests that they allocate time for resting at high tide as an antipredatory response.

I was unable to determine why site # 3 had the most snakes sighted over seagrass at high tide. The species and biomass of seagrass present in a habitat could potentially influence *H. elegans* sightings, as *A. antarticus* is much thicker then *P. australis,* and offers more refuge from predators for the snakes; *P. australis* consists of long thin strands that do not offer much cover. However, site #3 was not noticeably different from the other sites in this respect. Future studies could attempt to address this anomaly by focusing on the micro-habitat of this particular area, as well as snake eel availability and abundance within the five sites.

It is possible that the snakes are shifting habitat in response to factors other than predation risk, including variations in water current, temperature, etc.. Water temperature does not vary substantially between the shallow and deep water of my study site, and water currents are relatively low in shallow habitats in Shark Bay, rendering this possibility unlikely. Therefore, habitat use of *H. elegans* is most likely influenced by variation in predation risk with changes in water depth (tidal state) and snakes choose to forage over sand at low tide, when predation risk is lowest.

3.6 Acknowledgements

I thank David Charles for allowing me the use of the CALM boat during my second field season, as well as offering me much needed advice and support throughout. I offer my gratitude to the Monkey Mia Dolphin Resort and Dean Massey for providing me with accommodation and logistical support. Thank you to my two great field assistants, Trevor Bujas and Nadine Maynard, and to Aaron Wirsing and Mike and Linda Heithaus for helping me collect and organise my data, but more importantly, survive my field seasons!!! To Larry Dill and the rest of the Dillery, your positive criticism and support over the last three years have been tremendous and I truly appreciated it. This work was conducted under the authorities of the Department of Conservation and Land Mangement permits SF004410 and CE000532, and Simon Fraser University Animal Care permit #659B-03. Financial support was provided by NSERC grant A6869 to LM Dill, and PADI AWARE Australia.

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3.8 Figure Legends

Figure 3.1. a. Shark Bay, Western Australia (indicated by arrow). b. The study area was located offshore from the Monkey Mia Dolphin Resort (indicated by arrow).

Figure 3.2. The study area was located in the Eastern Gulf of Shark Bay, near Monkey Mia, and was divided into five paired sites, each containing a seagrass habitat, adjacent to a sand habitat. Two-km long transects were set using GPS waypoints in each of the five paired sites (n=5 for seagrass, n=5 for sand).

Figure 3.3. The number of *Hydrophis elegans* decoy sightings over sand at low and high tide from each set of 20 trials.

Figure 3.4. The number of *Hydrophis elegans* sighted/km surveyed over sand and seagrass at low and high tide. Habitat types (sand/seagrass at low/high tide) represented by different letters had significantly different numbers of sea snakes sighted.

Figure 3.5. The number of *Hydrophis elegans* sighted/km surveyed over sand and seagrass at low and high tide for the five paired sites.

Figure 3.6.a,b. The percentage of time *H. elegans* allocate to foraging over the four habitat categories, represented by a.) the number of snakes foraging/km surveyed during transects, and b.) the percent of time allocated to foraging recorded during focal follows.

3.9 Tables

Table 3.1. Results of an ANCOVA examining the effects of habitat (sand, seagrass), tide (low, high) and site on the number of *H. elegans* sighted per km surveyed. Other interactions were not significant.

Variable	F-value	P-value
Habitat	27.610	**<0.0001**
Tide	38.739	**<0.0001**
Site #	12.217	**0.0006**
Tide*Habitat	21.480	**<0.0001**

Table 3.2. **Individual focal follows broken down by habitat/tide category (sand or seagrass at low or high tide) showing the percent of time allocated to each behaviour by each snake.**

Category	Snake #	Total time	breathing	foraging	resting	travelling
sand low	1	86 min	25.6	39.5	2.3	32.6
	2	88 min	13.6	43.2	2.4	40.9
	3	64 min	40.6	50.0	9.4	0
	4	56 min	21.4	46.4	32.1	0
sand high	1	64 min	37.5	6.3	3.1	53.1
	2	18 min	33.3	0	0	66.7
seagrass low	1	38 min	36.8	0	0	63.2
	2	12 min	33.3	0	0	66.7
seagrass high	1	52 min	34.6	7.7	0	26.9

Note: There were times during the focal follow over seagrass at high tide when the snake was not visible for a period, and then would surface again to breathe (at the exact GPS point where it was last seen). This time (30.7%) was classified as unknown.

