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Spatial ecology of true sea snakes (Hydrophiinae) in coastal waters of North Queensland

Dissertation submitted by
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September 2015

For the degree of Doctor of Philosophy
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Animal Ethics

Research presented and reported in this thesis was conducted in compliance with the National Health and Medical Research Council (NHMRC) Australian Code of Practice for the Care and Use of Animals for Scientific Purposes, 7th Edition, 2004 and the Qld Animal Care and Protection Act, 2001. The proposed research study received animal ethics approval from the JCU Animal Ethics Committee Approval Number # A1799

Statement of the contribution made by others

My supervisory committee including Prof. Colin Simpfendorfer, Dr. Michelle Heupel, Dr. Mark Hamann, Dr. Mark Read and Dr. Tim Clark played a vital role in the consultation, development and the final outcome of the PhD project. I would like to specially acknowledge Prof. Colin Simpfendorfer, Dr. Michelle Heupel and Dr. Tim Clark for their editorial assistance that shaped the final version of this thesis.

The chapter dealing with the geographic distribution of sea snakes (Chapter 3) was only possible because of the collaboration with Dr. Mike Cappo from the Australian Institute of Marine Sciences (AIMS) and Dr. Vimoksalehi Lukosheck from the Australian Research Council Center of Excellence for Coral Reef Studies. Dr. Mike Cappo graciously allowed me to use the vast BRUVS dataset he collected as a means to quantify geographic scale distribution patterns of sea snakes on the Great Barrier Reef as well as giving valuable advice on statistical analyses that could be used to analyse the data. Dr. Vimoksalehi Lukoscheck contributed a lot of time to help sort through video frames to confirm identification of sea snakes as well as plan out the final version of the published paper.

The staff and students of the Centre of Sustainable Tropical Fisheries and Aquaculture provided numerous hours of assistance in the field to deploy transmitters and download telemetry data from Cleveland Bay. Numerous volunteers (full list in the acknowledgements) were integral in completing fieldwork on time as well as helping in maintaining captive sea snakes at the AIMS facility. Staff and volunteers at the SeaSim facility at AIMS were vital in helping set up, maintain and run the laboratory experiments conducted for Chapter 6.

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Publications arising from this dissertation and the contributions made by co-authors

Four scientific publications arising from this thesis have already been published:

Udyawer, V., Read, M. A., Hamann, M., Simpfendorfer, C. A. & Heupel, M. R. (2013). First record of sea snake (*Hydrophis elegans*, Hydrophiinae) entrapped in marine debris. *Marine Pollution Bulletin, 73*(1), 336−338.

This publication documented the finding of a sea snake entraped in marine debris during the fieldwork phase of the PhD project and discusses the importance of accurate reporting of marine strandings and entrapment for rare animals line sea snakes. Dr. Mark Read assisted in the field during capture of the injured sea snake and also provided editorial suggestions during the writing of the publication. Dr. Mark Hamann, Prof. Colin Simpfendorfer and Dr. Michelle Heupel contributed editorial suggestions towards the final version of the publication. This publication is presented in Appendix 8.1.

Udyawer, V., Cappo, M., Simpfendorfer, C. A., Heupel, M. R. & Lukoschek, V. (2014). Distribution of sea snakes in the Great Barrier Reef Marine Park: observations from 10 yrs of baited remote underwater video station (BRUVS) sampling. *Coral Reefs, 33*(3), 777−791.

This publication used long−term baited remote underwater video station (BRUVS) data collected by Dr. Mike Cappo from the Australian Institute of Marine Science as part of a large−scale project conducted in 2010. Data collection and video analysis was conducted by Dr. Mike Cappo, who also provided advice on statistical analysis. Dr. Vimoksalehi Lukoschek confirmed identification of sea snakes on videos and was part of the initial planning of analysis and write−up of the final publication. Prof. Colin Simpfendorfer and Dr. Michelle Heupel provided valuable editorial and analytical suggestions towards the final version of the publication. The findings of this publication are presented in Chapter 3 of the present thesis.

Udyawer, V., Read, M., Hamann, M., Simpfendorfer, C. A. & Heupel, M. R. (2015). Effects of environmental variables on the movement and space use of coastal sea snakes over multiple temporal scales. *Journal of Experimental Marine Biology and Ecology, 473*, 26−34.

This publication used passive acoustic telemetry to identify the effects of environmental variables on the spatial ecology of sea snakes. Prof. Colin Simpfendorfer and Dr. Michelle Heupel provided the tracking infrastructure of 63 acoustic recievers within the study site as well as financial assistance towards the purchase and deployment of acoustic transmitters used in the publication as well as valuable editorial comments on the final version of the publication. Dr. Mark Read and Dr. Mark Hamann provided valuable suggestions in the initial planning of the project as well as editorial suggestions in the final version of the publication. The findings of this publication are presented in Chapter 4 of the present thesis.

Udyawer, V., Simpfendorfer, C. A. & Heupel, M. R. (2015). Diel patterns in three−dimensional use of space by sea snakes. *Animal Biotelemetry*, *3:29*

This publication used passive acoustic telemetry to identify diel patterns in three−dimensional space use of sea snakes. Prof. Colin Simpfendorfer and Dr. Michelle Heupel provided the tracking infrastructure of 63 acoustic recievers within the study site as well as financial assistance towards the purchase and deployment of acoustic transmitters used in the publication as well as valuable editorial comments on the final version of the publication. The findings of this publication are presented in Chapter 4 of the present thesis.

At the time of submission, two additional manuscripts were under review for publication and are presented here in this thesis:

Udyawer, V., Simpfendorfer, C. A., Read, M., Hamann, M. & Heupel, M. R. (in review). Selection of habitat and notes on dietary composition in sea snakes from nearshore environments. *Marine Ecology Progress Series.* [Chapter 5]

Udyawer, V., Read, M., Hamann, M., Simpfendorfer, C. A. & Heupel, M. R. (in review). Importance of shallow tidal habitats as refugia for sea snakes from trawl fishing. *Journal of Herpetology*. [Chapter 7]

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This thesis also presents data that was the result of a collaboration with Dr. Mike Cappo from AIMS and Dr. Vimoksalehi Lukoschek (Chapter 3). I would like to thank Mike and Vee for generously allowing me to use the extensive BRUVs dataset and contributing all their time into planning and reviewing all the previous drafts of that manuscript. Mike's suggestions and assistance with R scripts was extremely valuable and helped me get my head around the complex analyses and machine learning we used for that manuscript. Vee's help with snake IDs, her encyclopaedic knowledge about sea snakes and numerous discussions were valuable in shaping my interpretation of the data and helping me learn more about these unique animals.

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Abstract

Aquatic snakes are a diverse group that represent multiple evolutionary transitions from a terrestrial to an aquatic mode of life. Current systematics of aquatic snakes identifies four independent lineages (file snakes, Acrochordidae; homalopsid snakes, Homalopsidae; sea kraits: Laticaudinae and 'true' sea snakes, Hydrophiinae), species of which are represented on almost every continent. Despite their widespread distributions, this group of snakes is under−represented in the scientific literature with many fundamental questions about their ecology and biology still unanswered. In Chapter 2 of this thesis, I review the current scientific literature on the spatial ecology of aquatic and semi−aquatic snakes and assess both the horizontal (i.e. geographic movements) and vertical (i.e. dive patterns) patterns in their movement. I also assess what is currently known about the intrinsic (e.g. food, predator avoidance, reproductive state, ontogenetic shifts, philopatry and homing) and extrinsic (e.g. temperature, salinity, lunar and tidal cycles) factors that drive movement and space use in this group of snakes and identify key knowledge gaps. Chapter 2 also reviews the current knowledge on natural and anthropogenic threats these animals face and how movement affects their susceptibility to these threats. Incidental trawl capture represents a major threat to sea snake populations throughout their global distribution where they often represent a large proportion of bycatch in artisanal and commercial trawl fisheries. Recent global assessments have highlighted the need for data regarding the distribution patterns and spatial ecology of sea snakes to better understand their interactions with trawl fisheries throughout their range.

This dissertation focuses on 'true' sea snakes, which are found in tropical waters of South East Asia, Australia and the Pacific Islands. Data obtained using multiple techniques were used to define the distribution patterns, spatial ecology and physiology of true sea snakes within the Great Barrier Reef Marine Park (GBRMP), Australia. These data were used to explore and better understand how sea snakes are distributed and utilise space throughout the GBRMP over multiple spatial (i.e., geographic to regional) and temporal (i.e., diel to seasonal) scales. In Chapter 3, data from baited remote underwater video stations (BRUVS) were used to estimate geographic−scale distribution patterns of three species of sea snake (*Aipysurus laevis, Hydrophis curtus* and *H. ocellatus*) over 14˚ of latitude within the GBRMP. A total of 2471 deployments of BRUVS were made in a range of locations, in sites open and closed to trawl fishing. Sightings of sea snakes were analysed alongside six spatial factors [depth, relative distance across (longitude) and along (latitude) the GBRMP, proximity to land, proximity to the nearest reef and habitat complexity] to determine the factors that most strongly influenced the distribution and abundance of sea snakes. The results showed a strong latitudinal effect on the distribution of all three species, with the highest densities and diversities occurring in central and southern GBRMP locations, while the northern Great Barrier Reef (GBR) was relatively depauperate in terms of both occurrence and diversity. Shallow inshore areas were identified as key habitats for *A. laevis* and *H. curtus*, whereas deeper offshore habitats were most important for *H. ocellatus*. No significant difference was found in the mean number of snakes sighted per hour between sites open and closed to trawling. Overall, sea snakes displayed ‘patchy’ geographic distribution patterns in the GBRMP. Inshore waters of the central GBR were one area that all three species had high abundances, indicating that this area is particularly favourable for sea snake populations on the GBR.

In Chapter 4, the movement patterns and three−dimensional home ranges of two species of sea snake (*Hydrophis curtus* and *H. elegans*) were examined at multiple temporal scales using passive acoustic telemetry. Over a diel period, monitored snakes exhibited a clear diel pattern in their use of space, with individuals displaying restricted movements at greater depths during the day, and larger movements on the surface at night. *Hydrophis curtus* generally occupied space in deep water within the bay, while *H. elegans* were restricted to mud flats in inundated inter−tidal habitats. The overlap in space used between day and night showed that individuals used different core areas; however, the extent of areas used was similar. The space use patterns of monitored sea snakes were also evaluated alongside environmental parameters to determine what factors influenced the spatial ecology of sea snakes in nearshore habitats. Presence, movement and three−dimensional home range metrics calculated from monitoring data were tested against environmental (water temperature, atmospheric pressure, wind speed, accumulated rainfall and tidal range) and biological (snout−vent length) factors on daily and monthly temporal scales to identify key environmental drivers of movement and the use of space. A generalised linear mixed model (GLMM) framework using Akaike information criterion (AIC) indicated that tidal reach and atmospheric pressure strongly influenced the daily presence and movements of tagged individuals, respectively.

Accumulated rainfall significantly influenced the volume of space used on a monthly timescale.

In Chapter 5, the data obtained from passive acoustic telemetry was used to determine how sea snakes select habitats based on habitat type, depth and proximity to sources of freshwater within a nearshore environment. A hierarchical Bayesian model was used to estimate if individuals were selecting habitats significantly more or less than random on a population− and individual−level. Composition of diet was also assessed using regurgitate from captured individuals. Selection of habitats by the two species differed with *H. elegans* displaying an affinity for mudflat and seagrass habitats less than 4 km from sources of freshwater and depths less than 3 m. *Hydrophis curtus* selected for slightly deeper seagrass habitats (1 – 4 m) further from freshwater sources (2 – 5 km). Data from regurgitate showed *H. curtus* displayed some level of intraspecific predation. Both species prominently selected seagrass areas indicating these habitats provide key resources for sea snakes within nearshore environments. Any degradation or loss of these habitats may have significant consequences for local sea snake populations. Understanding the habitat requirements of sea snakes is essential to defining how natural and anthropogenic disturbances may affect populations and is necessary to inform targeted management and conservation practices.

This thesis also explored the physiological basis of movement patterns in sea snakes and examined how environmental factors may affect their susceptibility to trawl fishing. In Chapter 6, laboratory observations showed that sea snakes displayed shorter dive durations and surfaced more frequently as water temperature increased. Animal−borne accelerometers were used to provide the first estimates of movement−associated energy expenditure in free−roaming sea snakes and explore diel and seasonal patterns in metabolic rates. The energy requirements of sea snakes estimated in the field showed a doubling of metabolic rate from the cooler dry season to the warmer wet season, which potentially increases their susceptibility to fishing activities that occur in summer months. In bimodally respiring animals like sea snakes, the up−regulation in cutaneous respiration is an important mechanism that can potentially prolong dive durations during periods of stress. This mechanism is important and can potentially allow sea snakes to prolong their dive durations when caught in trawl nets and increase their chances of survival. Results of this thesis showed that sea snakes may not have much control over the amount of oxygen they uptake cutaneously, which may impede their chances of survival once caught in fishing gear.

The use of spatial closures (e.g. Marine Protected Areas; MPAs) is effective in reducing the exposure of bycatch species to fishing activities in the GBRMP, and may be useful in managing fishing−related mortality in sea snakes. However, identifying important habitats for sea snakes is critical to ensure that MPAs function effectively. In Chapter 7, I examined the importance of protected, shallow coastal habitats as possible refuge sites for sea snakes in the GBRMP. Extensive boat−based surveys were conducted to investigate the assemblage and abundance of sea snakes within a protected, shallow coastal bay adjacent to trawl fishing grounds. *Hydrophis curtus* and *H. elegans* were the most commonly encountered species within the bay. Based on the age structure of these two species the bay was primarily used by juveniles. Temporal trends in age structure showed that *H. curtus* may use Cleveland Bay as a nursery ground with gravid females entering the bay in summer months to give birth. In contrast, *H. elegans* appears to use the bay more consistently through the year with approximately 30% of individuals being adult. This chapter also showed that shallow tidal habitats, which are too risky to undertake trawl fishing, are regularly used by sea snakes and may provide refugia for vulnerable life stages of sea snakes. The identification and protection of such habitats may further mitigate risks to sea snake populations from trawl fishing.

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General introduction

1.1. Introduction

Sea snakes are air–breathing marine reptiles in the family Elapidae that have adapted to living in the marine environment. The most identifiable characteristic of this taxa are their laterally flattened paddle like tail which are absent in all other aquatic or terrestrial snakes (Figure 1.1). Within the marine snakes, commonly referred to as 'sea snakes', two main clades are recognised: the *Laticaudid* and the *Hydrophiid* sea snakes. The main difference between these two clades is the reproductive mode. Species in the genus *Laticauda* are oviparous and display amphibious behaviours, traversing onto land to nest. The more speciose *Hydrophiid* clade is viviparous and has adapted to live their full life cycle in the marine environment (Heatwole 1999), representing the only extant group of fully marine reptiles (Rasmussen et al. 2011). As with the phylogeny of many reptile families, the taxonomy within the marine snake groups have not been completely resolved, with these lineages rearranged in several different configurations over the years (see review by Heatwole 2010). The most recent configuration of the taxonomy based on molecular evidence separates these two marine clades from African, Asian and American terrestrial elapids (Subfamily: Elapinae; Sanders & Lee 2008).

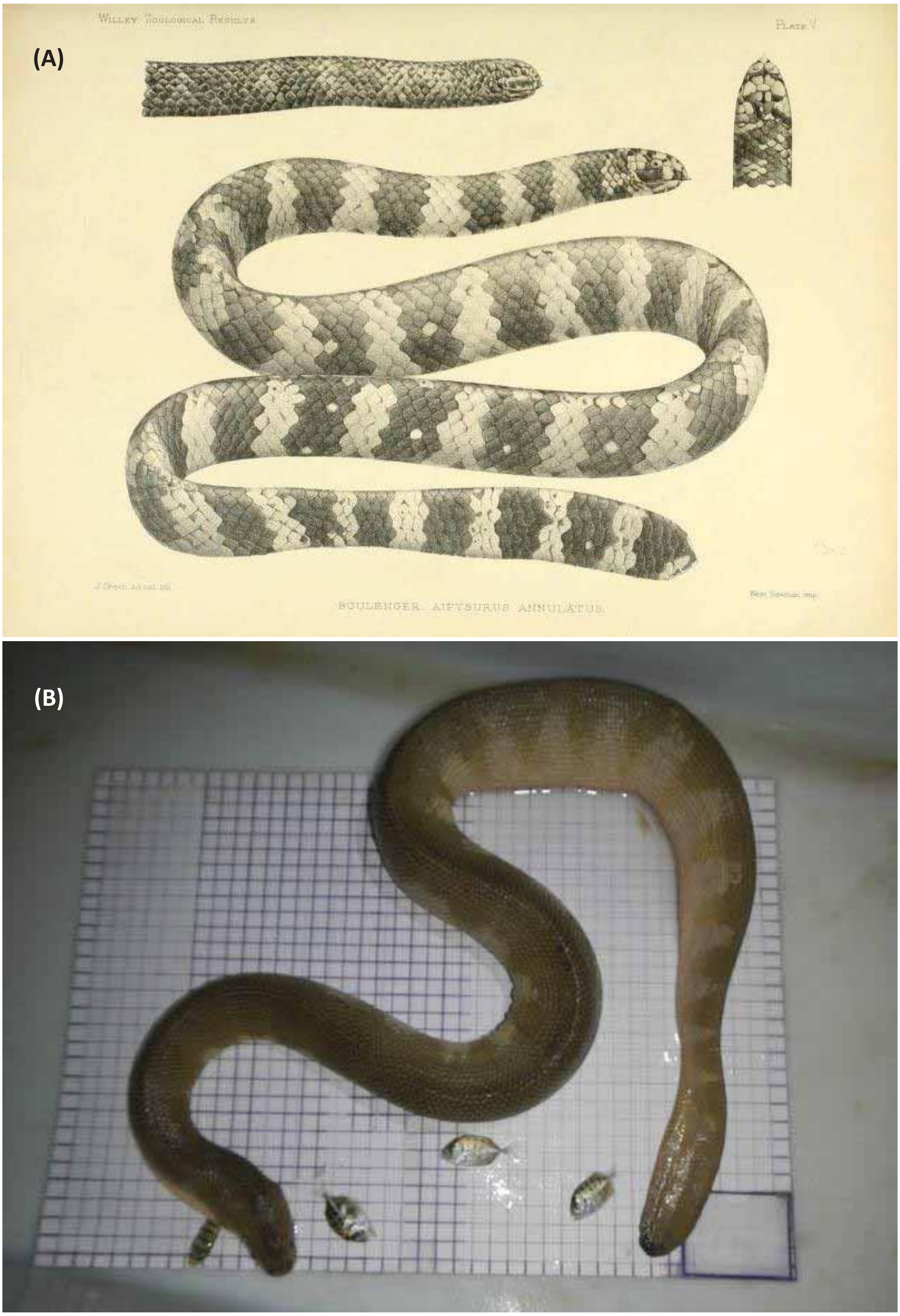

Figure 1.1.(A) Illustration of a turtle−headed sea snake, *Emydocephalus annulatus*, from a historic account of the biodiversity of the Loyalty islands (source: Boulenger 1898). (B) Photograph of a captured spine bellied sea snake, *Hydrophis* (*Lapemis*) *curtus*. A laterally flattened body and paddle−like tail are the distinguishing features of sea snakes.

The two marine clades independently transitioned into the marine environment, with the basal *Laticaudid* clade (Subfamily: Laticaudinae) first diverging from a Australasian common ancestor ~13 million years ago (Sanders et al. 2008). The *Hydrophiid* clade of ‘true sea snakes’ is nested within a larger ‘Australasian clade’ (Subfamily: Oxyuraninae) consisting of Australo−Papuan terrestrial elapid snakes (e.g. taipans, tiger snakes) and is thought to have transitioned into the marine environment more recently (~6−8 million years ago; Lukoschek & Keogh 2006). Species within the *Hydrophiid* clade can be further divided into two main evolutionary groups, the *Aipysurus* (10 species) and *Hydrophis* (49 species) (Lukoschek & Keogh 2006). Species from the *Aipysurus* group are typically found in coral reef habitats, whereas species from the *Hydrophis* group more commonly occur in inter−reef soft sediment habitats, although there are exceptions to this pattern (Cogger 2000). All true sea snake species, with the exception of the pelagic yellow−bellied sea snake, *Hydrophis* (*Pelamis*) *platura*, are strongly associated with benthic habitats, and occur in coastal, shallow water habitats (typically <100 m depth), as they regularly need to come to the surface to breathe (Heatwole 1999). This thesis focuses on the biology and ecology of species within the *Hydrophis* group, and more specifically species within the waters of the Great Barrier Reef, Australia. However, we will explore some biological aspects of the other groups (*Laticauda*, *Acrochordidae* & *Homalopsidae*) in the next chapter (Chapter 2). The information gathered here contributes to the need for fundamental biological, ecological and physiological data on these taxa (Elfes et al. 2013).

Sea snake distributions range throughout tropical and subtropical waters of the Indian and Pacific Oceans, with the greatest abundance and diversity in the waters off northern Australia and the Indonesian archipelago (Figure 1.2, Heatwole 1999). Currently there are ~70 identified species within both the Laticaudinae and Hydrophiinae subfamilies, of which 32 species have been recorded in Australian waters, and 14 of which are found on the Great Barrier Reef (GBR; Heatwole 1978). Sea snakes utilise a variety of habitats including coastal and freshwater, as well as coral reef systems and have been shown to be a good bio−indicator to assess the health of predator biodiversity in these habitats (Ineich et al. 2007, Brischoux et al. 2009a).

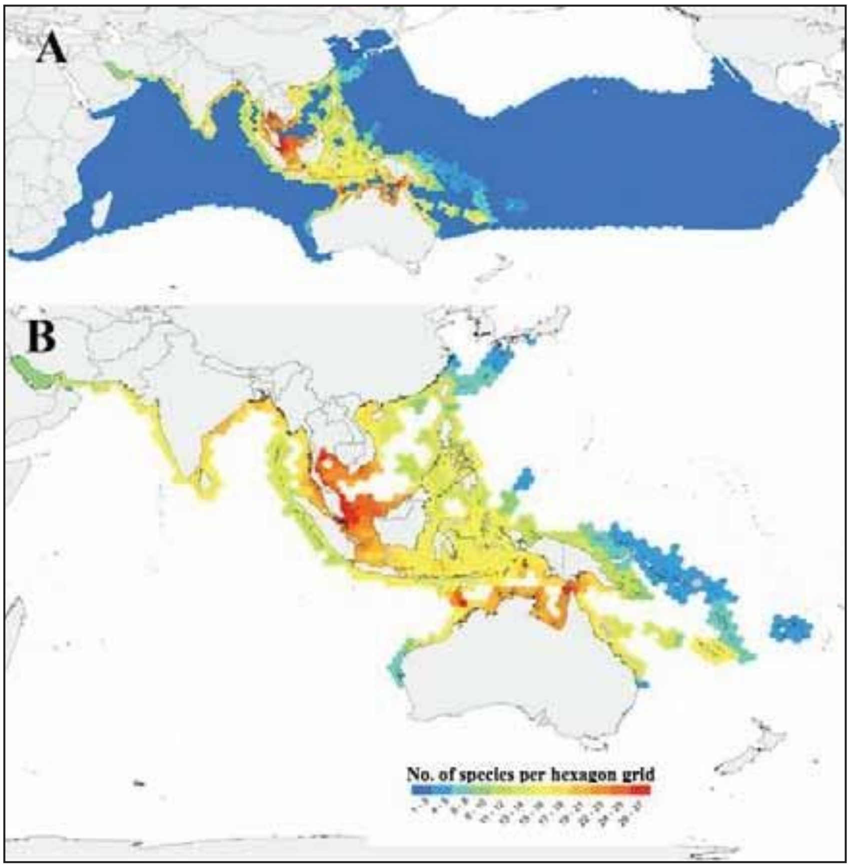

Figure 1.2. Global distribution and species richness of sea snakes (Hydrophiinae). (A) Including the widespread pelagic species *Hydrophis* (*Pelamis*) *platura.* (B) Distribution without *H. platura.* Figure uses IUCN Redlist distribution maps (source: Elfes et al. 2013)**.**

1.2. Global conservation status of sea snakes

Despite their widespread distribution, until recently there was very little information available to fully evaluate the status of sea snakes as a group. In 2009, the IUCN (International Union for Conservation of Nature) conducted its first global Red List assessment on this group, including 67 species of sea snakes (Laticaudinae and Hydrophiinae), 8 species of closely related aquatic Acrochordid snakes and 40 species of semi–aquatic Homalopsid snakes (Livingstone 2009). The assessment found that a large number of species of sea snakes (34%) were classified as 'Data Deficient' where insufficient scientific information is available to make an accurate assessment of their population health and risk of extinction (Elfes et al. 2013). Six species of sea snakes (9% of all assessed) were found to be at risk of extinction with two species 'Critically Endangered', one 'Endangered' and three classed as 'Vulnerable' to extinction. However, the majority of species (53%) are currently assessed as 'Least Concern' (Figure 1.3). Many species of sea snake are highly sought after for their meat, skin and internal organs, and often are traded internationally

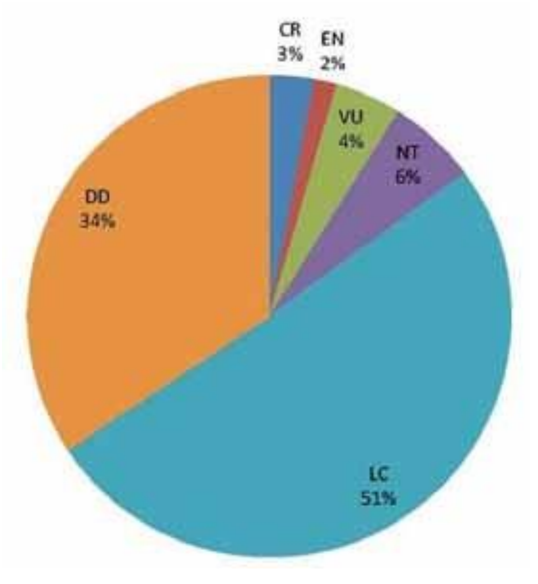

Figure 1.3. Percentage of all sea snake species assessed under the IUCN Red List categories. CR: Critically Endangered, EN: Endangered, VU: Vulnerable, NT: Near Threatened, LC: Least Concern, DD: Data Deficient (source: Elfes et al. 2013)

(Van Cao et al. 2014). Despite this, sea snakes are not currently protected under CITES (the Convention on International Trade in Endangered Species of Wild Fauna and Flora).