3.10 Figures

Figure 3.1

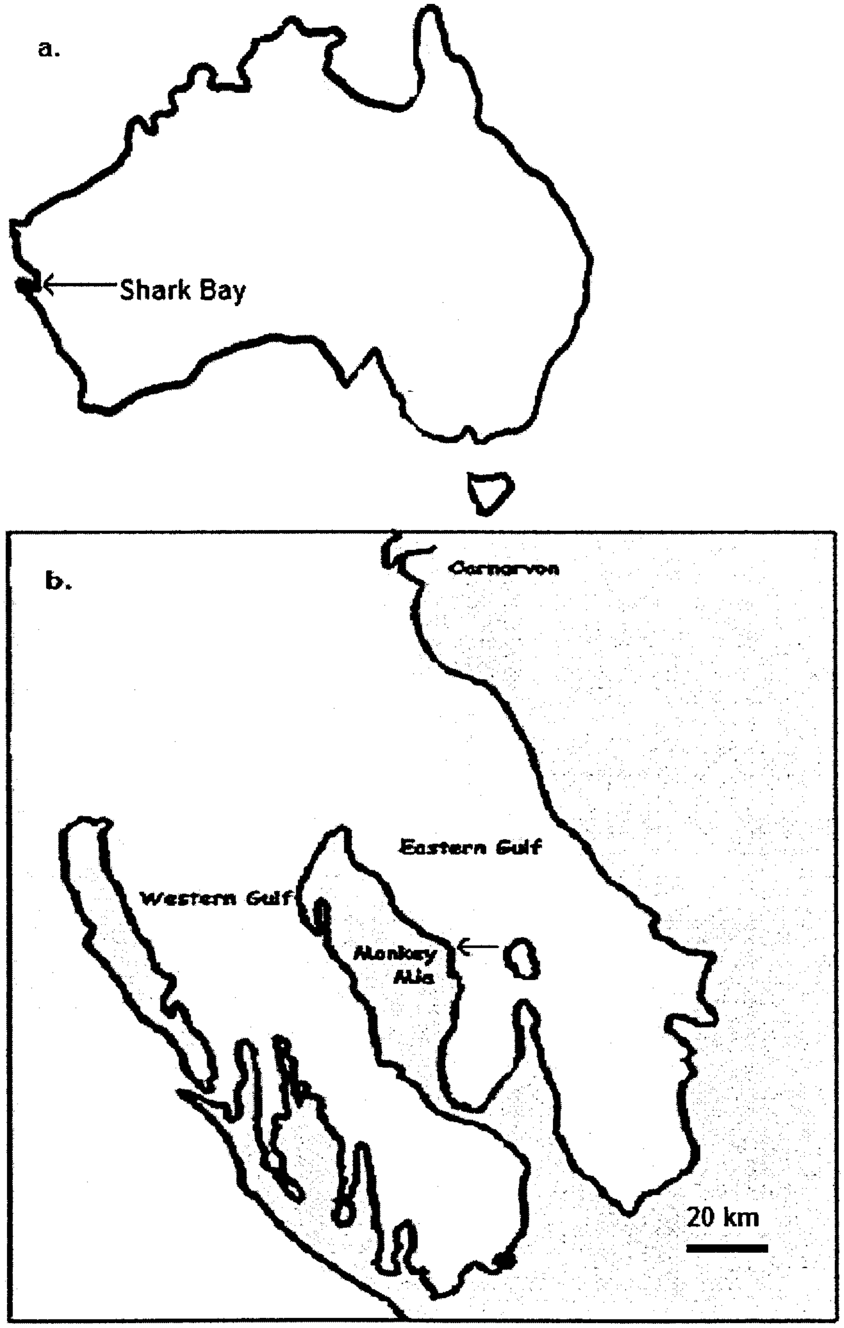


Figure 3.2

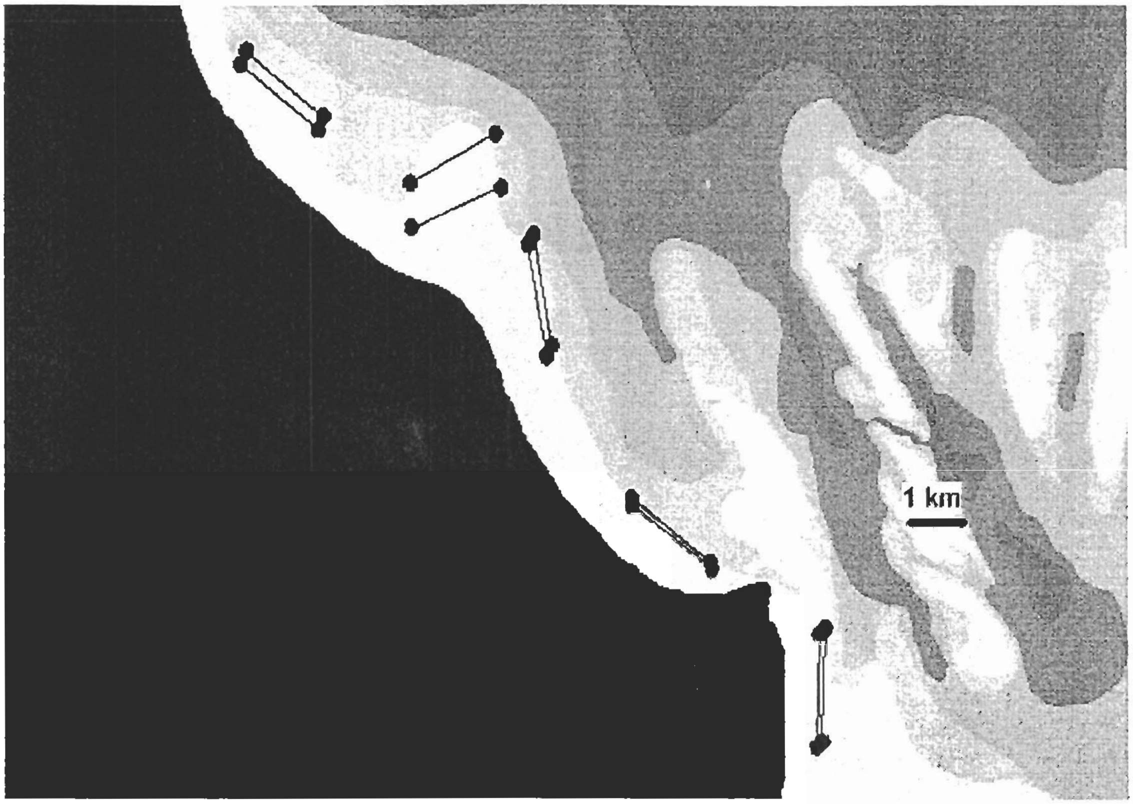


Figure 3.3