On a regional scale, sea snakes as a group are protected in Australian waters under Schedule 1 of the *National Parks and Wildlife Regulation 1994* and are 'Listed Marine Species' under the *Environment Protection Biodiversity and Conservation Act* of 1999 (EPBC Act). This stipulates that all Australian industries directly or indirectly interacting with protected species (including 'Listed Marine Species') have to demonstrate sustainable practices toward the species impacted by their activities (Milton et al. 2008). In addition, the *Queensland Fisheries Act* of 1994 requires trawl operators within state waters to reduce the incidental capture and mortality of protected marine species including sea snakes. This includes the mandatory use of bycatch reduction devices (BRDs) like turtle excluder devices (TEDs), square−mesh panels and fisheye BRDs. Despite these Commonwealth and state enforced legislature, large numbers of sea snakes are still captured incidentally in the productive tropical coastal trawl fisheries (Courtney et al. 2010).

1.3. Interaction with commercial fisheries

The life history traits of sea snakes (i.e. late maturity, low fecundity) mean they may be highly susceptible to natural and anthropogenic changes in their environment. In Australian waters, the main threat to sea snake populations is incidental capture in coastal trawl fisheries (Figure 1.4). Although the commercial fishing industry within the GBR is well managed, sea snakes are susceptible to fishing mortality (Ward 2001) and some species have been identified as having limited

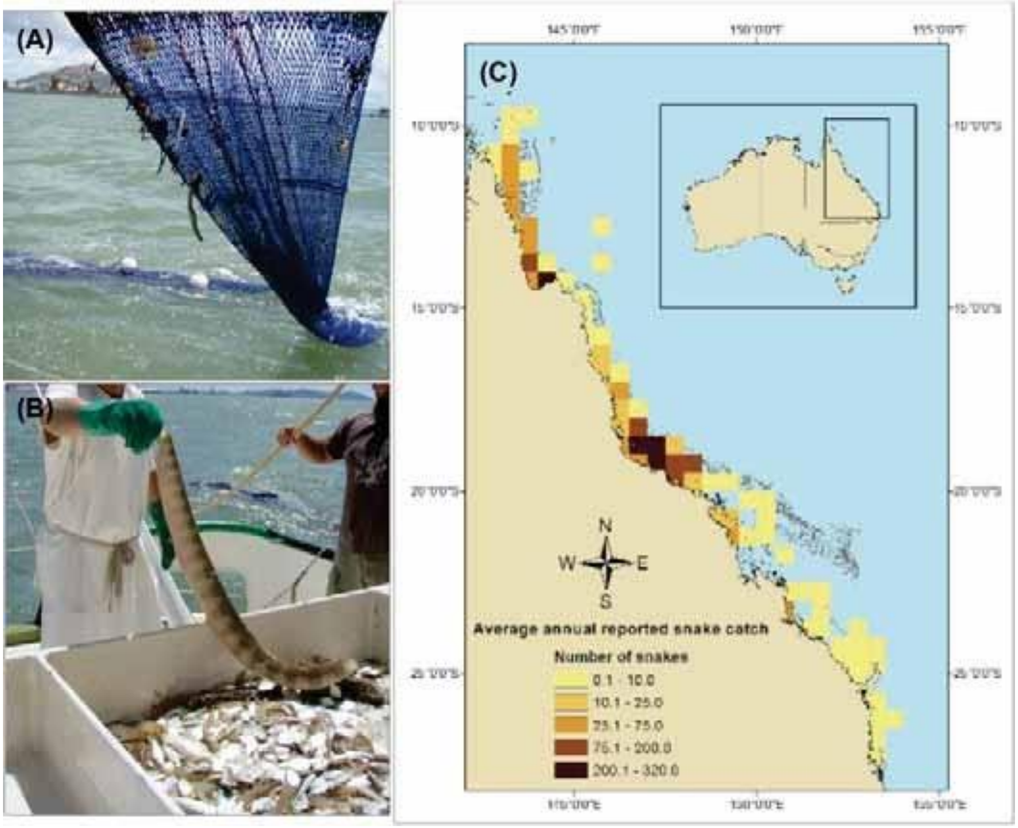

Figure 1.4. (A,B) Sea snakes form a large proportion of by−catch in tropical trawl fisheries (source: F&F database). (C) Average annual reported incidental catches of sea snakes between 2003−2008 based on the Queensland Species of Conservation Interest (SOCI) database (source: Courtney et al. 2010)

capacity to maintain viable populations in the face of continuing mortality (Milton 2001, Pears et al. 2012). Recent assessments of the impact of trawl fisheries on sea snakes around Queensland (Courtney et al. 2010) and the Gulf of Carpentaria (Milton et al. 2008) have highlighted a lack of biological information for the majority of sea snake species.

The Northern Prawn Fishery (NPF) and the Queensland East Coast Trawl fishery (QECTF) are large seasonal fisheries in Northern Australia and the coast of Queensland, respectively. The NPF targets a range of species including tiger prawns (*Penaeus esculentus* and *P. semisulcatus*), endeavour prawns (*Metapenaeus endeavouri* and *M. ensis*) and banana prawns (*Fenneropenaeus merguiensis and F.*

indicus) (Ward 1996). The QECTF targets tiger and banana prawns as well as eastern king and red−spot king prawns (*Melicertus latisulcatus* and *M. longistylus*), but also includes black tiger prawn (*Penaeus monodon*) broodstock collection and beam trawlers that target saucer scallops (*Amusium ballotti*) (Courtney et al. 2006, 2010). The QECTF has about 600 vessels operating annually, catching approximately 10,000 tonnes of product. Trawl fisheries use small meshed nets (generally > 50mm) that have poor selectivity, therefore they have high bycatch rates with the weight of bycatch often exceeding that of the targeted catch (Robins & Courtney 1998). Bycatch generally includes non−target teleosts, vulnerable species including sharks and rays and endangered and protected megafauna like turtles and sea snakes. The use of bycatch reduction devices (BRDs) has reduced bycatch of larger species like sharks, rays and turtles, but have had significantly less effect reducing bycatch of smaller species like sea snakes (Brewer et al. 1998, 2006).

An estimated 105,210 snakes of 12 species, including *Hydrophis* (*Lapemis*) *curtus*, *Aypisurus laevis*, *A. duboisii, Hydrophis* (*Acalyptophis*) *peronii* and *Hydrophis elegans,* are caught in the QECTF annually (Courtney et al. 2010). Incidental capture rates of sea snakes appear to be highest in productive inshore waters of the central GBR (Figure 1.4). Their high bycatch rate along with other life history traits makes sea snakes highly vulnerable to fishing pressure. Furthermore, because they are air−breathers and highly venomous, snakes that are caught in trawl nets have high mortality through drowning in the nets or being killed by the crew on−board (Milton 2001). In many cases, snakes caught in trawls are thrown back, however, post−release survival varies by species (Wassenberg et al. 2001). Post−release mortality of species that are less resilient [e.g. *A. laevis* and *Hydrophis* (*Astrotia*) *stokesii*] may have dire consequences for populations in areas used by trawl fisheries (Milton 2001). Apart from the use of BRDs, other methods can be implemented to reduce the effects of incidental trawl capture to ensure healthy populations and ecosystems. Spatial closures and restrictions on the activities that can be conducted in some areas have shown to be effective in management of commercially important populations of fishes or for animals of conservation value (Dryden et al. 2008, McCook et al. 2010). Such methods may be effective to protect sea snakes, but effective management can only be based on fundamental data on the spatial ecology of these species.

1.4. Spatial ecology

The movement and space use of marine snakes is poorly understood which has significant implications for the effectiveness of conservation and management planning for these taxa. Habitat use and movement studies of marine snakes to date have been restricted to large−scale movements with the majority of studies using visual survey, mark recapture and translocation methods (e.g. Shine et al. 2003, Lukoschek et al. 2007, Brischoux et al. 2009b, Lukoschek & Shine 2012). A limited number of studies have examined finer scale movement at the scale of individual reefs or coastal embayments (e.g. Rubinoff et al. 1986, Rubinoff et al. 1988, Burns & Heatwole 1998, Brischoux et al. 2007a).

Long−term movement and genetic data suggest that some species like *Emydocephalus annulatus* and *Aipysurus laevis* display restricted movement within reef environments and may be vulnerable to localised extinction (Lukoschek et al. 2007, Lukoschek & Shine 2012). Translocation studies have shown that snakes displayed high site fidelity, rapid homing and philopatry within fringing reef systems (Shetty & Shine 2002, Brischoux et al. 2009b). The majority of past studies have also focused on the ecology and habitat use of snakes on reef or reef−associated habitats, despite trawl bycatch (e.g. Ward 1996, Milton et al. 2008, Courtney et al. 2010) and visual surveys (M.Cappo, unpublished data) showing that there are a large number of species that utilise between−reef and coastal habitats that have not been accounted for in the literature. These between−reef and inshore coastal embayments are important habitats for sea snakes, and more information on how these animals use these habitats are required.

One aspect of the biology of mobile animals that is inherently linked to movement and activity is their energetics. However, in many cases examining metabolic rates of large or highly mobile animals is often overlooked, as it can be difficult to accurately measure or assess in the field. This thesis will examine some aspects of sea snake energetics in relation to their spatial ecology.

1.5. Energetics

Activity−related energy expenditure in ectotherms is a major factor that governs movement and drives behavioural responses (Dorcas & Willson 2009, Halsey et al. 2009b). The spatial ecology of many terrestrial and aquatic snakes can be explained, in part, by the variation in the energy requirements of individuals under specific biotic (e.g. reproductive energy requirements) and abiotic (e.g. environmental temperature) conditions (Carfagno & Weatherhead 2008, Lelievre et al. 2012). The three major components of the energy budget in reptiles are: (1) the standard metabolic rate (SMR), which is the metabolic rate of a resting animal that represents the cost of maintaining fundamental metabolic processes for survival, and (2) the specific dynamic action (SDA), which is the increased energy expenditure associated with digestion, assimilation and biosynthesis and (3) the active metabolic rate, which is the energitic expenditure relating to movements and activity (Secor & Diamond 2000, Hopkins et al. 2004). Energy expenditure in the form of aerobic metabolism can be directly measured using oxygen consumption under varying environmental conditions to assess the effect of abiotic factors on the energy budget. In many aquatic and marine reptiles, oxygen uptake occurs not only through the regular pulmonary pathway, but also through cutaneous gas exchange (Graham 1974, Mathie & Franklin 2006). To accurately estimate SMR and SDA in marine reptiles, both pulmonary and cutaneous respiration should be measured to estimate total oxygen uptake during metabolic studies (e.g. Heatwole & Seymour 1975, Seymour & Webster 1975, Pratt & Franklin 2010). Part of the present study will examine how factors like temperature influence the active metabolic rates of sea snakes, and how this in turn may have implications this may have on their spatial ecology.

With recent advances in biologging and biotelemetry technology, it is possible to measure body acceleration and estimate activity−associated energy expenditure at high resolution and over an extended period of time in animals in their natural environment (Cooke et al. 2004a, Clark et al. 2010, Payne et al. 2011, Wilson et al. 2015). The ability to use continuous field data coupled with lab based calibration experiments makes it possible to estimate field metabolic rates over the long−term. Vectorial dynamic body acceleration (*V*DBA) is a measure of the overall acceleration of an individual obtained from acceleration measures from multiple axes (Qasem et al. 2012). This measure has been shown to be a useful indicator of energy expenditure associated with locomotion in free–living animals (Wilson et al. 2006, Halsey et al. 2009a, Gleiss et al. 2010, Qasem et al. 2012). This study utilised acceleration measuring acoustic transmitters to measure VDBA and use this as a proxy to estimate movement–associated field metabolic rate and daily energy expenditure.

1.6. Relevance and objective of this study

As a group, sea snakes are considered threatened under the Environmental Protection and Biodiversity Conservation Act 1999 (EPBC). This means that vulnerable and critically endangered species within the taxa like *Aipysurus foliosquama* and *Aipysurus apraefrontalis* are listed as a conservation priority. In many cases, the cause for threatened status is habitat destruction and increased anthropogenic activity in critical habitats (Elfes et al. 2013). There is a need to understand the basic ecology, distribution and space use of marine snakes to assess the vulnerability of these taxa to anthropogenic activities like fishing and to design more effective conservation and management plans (Bonnet 2012, Zhou et al. 2012). This thesis aimed to answer some key questions regarding space use and movement of sea snakes in critical coastal environments and the efficacy of spatial closures, such as conservation park zones in coastal areas, for these species. The objective of this study was to provide information that can be used to better assess, conserve and manage marine snakes within habitats that overlap with anthropogenic activities.

1.6.1. Aims and structure of the thesis

This thesis will first examine the current literature on the activity patterns and spatial ecology of aquatic and semi−aquatic snakes, including sea snakes, and identify key knowledge gaps (Chapter 2). The thesis will then focus on answering two core research questions focusing on sea snake ecology:

1) *What are the movement and space use patterns of sea snakes in coastal ecosystems?*
2) *How do movement and space use patterns affect the vulnerability of sea snakes to anthropogenic activities?*

These questions are addressed in the subsequent data chapters which will focus on one of four aims:

Aim 1: Examine the landscape level distribution patterns of sea snakes within the GBR (Chapter 3)

Aim 2: Describe the space use and habitat selection patterns of sea snakes, and determine how environmental conditions influence use of coastal bays (Chapter 4 and Chapter 5)

Aim 3: Describe the energetics of sea snakes and determine the influence of metabolic rates on activity and space use (Chapter 6)

Aim 4: Evaluate the exposure of sea snakes to anthropogenic activities in coastal habitats (Chapter 7)

Chapter 2

A review on the activity patterns and space use by aquatic and semi-aquatic snakes: implications for management and conservation

2.1. Introduction

All animals, on an individual level, occupy space and often actively move to acquire resources such as food and water, mates and shelter during daily activities. The patterns of movement and associated space use of reptiles are greatly affected by both intrinsic (e.g. age, life history, size, sex) and extrinsic (e.g. temperature, season, habitat availability) factors (Vitt & Caldwell 2013). Chronic or acute changes in these factors can significantly influence the movements and space occupied by individuals and may therefore have further effects on global distributions and trophic interactions. Thus an understanding of the biology and ecology of species, and the characteristics of the environments they inhabit, is required to understand patterns of distribution and to define drivers of movements.

The space an individual uses and the extent of their movements are often closely correlated with intrinsic factors like body size and sex (Zug et al. 2001). The size of the individual influences its distribution and movement. Large individuals undertake broader movements and occupy larger areas, whereas smaller individuals (i.e. smaller species) tend to have limited distributions, shorter movements and occupy relatively small areas (Figure 2.1A, B; Perry & Garland Jr 2002, Reed 2003). Perry and Garland Jr (2002) found a strong relationship between the size (i.e. snout−vent

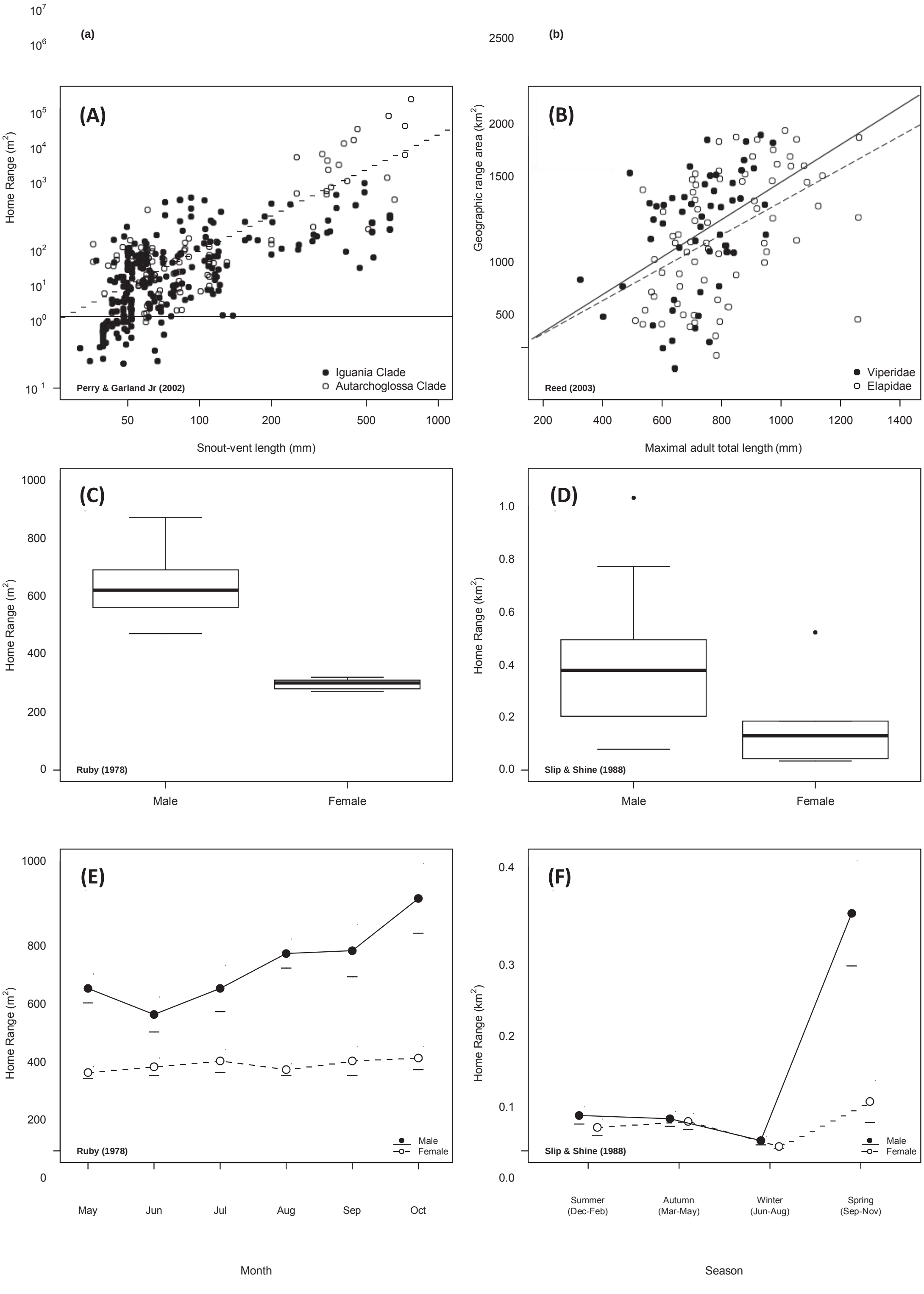

Figure 2.1. Intrinsic factors affecting space use in two groups of ectotherms (lizards: A,C,E; snakes: B,D,F). Size of individual (A,B) and sex (C–F) affects the size of home range in reptiles. (A) Data from two clades of lizards (Iguania and Autarchoglossa) show a positive correlation between body length and size of home range (adapted from Perry & Garland Jr 2002). (B) Similar correlation can be found between the maximal adult total length and geographic range size in two families of snakes (Viperidae and Elapidae) (adapted from Reed 2003). Sex influences the size of home ranges in Yarrow's spiny lizards (*Sceloporus jarrovi*) where (C) males occupy larger spaces than females, (E) which occurs during the breeding season to maximise overlap with female home ranges (adapted from Ruby 1978). Similar differences in

home ranges are observed between male and female Diamond pythons (*Morelia spilota spilota*) where (D) males occupy larger spaces than females, and (F) this pattern is closely related to mate−searching behaviours during the breeding season (adapted from Slip & Shine 1988).

length or mass) and patterns in space use (i.e. area of home range) in two clades of lizards (Iguania and Autarchoglossa), where increased body size was positively correlated with increased home range size (Figure 2.1A). Reed (2003) found a similar positive correlation between the lengths of adult individuals and the geographic range in two snake families (Viperidae and Elapidae), where species with larger adults displayed larger geographic ranges (Figure 2.1B). Regardless of sexual dimorphism, reptiles tend to display different activity and movement patterns between sexes due to differing resource requirements, mate searching behaviours and reproductive needs (Shine 1989). For example, Ruby (1978) found male Yarrow's spiny lizards (*Sceloporus jarrovi*) displayed larger home ranges (Figure 2.1C) and undertook larger movements to maximise overlap with female home ranges which were closely associated with nesting or over wintering sites (Figure 2.1E). Similarly, Slip and Shine (1988) observed a four−fold increase in movements and size of home ranges (Figure 2.1D) in male Diamond pythons (*Morelia spilota spilota*) during the breeding season which was closely associated with mate−searching behaviours (Figure 2.1F). Differential use of space and activity related to sex have been reported in a range of other terrestrial and semi−aquatic reptiles (e.g. Grass snakes; Madsen 1984, Snapping turtles; Brown & Brooks 1993, Eastern Indigo snakes; Hyslop et al. 2014) and show that the use of space and movements in males and females can be greatly influenced by specific reproductive behaviours (i.e. mate searching in males and nesting in females).

Extrinsic factors such as environmental temperature affect all aspects of reptile biology, from specific functions like ecdysis and embryonic development, to more general functions like digestion, growth and movement (Willmer 1991, Weatherhead

& Madsen 2009). Reptiles generally display higher rates of activity within a specific thermal range with environmental temperatures playing a critical role in small and large−scale movements and utilization of space (e.g. Webb & Shine 1998, Whitaker & Shine 2002, Abom et al. 2012). For example, thermally variable habitats influence movement in temperate snakes, in particular some individuals actively moved between habitats to maintain their body temperature within a narrow thermal range (Whitaker & Shine 2003). Studies conducted in the tropics however, suggest the influence of environmental temperature may have a limited effect as the temperature difference between habitats in the tropics are relatively small (Shine & Madsen 1996, Luiselli & Akani 2002). Therefore the amount of temperature change in combination with the environmental temperature range may be key to influencing small−scale reptile movement patterns.

The study of movement and space use in snakes in the past has focused on terrestrial species where monitoring techniques (e.g., mark−recapture, radio telemetry) were developed to more accurately study broad and small−scale movements of cryptic species in challenging environments (e.g. tall grass, forest canopies; Shine 1995). Monitoring of snakes in aquatic and marine environments present additional challenges, and in the last few decades there have been few studies focused on the movement and space use of snakes that inhabit these environments. This review aims to consolidate the current literature to improve our understanding of how intrinsic and extrinsic factors influence the movement and activity patterns of semi−aquatic and aquatic snakes, discuss what implications these might have on current and future conservation and management practices as well as identify significant knowledge gaps in the current literature.

2.2. Aquatic and semi-aquatic snake groups

The present understanding of the systematics of aquatic and marine snakes identifies four independent transitions of snakes from terrestrial to aquatic modes of life [Acrochordidae (Sanders et al. 2010), Homalopsidae (Alfaro et al. 2008), Laticaudinae and Hydrophiinae (Scanlon & Lee 2004, Sanders et al. 2008, Sanders et al. 2013)]. Apart from these four major phylogenetic groups, some species within the subfamily Natricinae (Colubridae) and family Viperidae inhabit regions adjacent to freshwater sources, and are known to forage and use space in aquatic habitats (Pauwels et al. 2008, Murphy 2012). For the purposes of this review, species within these phylogenetic groups will be grouped within two modes: (a) *aquatic*; species that move and use space exclusively in aquatic habitats, (b) *semi−aquatic*; species that move and utilise space in both aquatic and terrestrial habitats.