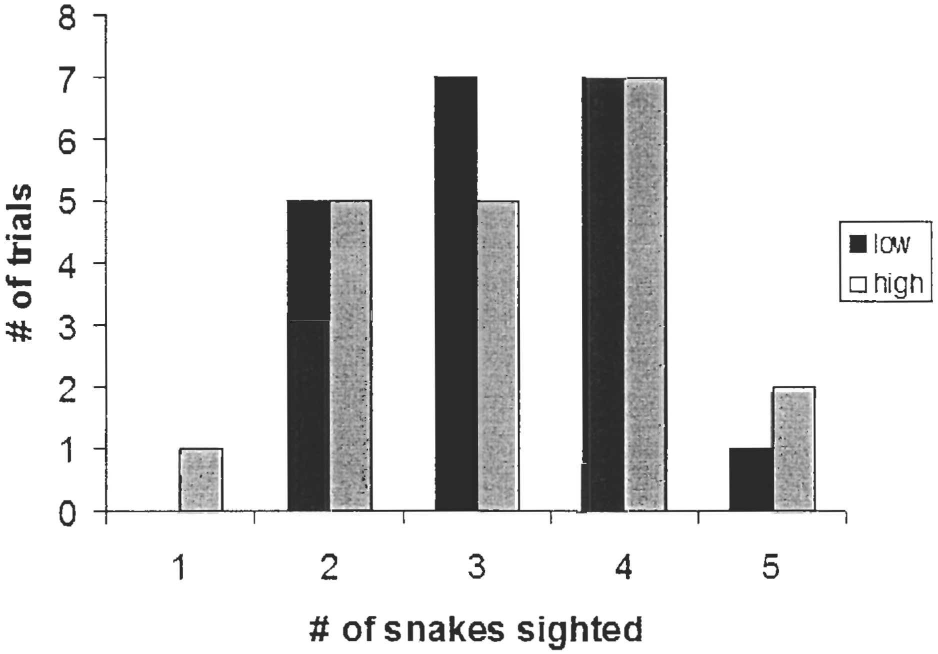
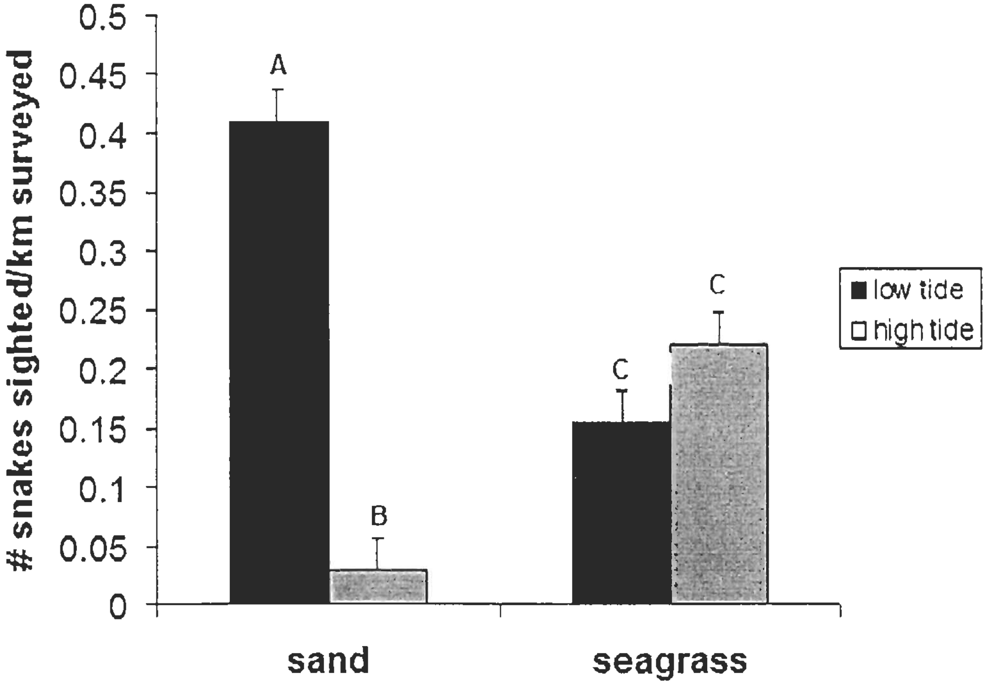
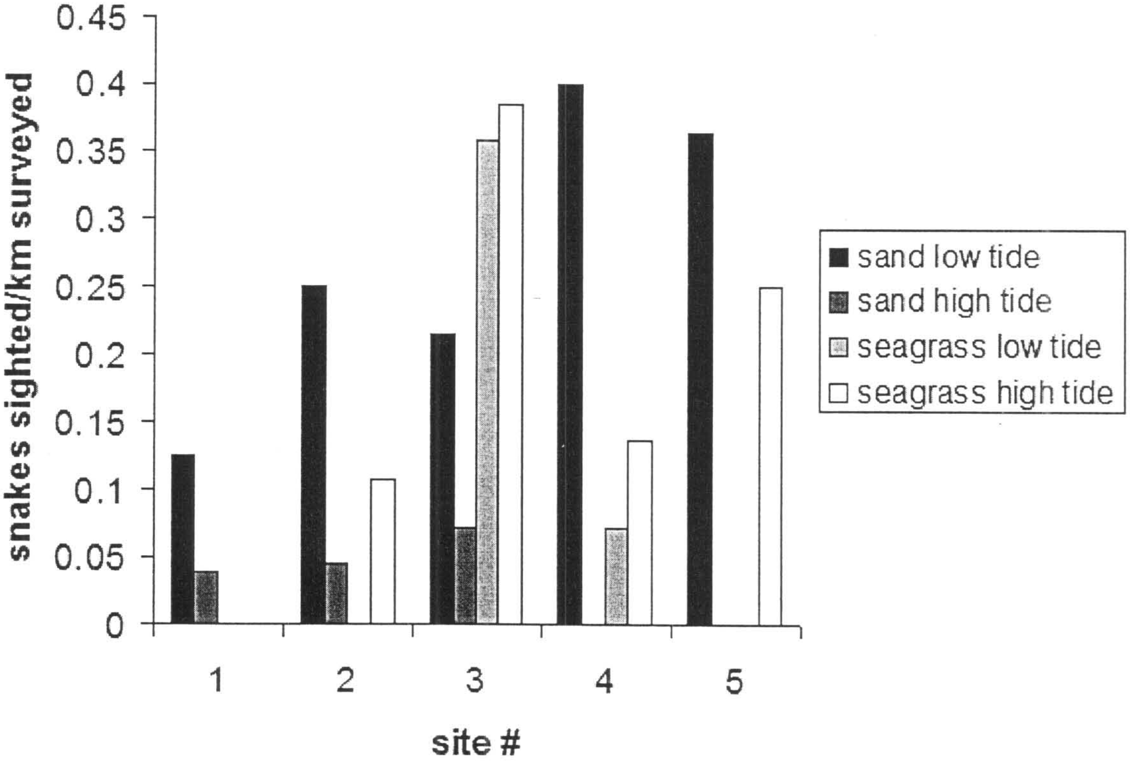


Figure 3.4



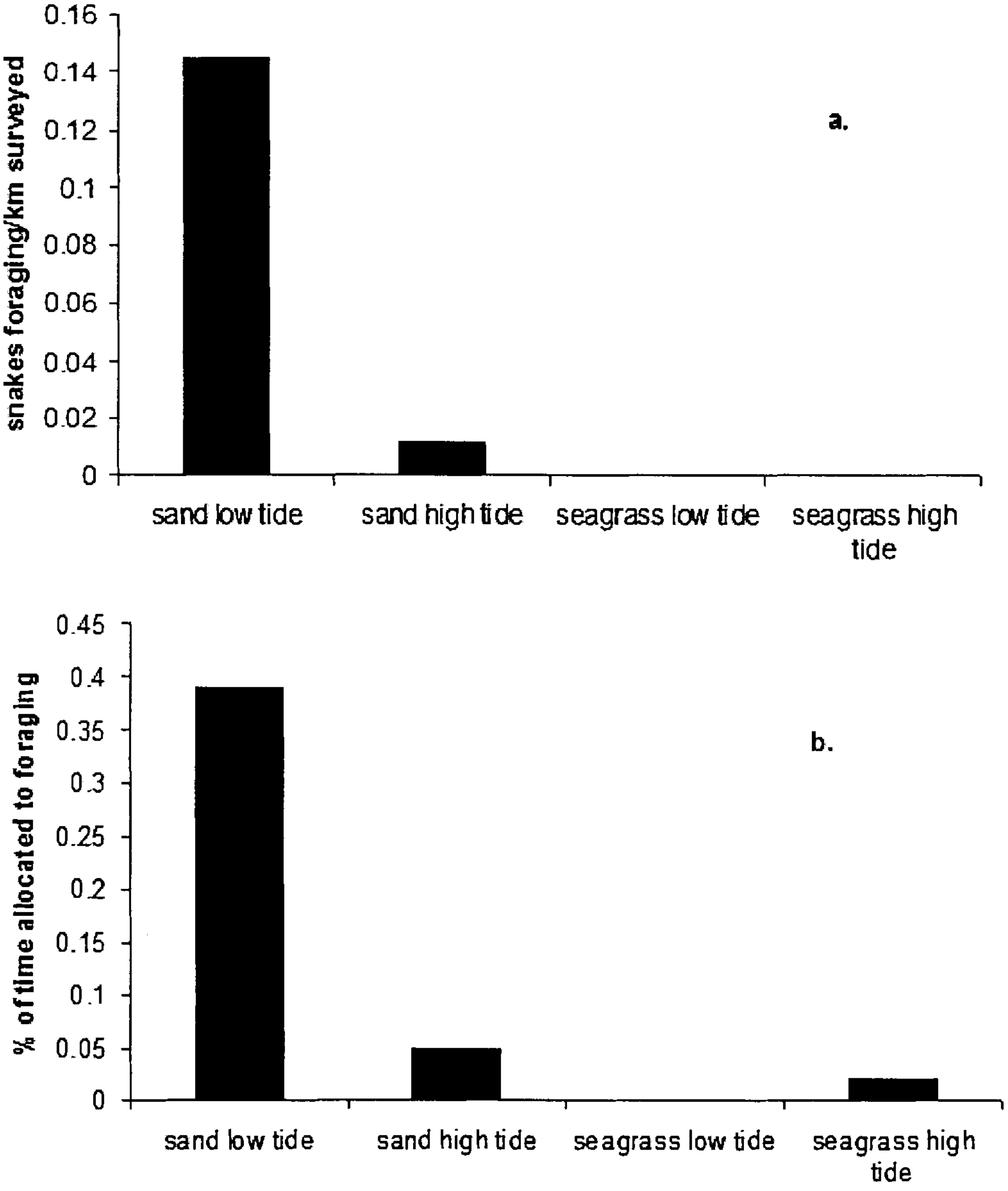
0.5
0.45
0.4
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
snakes sighted/km surveyed
A
B
C
C
■ low tide
□ high tide
sand
seagrass

Figure 3.5



0.45
0.4
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
snakes sighted/km surveyed
1
2
3
4
5
site #
■ sand low tide
▩ sand high tide
▨ seagrass low tide
□ seagrass high tide

Figure 3.6


a.
snakes foraging/km surveyed
0.16
0.14
0.12
0.1
0.08
0.06
0.04
0.02
0
sand low tide
sand high tide
seagrass low tide
seagrass high tide
b.
% of time allocated to foraging
0.45
0.4
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
sand low tide
sand high tide
seagrass low tide
seagrass high tide

CHAPTER 4:

Tides affect movements of fish across a sand-seagrass ecotone in a subtropical embayment

4.1 Abstract

Movements of aquatic species may be influenced by abiotic factors. I tested if tidal state influences movements of fish across a sand-seagrass ecotone in a subtropical embayment. Underwater video-cameras were used to record movements of several fish species over 2-h periods on flood tides at 5 sites. Each site consisted of a sand bank bordering a seagrass meadow; water depths were similar among sites. Fish were recorded as moving towards either the sand or seagrass habitat as they passed through a camera's field of view. The total net movement of fish was from sand to seagrass, and this trend was consistent among the size classes except for large fish (≥30 cm), for which movement was equal with respect to habitat type. This result suggests that as the tide rises, small to medium sized fish (< 30 cm) move from shallow sand habitats to seagrass meadows, potentially seeking refuge from predators, whereas larger fish, less susceptible to predation, do not respond to incoming tides with habitat shifts.