2.3. Types of movements and space use in aquatic snakes

2.3.1. Horizontal movement

Movement of individuals over the horizontal plane defines the geographical distribution and connectivity between populations in patchy environments. Studies on horizontal movements of aquatic and semi−aquatic snakes show a range of daily movements (Table 2.1). Previously, a combination of techniques have been used from long−term mark−recapture methods to radio telemetry to monitor movements of individuals at varying levels of temporal and spatial resolution. Overall, there were no general trends or patterns in horizontal movements between species, populations or individuals. Some studies found that males generally displayed larger movements and home ranges than females (e.g. Karns et al. 2000, Roe et al. 2004, Roth 2005, Welsh Jr et al. 2010). However studies on the aquatic *Acrochordidae* *arafurae* (Shine & Lambeck 1985, Houston & Shine 1994) and *Aipysurus laevis* (Burns & Heatwole 1998) revealed the opposite pattern with females displaying larger movements and home ranges indicating that there may not be a universal correlation between sex and movement metrics in all species of aquatic and semi–aquatic snakes. Similarly, patterns between life stages were not studied in most cases, with the majority of studies focusing on adult movements. Thus the movements of juveniles remain largely unstudied.

Past studies also looked at how movement and space use metrics related to environmental and biotic factors. The geographic distributions, movement and activity of aquatic snake species have been correlated to extrinsic factors such as moon phase (Lillywhite & Brischoux 2012b), water temperature (Heatwole 1999, 2010) and salinity (Lillywhite et al. 2008, Brischoux et al. 2012b), as well as intrinsic factors like reproductive state (Lynch 2000) and predation pressure (Kerford et al. 2008). These correlations will be discussed in more detail later in this review.

Table 2.1. Horizontal movement and space use data for several aquatic and semi–aquatic snakes in current literature. Modes defined by the environment snakes are most commonly encountered in (T: terrestrial, F: freshwater, M: marine). Most studies used either one or a combination of trapping (T), mark–recapture (MR) and radiotelemetry techniques (RT) to calculate rates of movement. Space use was calculated using the Maximum Convex polygon method (MCP), 50% and 95% Kernel Utilisation Distribution methods (KUD 50%, KUD 95%).

Species	Mode (Environment: T,F,M)	Monitoring method	Period monitored	Daily rate of movement (m/day) [mean ± SE *(n)*]	**Space Use (km²)** [mean ± SE]			Reference
					MCP	**KUD 50%**	**KUD 95%**	
Colubridae, Natricinae								
Tropidonophis mairii	Semi–aquatic (T,F)	RT	28 days	17.11 ± 3.7 *(50)*				Abom et al. (2012)
Natrix natrix	Semi–aquatic (T,F)	RT	6 – 91 days	M: 33.9 ± 12.7 *(4)* F: 57.2 ± 37.25 *(4)*	M: 0.099 ± 0.019 F: 0.136 ± 0.057			Madsen (1984)
Thamnophis atratus hydrophilus	Semi–aquatic (T,F)	MR	15 years	M: 1.86 ± 0.58 *(770)* F: 0.833 ± 0.54 *(960)*				Welsh Jr et al. (2010)
Nerodia taxispilota	Semi–aquatic (T,F)	MR	2 years	13 ± 33 *(361)*				Mills et al. (1995)
Nerodia harteri paucimaculata	Semi–aquatic (T,F)	MR, RT	14 – 156 days	M: 55.4 ± 26 *(4)* F: 26.7 ± 4.5 *(4)*				Whiting et al. (1997)
Nerodia rhombifer	Semi–aquatic (T,F)	MR		M: 10.7 F: 0.5				Preston (1970)

Nerodia erythrogaster neglecta	Semi–aquatic (T,F)	RT	1 year	M: 60.7 ± 11.7 *(8)* F: 44.8 ± 7.1 *(7)* All: 53.3 ± 7.1 *(15)*	M: 0.189 ± 0.039 F: 0.121 ± 0.033	M: 0.022 ± 0.006 F: 0.011 ± 0.003 All: 0.017 ± 0.004	M: 0.160 ± 0.037 F: 0.097 ± 0.029 All: 0.131 ± 0.025	Roe et al. (2004)
		MR		M: 3.1 F: 11.7				Preston (1970)
Nerodia faciata faciata	Semi–aquatic (T,F)	RT	10 months? – 1 year?	46.47 ± 11.39 *(22)*	0.0354 ± 0.0175	0.0295 ± 0.0378	0.1095 ± 0.1003	Camper and Chick (2010)
Nerodia sipedon sipedon	Semi–aquatic (T,F)	RT	1 year	M: 31.5 ± 6.2 *(4)* F: 22.9 ± 7.7 *(9)* All: 25.6 ± 2.7 *(13)*	M: 0.056 ± 0.029 F: 0.033 ± 0.006	M: 0.016 ± 0.01 F: 0.004 ± 0.001 All: 0.008 ± 0.003	M: 0.069 ± 0.036 F: 0.031 ± 0.009 All: 0.043 ± 0.013	Roe et al. (2004)
		RT	29 – 116 days	M: 48.8 ± 5.3 *(8)* F: 49.3 ± 8.3 *(9)*		M: 0.38 ± 0.09 F: 0.33 ± 0.17	M: 2.92 ± 0.79 F: 2.72 ± 1.15	Roth et al. (2006)
		RT	4 – 35 days	4.0 *(4)*				Fitch and Shirer (1971)
		RT	17 – 75 days	*(10)*		4.19x10^{-3} ± 4.793x10^{-3}	0.054185 ± 0.05983	Tiebout III and Cary (1987)
Nerodia spp. (three species)	Semi–aquatic (T,F)	RT	> 1 year		0.057			Michot (1981)
Acrochordidae								
Acrochordus arafurae	Aquatic (F)	RT	2 – 24 days	M: 116.5 ± 58.04 *(6)* F: 133.8 ± 83.5 *(9)*	2.65x10^{-2} ± 6.36x10^{-3}			Shine and Lambeck (1985)
		MR	4 years	M: 211.3 ± 326.6 *(148)* F: 286.8 ± 530 *(190)*				Houston and Shine (1994)

Elapidae, Hydrophiinae						
Aipysurus laevis	Aquatic (M)	RT	6 – 9 days	M: 14.9 ± 1.59 *(5)* F: 20.4 ± 1.53 *(7)*	M: $1.471x10^{-3} \pm 1.28x10^{-4}$ F: $1.817x10^{-3} \pm 2.47x10^{-4}$	Burns and Heatwole (1998)
Homalopsidae						
Enhydris enhydris	Semi–aquatic (T,F)	T, MR, RT	8 – 19 days	M: 22.5 ± 2.89 *(6)* F: 16.7 ± 4.09 *(5)*	M: $3.6306x10^{-3} \pm 2.0009x10^{-3}$ F: $2.4271x10^{-3} \pm 9.1169x10^{-4}$	Murphy et al. (1999),Karns et al. (2000)
Enhydris plumbea	Semi–aquatic (T,F)	T, MR, RT	7 – 9 days	4.4 ± 1.7 *(6)*		Voris and Karns (1996)
Cerberus schneiderii	Semi–aquatic (T,F)	MR	~ 12 months	Maximum displacement: M: 851 m; F: 555 m Average movement: 197.63 ± 221.23 m		Chim and Diong (2013)
Fordonia leucobalia	Semi–aquatic (T,F)	MR, RT	14 – 22 days	M: 6.9 ± 0.64 *(3)*	M: $9.23x10^{-5} \pm 1.608x10^{-5}$	Karns et al. (2002)

Viperidae								
Agkistrodon piscivorus	Semi–aquatic (T,F)	RT	26 – 81 days	M: *(5)* *F: (15)*	All: 0.0106 ± 0.00864 M: 0.0186 ± 0.00407 F(gravid): 0.00963 ± 0.00264 F(non–gravid): 0.00372 ± 0.00081		All: 0.0304 ± 0.038 M: 0.0674 ± 0.0475 F(gravid): 0.01775 ± 0.01235 F(non–gravid): 0.00617 ± 0.00227	Roth (2005)
		MR	19 months		M: 0.0017 F: 0.0014			Wharton (1969)

2.3.2. Vertical movement

In the aquatic environment, use of the water column is an added dimension that needs to be considered when examining movement and space use. As aquatic snakes are air−breathing reptiles, the ability to access different depths is restricted by apnoeic ability (Heatwole 1975c). Extensive studies on pelagic and benthic sea snakes have shown that marine snakes display a remarkable range of voluntary submergence times, with animals diving for up to 3.5 hours during periods of inactivity (Table 2.2). In most cases, diving profiles of snakes have been recorded with snakes in captivity or anecdotal field observations (e.g. Heatwole 1975c, Pratt & Franklin 2009), however a few studies have used field based telemetry techniques to quantify short−term behaviours and define dive profiles in the natural environment (Brischoux et al. 2007a, Pratt et al. 2010, Cook & Brischoux 2014).

One aspect of vertical movement that has not been examined is the pattern of space use of snakes at particular depths and how this is driven by intrinsic and extrinsic factors. This has been due to a limited ability to accurately measure swimming depths of animals in the natural environments over extended periods and limited computational techniques to calculate the use of space in three dimensions. New technologies and analysis techniques can now be used to address these questions and can provide more detailed insight into how marine animals use space though time in a three dimensional environment (Hays et al. 2001, Campbell et al. 2010, Simpfendorfer et al. 2012).

Table 2.2. Vertical movement data for aquatic and semi−aquatic snakes in current literature during periods of activity and inactivity. Modes defined by the environment snakes are most commonly encountered in (T: terrestrial, F: freshwater, M: marine). Most studies used one or a combination of field observations (FO), radio−telemetry (RT), Acoustic telemetry (AT) and data from captive animals (C). All dive depths were standardised in meters and dive duration in seconds.

Species	**Mode** (Environment: T,F,M)	**Monitoring method**	**Period monitored**	**Dive Depth (m)** [mean depth ± SE *(max depth)*]	**Dive Duration (sec)** [mean duration ± SE *(max duration)*]	**Reference**
Elapidae, Hydrophiinae						
Acalyptophis peronii	Aquatic (M)	C, FO			Active: 1813 Inactive: 1110 *(3246)*	Heatwole (1975c)
Hydrophis belcheri	Aquatic (M)	C, FO			Active: 244 Inactive: 582 *(2220)*	Heatwole (1975c)
Hydrophis (Pelamis) platura	Aquatic (M)	RT	3 − 29 hours	14 ± 8.7 *(50)*	2226 ± 1038 *(12810)*	Rubinoff et al. (1986), Cook and Brischoux (2014)
Hydrophis elegans	Aquatic (M)	C, FO			Active: 194 Inactive: 920 *(2820)*	Heatwole (1975c)
Aipysurus laevis	Aquatic (M)	C, FO			Active: 888 Inactive: 1461 *(4200)*	Heatwole (1975c)
Aipysurus duboisii	Aquatic (M)	C, FO			Active: 1322 *(2746)* Inactive: 940	Heatwole (1975c)
Emydocephalus annulatus	Aquatic (M)	C, FO			Active: 1712 *(5005)*	Heatwole (1975c)

Elapidae, Laticaudidae						
Laticauda colubrina	Semi–aquatic (T,M)	C, FO			Active: 40 Inactive: 268	Heatwole (1975c)
Laticauda saintgironsi	Semi–aquatic (T,M)	RT	8 – 11 weeks	12 ± 8 (83)	960 ± 720 *(8280)*	Brischoux et al. (2007a)
Laticauda laticaudata	Semi–aquatic (T,M)	RT	8 – 11 weeks	(32)		Brischoux et al. (2007a)
Acrochordidae						
Acrochordus javanicus	Aquatic (F,M)	C			Active: 60 *(174)* Inactive: 1350 *(1920)*	Pough (1973)
Acrochordus arafurae	Aquatic (F)	C			Active: 577 ± 104 Inactive: 1967 ± 154	Pratt and Franklin (2009)
		AT	6 – 14 days	0.62 ± 0.2 (>3)	400 ± 72 *(4512)*	Pratt et al. (2010)
Acrochordus granulatus	Aquatic (F,M)	C, FO			Active: 122 Inactive: 1050 *(7014)*	Heatwole (1975c)

2.4. Drivers of movement and space use in aquatic and semi-aquatic snakes

As apex and meso−predators, aquatic and semi−aquatic snakes play an important role in a range of habitats including freshwater and marine systems, and can serve as bio−indicators for ecosystem health (Brischoux et al. 2009a). However, these groups are often under−represented in the literature due to their rarity and difficulty to work with, and therefore large knowledge gaps exist in their fundamental ecology (Hazen et al. 2012, Shillinger et al. 2012, Elfes et al. 2013). One aspect of aquatic and semi−aquatic snake ecology that this literature review will address is the effect of environmental and biological variables that may influence movement and activity patterns in wild populations. The patterns of movement and space use exhibited by terrestrial snakes are heavily influenced by a suite of factors (e.g., temperature, reproductive state), however when considering species that inhabit aquatic environments, additional factors (e.g., salinity, tidal cycle) also need to be considered (Heatwole 1978, Brischoux & Shine 2011).

2.4.1. Extrinsic drivers

2.4.1.1. Temperature

Temperature has been demonstrated to have a strong influence on the biology, ecology and distribution of reptiles. The global distribution of aquatic and semi−aquatic snakes is restricted to areas with habitats that maintain environmental temperatures within a suitable thermal range. The thermal tolerance of most aquatic snakes ranges from ~18−20˚C to ~39−40˚ C (Heatwole 1999, Heatwole et al. 2012) and thus they are most commonly found within sub−tropical and tropical waters. On a smaller scale, thermoregulation by means of moving from habitats with unfavourable temperatures to habitats with favourable temperatures is an important process that many reptiles use to maintain body temperature within their preferred thermal range. Aquatic snakes display this behaviour not only by selecting suitable sites in estuarine and coastal areas, but also by diving into and out of thermoclines in the water column to regulate their body temperature (Dunson & Ehlert 1971). Some aquatic snakes exhibit a different strategy and instead of regulating their body temperature by moving between areas that offer different temperature regimes, they simply allow their body temperature to heat up or cool down with the environment (i.e., thermoconform). This strategy has been observed in the freshwater snake *Acrochordus arafurae,* where individuals undertake shallow dives during the day in restricted pools and the water temperature determines their body temperature (Shine & Lambeck 1985, Pratt et al. 2010). Therefore, temperature as a driver for movement and activity may only apply to aquatic and semi−aquatic snakes that are inherent thermoregulators, and may play a smaller role in thermoconforming species. Thus physiological and behavioural strategies combine to determine movement patterns in relation to temperature. The movement and activity of aquatic and semi−aquatic snakes in response to unfavourable temperatures have not been directly tested in the current literature and remain a question that needs to be addressed.

2.4.1.2. Salinity

Salinity plays an important role in the geographic distributions of estuarine and marine reptiles (Dunson & Mazzotti 1989, Lillywhite et al. 2010). Freshwater semi−aquatic snake assemblages as well as movement and spatial use by water snakes (*Enhydris enhydris* and *E. plumbea*) in Southern Thailand were influenced by water level (associated with the monsoon) and salinity (Karns et al. 2000). Previous studies have also shown that semi−aquatic snakes that inhabit freshwater and estuarine areas have markedly varying tolerances to sea water (Dunson 1980), which directly affects their survival and restricts their movements to environments outside a suitable salinity range (Zug & Dunson 1979). The requirement to access fresh water for nitrogen excretion, osmoreglation and water balance was found to be a potential limitation for seaward migration in aquatic Acrocordid snakes (Lillywhite & Ellis 1994). The gradual transition from terrestrial to estuarine, and finally, to a marine environment by snakes meant that several adaptations in morphology and physiology were needed to maintain internal homeostasis in new environments. Maintaining water balance in a hyperosmotic environment, like in the marine environment, is challenging and despite the presence of functional salt glands in most species of marine snakes, dehydration remains a serious problem (Lillywhite et al. 2012, 2014a). Recent studies on the pelagic yellow−bellied sea snake, *Pelamis platura*, have revealed that these snakes can remain in a dehydrated state for six to seven months at a time following seasonal dry spells (Lillywhite et al. 2014b).

On a global scale, the species richness of marine aquatic and semi−aquatic snakes are highest in areas of relatively low, but seasonally variable salinities (Brischoux et al. 2012b). Field observations and captive dehydration experiments have shown that marine aquatic snakes are regularly encountered on the water surface right after heavy rainfall and have been observed to leave refuge sites to access the ‘lens’ of fresh or brackish water that forms on the surface after these events (Bonnet & Brischoux 2008, Lillywhite et al. 2008, Lillywhite & Tu 2011). However, one question that remains to be fully addressed is if pelagic snakes in isolated ecosystems have the ability to track heavy rainfall events and if these animals can use environmental cues to predict and move toward the surface to take advantage of the freshwater lens. Physiological challenges faced by marine aquatic snakes in maintaining water balance can have potential effects on energy expenditure, activity patterns and movement (Lillywhite & Ellis 1994). However, the link between the state of dehydration and activity patterns in aquatic snakes has yet to be fully explored.

2.4.1.3. Lunar and tidal cycles

Lunar and tidal cycles are two mechanisms that are intrinsically linked and play a vital role in driving biological processes in estuarine and marine environments (Naylor 1999). This environmental driver influences coastal and estuarine areas more than anywhere else, and affects the ecology of aquatic and semi−aquatic snakes that inhabit these regions. Houston and Shine (1994) found a strong influence of lunar phase on the activity of aquatic file snakes (*Acrochordus arafurae*), with less movement observed on moonlit nights. The authors suggested that file snakes reduced their movements and activity in increased lunar light levels to reduce their vulnerability to predation. Whereas, Lillywhite and Brischoux (2012b) found the opposite trend in semi−aquatic cottonmouth snakes (*Agkistrodon piscivorus*), this species increased foraging and scavenging activity during full moon nights to increase prey capture efficiency. This demonstrates that movements of semi−aquatic and aquatic snakes in relation to moon phase are varied and can be highly influenced by a trade−off between predator avoidance and prey capture efficiency.

The tidal cycle also seems to be an important factor with respect to diurnal and nocturnal activity patterns of sea snakes (Ineich & Laboute 2002). In marine systems, the tidal cycle is most clearly felt by tidal currents that are strongest during the full and new moon phases (spring tides) and weakest during the quarter phases (neap tides). Tidal currents are significant in coastal habitats and can influence movement and activity patterns of animals that inhabit these environments (Naylor 1999). Lynch (2000) observed a strong correlation between tidal cycle and activity patterns of adult male *Aipysurus laevis* in coral reef habitats, where individuals were more active within the water column during neap tidal periods. Lynch (2000) hypothesised that activity may be related to predator avoidance or feeding behaviours. Similarly, coastal species like *Hydrophis* (*Disteira*) *major* and *H. elegans* may use the tidal cycle as a cue to move in and out of seagrass habitats to avoid predation by tiger sharks (*Galeocerdo cuvier*) (Kerford et al. 2008, Wirsing & Heithaus 2009). Heatwole (1999) noted the beaked sea snake (*Hydrophis zwefeli,* previously *Enhydrina schistosa*) inhibited its activity during spring tides with increased tidal current. As most species of aquatic or semi−aquatic snakes occupy habitats adjacent to or within coastal waters, tidal currents are likely to directly or indirectly (via patterns in prey movements or predator behaviours) play an influential role in their movement and habitat use patterns.

Extrinsic factors alone may not fully explain movement in aquatic and semi−aquatic snakes, but the factors discussed above in combination with intrinsic drivers may improve our understanding of movement and activity patterns in snakes.

2.4.2. Intrinsic drivers

2.4.2.1. Food

The need to acquire food is an obvious driver of movement and activity in mobile animals, and can be greatly influenced by the movement of prey species and foraging modes used to search for and access these resources. Aquatic snakes have varied diets from the highly specialised, reef−associated *Emydocephalus annulatus,* that only feed on reef fish eggs, and near-shoreʃcoastal species that specialise in feeding on eel or goby−like fishes (e.g. *Hydrophis* spp., *Acrochordus* spp.), to generalists where prey type is only restricted by its size (e.g. *Hydrophis* [*Lapemis*] *curtus*) (Voris & Voris 1983). The diets of semi−aquatic snakes are also varied, from generalists like the Natricine and Homalopsine snakes that are largely piscivorous but also feed on anurans, crustaceans and snails (Mushinsky & Hebrard 1977, Jayne et al. 1995), to some species of Laticaudid snakes that specialise in feeding on eels (Brischoux et al. 2007b). Foraging patterns of aquatic and semi−aquatic snakes include specific modes (e.g. 'cruising near the bottom'; Voris et al. 1978, 'crevice−foraging'; Shine et al. 2004, 'float−and−wait' foraging; Brischoux & Lillywhite 2011), which result in specific movement and activity patterns.

Apart from foraging modes, the abundance and activity of prey species greatly influences activity and movement patterns of aquatic snake species. Past studies have shown that the diets of many species of reef−associated sea snakes (e.g. *Aipysurus* spp.) are closely correlated to prey fish abundance within the ecosystem (e.g. Reed et al. 2002, Ineich et al. 2007, Brischoux et al. 2009a). A close association between snake distribution and prey have been suggested as reasons for restricted home ranges over the short−term in reef−associated snakes. Large seasonal migrations in and out of the Mekong River basin by *Hydrophis* (*Enhydrina*) *schistosa* in Cambodia were correlated with the movement of prey fish species (Ineich & Laboute 2002). Similar close relationships between prey populations and semi−aquatic Laticaudid snakes have been demonstrated in coastal reef systems in New Caledonia (Ineich et al. 2007), where local sea snake surveys were successfully used as bio−indicators for the abundance of anguilliform fish species (Brischoux et al. 2009a). The relationship between snake populations and prey species are important and any alteration or decrease in prey populations may have consequences on the movements of semi−aquatic and aquatic snake populations.

2.4.2.2. Predator avoidance

Predation risk is a powerful driver for animal behaviour (Lima & Dill 1990). In many species of venomous sea snakes, warning colouration has been shown to dissuade potential predators (Caldwell 1983), but other species have been observed to actively avoid predators. Predation on aquatic and semi−aquatic snakes comes from both the aerial and aquatic realm. The gut contents of tiger sharks (*Galeocerdo cuvier*) captured in several locations around Australia, New Caledonia and Thailand contained aquatic (*Hydrophis curtus*, *Aipysurus laevis*) and semi−aquatic (*Cerberus rynchops*, *Fordonia leucobalia*) snakes and suggest these species comprise a regular part of their diets (e.g. Simpfendorfer 1992, Simpfendorfer et al. 2001, Ineich & Laboute 2002, Voris & Murphy 2002, Wirsing & Heithaus 2009). The predator−prey interaction between sharks and sea snakes have been intensely examined by Wirsing and colleagues (Kerford et al. 2008, Wirsing & Heithaus 2009) who have found that sea snakes (*Hydrophis major* and *H. elegans*) actively move between sandy bottom and seagrass habitats at different stages of the tide to avoid predation by sharks.

Snakes foraged in sandy bottom habitats during low tides when these areas were not accessible to sharks, and moved into shallower seagrass habitats during high tide, using these habitats as refugia. Apart from large sharks, aquatic snakes are also preyed on by invertebrates including mud crabs (*Scylla serrata*), as well as other semi−aquatic reptiles (e.g. long−necked turtle, *Chelodina rugosa*; salt−water crocodile, *Crocodylus porosus*; mangrove monitors, *Varanus indicus*) (Voris & Murphy 2002).

Birds of prey like sea eagles (*Haliastur indus* and *H. leucogaster*) are one of the main non−aquatic predators of aquatic and semi−aquatic snakes (Heatwole 1975a, 1999, Voris & Murphy 2002). The risk of predation on aquatic snakes by aerial predators is highest during intervals when snakes come to the surface to breathe. Altering diving behaviour has been shown to be an effective strategy to reduce this risk of predation in other air−breathing aquatic foragers (Heithaus & Frid 2003). However, diving patterns of *Acrohcordus arafurae,* observed in captivity by Pratt and Franklin (2009), showed that aerial predation did not alter diving behaviours. The authors concluded that diel diving patterns in this nocturnal snake (i.e. more active at the water surface at nights) might have already provided an inbuilt anti−predatory response to aerial predation. Anti−predatory behaviours may influence diving patterns of other diurnally active snakes, however this has not yet been observed in the current literature.