4.2 Introduction

Abiotic factors such as temperature, salinity and tidal state can affect the behaviour of aquatic species, including their patterns of movement. For example, water temperature affects the migratory movements of many species of fish (Zurstadt and Stephan 2004, Albanese et al. 2004, Hohausova et al. 2003), and salinity influences migratory movements in crabs (Turner et al. 2003, Carr et al. 2004). Tidal state could also be an important factor in the habitat selection of fish because some species are limited by water depth. However, recent studies of effects of tidal state on fish behaviour have addressed mainly spawning time (Rijnsdorp et al. 1985, Hay 1990) and the foraging behaviour of several marine predators (Medved and Marshall 1983, Ackerman et al. 2000, Zamon 2001), but effects on movements and habitat selection have not been examined.

Some habitats may be safer at low tide when larger predators are unable to enter them (Medved and Marshall 1983, Ackerman et al. 2000). Consequently, to avoid predation, small fish may shift habitats (move) in response to changes in water depth, imposed by tidal state. The aim of this study was to determine if fish movements across shallow sand-seagrass interfaces are affected by tidal state in Shark Bay, Western Australia. I addressed this question using underwater video-cameras placed haphazardly along the common border between unvegetated (sand) and vegetated (seagrass) habitats during incoming tides. The use of underwater technology provides opportunity to observe fish behaviour in a natural setting while causing very little disturbance.

4.3 Methods

4.3.1 Study site

Shark Bay is situated approximately 800 km north of Perth on the westernmost point of Western Australia (approx. 25° 45'S, 113° 45'E) (Figure 4.1a). It is a large, semi-enclosed body of water consisting of a several peninsulas and islands surrounded by large areas of dense, species-rich seagrass beds, deeper channels, and large shallow sand flats (Humphries 1990). The tide cycle is mixed semi-diurnal. The study area was the Eastern Gulf, offshore from the Monkey Mia Dolphin Resort (Figure 4.1b), and comprised five sites consisting of sand habitat bordering seagrass habitat. The minimum and maximum water depths at each site, recorded throughout the field season at low and high tide, were similar; seagrass coverage was also similar among sites, except site 1, which contained relatively more *Posidonia australis* (Table 4.1).

4.3.2 Video recording

Underwater video recordings were made between 18 February and 21 April, 2004. There were 10 recordings per site, and each recording was 2 h in length, for a total of 100 h. At each site a camera (8 mm Samsung camcorders encased in an underwater housing unit) was placed haphazardly along sand-seagrass borders one 1 h after low tide, with half the camera's field of view capturing sand and the other capturing seagrass. The sand habitat was always slightly shallower because it was the habitat closest to shore. A ruler attached horizontally in front of the camera allowed estimation of fish size. All fish passing through a camera's field of view during each recording period were noted and classified as small (<5 cm), small/medium (5-14 cm), medium (15-29 cm), or large (≥30 cm). I also noted whether individual fish moved towards sand or seagrass as they left the field of view of a camera. Net fish movement was expressed as the proportion of fish moving towards seagrass (i.e., the number of fish heading towards seagrass per recording divided by the total number of fish observed during that recording); a similar calculation was made for each size class. Proportional values tend to have a binomial distribution, so to achieve a normal distribution the data were arcsin square root transformed (Zar 1999).

4.3.3 Statistical analysis

Data were analyzed using the statistical program JMP (Sall et al. 2001). ANOVA was used to test whether the total number of fish observed differed among sites, and *post hoc* Tukey tests to determine which sites had significantly fewer fish overall. A one-tailed t-test was performed to determine whether the net movement of fish towards seagrass was significantly greater than the predicted mean value of 0.785 radians (the arcsin square root of 0.5). The same analysis was used to test the net movement of individual size classes. Recordings with 0 or 1 fish observed for a particular size class were removed from analyses because a proportional value could not be calculated; this mainly affected the large fish data set (Table 4.2). An analysis of covariance (ANCOVA) was used to test whether net movement differed between sites and size classes. For this analysis, arcsin square root transformed values for each size class served as the dependent variable, with size class and site as covariates. *Post hoc* Tukey tests were performed to determine which size classes were responsible for any differences detected.

4.4 Results

The total number of fish observed per recording ranged from 104 to 818. There were no significant differences between the number of fish observed between sites, except that significantly fewer fish were observed at site 1 than at sites 3 and 5. In total, 64 different fish species were recorded. The small and small/medium size classes consisted mainly of western butterfish (*Pentapodus vitta)*, whiting (*Sillago* spp.), and gizzard shad (*Anodontostoma chacunda*), the medium size class consisted mainly of striped sea pike (*Selenotoca multifasciata)*, black snapper (*Lethrinus laticaudis),* and yellowtail trumpeter (*Amniataba caudavittata)*, and the large size class consisted mainly of the banded goatfish (*Parupeneus multifasiatus*), giant herring (*Elops hawaiiensis*), hump-headed bat fish (*Platax batavianus*) and norwest blowie (*Lagocephalus sceleratus*). Three species of sea snakes (*Hydrophis elegans, Disteria major,* and *Aipysurus leavis*) were also observed, as well as sharks (*Triakis* spp., *Asymbolus* spp., and Carcharhinidae spp.) and a variety of rays (*Taeniura lymma, Pastinachus sephen, Aetobatus* spp., *Himantura* spp., and Rhinobatidae spp.).