2.4.2.3. Reproductive state

The reproductive state of individuals often influences the seasonal activity and movement patterns of squamate reptiles, where in some species males tend to display larger movements and activity spaces during the mating season, whereas females tend to maintain a fairly constant pattern of movement throughout the year (Figure 2.1, Southwood & Avens 2010). These patterns are also evident in aquatic and semi−aquatic species. For example, movement patterns in male *Aipysurus laevis* were more extensive during the mating season as males searched for potential mates (Lynch 2000). Similar patterns of movement were observed in northern water snakes (*Nerodia sipedon*), where mature males had larger home ranges during the mating season (Brown & Weatherhead 1999). Males also covered larger areas searching for mates when females were dispersed than when females were clumped. Female aquatic and semi−aquatic snakes on the other hand, generally display restricted movements and occupy smaller areas during mating seasons and are often sedentary during gestation. Shine (1988) hypothesised that gravid or egg−bearing female aquatic snakes may have impaired locomotory ability, hence they may seek out shallower waters to reduce energy costs of deep diving to find prey and return to the surface to breath. Restricted movement of female aquatic snakes in shallow coastal environments during mating seasons has been observed in several species (e.g. *Hydrophis curtus, H. elegans, Acrochordus granulatus*) (Dunson 1975, Houston & Shine 1994). Similarly, female semi−aquatic snakes *(*e.g. *Natrix natrix, Agkistrodon piscivorus*) display more restricted movements than males during mating season and are almost sedentary weeks prior to oviposition (Madsen 1984, Roth 2005). Therefore, repropductive state may not only influence individual movement and space use patterns, but may also influence how aquatic and semi−aquatic snakes use different habitats. Currently, few studies have directly examined how reproductive state or life stage of individuals influence energetic requirements and movement patterns, and should be a focus of future work on these groups of animals.

2.4.2.4. Ontogenetic shifts

Few studies on aquatic snakes have focused on changes in habitat use between juveniles and adults. However, catch data from trawl fishing and coastal netting have shown a pattern that may suggest a strong ontogenic change in habitat use by snakes at different life stages. Wassenberg et al. (1994) noted that juvenile snakes were rarely caught in commercial trawl grounds (>30 m) in the Gulf of Carpentaria, Northern Australia. They suggested that gear selectivity (large mesh sizes) was not a reasonable explanation for the lack of juveniles as bycatch and that this size class may not inhabit trawl grounds, but instead utilise shallower habitats adjacent to reefs, coastal and estuarine environments (Wassenberg et al. 1994). Similarly, a study of *Hydrophis schistosa* in coastal habitats in Malaysia reported 59% of snakes caught in shallow estuarine waters were juvenile (Voris & Jayne 1979). This pattern of differential habitat use between juveniles and adults was suggested by Wassenberg et al. (1994) as a strategy to maximise survival of juveniles by reducing the energetic costs of swimming to the surface for air. Although supporting evidence is limited, life stage may play a key role in movement and distribution patterns in these species and future research should consider size class distribution across different habitats.

2.4.2.5. Philopatry and homing

The affinity toward particular habitats in many mobile animals is often displayed in their ‘homing’ ability, where animals displaced from favourable habitats actively navigate back to these areas. Homing is an important factor that can drive large and small−scale movements and activity patterns (Southwood & Avens 2010). Snakes in the subfamily Laticaudinae have been shown to display a high degree of site fidelity

(*Laticauda saintgironsi* & *L. laticaudata*; Brischoux et al. 2009b) and large scale ‘homing’ ability (*L. colubrina*; Saint Girons 1990, Shetty & Shine 2002). The close association of individuals to one particular habitat or area was hypothesised to be due to an intrinsic behavioural mechanism rather than obstacles to dispersal.

Similarly, reef associated sea snakes have also been observed to have a high degree of site fidelity and display philopatry (Lukoschek et al. 2007, Lukoschek & Shine 2012). Work conducted by Lukoschek and colleagues in Australia (Lukoschek et al. 2007) and New Caledonia (Lukoschek & Shine 2012) have shown that individuals from two species of sea snakes (*Aipysurus laevis* and *Emydocephalus annulatus*) displayed a high degree of site attachment with few movements between adjacent reefs despite being separated by small distances. Limited connectivity between discrete populations in the reef environment was considered likely to make them highly vulnerable to localised extinction events.

Strong attachment to particular areas and the potential for localised extinction presents significant conservation and management implications when considering populations of critically endangered (IUCN listing) species like *Aipysurus apraefrontalis* and *A. foliosquama* that have restricted distributions and are the only Australian sea snakes listed as ‘threatened’ under the Environmental Protection and Biodiversity Conservation (EPBC) Act of 1999. Long−term mark−recapture studies conducted by Bonnet and colleagues (2014) in New Caledonia have shown that certain coastal sites were dominated by neonates and juveniles and considered to represent nursery habitats for amphibious yellow sea krait populations (*Laticauda saintgironsi*). Bonnet et al. (2014) also recorded mature females returning to these coastal sites to lay their eggs seasonally. Natal philopatry to particular sites is an important factor that drives seasonal movements in many aquatic and semi−aquatic snake species.

2.5. Implications for management and conservation

2.5.1. Targeted harvesting

Aquatic and semi−aquatic snakes are commercially targeted in artisanal ‘fisheries’ in several countries in South East Asia, largely for rawhides and for meat, and also as aphrodisiacs and traditional medicines in other Asian countries (Heatwole 1999, Van Cao et al. 2014). Around ~6.3 million homalopsine water snakes (*Enhydris* spp. and *Homalopsis* spp.) are harvested annually in Cambodia for leather and meat (Brooks et al. 2007). Punay (1975) found that hunters in the Philippines targeted a small number of aquatic species that have high export value: *Laticauda semifasciata*, *L. laticaudata* and *Hydrophis inornatus.* A recent assessment of the sea snake trade in the Gulf of Thailand highlighted the extent of the harvests in the area (Van Cao et al. 2014). The assessment found that 82 tonnes (roughly 225,500 individuals) of live sea snakes were harvested annually, which constituted one of the largest harvests of wild marine reptiles in the world to date. The species compositions of these harvests were dominated by two species, *Hydrophis curtus* and *H. cyanocinctus*, but included a wide range of other aquatic snakes (*Acalyptophis peronii, Aipysurus eydouxii, H. atriceps, H. belcheri, H. lamberti* and *H. ornatus*). The assessment also observed a decline in the biomass of harvests over the study period (~30% decline over 4 years), citing overharvesting or targeting of smaller (or younger) snakes as possible reasons for such declines. As this was the first assessment of its kind, it serves as a baseline study for the harvests, and further long−term monitoring is required to accurately assess the effect of harvesting on the local marine snake populations (Van Cao et al. 2014).

Other taxa like Acrochordidae are seasonally hunted for their skin in Sumatra, Indonesia and are considered predators in fish ponds and culled to reduce predation on target fish species (Shine et al. 1995). All of these targeted snake species display relatively restricted movements; therefore catching them in large numbers is relatively easy which can have dramatic effects on their populations (Bacolod 1984, 1990). Hunting snakes for leather and meat represents an important source of income in many parts of Asia, where weak or under−resourced governance systems are unable to restrict trade or properly manage these resources (Brooks et al. 2007). Therefore understanding the movement ecology and distributions of these animals is crucial to management agencies tasked with conserving and ensuring the sustainable use of these species, and for NGOs who may use these data to lobby for improved protection.

2.5.2. Incidental trawl capture

Apart from targeted fishing, a significant threat to aquatic and marine snake populations is incidental catch in trawl fisheries. The impacts of trawl fishing have been well studied in two large coastal fisheries in tropical waters of Australia. The Northern Prawn Fishery (NPF), an extensive trawl fishery operating in the Gulf of Carpentaria and Northern Australia; and the East Coast Otter Trawl Fishery (ECOTF) which operates along the east coast of Australia, both record large incidental catches of sea snakes (Milton et al. 2008). Grech and Coles (2011) observed that trawl activity around the eastern coast of Australia was highly clumped in specific coastal habitats, despite large areas of the coast being open to trawl fishing. This suggests species that utilise these non−reef areas are at high risk of exposure to trawl fishing. Courtney et al. (2010) found that within and post−trawl mortality of sea snakes could be as high as 50%, and varied between species and trawl sector. They estimated > 100,000 sea snakes were captured per year within the ECOTF. This led the authors to identify sea snakes as a bycatch species at high risk (Courtney et al. 2010). Movement and space use data on snakes that utilise non−reef and coastal areas are sparse, and understanding the extent of the overlap between snakes and trawl activity is critical to minimising bycatch of this group in trawl fisheries.

2.5.3. Declines in populations

In recent years, a largely unexplained decline in the diversity and abundance of aquatic snakes has been reported in areas that were once considered 'hotspots' for sea snake biodiversity (e.g. Guinea 2012b, New Calidonia: Goiran & Shine 2013, Ashmore Reef, Australia: Lukoschek et al. 2013). These declines have taken place in the last decade and have been reported in areas that are protected under local management practices and have had little anthropogenic modification. The authors of these studies considered a range of factors that may be impacting these populations (e.g. habitat loss, declines in prey availability, disease, recruitment failure and illegal harvests) and concluded that none of them appropriately explained such declines (Goiran & Shine 2013, Lukoschek et al. 2013). There is a need to identify and understand these cryptic causes of declines, and filling knowledge gaps in fundamental biology and ecology of marine snakes may help to better direct conservation and bycatch management efforts for this taxa (Elfes et al. 2013).

2.6. Concluding remarks

Aquatic and semi–aquatic snakes form a diverse group and species within this group are represented in almost every continent (Rasmussen et al. 2011). Despite this, these species are under–represented in the scientific literature. Understanding how these species react to extrinsic and intrinsic factors is important when considering the spatial ecology of these animals. Here, I have reviewed findings from previous work and have highlighted the need for more data to better inform management policy and ensure healthy populations of aquatic and semi–aquatic snakes. The current thesis mainly focuses on aquatic sea snakes (Hydrophiinae), which are currently facing a multitude of natural and anthopogenic threats world–wide. Scientific research on the physiology, behaviour and spatial ecology of these taxa of have historically been challenging owing to their rarity and difficulty to handle and keep in captivity. Despite these challenges, a few prominent authors (e.g. Harold Heatwole, William Dunson) have contributed the majority of what we know about these animals from the 1960's and 1970's (Lillywhite & Brischoux 2012a). Following a decline in scientific publications on sea snakes in the 1990's there has been a ressurgence of scientific interest in these taxa with many authors using an array of new techniques to answer fundamental questions on the biology of sea snakes. This thesis aims to contribute to this endevour using new methods like baited video surveys, passive acoustic telemetry and accelerometry to examine the spatial ecology of sea snakes to help inform management policy to better conserve these animals on the Great Barrier Reef, Australia.

Chapter 3

Distribution of sea snakes on the Great Barrier Reef

3.1. Introduction

Fundamental information about the distribution and abundance of marine organisms is vital for understanding their biology, ecology and conservation status (Brooks et al. 2006, Hoffmann et al. 2008). Management of harvests and conservation practices are based on this knowledge (Ward et al. 1999, Roberts et al. 2003). In recent years, animals have been observed shifting historical global distributions in response to climate change (see Zacherl et al. 2003, Perry et al. 2005), therefore understanding current distribution patterns is critical for identifying any potential effects of a warming climate (Walther et al. 2002, Parmesan 2006). Estimating the distribution and abundance of animals over large spatial scales has historically been difficult because of the amount of resources (time and money) needed to undertake large−scale sampling in marine habitats.

The challenges of estimating the distribution and abundance of marine vertebrates becomes more extreme when the target group is comprised of relatively rare and potentially highly mobile animals that are not frequently encountered (Thompson 2004). Technological advances are providing marine researchers with the ability to conduct remote surveys over large spatial and temporal scales and are increasingly being used to quantify the distribution and movements of commercially important species, as well as other species of conservation concern (Cooke et al. 2004a, Hodgson et al. 2013). One such approach is baited remote underwater video stations (BRUVS), which have been used to provide information about the distribution and abundance of demersal vertebrate communities (Cappo et al. 2007) and quantifying the effects of spatial closures to fish stocks (Cappo et al. 2012). The nature of BRUVS surveys is that all animals in the field of view are recorded, providing an opportune source of data about the distribution and abundance of non−target species that receive little research focus.

One group of mobile marine vertebrates that is largely neglected by the research community is the true sea snakes (Elfes et al. 2013). True sea snakes (Family Elapidae; Subfamily Hydrophiinae) are a group of approximately 60 species of air breathing marine reptiles that occur in tropical marine habitats throughout the Indo−West Pacific (Heatwole 1999). A total of 36 species occur in Australian waters, 16 of which have been recorded within the waters of the Great Barrier Reef (GBR) (Heatwole 1999). True sea snakes comprise two main evolutionary groups, the *Aipysurus* and *Hydrophis* groups (Lukoschek & Keogh 2006), with species from the *Aipysurus* group typically found in coral reef habitats, whereas species from the *Hydrophis* group more commonly occur in inter−reef soft sediment habitats, although there are exceptions to this pattern (Cogger 2000). All sea snake species, with the exception of the pelagic yellow−bellied sea snake, *Hydrophis* (*Pelamis*) *platura*, are strongly associated with benthic habitats, and occur in coastal, shallow water habitats (typically <100 m depth), as they regularly need to come to the surface to breathe (Heatwole 1999). Sea snakes typically have highly aggregated distributions, with genetic (Lukoschek et al. 2007, Lukoschek & Shine 2012) and mark−recapture (Lukoschek & Shine 2012) evidence indicating limited dispersal and connectivity among populations, particularly for reef−associated species in the

Aipysurus group. Although there is evidence that global distribution patterns of amphibious marine snakes (Elapidae, *Laticauda*) are influenced by salinity and temperature (see Brischoux et al. 2012b, Heatwole et al. 2012), the distributions of the fully marine true sea snakes are most strongly influenced by proximity to coastlines (Brischoux et al. 2012b).

Sea snakes form a significant component of bycatch in trawl fisheries that operate in tropical waters around the world (Heatwole 1997). The Queensland east coast trawl fishery (QECTF) is the main trawl fishery targeting penaeid prawns that operates within the GBRMP and an estimated 105,210 sea snakes (standard error = 18,828) are caught annually in this fishery (Courtney et al. 2010). True sea snakes are Listed Marine Species under the Commonwealth Environment Protection and Biodiversity Conservation (EPBC) Act, which requires fishers to return all snakes (living and dead) to the ocean. Approximately 26% of sea snakes are either landed dead or die within 72 hours following release (Courtney et al. 2010). In the past, a combination of incidental catch data in the Australian trawl fishery (Wassenberg et al. 1994, Ward 2000, Courtney et al. 2010), as well as fisheries−independent data (Dunson 1975, Heatwole 1975b, Limpus 1975), have provided some understanding of how commonly sea snakes occur and have been used to evaluate distribution and abundance of sea snakes along the GBR.

All sea snake species typically occur in dense aggregations in some locales throughout their geographic ranges, but not in other apparently ecologically similar areas (Heatwole 1975b, 1997), and this aggregated pattern of distribution is exhibited at a range of spatial scales. For example, long−term surveys (>30 years) in the Swains and Pompey reef regions of the southern GBR showed that the olive sea snake, *Aipysurus laevis,* and the turtleheaded sea snake, *Emydocephalus annulatus,* have highly aggregated distributions, with high abundances on some reefs but none on neighbouring reefs (Lukoschek et al. 2007). This long−term study also found that sea snakes had disappeared from some reefs on which they had previously been abundant (Lukoschek et al. 2007). Recent studies also have revealed declines in the abundance and distribution of sea snakes in isolated areas that have historically been hotspots for sea snake diversity (New Caledonia: Goiran and Shine 2013; Ashmore Reef: Guinea 2012, Lukoschek et al. 2013). Given growing concerns about the declines in the abundance of sea snakes, there is a need to better understand their distribution and abundance and assess the effectiveness of spatial conservation tools like Marine Protected Areas (MPA) for conserving populations (Elfes et al. 2013).

The use of trawl fishery data (e.g. Courtney et al. 2010), as well as fisheries−independent sampling using commercial fishing techniques (e.g. Dunson 1975) and underwater visual surveys (e.g. Heatwole 1975b, Lukoschek et al. 2007), has provided some useful data for management of sea snakes on the GBR. However, these techniques have inherent limitations that restrict the spatial range of sampling. In addition, the use of trawl by−catch data to estimate the distribution and relative abundance of sea snakes is biased by gear selectivity (Wassenberg et al. 1997) that can potentially underestimate relative abundances. Specifically, trawl fisheries only operate in flat, soft sediment habitats, and the use of mandatory bycatch reduction devices (BRDs), such as turtle exclusion devices (TEDs) and fisheye BRDs, significantly reduce the number of sea snakes caught (Courtney et al. 2010).

Underwater visual census (UVC) have been used to assess the distribution and abundance of sea snakes around coral reefs (Lukoschek et al. 2007, Lukoschek & Shine 2012); however, short survey times and depth constraints restrict the amount of habitat that can be surveyed. In addition, response to observers has been shown to influence the accuracy of estimates of abundance for marine fish by either underestimating (Jennings & Polunin 1995) or overestimating (Ward−Paige et al. 2010) counts. Similar biases may also occur for estimates of abundance for sea snakes, but such effects have not been quantified. Alternative approaches are required to estimate distribution and abundance of sea snakes at ecosystem scales.

Baited remote underwater video stations (unlike trawls) can be deployed on any seafloor topography and (unlike diver−based UVC) can provide long periods of observation in deep water at any time of day. However, as with all survey techniques, BRUVS have biases due to the use of bait (Bernard & Götz 2012, Dorman et al. 2012, Wraith et al. 2013), the behaviour of animals in the field of view (Birt et al. 2012), and reduced effectiveness in low light or high turbidity conditions (Cappo et al. 2004, Merritt et al. 2011). However, the numerous benefits offered by a non−extractive sampling technique (see Cappo et al. 2006, Shortis et al. 2008 for reviews) have been recognised for the study of larger, rare species, such as elasmobranchs (Brooks et al. 2011, White et al. 2013), and for surveys in environmentally sensitive areas such as MPAs (Fitzpatrick et al. 2013, Moore et al. 2013). This study evaluates the use of BRUVS as an alternative sampling technique for estimating the distribution and abundance of sea snakes at an ecosystem scale, and addresses the first aim of the overall thesis (Aim 1:).

In this chapter, BRUVS techniques are used to (a) describe the distribution of commonly encountered sea snake species in the GBRMP, (b) investigate how spatial factors (depth, latitudinal and longitudinal distances along the GBR, proximity to reef systems and proximity to land) in the GBRMP influenced the presence and species composition of sea snakes, and (c) evaluate whether there were significantly more sea snakes in no−take reserves established in 2004 compared with areas open to trawling.

3.2. Methods

3.2.1. Field methods

A total of 2471 BRUVS were deployed between March 2000 and May 2010 at sites spanning a range of latitudes (10.7˚S − 24.2˚S) and longitudes (143.38˚E − 152.36˚E) of the GBR as part of several research projects (Cappo et al. 2004, Cappo et al. 2007, Cappo et al. 2012). BRUVS were deployed at depths of 7 to 115 m (mean ± SD; 36.7 ± 15.6 m). Each BRUVS consisted of a galvanised, steel frame with a detachable arm (20 mm plastic conduit), which positioned a 350 mm plastic mesh canister containing 1 kg of crushed oily sardines (*Sardinops* or *Sardinella* spp.) as bait on the sea floor. A roll−cage frame was used prior to 2003 (shown in Cappo et al. 2004), after which a trestle−shaped frame was used for the majority of deployments (Figure 3.1A). A simple camera housing made from PVC pipe with acrylic front and rear ports was situated inside the frames to deploy either a Sony™ Hi−8 (model TR516E; prior to 2003) or a Sony™ Mini−DV (models TRV18E, TRV19E) HandiCam. Wide−angle lens adapters (Hama™ 0.5X or Sony™ 0.6X) were fitted to the cameras, the exposure was set to 'Auto', focus was set to 'Infinity/Manual', and 'Standard Play' mode was selected to provide at least 45 min (53.3 ± 11.3 min) of filming around the bait (Figure

3.1A). BRUVS were deployed with 8 mm polypropylene ropes and polystyrene surface floats bearing a marker flag, and were retrieved with a hydraulic pot−hauler.

BRUVS were generally set in groups of 3−5 about 300−450 metres apart along transects bracketing sampling locations. This spacing was designed to minimise the possibility of large−scale interference between BRUVS deployments. The prevailing currents within the GBRMP flow at approximately 0.2 ms^{-1} (Luick et al. 2007). Data obtained from the seafloor biodiversity project models [Lance Bode & Lou Mason models, JCUƒReef−CRC] show that seabed current sheer stress is spatially variable with stronger average currents in the southern GBRMP (south of 20˚S latitude; [$\bar{x}$ ± SE] 0.31 ± 0.02 Pascals), and weaker currents in the central (20˚−16˚S latitude; 0.17 ± 0.03 Pa) and northern GBRMP (north of 16˚S latitude; 0.08 ± 0.01 Pa) (Pitcher et al. 2007). The currents along the GBR are also seasonally variable; therefore an approximate effective range of attraction was calculated using the mean flow rate throughout the GBRMP. A 60 minute BRUVS soak time potentially had an effective range of attraction of ~480 m for sea snakes, which have average swimming speeds of ~0.6 ms^{-1} (1.9 kmh^{-1}; Rubinoff et al. 1988). This range comprised 40 minutes of advection of the bait plume down current and 20 minutes of swimming time up current to reach the field of view in time to be recorded on the BRUVS (see Cappo et al. 2004, Farnsworth et al. 2007).

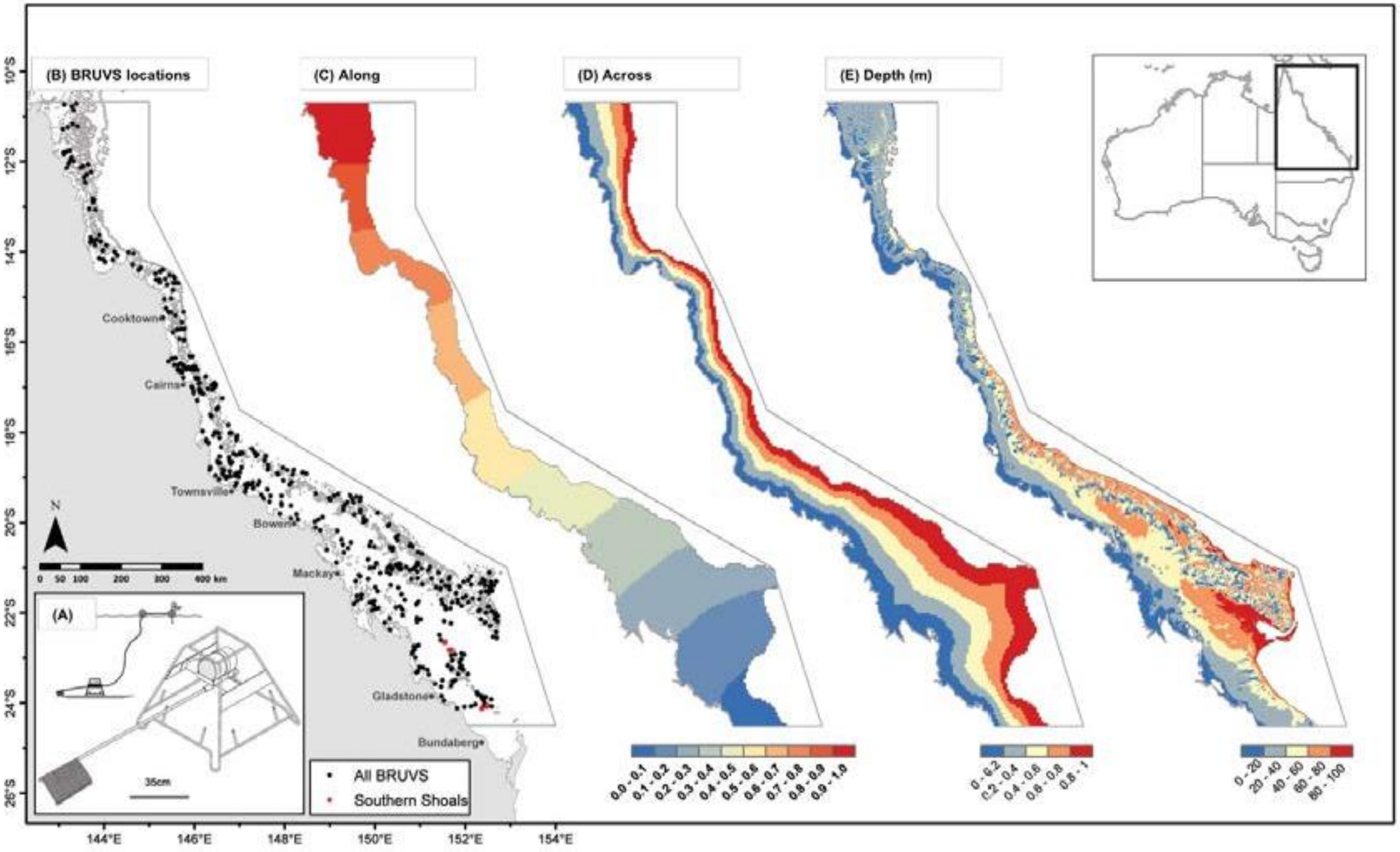

Figure 3.1. BRUVS setup, locations and spatial factors used in analysis (A) Baited remote underwater video station (BRUVS) showing deployment on the seabed and details of the removable bait arm and camera housing. (B) Red points in left plot represent the Southern Shoals sampled as part of intensive study (see Stowar et al. 2008, Cappo et al. 2012) and black points represent the locations of the remaining BRUVS deployed (total=2471). Spatial patterns used for analysis of (C) Along, (D) Across and (E) Depth (m) on the GBR [depth data sourced from project 3DGBR (Beaman 2010)]

During 2007−2010, intensive BRUVS sampling was conducted on four deep banks off the coast of Gladstone in the southern GBR (Figure 3.1B) to examine short−term (hours and days) and long−term (years) variability in samples (Stowar et al. 2008, Cappo et al. 2012). The four banks surveyed were Karamea Bank (22˚38.6 S, 151˚32.4 E), Barcoo Bank (22˚49.6 S, 151˚39.9 E), West Warregoes (24˚07.0 S, 152˚22.1 E) and East Warregoes (24˚02.9 S, 152˚29.2 E)(Figure 3.1B). The BRUVS footage showed that these four deep−water banks were mesophotic coral reef systems that do not appear as 'reef' features in the current maps of the GBRMP. These studies showed that there were significantly larger numbers of target teleost species (e.g. coral trout *Plectropomus leopardus,* red−throat emperor *Lethrinus miniatus*) sighted in shoals closed to fishing than the shoals open to fishing, in both the short and long−term (Stowar et al. 2008). The high spatial and temporal intensity of BRUVS sampling at these four shoals potentially resulted in recounting of snakes at intervals of hours, days and years. In order to account for the possible recounting of snakes, all spatial analyses were conducted including and excluding data from these four shoals. The BRUVS surveys did not conduct temporal sampling at most sites, so temporal effects (e.g. season, year) could not be examined in this study.