Overall, the net movement of fish during incoming tides was towards seagrass (t=18.8, 48 df, P<0.001) with a proportional mean value of 0.617 (95% CI, 0.573 to 0.660). This proportion did not vary between sites (P=0.9) and remained for small, small/medium, and medium fishes when size classes were considered separately (Table 4.2). However, larger fish did not show a tendency to move towards seagrass. The result of the *post hoc* Tukey tests showed that there was no significant difference between the movements of small, small/medium, and medium size fish, but that movement of large fish was significantly different from that of the other three size classes (Figure 4.2). As the tide rises, the net movement of smaller fish is towards seagrass, whereas larger fish tend to move equally between the two habitats. Net movement of individual size classes did not differ among sites (F=0.5, 4 df, P=0.7).

4.5 Discussion

My findings suggest that fish in nearshore shallows shift habitats in response to increases in water depth associated with tidal influx. On incoming tides, fish tended to move from an unvegetated (sandy) habitat to a vegetated (seagrass) habitat. It is important to note, however, that fish behavioural data were not collected during periods of tidal eflux. Therefore, I am cautious when trying to explain why this shift may have occurred.

One possible explanation for the shift is an increase in predation risk as the tide rises. Animals can assess predation risk and modify their behaviour accordingly (Lima and Dill 1990), and such modifications can involve habitat shifting (Sih, 1983). Dorenbosch et al. (2004) suggested that fish may shift habitats in an effort to avoid larger predators that are unable to enter a habitat at low tide, but can do so as the tide rises. This concurs with previous research on predatory sharks that suggested they are unable to enter certain habitats at low tide (sandbar shark, *Carcharhinus plumbeus,* Medved and Marshall 1983; leopard shark, *Triakis semifasciata*, Ackerman et al. 2000; tiger shark, *Galeocerdo cuvier*, M. Heithaus, Fla. Int. Univ., Miami, pers. comm.). This would suggest that sand habitat is potentially safe from predation at low tide, but as the tide rises the fish are forced to seek refuge within the protective cover of seagrass. Although seagrass habitats were always further offshore, and thus slightly deeper, than sand habitats, it is unlikely that the depth difference *per se* caused the habitat shift because this likely would have increased the fishes' risk of predation.

The size class of fish is also an important factor when examining the effects of incoming tides on fish movement. This research suggests that the movements of the smaller fish are affected by incoming tides, whereas those of larger fish are not. This difference between the size classes may occur because smaller fish are more susceptible to predation than the larger fish. Also, these smaller fish are potential prey for some of the larger fish (sharks and rays) that may not be able to forage successfully over the sand at low tide. As the water depth and volume increases, the risks in unvegetated shallow habitats may increase, potentially forcing the smaller fish into the seagrass for refuge. Gotceitas et al. (1997) observed that young Atlantic cod (*Gadus morhua)* increased their use of eelgrass habitat over that of sand and cobble when a predator was present, and Warfe and Barmuta (2004) determined that an increase in habitat complexity (i.e., macrophyte beds) decreased the success of aquatic predators. Both results suggest that Shark Bay's seagrass habitats might grant the smaller fish increased safety from predation.

All recordings were on incoming tides, and to properly assess the effects of tidal state on behaviour, the effect of outgoing tides must be addressed as well. However, I have shown that the use of underwater video recordings is an excellent way to record and potentially monitor fish behaviour and habitat use in a non-invasive manner.

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4.8 Figure Legends

Figure 4.1. a. Shark Bay, Western Australia (indicated by arrow). b. The study area was located offshore from the Monkey Mia Dolphin Resort (indicated by arrow).

Figure 4.2. The number of recordings that had particular proportions of small fish (size classes small, small/medium and medium combined as they were not significantly different from one another) and large fish moving towards seagrass.

4.9 Tables

Table 4.1. The minimum and maximum water depths recorded at each of the five sites at low and high tide, as well as the seagrass species present within each site, where A= *Amphibolis antarctica* and P= *Posidonia australis*.

	Water depth (m)		Seagrass species
Site #	**Minimum**	**Maximum**	**(% cover)**
1	0.75	4.0	27% A: 73% P
2	1.5	4.5	100% A
3	1.0	4.0	100% A
4	1.0	5.0	95% A: 5% P
5	1.0	4.0	100% A

Table 4.2. Results of one-tailed t-tests of whether net movement of individual size classes of fish towards seagrass was significantly greater than the predicted mean value of 0.785 radians (the arcsin square root of 0.50). NB: The p-value for large fish tests whether net movement towards sand was significant.

Size class	Observed value		df	St. dev.	t-value	P-value
	Radians	Proportion				
Small	0.884	0.598	48	0.222	3.153	**0.002**
Small/medium	0.930	0.643	49	0.241	4.257	**<0.0001**
Medium	0.917	0.630	45	0.215	4.146	**0.0001**
Large	0.718	0.433	15	0.134	-2.002	(0.064)

Note: Significant P-values are in bold.

4.10 Figures

Figure 4.1

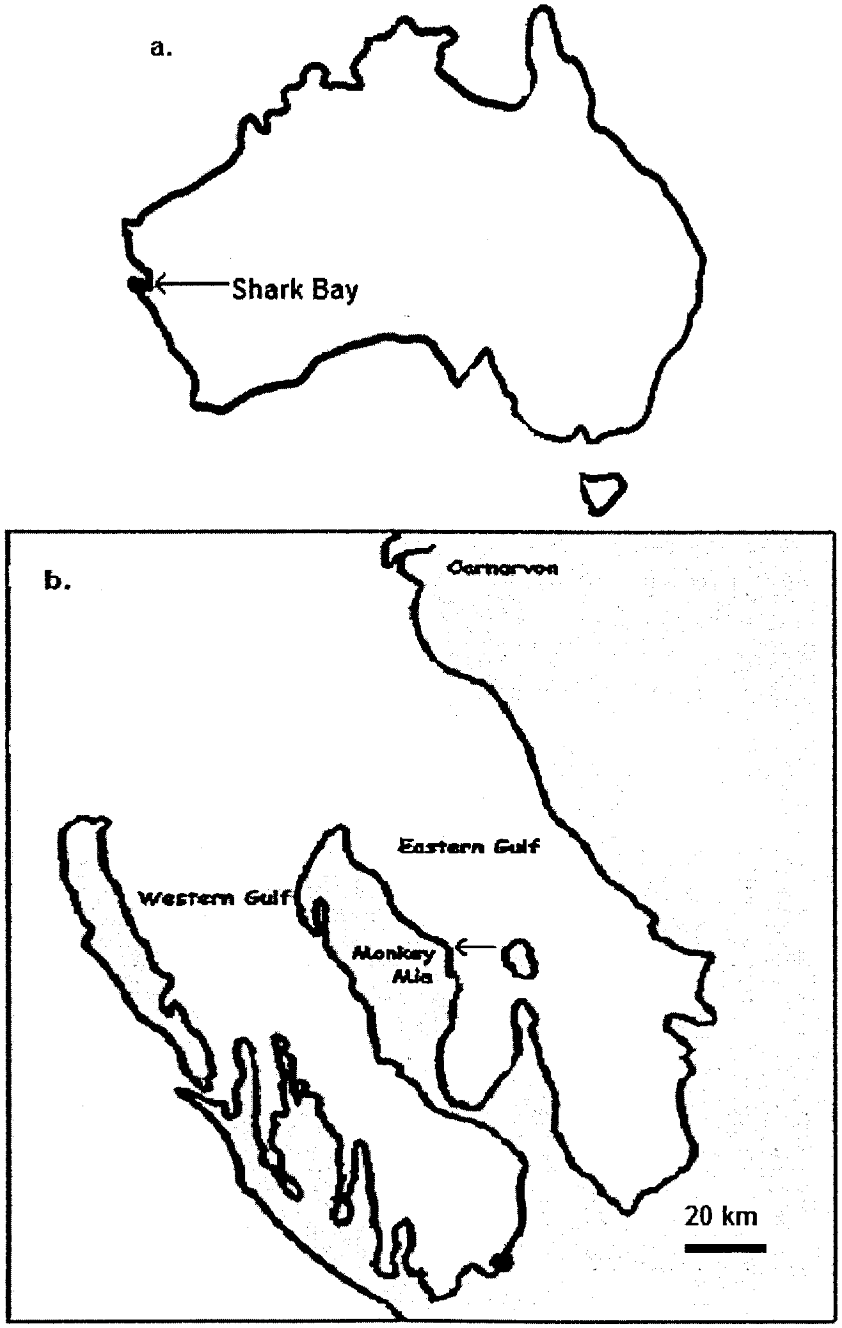
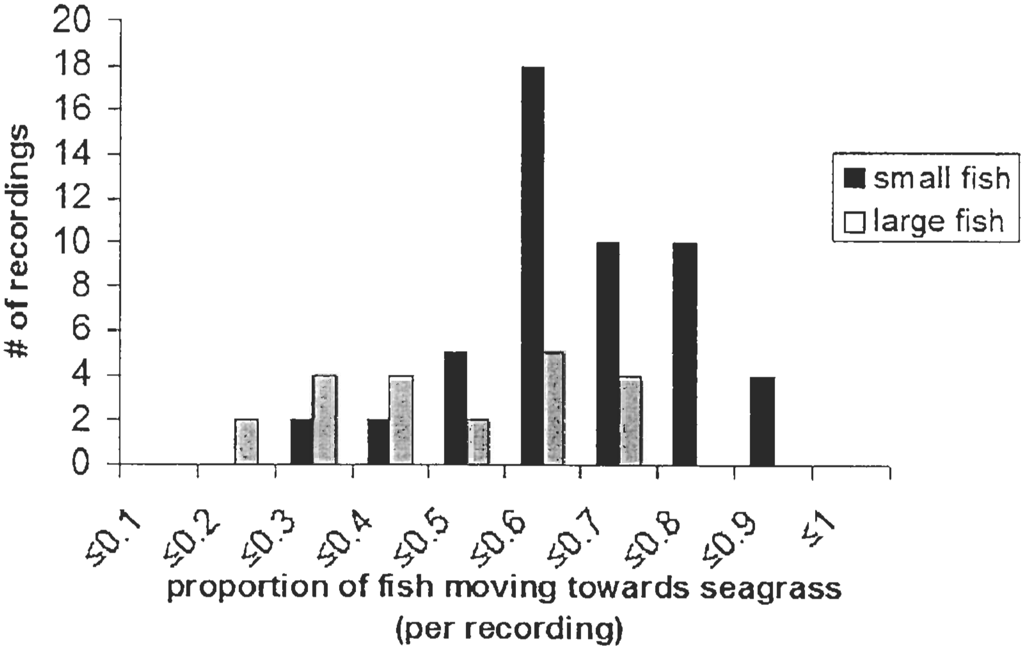


Figure 4.2


20
18
16
14
12
10
8
6
4
2
0
# of recordings
■ small fish
□ large fish
≤0.1
≤0.2
≤0.3
≤0.4
≤0.5
≤0.6
≤0.7
≤0.8
≤0.9
≤1
proportion of fish moving towards seagrass (per recording)

CHAPTER 5:

General Discussion

Competition, predation, and prey availability can influence an animal's habitat use. Animals have developed ways in which to deal with these ecological interactions; they can reduce the effects of competition through intra- and inter-specific resource partitioning within a habitat, avoid predation by not performing risky behaviours when predation risk is high, or by shifting to a habitat with lower predation risk, and choose habitats where prey availability is the highest. However, animals usually make decisions based on all three of these factors simultaneously, and these decisions ultimately affect the behavioural decisions of other animals within their community, either directly or indirectly. The chapters of this thesis addressed these three ecological interactions separately; however, the next logical step is to incorporate these results with previous data collected from Shark Bay in an attempt to determine their implications in a community context.