3.2.2. Tape Interrogation

Interrogation of each tape was conducted using a custom interface (BRUVS2.1.mdb, Ericson and Cappo, unpublished, Australian Institute of Marine Science 2006) to store data from field operations and tape reading, to capture the timing of events, and reference images of the sea snakes and seafloor habitat in the field of view. The maximum number of snakes seen together at any one time (*MaxN*) was recorded at each site, for each species sighted on the BRUVS. Whilst the use of

MaxN potentially underestimates the numbers of individuals per species at each site, it overcomes the potential for double counting individuals within the same tape. For example, if five individuals are passing back and forth through the field of view, but only three are visible at one time, then *MaxN*=3. Species identifications were made according to the Australian CAAB codes national standard (Yearsley et al. 1997).

3.2.3. Data preparation and analysis

As the GBR runs from the SE to the NW, the latitude and longitude of BRUVS deployments were converted to relative distances across and along the GBRMP shelf to allow for improved analysis and graphical representation (Fabricius & De'ath 2001). The relative distance along the GBR (‘Along’) was defined as the distance from the BRUVS site to the northern end of the GBR divided by the sum of distances to the northern and southern ends of the GBR for each BRUVS site sampled (Figure 3.1C). Relative distance across the GBR (‘Across’) was defined as the distance of a BRUVS site to the coast, divided by the sum of distances to the coast and to the outer edge of the GBR shelf (80 m isobath) from each BRUVS site sampled (Figure 3.1D). Therefore, each BRUVS site was given an ‘Along’ value, from 0 (southernmost edge of the GBR) to 1 (northernmost edge of the GBR) measuring its position along the length of the GBR and ‘Across’, from 0 (on the coast) to 1 (on the outer shelf) measuring its position across the continental shelf of the GBR (Figure 3.1C, D).

The seafloor reference image at each BRUVS site was processed visually to score a subjective habitat complexity index (‘CI’) based on rugosity and type of the substratum. Two readers assessed images independently and in random order, with sites that had conflicting ‘CI’ values reassessed by both readers together. The CI ranged from 1, representing the least complex habitat (single substratumƒ flat sandy habitats) to 4, representing the most complex habitat (multiple substrataƒ high relief reef habitats). The depth (‘Depth’, Figure 3.1E) of each BRUVS site was also recorded in the field by echosounder. The shortest distances from the BRUVS to the mainland (‘DistLand’) and to the closest exposed reef edge (‘DistReef’), as per the current GBRMPA spatial data (http:ƒƒe-atlas.org.auƒdataƒuuidƒac8e8e4f-fc0e-4a01-9c3d-f27e4a8fac3c), were also calculated using ArcMap® (Version 10.0, Environmental Systems Research Institute, 2012) and customized scripts in the *R* environment (*R* Development Core Team 2014). Un–mapped mesophotic coral reefs present in the GBRMP significantly increase the availability of coral reef habitat in the GBR (Harris et al. 2013), yet they do not appear on the current GBRMPA spatial data layer. Therefore, sites in the southern banks and other inter–reef areas distant from any exposed reef edges may have had coral cover characteristic of exposed coral reefs in the GBRMP.

3.2.3.1. *Spatial analysis*

The number of sea snakes detected on each BRUVS throughout the GBRMP was standardised using a catch (sightings) per unit effort (CPUE) approach. The CPUE for each BRUVS deployment (*i*) was calculated by dividing the number of snakes sighted on each BRUVS (*MaxN*) by the duration of filming for each BRUVS:

(Eq: 3.1) [illegible]

A GIS framework using the following approach was used to graphically represent the large−scale distributions of each species on the GBR. The Great Barrier Reef World Heritage Area (GBRWHA) was divided into grid squares with edges of 50 km (g) and the mean CPUE of all BRUVS deployments within each grid ($\bar{x}_{\mathrm{CPUE}g}$) was calculated. The non−uniform shape of the GBRWHA meant that the areas within each grid square along the coast were not identical; therefore, the area of each grid (Area_g) was taken into account to calculate an Area−weighted CPUE (AWCPUE):

(Eq: 3.2) ژ‥١ﻢ = ٣□ □٣:ﻢ١□ ‥+ﻋﺪ ژ
☐

□

3.2.3.2. *Factors influencing species assemblage*

The BRUVS sampling allowed for a multivariate analysis (a multivariate response to multivariate predictors) to examine how spatial covariates influenced the species assemblage of sea snakes within the GBR. A multivariate regression tree analysis (MRT; De'ath 2002) was used to determine the influence of six spatial factors (‘Across’, ‘Along’, ’DistReef’, ‘DistLand’, ‘Depth’, ‘CI’) on the assemblage of sea snakes (four response variables) and identify which species were responsible for the MRT groupings. For this analysis, the CPUE of each species at each BRUVS deployment *(Eq: **3.1**)* was used to assess the abundance and diversity of sea snakes on each BRUVS.

Multivariate regression tree analyses are a useful tool for analysing complex ecological data with high order interactions and non−linear distributions while producing models that are easy to interpret (De'ath & Fabricius 2000, De'ath 2002). The MRT attempts to explain the variation in the response variable (CPUE of each sea snake species) by repeatedly partitioning the data into homogeneous groups based on a single explanatory variable (e.g. depth, proximity to closest reef). In this analysis, the species and site variables were standardised to the same mean to increase the strength of the relationship between species dissimilarity and ecological distance gradients (see De'ath 2002). MRT analyses were conducted using all BRUVS samples (n=2471) and excluding the samples from the southern shoals (n=2208) to examine the effects of the potential recounting on the tree groupings. The MRT analyses were conducted using the ‘rpart’ and ‘mvpart’ packages in the *R* environment.

3.2.3.3. Factors influencing species occurrence

The presence/absence of each species at each BRUVS was used to determine how spatial factors influenced species occurrence. Again, a tree−based approach was used to examine how the measured spatial variables (‘Across’, ‘Along’, ’DistReef’, ‘DistLand’, ‘Depth’, ‘CI’) influenced the occurrence of each species in the BRUVS dataset. A boosted regression tree (BRT) analysis uses a tree based model that relates a response variable to multiple predictors using recursive partitioning with the added advantage of improved predictive performance achieved by boosting (De'ath 2007, Elith et al. 2008). The BRT analysis fitted a proportion of the data (training set), randomly selected at each iteration, into several initial models consisting of simple classification trees. The remaining data (testing set) was then run though the parameters of the initial model trees and at each stage of the analysis, each explanatory variable was weighted according to predictive error. The weighting of each variable was determined by a user−defined learning rate (*lr*). A large *lr* results in an over−fitted model and a small *lr* results in diminished model performance (Elith et al. 2008). Model performance was determined by a cross validation of the training set and the optimal number of trees for each model. The BRT analysis then ran these models with the weighted data until the predictive error was at its minimum.

The relative influence of each predictor in the BRT analysis was calculated by the number of times the variable was selected for splitting and the squared improvements to the predicted values resulting from the splits (Friedman 2001). Higher percentages of relative influence indicate a stronger influence of predictors on the response variable. BRT analyses were run in the *R* environment using the ‘gbm’ and ‘dismo’ packages supplemented with functions from (Elith et al. 2008) and (De'ath 2007). The presence/absence of each species of sea snake was used as the response variable, a training set of 0.5 was chosen and a *lr* of 0.001, with a 5−fold cross validation used to find the optimal number of trees. The BRT analyses were run with all BRUVS samples and excluding the samples from the southern shoals to examine the effect of the potential recounting of individuals.

3.2.3.4. Influence of zoning on the abundance of sea snakes

In 2004, the GBRMP was rezoned as part of the representative areas program (RAP; Fernandes et al. 2005) and a large number of marine protected areas closed to trawl fishing were established reducing the proportion of the GBRMP open to trawling from 51% pre−2004 to 34% post−2004 (Grech & Coles 2011). To simplify comparisons in the abundance of sea snakes in areas open and closed to trawling, these analyses were conducted using only BRUVS data collected after the enforcement of the new RAP zoning scheme on July 1st 2004. Sites open and closed to trawling were determined using the coordinates of each BRUVS in the post−RAP zoning scheme. The number of days between enforcement of the post−RAP zoning scheme and BRUVS sampling was used as a covariate in the analysis to incorporate the lag effects of no−take areas. A zero−inflated negative binomial (ZINB) model was used (Cunningham & Lindenmayer 2005) to account for the over−dispersion caused by the large numbers of BRUVS with no snakes sighted. The ZINB model, with the number of days post RAP zoning as a covariate, was used to examine if there was a significant difference in the sighting rate of sea snake species between sites open and closed to trawling. The ZINB analysis was conducted using the ‘pscl’ package in the *R* environment.

3.3. Results

A total of 572 snakes were detected in 467 of the 2471 (19%) BRUVS deployments. Three species of sea snake (olive sea snake: *Aipysurus laevis*, spine−bellied sea snake: *Hydrophis* [*Lapemis*] *curtus* and ornate sea snake: *Hydrophis ocellatus*) were readily identified (Figure 3.2). Snakes that could not reliably be identified to species or genus because of low light conditions or bad visibility were grouped as ‘other species’. The majority of snakes detected by BRUVS were olive sea snakes, *A. laevis* (441, 77%), with smaller numbers of *H. curtus* (53, 9%) and *H. ocellatus* (44, 8%) recorded. A total of 34 sea snakes (6%) could not be identified reliably. The distribution of snakes was non−uniform, with *A. laevis*, *H. curtus* and other species clumped around inter−reefal and coastal areas, while *H. ocellatus* were less clumped and found predominantly close to mid− and outer−shelf reefs (Figure 3.3, Figure 3.4). Mapping the results showed a high AWCPUE for *A. laevis* in the southern−most quadrants (Figure

3.4B), which is possibly due to recounting snakes on multiple cameras or repeated deployments on the four southern shoals.

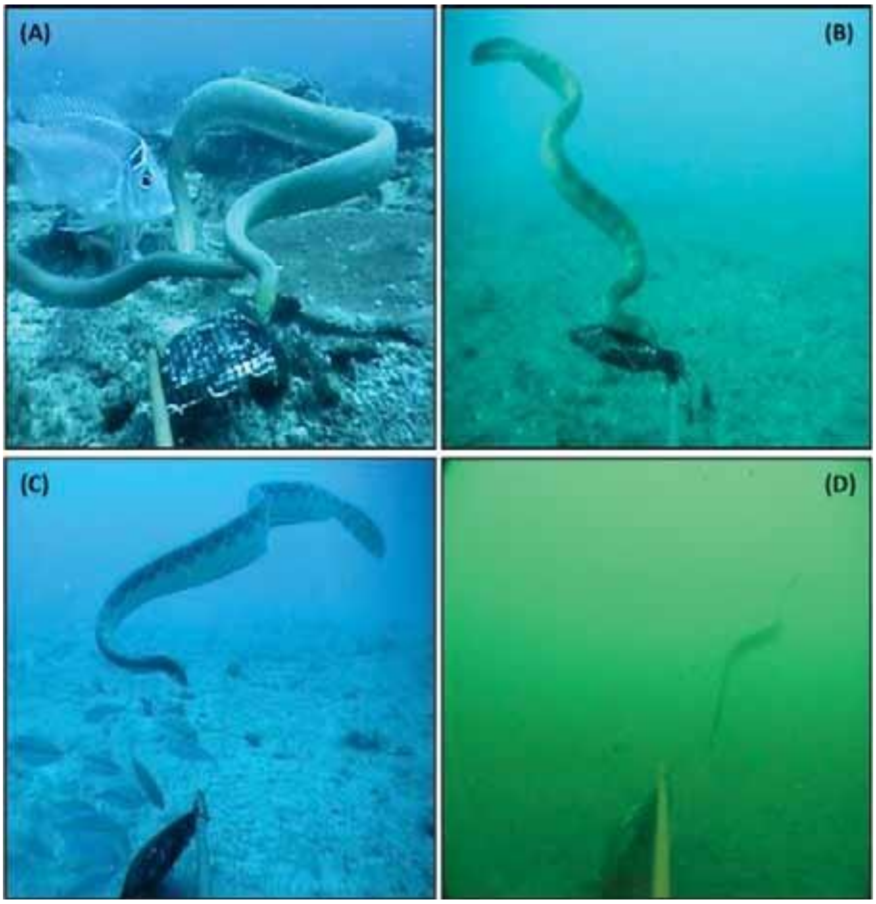

Figure 3.2. Screen−captures of sea snakes observed on BRUVS (A) *Aipysurus laevis*, (B) *Hydrophis curtus*, (C) *Hydrophis ocellatus*, (D) ‘other species’, category for unidentifiable snakes.

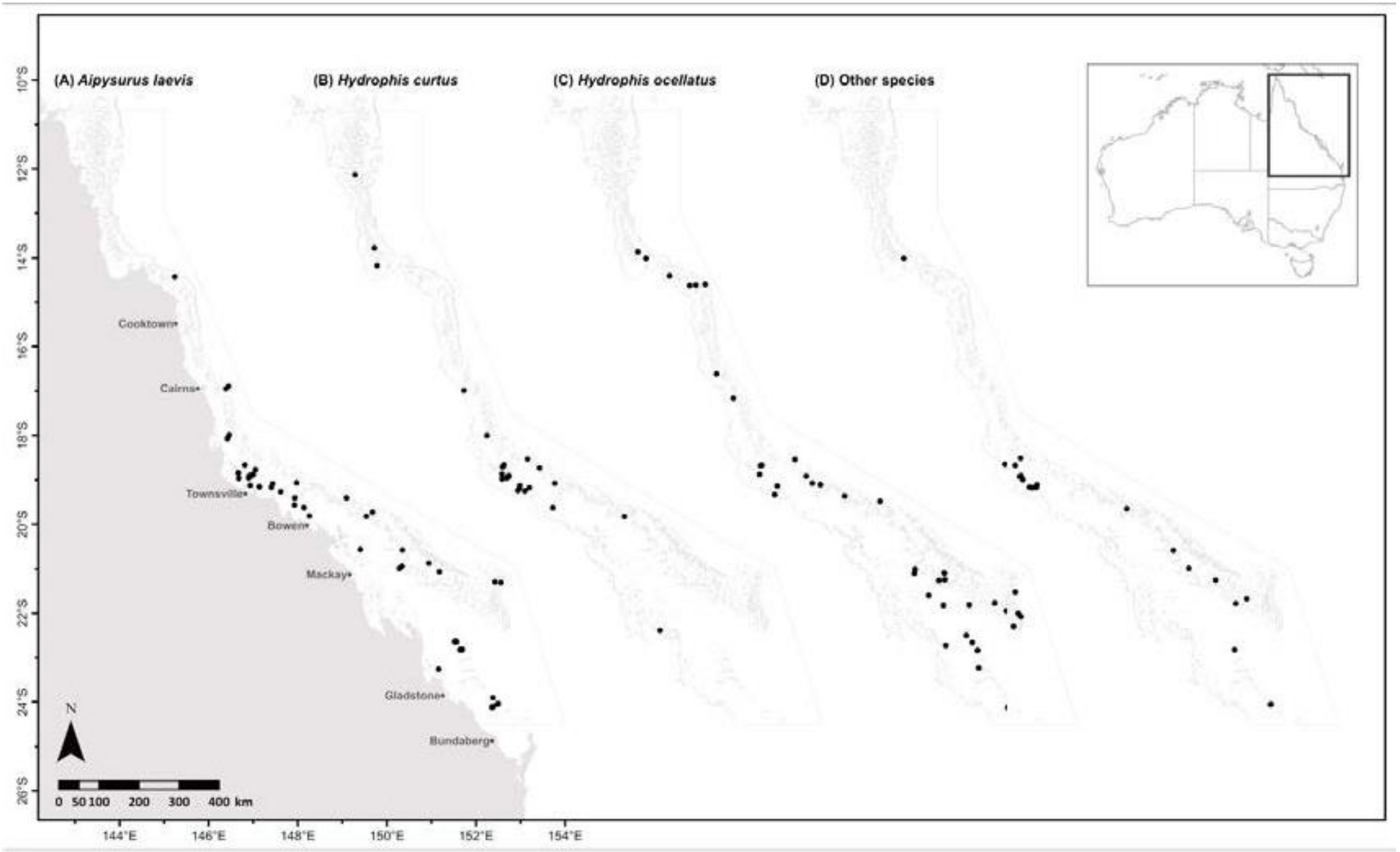

Figure 3.3. Sequential plots of locations of BRUVS on which sea snake species were sighted (A) *Aipysurus laevis*, (B) *Hydrophis curtus*, (C) *Hydrophis ocellatus* and (D) 'other species' sightings.

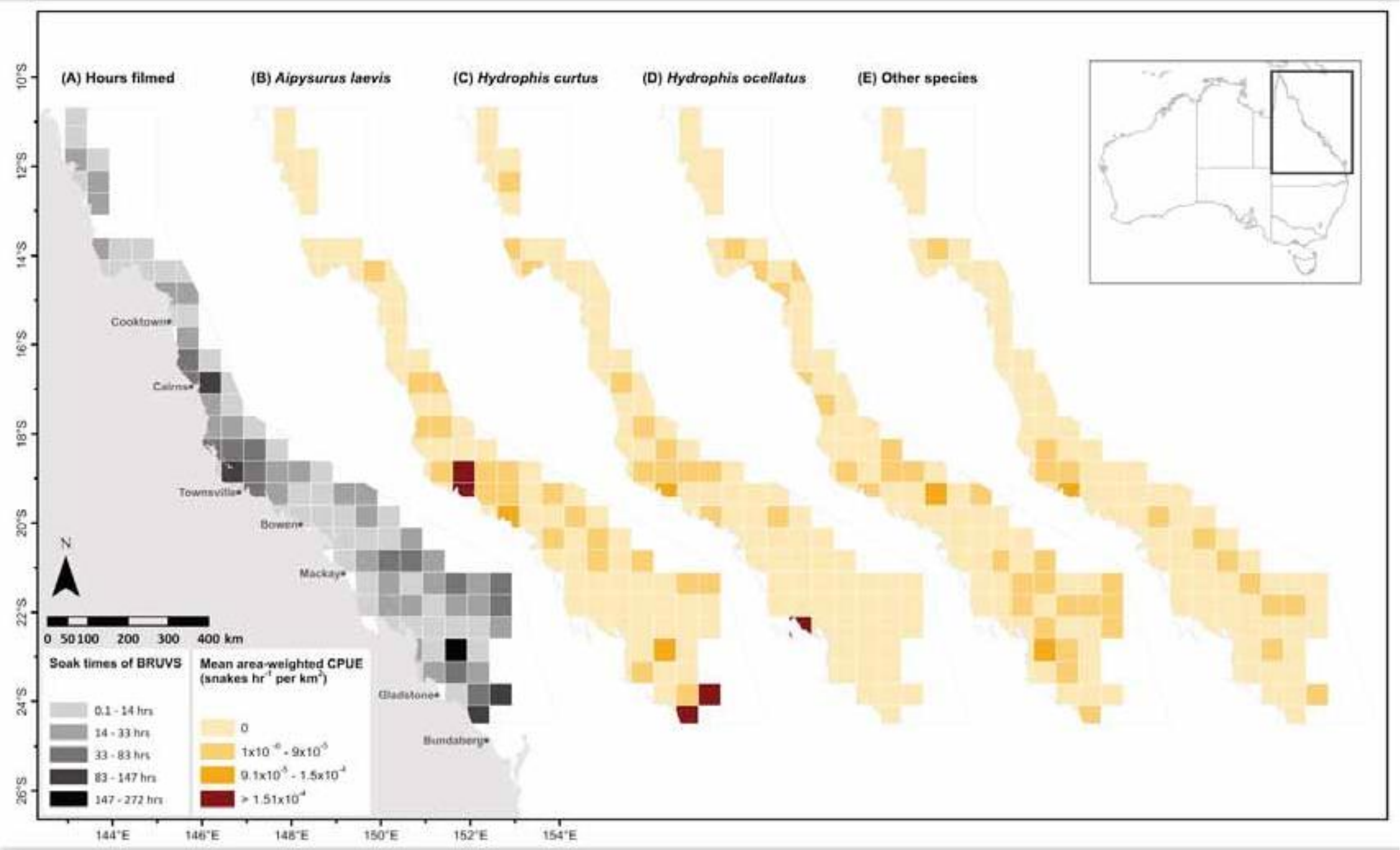

Figure 3.4. Sequential plots of (A) total number of hours filmed within each grid. Subsequent plots represent mean area−weighted catch per unit effort plot for (B) *Aipysurus laevis*, (C) *Hydrophis curtus*, (D) *Hydrophis ocellatus* and (E) ‘other species’.

3.3.1. Factors influencing species assemblage

The MRT model resulted in an optimum tree of three splits for trees with, and without, the southern shoals samples (Figure 3.5A, B). The optimum tree with all BRUVS deployments (Figure 3.5A) grouped the results based on two parameters, 'Along' and 'Depth', with a cross−validation relative error of 0.83. The primary split in the tree with all BRUVS was based on the relative latitudinal distance along the GBR, with *A. laevis* having the highest mean CPUE in the southern latitudes (<0.13 Along, south of ~22˚S latitude). Samples north of 22°S were further split based on depth ('Depth'), with *H. ocellatus* having the highest mean CPUE in deeper water (> 47 m). The third split in this tree represented a grouping of snakes found in shallower depths (< 47 m) with *A. laevis* having the highest mean CPUE in the southern central GBR (<0.48 Along; south of ~20˚S latitude) with all species relatively equally represented in shallower waters of the central GBR (north of ~20˚S latitude).

The MRT excluding the southern shoals BRUVS grouped the samples based on 'Depth', 'Along' and 'DistLand' with a higher relative error by cross−validation of 0.88 (Figure 3.5B). The primary split in this tree was based on the depth ('Depth'), with *H. ocellatus* again having the highest mean CPUE in deeper waters (> 52m). The shallower samples were then split by 'Along', with all species relatively equally represented in the central GBR (>0.47; north of ~20˚S latitude). The third split in this tree separated species distributions in the southern central GBR (south of ~20˚S latitude), with *A. laevis* having the highest mean CPUE in samples further away from the mainland (> 28km from the coast). Apart from the primary split, this tree (Figure 3.5B) displays similar groupings to the tree that included the southern shoals deployments (Figure 3.5A). This result indicates that the high numbers of *A. laevis* in the southern shoals was the main driver of the primary split when all BRUVS samples were included (Figure 3.5A).

3.3.2. Factors influencing species presence

The five−fold cross validation method for the optimal number of trees for the BRT analysis with the full BRUVS dataset (n=2471) showed that the presence/absence data optimally with 5500 trees for *A. laevis*, 2000 trees for *H. curtus,* 550 trees for *H. ocellatus* and 2200 trees for 'other species'. The presence of sea snakes was most strongly influenced on average by the relative latitudinal distance ('Along'), distance

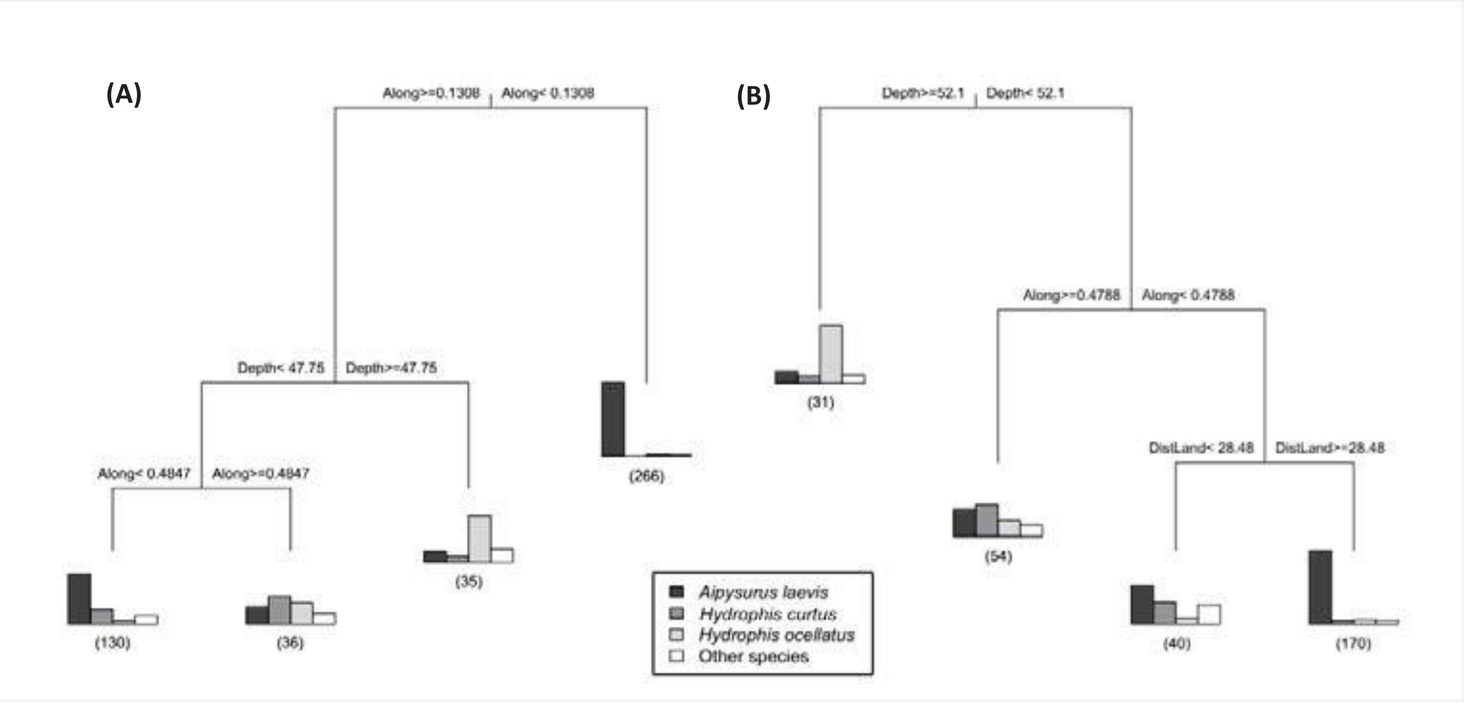

Figure 3.5. Multivariate regression tree analysis. Data were standardized to the same mean by species and site. Euclidean distance was used for splitting. Barplots show the multivariate species mean at each node with the number of sites included indicated in parentheses. (A) Tree including data from all locations (n=2471) showing 'Along' as the most influential parameter (B) Tree with data excluding the southern shoal BRUVS (n=2208) showing 'Depth' as the most influential parameter.

to the closest exposed reef (‘DistReef’) and depth (Figure 3.6A). The occurrence of *A. laevis* was most strongly influenced by the distance to the closest exposed reef, whereas the presence of *H. curtus* and ‘other species’ were most strongly influenced by latitude (‘Along’). The presence of *H. ocellatus* was most strongly influenced by depth (Figure 3.6A).

The analysis excluding the southern shoal samples (n=2208) resulted in the models fitting the presenceƒabsence data optimally with 3450 trees for *A. laevis*, 1700 trees for *H. curtus,* 250 trees for *H. ocellatus* and 800 trees for ‘other species’. On average, the presence of sea snakes on BRUVS was most strongly influenced by the distance to the closest exposed reef (DistReef), followed by latitude (‘Along’) and depth (Figure 3.6B). Within each model, the presence of *A. laevis* and ‘other species’ were most strongly influenced by the distance to the closest exposed reef edge, whereas the latitudinal distance along the GBR had a marginally stronger influence on the presence of *H. curtus*. The presence of *H. ocellatus* was again influenced most strongly by depth, with this species sighted at a maximum depth of 84.6 m (Figure 3.6B).

Partial dependency plots of the four most influential factors in the BRT model excluding the southern shoals suggested that *A. laevis* were most likely to be sighted on BRUVS between 15 and 25 km away from the closest exposed reef edge, within the southern central GBR (<0.2 Along) (Figure 3.7). In contrast, *H. curtus* were more likely to be sighted in areas closer to the coast (<50 km from the mainland) in the central GBR (between 0.4 and 0.6 Along, between ~20˚ and 17˚ S latitude), and *H. ocellatus* in depths between 45 and 60 m on the outer shelf of the GBR (>0.7 Across

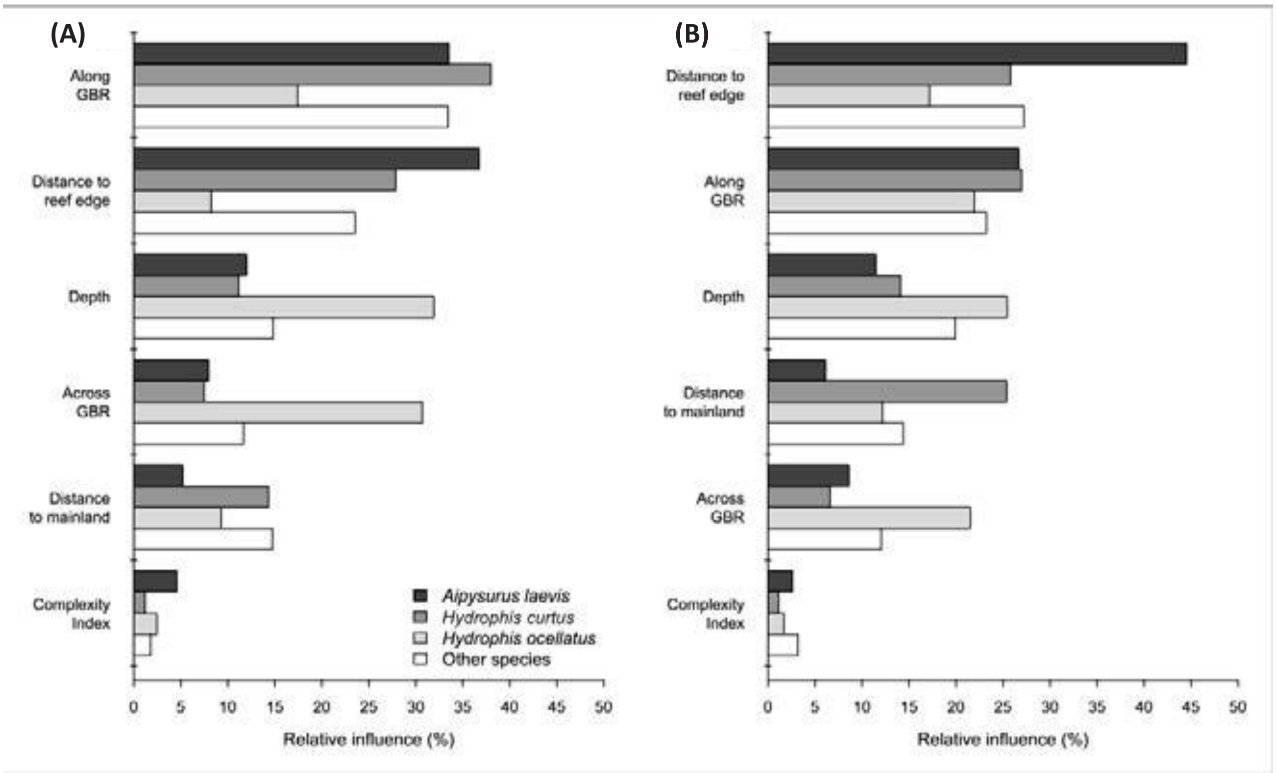

Figure 3.6. Relative influence of spatial factors predicting the presence/absence of sea snakes (*Aipysurus laevis*, *Hydrophis curtus*, *Hydrophis ocellatus* and other species) assessed by a boosted regression tree model with (A) all full BRUVS dataset (n=2471) and (B) excluding the southern shoal BRUVS (n=2208). Variables on y−axes are ranked in decreasing order based on average overall influence.

the GBR shelf). These results are broadly consistent with the MRT analysis, where latitudinal distance along the GBR strongly influenced sea snake diversity.

3.3.3. Influence of zoning

The zoning analysis used data obtained after the 2004 RAP rezoning and included 1755 BRUVS samples, with 539 samples in areas open to trawling and 1216 samples in areas closed to trawling. The ZINB model showed that there was no significant difference in the rate of sightings of all species in areas open or closed to trawling (Response variable, Table 3.1). However, significantly more *A. laevis*, *H. curtus* and

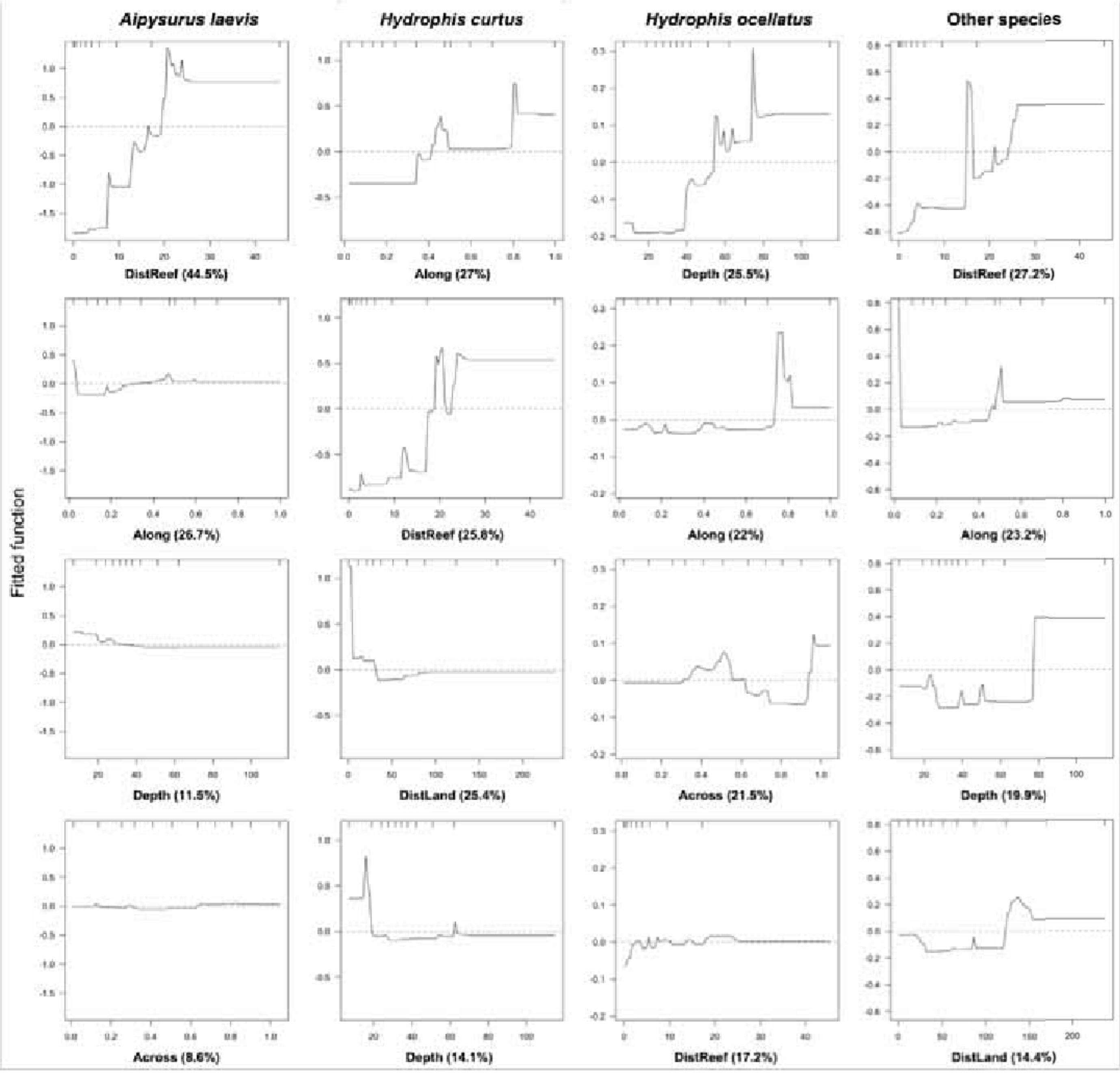

Figure 3.7. Partial dependency plots for boosted regression tree (BRT) analysis. Plots show the fitted functions of the presence or absence of each species with the four most influential predictors for each species in the BRT model excluding the southern shoal BRUVS (n=2208). X−axes represent continuous variables: relative longitudinal distance along the GBR (‘Along’), relative longitudinal distance across the GBR shelf (‘Across’), distance to the closest exposed reef edge (‘DistReef’, km), distance to the mainland (‘DistLand’, km) and depth (‘Depth’, m).

Table 3.1. Results from zero−inflated negative binomial regression analysis with a 'logit' link function examining differences in the catch per unit effort (CPUE) of the four species groups in sites open and closed to trawling. All tests were based on 1755 BRUVS sites deployed after the 2004 Representative Areas Program (RAP) and rezoning of the Great Barrier Reef Marine Park. The number of days from the RAP rezoning to the deployment of the BRUVS was used as a covariate for all tests. The wald statistic (z) and p values presented in the table for the response of zoning and effect of the covariate correspond to the zero−inflated part of the mixture model (α=0.05). Significant p values are represented in bold font.

Taxa	Number of snakes sighted (*Open*|*Closed*)	Mean sightings per hour in sites open to trawling (snakes h^{-1})	Mean sightings per hour in sites closed to trawling (snakes h^{-1})	Source	z	p
Aipysurus laevis	421 (*133*|*288*)	0.240	0.229	Response	−0.697	0.486
				Covariate	−6.797	**< 0.001**
Lapemis curtus	21 (*5*|*16*)	0.010	0.013	Response	−0.264	0.792
				Covariate	−3.349	**< 0.001**
Hydrophis ocellatus	30 (*15*|*15*)	0.028	0.013	Response	−0.058	0.953
				Covariate	−1.754	0.080
Other species	21 (*8*|*13*)	0.015	0.010	Response	−1.411	0.158
				Covariate	−3.071	**< 0.001**

‘other species’ were sighted with time post−RAP zoning (Covariate, Table 3.1) in areas open and closed to trawling.

3.4. Discussion

The distribution of *A. laevis* suggests that individuals occur in both coral reef environments and coastal embayments in the central GBR. The distribution of *H. curtus* indicated high abundance in nearshore habitats in the central GBR, whereas *H. ocellatus* was more abundant in offshore inter−reefal areas in the southern GBR. The fact that all sea snake species occurred in nearshore areas in the central GBR (between ~20˚ and ~18˚ S latitudes) indicates that this region is important in terms of both species diversity and abundance. Previous studies using incidental catch rates in the Queensland trawl fishery (Courtney et al. 2010) and other trawl−based studies (Dunson 1975) match the BRUVS results, with a high abundance of sea snakes (dominated by *H. curtus*) reported in nearshore areas around Townsville (~19˚S latitude), suggesting that this area may be an important habitat for sea snakes. The similarity of BRUVS data with previously documented spatial distribution patterns for these species also suggests this method could be a suitable non−extractive surrogate for monitoring.

Nonetheless, the diversity of species identified on the BRUVS footage was low (three out of 16 species known from the GBRMP), with species that are generalist foragers that feed on a range of small fish and invertebrates commonly found in inter−reefal or nearshore habitats (Voris & Voris 1983, Fry et al. 2001). Fry et al. (2001) examined the diets of nine sea snake species collected from trawls in northern Australia and found that *H. curtus* had the most varied diet, consisting of a range of demersal and bentho−pelagic fish and squid. The diets of *H. ocellatus* (previously *Hydrophis ornatus*) and *A. laevis* consisted of a range of fish species but with little overlap between the two species (Fry et al. 2001). *Hydrophis ocellatus* largely fed on benthic or substrate associated fish species (e.g. Apogonidae) while the diets of *A. laevis* largely consisted of bentho−pelagic fish species (e.g. Nemipteridae) (Fry et al. 2001). The abundance and diversity of prey species in nearshore and outer−shelf areas of the GBR (Williams & Hatcher 1983) may explain some of the observed cross shelf or along−shore distribution and abundance patterns of the three sea snake species. However, a closer examination of diet of sea snakes in these regions within the GRB would be required to substantiate this hypothesis.

Many sea snake species that are commonly caught in trawl surveys on the GBR (Dunson 1975, Limpus 1975, Courtney et al. 2010) were not represented in the BRUVS data. For example, Courtney et al. (2010) recorded twelve sea snake species from trawl bycatch and research trawls on the GBR, with *H. curtus* being most abundant, followed by *A. laevis.* One possible explanation for the fewer numbers of species recorded by BRUVS is the selective effect of bait (Wraith et al. 2013), with BRUVS being more likely to attract predatory and scavenging sea snake species over animals with highly specialised diets. For example, several species in the *Hydrophis* group that commonly occur in trawls on the GBR (e.g. *Acalyptophis peronii, H. elegans* and *H. mcdowelli*) (Courtney et al. 2010) are known to be dietary specialists on burrowing gobies and eels (Voris & Voris 1983, Fry et al. 2001). Their foraging mode consists of probing holes in the sand and crevices in the reef matrix for potential prey items (Heatwole 1999) and they may not have been attracted to BRUVS by the bait plumes. The scavanging behaviours and attraction to bait plumes in some species of sea snakes highlights a bias in using BRUVS to survey sea snakes, where bolder, generalist feeders are potentially more likely to be surveyed using this technique.

The attraction of larger, predatory teleosts and sharks to BRUVS may also have dissuaded some sea snake species from approaching the BRUVS field of view. The historical BRUVS dataset used in this study has recorded a large assemblage of predatory species (e.g. whaler sharks *Carcharhinus* spp., tiger sharks *Galeocerdo cuvier*; M. Cappo, unpublished data) within the GBRMP that may have had an influence on sighting rates of sea snakes. Similar effects have been recorded previously where the presence of predatory sharks (gummy sharks, *Mustelus antarcticus*) have influenced behaviour of smaller species and affected the composition of fish fauna recorded on BRUVS (Klages et al. 2013). Previously, Kerford et al. (2008) found *H. elegans* actively avoided habitats accessible to large predators like tiger sharks (*Galeocerdo cuvier*). Therefore the presence of large predators may have produced avoidance in some sea snake species. These factors may explain the low diversity of sea snakes species identified using BRUVS and indicate that other sampling approaches are required to define the distribution of other sea snake species on the GBR.

The use of CPUE in the MRT model and presenceʃabsence in the BRT analysis showed a strong latitudinal influence in the abundance and presence of sea snakes. This strong division was defined by *A. laevis* as the most frequently sighted species in the southern latitudes. The increased intensity of sampling in the southern shoals was the major driver of this pattern and excluding the southern shoals data removed the primary split based on latitude (0.13 Along, ~22˚S latitude) from the MRT.

Nonetheless, latitude (0.48 Along, ~20˚S latitude) did account for the patterns of distribution of sea snakes on the GBR. Specifically, a more abundant and diverse assemblage of sea snakes were sighted in the middle latitudes, with few individuals sighted in the far northern GBR and *A. laevis* dominating in southern latitudes. Previously, Heatwole (1999) also identified an effect of latitude in the diversity of sea snakes on the north−eastern coast of Queensland and within the GBRMP using established species range distributions from museum samples and sighting records. However, Heatwole (1999) identified a gradual decreasing trend southward from 16 species in the far northern GBR to eight species in the Swain reefs. Heatwole (1999) also reported 14 species in coastal areas between Hinchinbrook and Fraser Islands and reduced species diversity offshore at the same latitudes. Despite the incongruence in species diversity in the north from range distributions by Heatwole (1999) and the present observations using BRUVS, in both cases the central GBR had high species diversity suggesting that it is an important area with suitable environmental conditions and habitats for sea snakes.

The MRT and BRT analyses identified depth as an important factor influencing the diversity and presence of sea snakes. The analysis indicated *H. ocellatus* was most abundant at greater depths (>52 m), and at greater distances across the continental shelf. Similarly, Dunson (1975) previously observed that *H. ocellatus* (formerly *H. ornatus*) were strongly associated with deeper waters in the central GBR, and were only caught in trawl samples conducted in waters greater than 10 fathoms (~18 m). This strong association with deeper water by *H. ocellatus* was also observed outside the GBR, in the Gigante Islands in the Philippines, where *H. ocellatus* comprised the predominant catch in offshore shoals and channels of deeper water (15−30 m) between coral reefs (Dunson & Minton 1978). This close association with deeper water by some species may be explained by a range of factors like abundance and distribution of prey species or availability of suitable habitat however will require the collection and examination of species−specific habitat use patterns.

The global distribution of sea snakes is restricted to waters where snakes can maintain their body temperature within their thermal tolerance (~ 18−40˚C; Heatwole et al. 2012) and there is a general pattern of high sea snake species diversity at lower latitudes, which decreases at higher latitudes, both north and south of the equator (Heatwole 1999). A decreasing north to south gradient for sea snake species richness has been documented along the Western Australian coastline and (as noted above) on the GBR (Heatwole 1999, Cogger 2000). Although the BRUVS data are not consistent with known temperature gradients on the GBR (Wolanski & Pickard 1985), the extremely patchy distribution of sea snakes throughout their known ranges (Cogger 2000, Lukoschek et al. 2007) indicates that temperature gradients alone do not account for observed distribution and abundance patterns of sea snakes. Many other factors (e.g. depth, prey and habitat availability, and historical factors) are likely to have shaped current biodiversity patterns of sea snakes (Heatwole 1999). In addition, methodological factors (e.g. the limited field of view of the BRUVS), combined with the highly patchy distributions of sea snakes, may have resulted in BRUVS not recording sea snakes in relatively close proximity to the BRUVS.

The relatively large numbers of sea snakes (105,210 individuals; Courtney et al. 2010) caught annually as bycatch within the highly clumped QECTF (Grech & Coles 2011) suggests that populations in areas with high trawl fishing effort would be considerably diminished compared to those in protected areas. However, there was no significant difference in overall sighting rates between areas open and closed to trawling. Since the majority of the sampling was conducted two to three years after rezoning of the GBR, the effects of closures established in 2004 may not have been observable because of sea snake life history traits. For example, *H. curtus* and *H. ocellatus* are sexually mature at young ages (1−2 years) and reproduce annually, but have small clutch sizes (Ward 2001) whereas *A. laevis* mature later (~3−5 years) and give birth to 2−5 young every two years on average (Heatwole 1999, Burns & Heatwole 2000).

Considering the life history traits of sea snakes, the temporal spread of sampling was possibly not sufficiently long to produce any detectable differences in relative abundance. The results of this analysis, therefore, cannot be used to assess the effectiveness of spatial closures and MPAs on the abundance of sea snakes. A more appropriately designed sampling strategy inside and outside known trawling grounds with long−term (>10 yr) closures is needed to elucidate any true effects of zoning on the abundance of sea snakes. However, previous studies on other animals with similar life−history characteristics like reef associated sharks (e.g. whitetip sharks, *Triaenodon obesus*; grey reef shark, *Carcharhinus amblyrhynchos*) have shown that the post−RAP zoning has benefited these populations with larger abundances found in protected zones as compared to areas open to fishing (Ayling & Choat 2008, Heupel et al. 2009, McCook et al. 2010).