Data collected for Chapter 2 suggested that bar bellied sea snakes (*H. elegans*) in Shark Bay are specialized feeders, eating only sand-dwelling snake eels. *D. major*, a similar species with respect to geographical range and phenotype, consumed larger fish from a greater array of taxa. Morphological data showed that although *H. elegans* grow longer than *D. major*, their heads are significantly smaller. Presumably, the shape of their head allows them to burrow into the sand and seek out the snake eels, whereas *D.*

major's large head allows them to consume larger, non-burrowing fish found in and around the seagrass. The difference in the head morphology of these two species has probably enabled them to partition the available prey based on size and thus reduce competition. This partitioning of prey has also reduced the possibility of the two snakes interacting because *H. elegans* forage over the sand and appear to rest when over the seagrass, whereas transect data for *D. major* suggested that they are always over the seagrass.

Chapter 3 showed how tidal state influences the habitat use of the bar bellied sea snake, which is likely due to an avoidance of predators at high tide. If prey availability were the main factor affecting the snakes' habitat use then we would expect to find them over the sand at the same frequency, regardless of tidal state. However, this was not the case, because the snakes chose to forage over sand at low tide, but at high tide, when the risk of predation is greater, the snakes shifted out of the sand habitat and into alternate habitats, perhaps including seagrass. The seagrass likely offers more cover for predator avoidance and escape.

Previous diet data for *H. elegans* suggested that they ate a combination of snake eels (Ophichthidae), catfish (Plotosidae) and whiting (Sillaginidae) (Voris and Voris 1983). Based on these data, in Chapter 4 I examined the net movement of fish between habitats as the tide rises to address whether prey availability for *H. elegans* was potentially influencing the habitat selection and subsequent habitat shift of the snakes. The results suggested that as the tide rises, small to medium sized fish were shifting from the sand habitat into the seagrass, similar to *H. elegans*. Unfortunately, it wasn't until after all the video recordings from the field were complete that the gut contents were analysed in lab, revealing that *H. elegans* along the West Coast of Australia were actually highly specialized feeders, consuming only snake eels, which were not observed on any of the video recordings. However, the fish seen in the videos are prey for *D. major*, who were only sighted over seagrass and the transitional zone between sand and seagrass habitats. These data could potentially address whether the habitat use and activity budget of *D. major* are affected by tidal state, as it influences the local abundance of their prey. The results from this chapter allowed me to make general predictions regarding the influence of tidal state on potential prey availability as well as master a technique of monitoring fish behaviour and habitat use in a non-invasive manner.

5.1 Future Studies

This study focused on the habitat use of one species within the Shark Bay: the bar bellied sea snake. However, to fully address the behavioural decisions associated with habitat selection, we need to look at it in a broader community context. For example, there is another species of sea snake, the Shark Bay sea snake (*Aipysurus pooleorum*) found within the Bay. In general, these snakes are a rich dark brown on top, fading to a lighter shade on the ventral surface (Cogger 2000). Their head width/girth ratio was 0.25 (n=7), larger than both *D. major* and *H. elegans* (0.19 and 0.14, respectively). They were also observed only over the seagrass regardless of tidal state. Future research should address how these three species co-exist, and how their interactions, both direct and indirect, influence habitat choice.

Owing to the constraints of a small boat and limited time, I was restricted to the shallow sand flats and seagrass beds. I would have liked to have addressed whether the snakes also utilize the deep channels within the bay, and if so, whether this use is influenced by tidal state. These deep channels have sandy bottoms, and therefore should have snake-eels present (i.e., high prey availability), and according to previous research the predation risk in this habitat is minimal (Heithaus and Dill 2002) suggesting that the snakes should be found in these deep channels. However, even if there are fewer sharks present in the deep channels than the sand at low tide, the intrinsic risk (*sensu* Hugie and Dill 1994) could still be higher because the snakes are extremely vulnerable as they surface to breath. Because shark abundance fluctuates seasonally (Heithaus and Dill 2002), the snakes may choose the deep habitats when predation risk is low, but when it is high, they may choose to stay in the shallower sand and seagrass habitats.

Measuring predation risk over sand at low at high tide is something I wanted to address as well. I had planned on setting out snake decoys resembling foraging *H. elegans* by half burying them in the sand with their ends sticking up and counting how many were attacked over sand at low compared to high tide. Although previous research has suggested that that some shallow areas may be inaccessible to sharks at low tide (Medved and Marshall 1983, Ackerman et al. 2000), smaller species of sharks (i.e., nervous shark, *Carcharhinus cautus*) may be able to hunt the snakes over sand at that time.

Future research should also focus on the snakes' prey, the snake eels. There is a paucity of data available regarding snake eel behaviour and ecology (McCosker and Rosenblatt 1993), and these fish are potentially very important determinant of habitat use in the bar bellied sea snake. Had I performed my gut content analyses in advance of my last field season, I would have performed night transects as snake eels are reported to be more active then (Starck and Davis 1966, McCosker and Rosenblatt 1993), and thus more available to the snakes.

Shark Bay provides the ideal environment in which to address predator/prey interactions because it offers a very simple system with only one main predator, the tiger shark, and its prey, predominantly turtles, dugongs, sea snakes and the occasional dolphin. Heithaus and Dill (2002) concluded that predation risk from tiger sharks influences the habitat use of the bottlenose dolphin. During summer, when there are numerous tiger sharks present, the dolphins select deeper, low prey density waters where tiger sharks are less abundant. The tiger sharks themselves prefer shallow seagrass habitats (Heithaus et al. 2002), where they are potentially targeting alternate prey, i.e., sea snakes, turtles and dugongs. Heithaus (2001) suggested that these alternate prey influenced habitat use by the dolphins indirectly. These indirect interactions are called behaviourally mediated indirect interactions (BMII) (Dill et al. 2003). Because *H. elegans* is an important prey of the tiger shark, it is highly likely that the habitat choices the snakes make are indirectly affecting the habitat choices of other species within the bay, by affecting the behaviour of the sharks. By understanding how all the members of a community are interacting, either directly or indirectly, we could make predictions regarding their habitat use and how behavioural or abundance changes of one species may affect their local population and/or their community.

5.2 Literature cited

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