The lack of an effect of zoning in the present study may also be due to any potential large−scale or long−term movement of sea snakes between zones open and closed to trawling. The effects of large−scale and long−term movements have been previously identified as important factors that need to be taken into account when assessing the effectiveness of zoning in the GBR on mobile animals (e.g. GBR Dugong, *Dugong dugon*; marine turtles; McCook et al. 2010). Very little is known about long−term movements of sea snakes within and between habitats in the GBR and cannot be accounted for in the present study. Additional information on the long−term movements of sea snakes is needed to accurately understand the effects of MPAs and fishing closures on sea snake populations.

3.5. Conclusions

Due to the broad distribution, but local rarity of sea snakes, assessments of their distribution and abundance in the past have mostly been restricted to localised scales of reefs and bays. The BRUVS sampling used in this study provided an understanding of the broad−scale distributions of sea snake species typically found in coral reef habitats (e.g. *A. laevis*) and inter−reefal and nearshore habitats (e.g. *H. ocellatus, H. curtus*). The advantage of the data collected using BRUVS is the spatial and temporal independence to the trawl fishing industry. These data were collected in areas that trawl fisheries cannot opperate in and during seasons when the trawl industry is restricted from fishing. Like all methods used to estimate the distribution and abundance of large mobile marine vertebrates, BRUVS have some limitations that need to be considered in the interpretation of the results. Nonetheless, the BRUVS information generated by this study, when used in conjunction with trawl and UVC data, provides ecosystem−scale information and a valuable contribution to our understanding of the distribution, abundance and spatial ecology of sea snakes on the GBR.

Chapter 4

Movement patterns and home ranges of sea snakes within a nearshore environment

4.1. Introduction

Coastal ecosystems are complex and highly variable, and as we have seen from the previous chapter, inshore waters of the Great Barrier Reef (GBR) are important habitats with high abundances of sea snakes. Unfortunately, coastal habitats and the animals that occupy them are under increasing pressure around the world and are highly vulnerable to degradation from anthropogenic and natural drivers (Beck et al. 2001, Halpern et al. 2008). Acute or chronic changes to these environments can significantly affect movement and habitat use patterns of animals occupying these environenments with varying temporal scales of influence (Thistle 1981, Heupel 2007). Daily activity of animals can be driven by an environmental factor that varies over a daily cycle (e.g. tidal currents, moon phase; Naylor 1999) while seasonal movements may be governed by more gradual environmental changes (e.g. photoperiod, water temperature; Heupel 2007). Gradual changes in environmental variables often act as cues for seasonal changes of behaviour in animals, especially in coastal ecosystems (Heupel 2007, Froeschke et al. 2010, Schlaff et al. 2014), whereas acute changes in these same variables may trigger different behavioural responses (Jury et al. 1995, Liu et al. 2010, Udyawer et al. 2013).

The identification of patterns in the movements of individuals, and their relationship to ecological phenomena, have been critical aspects in past studies of terrestrial, avian, and marine organisms (Cooke et al. 2004a, Wilson et al. 2015).

Traditionally, studies on the movement and use of space by animals have been represented in two dimensions (e.g. Latitude−Longitude or Easting−Northing); this, however, may not fully represent the reality of the environment that many animals occupy. Recent advances in technology and analytical techniques have allowed integration of the vertical axis into studies examining the use of space to a high degree of spatial resolution. These advances have improved our understanding of the spatial ecology of a range of terrestrial, avian, and marine organisms (Shepard et al. 2008, Simpfendorfer et al. 2012, Cooper et al. 2014, Tracey et al. 2014).

Since aquatic animals, like sea snakes, live in a three−dimensional environment and have the ability to move in all three dimensions, their use of space is most accurately represented in the same number of dimensions. A few attempts to understand movement and use of space by reef−associated (Burns & Heatwole 1998, Shetty & Shine 2002) and pelagic sea snakes (Rubinoff et al. 1986, Rubinoff et al. 1988) have contributed the majority of what is currently known about these taxa. Rubinoff and colleagues (Rubinoff et al. 1986, Rubinoff et al. 1988) studied the short−term movements (3.8 – 31.2 h monitored) of fifteen *H. platura* tagged with depth−sensing ultrasonic tags and examined vertical and horizontal patterns of movement separately, publishing their results in two articles. They first, examined the movements of tagged snakes in the vertical axis, looking at the depths and durations of dives (Rubinoff et al. 1986) followed by the second, that focused on the horizontal movements of tagged individuals (Rubinoff et al. 1988). They found that despite *H. platura* being considered a surface−dwelling pelagic sea snake, tagged individuals spent the majority of the monitoring period (87%) underwater and dove as deep as 50 m. Burns and Heatwole (1998) found that *A. laevis* displayed restricted movements around their home reef with small home ranges (1500 – 1800 m^2) and that home ranges of all snakes (n = 11) overlapped with two or more individuals. Estimates of space used and overlap between monitored individuals, however, did not consider their use of depth. Studies of eel movements by Simpfendorfer et al. (2012) revealed that failure to consider vertical movement can result in an overestimation of home range overlap if individuals are using the same two−dimensional location but different depths.

Majority of past studies exploring sea snake populations in inshore habitats focus on abundance and diversity based on incidental capture in trawl fisheries (Dunson 1975, Wassenberg et al. 1994). Studying activity patterns of sea snakes in shallow, murky nearshore habitats using traditional visual survey or mark−recapture techniques is logistically difficult and rarely provides enough temporal resolution to explore links with long− or short−term environmental changes. This chapter uses data obtained using passive acoustic telemetry to provide information to better understand and visualise how sea snakes move and use space within the water column in nearshore habitats, and addresses the second aim of the overall thesis (Aim 2:). The objectives of this chapter were to: (a) examine any short term, diel patterns in the use of three−dimensional space by tagged sea snakes and (b) explore longer−term, daily and monthly, patterns of movements and identify potential environmental drivers of such patterns.

4.2. Methods

4.2.1. Study site

This study was conducted in Cleveland Bay (19.20˚S, 146.92˚E), on the northeast coast of Queensland, Australia (Figure 4.1). Cleveland Bay is a shallow coastal bay (<10 m deep) with a maximum tidal range of approximately 4 m. The bay covers an area of approximately 225 km^2 with the western and southern margin bounded by the mainland and Cape Cleveland, respectively, and a large continental island, Magnetic Island, to the north of the bay (Figure 4.1). The southern shore is lined with mudflats and mangroves. Several waterways flow into the southern portion of the bay and provide the major input of freshwater. Water temperature within the bay averages 28.6˚C (range: 26.9 − 30.6˚C) during the warmer wet season (November − April) and 24.1˚C (21.4 − 27.5˚C) in the cooler dry season (May − October)(Figure 4.2).

4.2.2. Field methods

Two species of sea snake (Spine−bellied sea snake; *Hydrophis curtus* and Elegant sea snake; *H. elegans*) were targeted for this part of the study. Sea snakes were located after dark and captured off the surface using dip nets. Once captured, the maturity of each individual was recorded as either juvenile or adult, with the sex of adults determined using external morphological features (by investigating hemipenal bulges or exposing the hemipenes). The determination of sex in juvenile individuals was unreliable using external morphological features, therefore the sex of juveniles was not considered in the present study. Snout−vent length (SVL) and mass of each

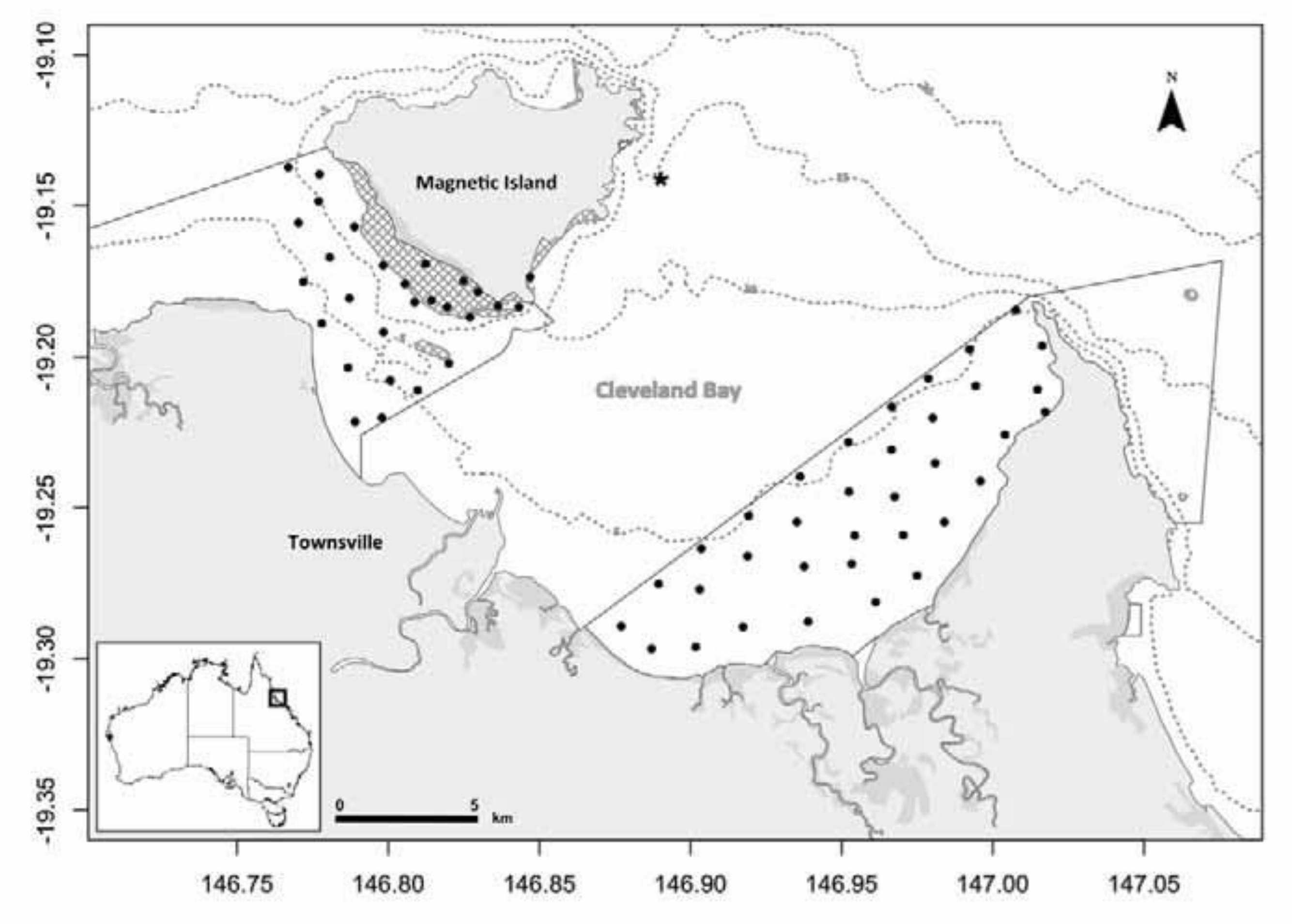

Figure 4.1. Map of study site within Cleveland Bay, Queensland. Points represent locations of acoustic receiver stations deployed on the east and western side of Cleveland Bay divided by a port area. Broken grey lines indicate bathymetry and solid lines are boundaries of Conservation Park zones (no trawling or netting). Cross−hatching indicates fringing reefs and dark grey areas along the coast indicate mangrove habitats. Note rivers serving as sources of freshwater in the southeast of the bay. The location of the weather buoy operated by the Australian Institute of Marine Science within the study site is displayed as an asterix (*). An interactive, three−dimensional model of the study site is available in Appendix 4.5.1. Please refer to the Note for a list of suitable desktop and mobile browsers.

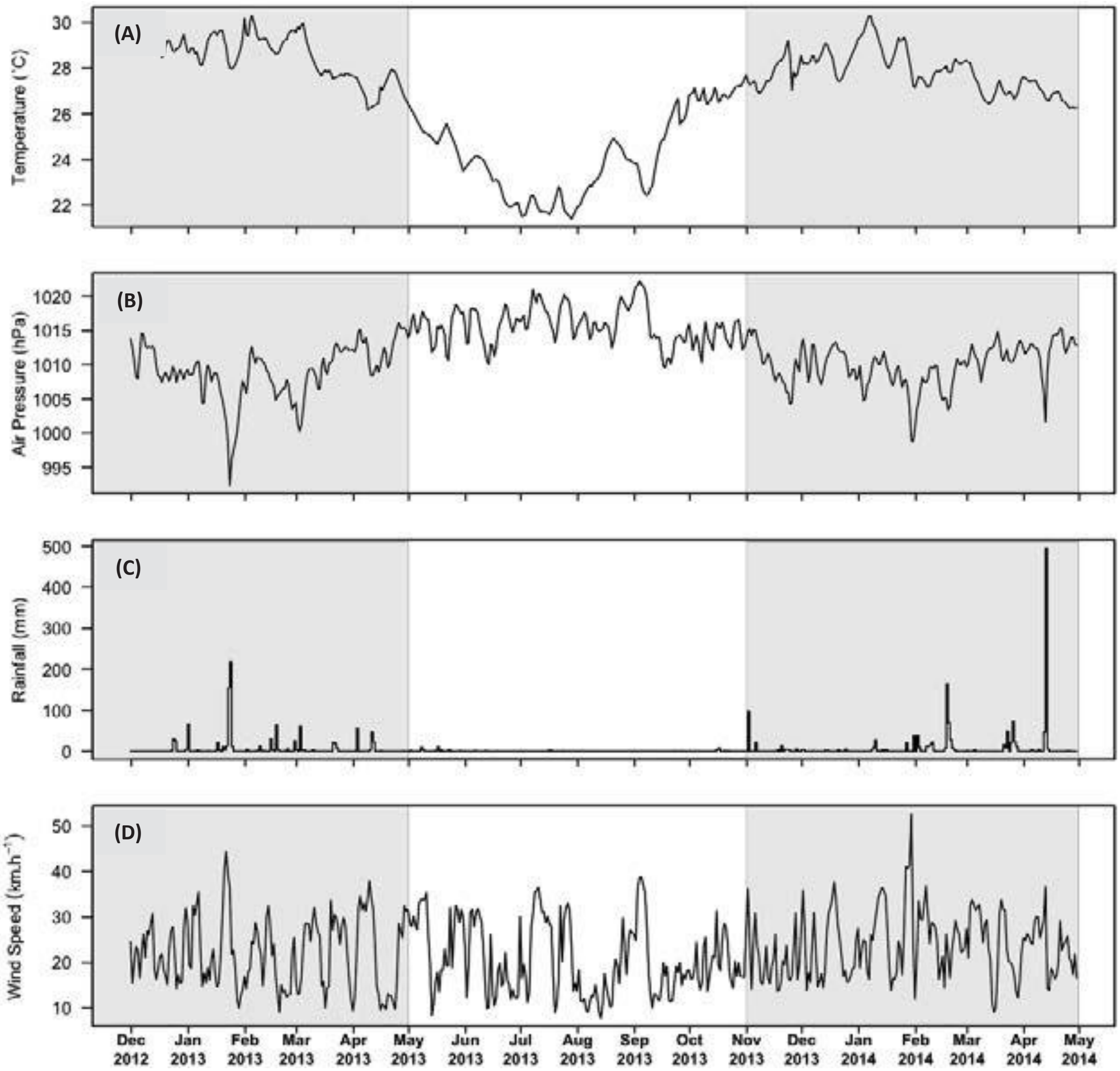

Figure 4.2. Daily environmental measurements within Cleveland Bay over the study period (A) mean water temperature, (B) mean air pressure, (C) daily rainfall accumulation and (D) mean wind speed. Wet (grey background) and dry (white background) seasons are also represented.

captured snake were recorded, and each individual was fitted with a passive integrated transponder (PIT) tag for future identification. Individuals in good condition and large enough to carry a transmitter were surgically implanted with acoustic transmitters with depth sensors (V9P−2H, Vemco Ltd.). Transmitters were small (diameter 9 mm, length 29mm, weight 2.9g) and less than 1% of the body weight of the individuals tagged (*mean ± se*; 0.91 ± 0.11%) to avoid any deleterious effects of transmitter implantation. The method of implanting tags was similar to those 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 minutes 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 69kHz and had a battery life of approximately 215 days.

An array of 63 VR2W underwater acoustic receivers (Vemco Ltd.) was used to passively monitor the movements of tagged sea snakes between January and November 2013 (Figure 4.1, Appendix 4.5.1). Sentinel tag range testing indicated stations had a maximum detection range of 525 m with no overlap between stations (unpublished data, M. Heupel). Receivers were suspended in the mid−water column and anchored at fixed locations within the study site (Figure 4.1). The acoustic array covered the eastern and western sections of the bay that corresponded to Conservation Park zones (no trawling or net fishing allowed) within the Great Barrier Reef Marine Park. The area between the two 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 for any period of time was not logistically feasible. Receiver densities on both the eastern and western sections were similar (east: 0.38 receivers per km^2; west: 0.53 receivers per km^2) with similar average distances between receivers (east: 6.45 ± 0.11 km, n= 35; west: 4.13 ± 0.09 km, n=28). Data from the acoustic receiver array was downloaded every 3 – 4 months.

4.2.3. Data analysis

4.2.3.1. Patterns in short-term diel movements

Short−term, diel movements of tagged individuals were explored using the detection data by comparing diving patterns and metrics of activity space (home range) between day and night. As the diving behaviours in these species are an important aspect of their movements in their natural environment, calculations of home ranges in this study incorporated all three dimensions of movement using a three−dimensional Kernel Utilisation Distribution (3DKUD) analysis. Raw data were first standardised for temporal variation in detections through a position−averaging algorithm that computed an individual's centre of activity (COA) at 30 min intervals (Simpfendorfer et al. 2002). The COAs provided mean latitudinal and longitudinal position as well as depth for individuals within 30 min intervals. The COAs calculated for each individual were then used to calculate 3D home ranges. The volume of the home ranges of tagged individuals was examined by calculating 3DKUDs for both species in the *R* environment (R Development Core Team 2014) using the 'ks package (Duong 2007) and rendered using the 'rgl' and 'misc3d' packages (Feng & Tierney 2008, Adler & Murdoch 2014). Calculations of 3DKUD and estimation of volume of core home range (50% contour; 50% 3DKUD, m^3) and the extent of home range (95% contour; 95% 3DKUD, m^3) used by tagged individuals were conducted using code adapted from Simpfendorfer et al. (2012) and Cooper et al. (2014). Interactive plots of diel patterns in 3DKUD were rendered using the 'brainR' package in *R* and code adapted from Muschelli et al. (2013). The proportion of overlap in the home ranges between day and night was also calculated for 50% 3DKUD and 95% 3DKUD for both species using *R* code from Simpfendorfer et al. (2012).

Estimations of volume of 50% 3DKUD and 95% 3DKUD were log−transformed prior to statistical analyses. The differences in the volume of home ranges between day and night were compared using generalised linear mixed models (GLMM) with individuals' ID treated as a random factor within each model (~1|ID) to account for variability between individuals and the repeated measures nature of the data. Additionally, t−tests ($\alpha = 0.05$) were conducted to examine whether the mean proportion of overlap between home ranges used during the day and at night (both 50%−3DKUD and 95%−3DKUD) varied from that expected if there were no pattern in proportions of overlap (i.e. mean proportion = 0.5). The data for proportional overlap of the occupied spaces were arcsine−transformed prior to analysis. All statistical analyses and plotting were conducted in the *R* statistical environment (R Development Core Team 2014).

4.2.3.2. Environmental drivers of daily and monthly patterns of movement

Detection data from tagged sea snakes were also used to assess longer−term patterns in movement within Cleveland Bay and the data was used to identify any environmental drivers of such patterns. To assess environmental drivers of movement and the use of space in sea snakes, environmental variables were examined alongside metrics of presence, movement and home range over two temporal scales; daily and monthly. The relationships between environmental variables and response metrics were evaluated using a generalised linear mixed model (GLMM) framework. Firstly, the presence and movements of individuals were examined on a daily timescale. Secondly, the movements and activity spaces (home range) of individuals were examined on a monthly timescale to assess if environmental drivers were consistent over the two temporal scales.

4.2.3.2.1. Response variables: presence, movement and home range metrics

On a daily timescale, the presence/absence (pa) of individuals was determined by a decision rule whereby an individual was considered present within the array on a particular day if two or more detections were recorded from that individual during that 24−hour period. If fewer than two detections were recorded, individuals were considered absent to eliminate any false positive detections. A ‘Roaming Index’ (*Rom*) was calculated as a proxy for movement on a daily temporal scale. *Rom* (between 0 and 1) represented the proportion of receiver stations at which each individual was detected daily within Cleveland Bay. A *Rom* of 0 indicated an individual was not detected on any receivers and 1 indicated that an individual was detected on all receivers, and therefore highly active within the array.

The movements of individuals were also examined on a monthly timescale using *Rom*. The *Rom* calculated on a monthly scale represented the proportion of receiver stations at which each individual was detected each month within Cleveland Bay. The space used by tagged individuals each month was evaluated using volumes of three−dimensional home ranges. Similarly to the method of analysis in section

4.2.3.1. , a three−dimensional Kernel Utilisation Distribution (3DKUD) analysis was used to incorporate the diving ability of individuals using data from depth sensors, and to calculate the volumes of core (50% 3DKUD, m^3) and the extent (95% 3DKUD, m^3) of home ranges over a monthly time scale. Raw detection data were first standardised for temporal variation in detections through a position−averaging algorithm that computed an individual's centre of activity at 30 min intervals (Simpfendorfer et al. 2002).

Individuals that were not detected within the array for more than five days were excluded from further analyses to rule out potential tag failure, migration out of the array or post−surgery mortality. Additionally, months that had fewer than 10 detections due to low sample sizes were excluded from further calculations. Calculations of 3DKUDs were conducted in the *R* environment (R Development Core Team 2014) using the 'ks' package (Duong 2007) and using code adapted from Simpfendorfer et al. (2012) and Cooper et al. (2014). Monthly 3DKUDs were rendered using the 'rgl' and 'misc3d' packages (Feng & Tierney 2008, Adler & Murdoch 2014) and interactive plots were generated using the 'brainR' package in *R* and code adapted from Muschelli et al. (2013).

4.2.3.2.2. Explanatory variables: environmental and biological

Local environmental data was sourced from a fixed weather buoy operated by the Australian Institute of Marine Science, and located within Cleveland Bay (Figure 4.1). The buoy collected semi−continuous data on water temperature (temp, ˚C), air pressure (press, hPa), wind speed (wind, $km.h^{-1}$) and rainfall (rain, mm; Figure 4.2). Daily and monthly mean values of environmental variables were calculated for further analyses. Tidal height data at the Townsville port were sourced from the

Australian Bureau of Meteorology. Tidal reach (tide, cm) was calculated as the difference between daily maximum and minimum tidal heights. The snout−vent length (SVL, mm) of snakes was also included in all models to examine any potential biological influences on movement, presence and home range on both daily and monthly timescales.

4.2.3.2.3. Model construction

A logistic regression approach was chosen over the analysis of arcsine−transformed data to account for proportional data (*Rom*) and its improved power and interpretability (Warton & Hui 2011). To account for the repeated measures nature of the data and variability between individuals, snake ID (ID) was treated as a random factor within each model, using a binomial distribution (logit link function). Candidate models for each response variable were constructed in the *R* environment using the 'glmer' function within the 'lme4' package (Bates et al. 2014). Candidate models were constructed using all possible combinations of biological and temporally relevant environmental factors using the 'MuMIn' package in *R* (Bartoń 2014).

Analyses of daily movements (*Rom*) and presence (pa) were examined with daily averaged environmental variables [full model: ~ temperature + pressure + wind + rain + tide + SVL + (1|ID)]. We then analysed monthly movements (*Rom*), core (50% 3DKUD) and extent (95% 3DKUD) of home ranges of sea snakes alongside monthly averaged environmental variables [full model: ~ temperature + pressure + wind + rain + SVL + (1|ID)].

4.2.3.2.4. Model validation and selection

Candidate models were compared using the second order Akaike information criterion corrected for small or finite samples (AICc; Burnham & Anderson 2002). Environmental or biological variables in the model with the lowest AICc value were considered to be the most significant drivers of movement or home range. If the null model [M_O: ~ 1 + (1|ID)] had the lowest AICc value, the chosen environmental and biological variables were poor predictors of the response variable and the data were considered random relative to the tested variables. Candidate models were then compared against the null model (M_O) and significant differences were evaluated with maximum likelihood ratio tests (χ^2, $p < 0.05$).

4.3. Results

Initial tagging trips focused within the full extent of the bay, however no sea snakes were captured in the western section, 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 individuals of both species were predominantly detected in this area. A total of twenty−five individuals (19 spine−bellied sea snakes, *Hydrophis curtus* and six elegant sea snakes, *H. elegans*) were monitored within Cleveland Bay between January and November 2013 (Figure 4.3, Table 4.1). Tagged *H. curtus* ranged in size from 501 – 1125 mm SVL (4 female, 1 male and 14 juveniles; Tag codes starting with ‘S’, Figure 4.3A, Table 4.1) and *H. elegans* ranged in size from 865 – 1242 mm SVL (1 male, 1 female and 4 juveniles; Tag codes starting with ‘E’, Figure 4.3B, Table 4.1).

Table 4.1. Summary of morphometrics and detection patterns of tagged sea snakes in the present study. Age estimates were calculated using established age–growth curves previously published by Ward (2001). Individuals that were detected for fewer than five days (*) were excluded from analyses.

Species	Tag code	Snout-vent length (mm)	Body mass (g)	Life stage (Adult/Juvenile)	Estimated Age (years)	Number of receivers detected on	Number of days detected
Hydrophis curtus (Spine–bellied sea snake)	S1	501	170	Juvenile	0.67	9	7
	S2	563	220	Juvenile	0.92	9	7
	S3	536	110	Juvenile	0.81	9	56
	S4	592	260	Juvenile	1.04	13	17
	S5*	704	400	Juvenile	1.60	3	4
	S6	527	240	Juvenile	0.77	7	10
	S7	705	420	Juvenile	1.60	7	8
	S8	992	1510	Adult (F)	4.21	11	8
	S9	665	370	Juvenile	1.39	22	128
	S10*	1125	1410	Adult (F)	6.45	1	1
	S11	615	300	Juvenile	1.15	5	8
	S12	635	350	Juvenile	1.24	10	13
	S13*	979	1390	Adult (F)	4.00	6	4
	S14*	932	740	Adult (M)	3.48	2	1
	S15	634	250	Juvenile	1.24	16	93
	S16	571	310	Juvenile	0.95	15	72
	S17	556	290	Juvenile	0.89	21	62
	S18	626	290	Juvenile	1.20	12	45
	S19	994	1560	Adult (F)	4.24	6	7
Hydrophis elegans Elegant sea snake	E1	1213	650	Adult (F)	3.10	18	39
	E2	1242	800	Adult (F)	3.30	19	17
	E3*	865	280	Juvenile	1.09	6	4
	E4	947	290	Juvenile	1.44	8	20
	E5	1072	380	Juvenile	2.04	9	69
	E6	1167	410	Juvenile	2.56	3	8

Detection data showed that individuals from both species (S3, S9, S17, E1 and E5; Figure 4.3) moved between both sections of the array, making short excursions to the western section of the bay lasting ~1 hr – 2 days before returning to the eastern side, where the majority of detections were recorded. Of the 5 adult *H. curtus* individuals monitored, only one was male (S14) and was detected in the array for a single day. Four sexually mature female *H. curtus* were monitored (S8, S10, S13, S19) and were detected for short periods (1 – 26 days), with three of those individuals gravid (S8, S10, S19). In total, four tagged *H. curtus* (S5, S10, S13, S14; Figure 4.3A in red) were excluded from further analyses as they were detected within the array for fewer than five days. Both adult *H. elegans* monitored were female (E1 and E2) and one male (E2). One of the six tagged *H. elegans* (E3; Figure 4.3B in red) was excluded from analysis due to low numbers of detections. After excluding all individuals with low numbers of detections, the majority of monitored sea snakes were juvenile with only two adult female *H. curtus*, one adult male and one adult female *H. elegans* included in the dataset. Therefore, to avoid inaccurate conclusions related to the small sample size of reproductively mature individuals in this study, sex was excluded as a covariate in further analyses.

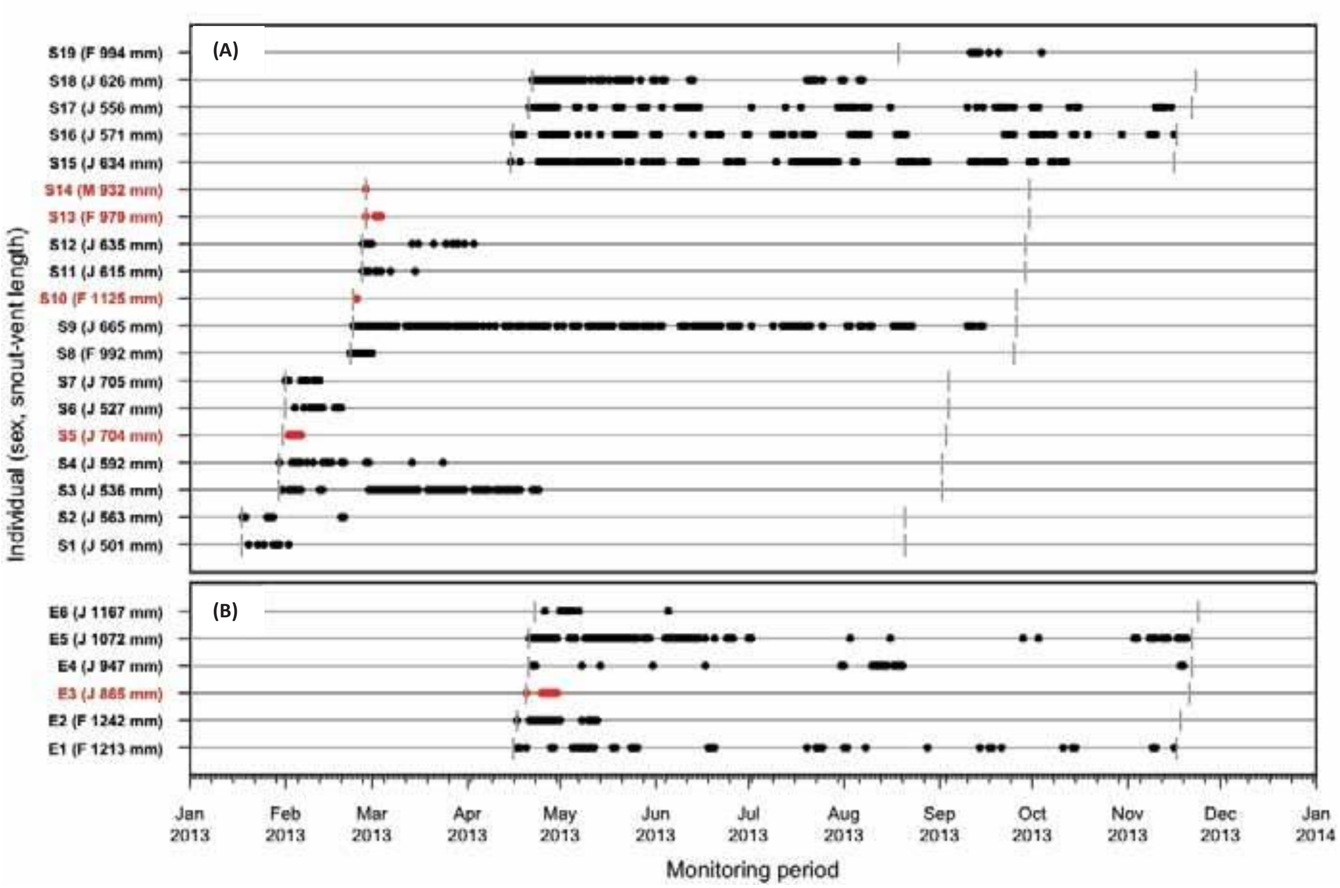

Figure 4.3. Daily detection plot of (A) 19 tagged *Hydrophis curtus* and (B) six tagged *H. elegans*. The lifestage and sex (J= juvenile, F= adult female, M= adult male) of each individual along with snout−vent length (mm) is presented along the y−axis. Animals in red were excluded from analyses due to low numbers of detections. Short vertical grey lines represent dates animals were tagged and expected date of the end of tag life (tag life = 215 days).

4.3.1. Patterns in short-term diel movements

Data from depth sensors showed that individuals from both species displayed a strong diel pattern in use of the water column (Figure 4.4). Snakes were found at significantly greater depths during the day (06:00 – 18:00 hr) and were active on the surface at night (*t*−*test*, *H. curtus*: $t = 26.37$, $p<0.05$, *H. elegans*: $t = 9.51$, $p<0.05$). *Hydrophis curtus* displayed a more varied dive profile, diving to an average depth of 3.2 m (se: ± 0.03 m; max depth = 7.5 m) during the day and 2.1 m (se: ± 0.03 m; max depth = 7.4 m) at night. While, *H. elegans* generally used comparatively shallower water and dived to an average of 2.5 m (se: ± 0.05 m; max depth = 5.7 m) during the day and 1.8 m (se: ± 0.04 m; max depth = 6.2 m) at night. Individuals of *H. curtus* were generally present in deep water on the eastern side of Cleveland Bay (Figure 4.5A, Appendix 4.5.2), whereas *H. elegans* were restricted to shallow water directly adjacent to the southern shore (Figure 4.5C, Appendix 4.5.4).

The integration of depth data into analysis of space use showed a difference in the three−dimensional kernel utilisation distributions (3DKUD) for individuals of both species during day and night (Figure 4.5B, D; Appendix 4.5.3, Appendix 4.5.5). Sufficient data from 12 of the 19 tagged *H. curtus*, and five of the six *H. elegans* was available to calculate reliable 3DKUDs to compare diurnal and nocturnal home ranges. Despite the difference in depths occupied by individuals, GLMMs showed that volumes of core (50% 3DKUD) and extent (95% 3DKUD) of home ranges in *H. curtus* were not significantly different between day and night (50% 3DKUD: $F_{1,11} = 0.44$, $p = 0.52$; 95% 3DKUD: $F_{1,11} = 0.20$, $p = 0.66$; Figure 4.6A). Similarly, the volume

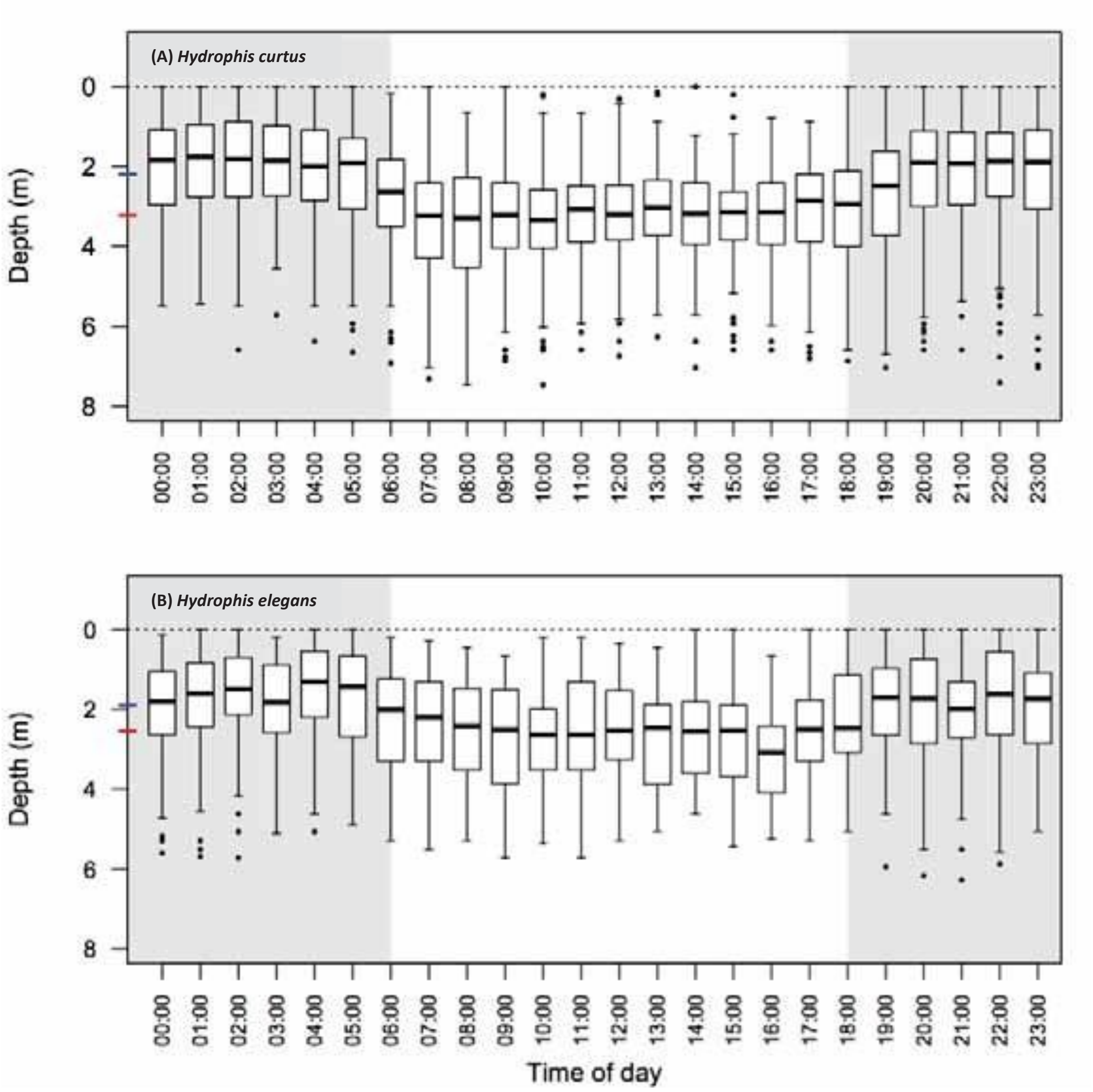

Figure 4.4. Patterns in diel use of different depths by tagged (A) *Hydrophis curtus* [*n* = 19] and (B) *Hydrophis elegans* [*n* = 6] over the monitoring period. Mean depths recorded by day (red) and night (blue) are represented as ticks on the y−axis.

of 50% 3DKUD used by *H. elegans* was not significantly different between day and night ($F_{1,4} = 5.58$, $p = 0.07$); however, *H. elegans* displayed significantly larger 95%–3DKUD volumes at night compared to the day ($F_{1,4} = 18.79$, $p = 0.01$; Figure 4.6B).

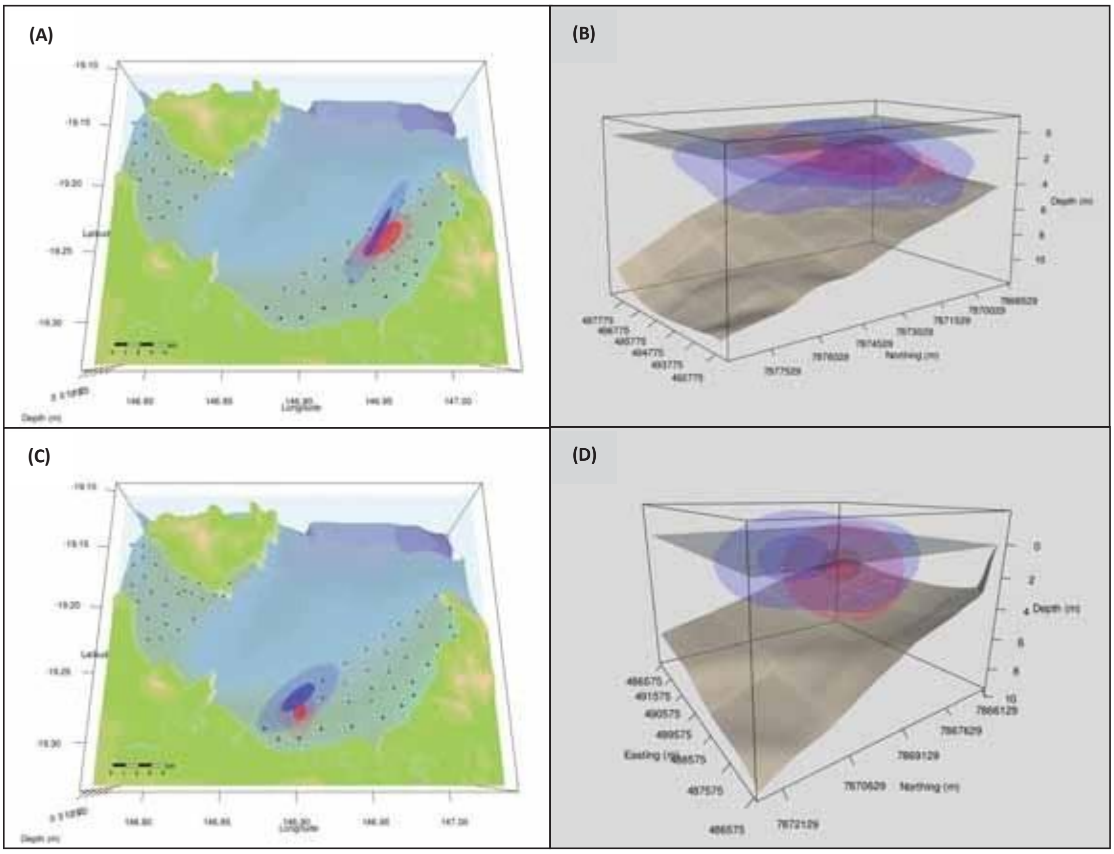

Figure 4.5. Three–dimensional home range of a representative *Hydrophis curtus* (A) within the study site and (B) in closer detail, and by a representative *Hydrophis elegans* (C,D). Screenshots showing day–time core (50% 3DKUD; dark red) and extent (95% 3DKUD; light red) 3DKUD as well as night–time core (50% 3DKUD; dark blue) and extent (95% 3DKUD; light blue) 3DKUD. Surrounding bathymetry and sea surface are also rendered to provide context. Black points in panels (A,C) represent the locations of acoustic receivers within the study site. Online links to interactive, three–dimensional versions of these 3DKUD models are available in the appendices (Appendix 4.5.2 – 4.1.5); please refer to the Note for a list of suitable desktop and mobile browsers.

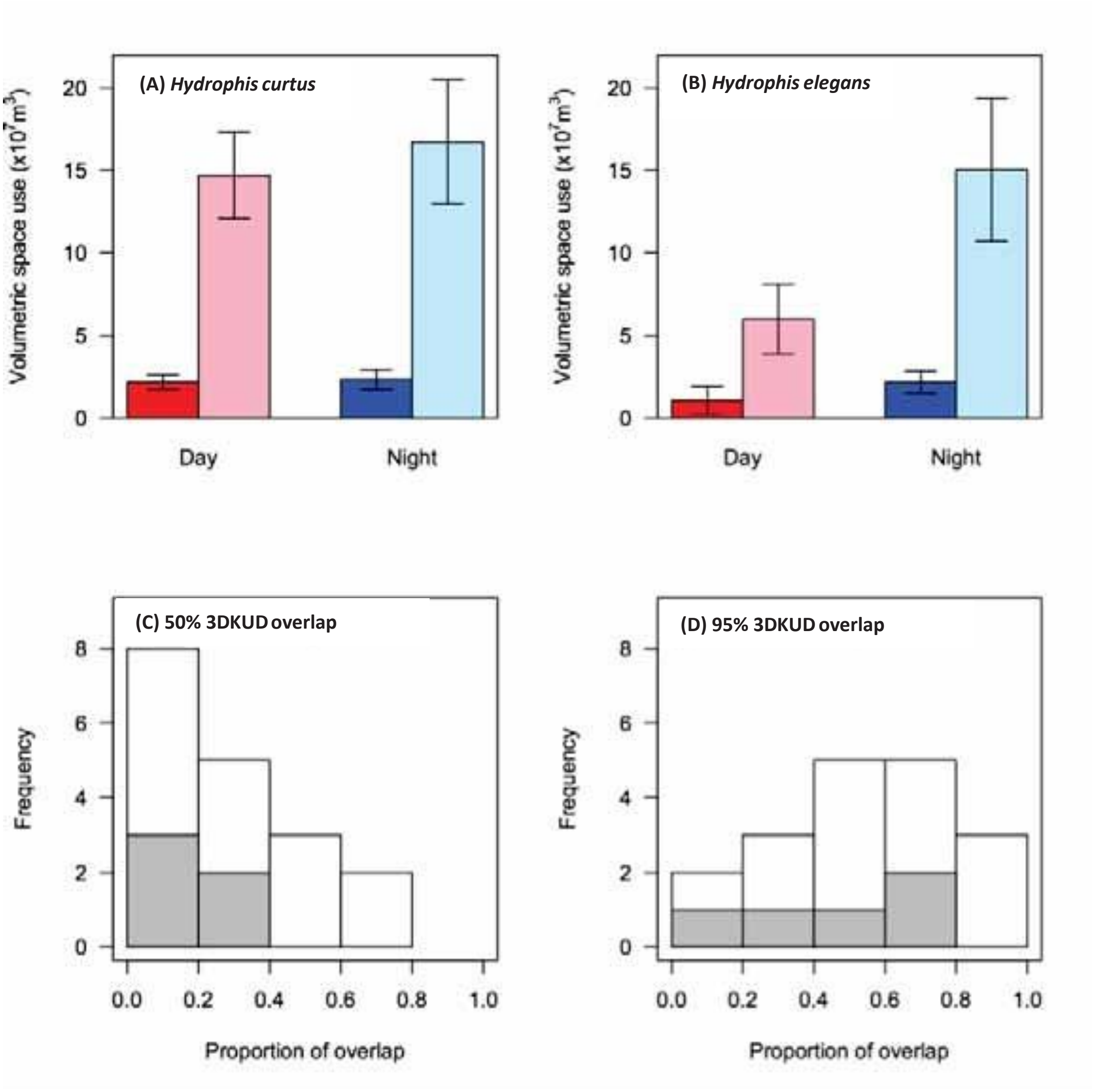

Figure 4.6. Diel differences in three−dimensional home range by tagged sea snakes. Mean diurnal (50% 3DKUD: dark red; 95% 3DKUD: light red) and nocturnal (50% 3DKUD: dark blue; 95% 3DKUD: light blue) home ranges of (A) *Hydrophis curtus* [*n* = 12] and (B) *H. elegans* [*n* = 5]. Overlap between (C) 50% 3DKUD and (D) 95% 3DKUD diurnal and nocturnal use of space by *H. curtus* (white bars) and *H. elegans* (grey bars).

The overlap between home ranges occupied by individuals during the day and at night showed that 50% 3DKUDs of both species had a low proportion of overlap (Figure 4.6C), suggesting that despite similar volumes, there was little overlap in the core areas used. The mean proportion of overlap in 50% 3DKUDs between day and night was significantly lower than that of a random pattern for both species (*t−test, H. curtus*: t = −2.47, p = 0.02; *H. elegans*: t = −3.93, p = 0.02). In contrast, 95% 3DKUDs showed a high degree of overlap between day and night (Figure 4.6D). The mean proportion of overlap in 95% 3DKUD between day and night for both species was not significantly different from random (*t−test, H. curtus*: t = 1.52, p = 0.15; *H. elegans*: t = 0.07, p = 0.94).

4.3.2. Environmental drivers of daily and monthly patterns of movement

Analysis of daily presence (pa) and movement (*Rom*) each resulted in 64 candidate models for each species (*Hydrophis curtus*: Table 4.2, Appendix 4.6.1; *Hydrophis elegans*: Table 4.2, Appendix 4.6.2). The models showed that for *H. curtus*, daily presence was most influenced by tidal reach, as represented by the model with the lowest AICc score (277.5; Table 4.3, Appendix 4.6.1), which was significantly better than the null model. The probability of daily presence of *H. curtus* was marginally higher on days with larger tidal ranges (Figure 4.7A). Tidal range was also represented as an explanatory variable in the top five ranked models (Table 4.2) suggesting that this variable was a significant predictor of presence of individuals within the array on a daily timescale. Daily air pressure, accumulated rainfall and snout−vent length of individuals were also consistently present within the top seven ranked models, suggesting that these variables also had some influence on the daily presence of *H. curtus*. In *H. elegans*, the low numbers of detections resulted in weaker relationships between the probability of presence and measured environmental variables, with wind speed and air pressure represented in the top two models (Table 4.2, Appendix 4.6.2), however these models were not significantly

Table 4.2. Top fifteen models exploring the effect of biological and environmental drivers on presence and movement of monitored ***Hydrophis curtus*** over a **daily** temporal scale. A Generalised Linear Mixed Model (GLMM) framework was used with individuals treated as a random factor (1|ID). Candidate models were compared to a null model [M_O:~ 1 + (1|ID)] and significant differences were evaluated with maximum likelihood ratio tests (χ^2, $p < 0.05$). *Rom*: roaming index, pa: presenceꞬabsence, SVL: snout–vent length (mm), temp: water temperature (˚C), press: atmospheric pressure (hPa), rain: accumulated rainfall (mm), wind: wind speed (km.hr^{-1}), tide: daily tidal range (mm); *: models that significantly differed from null model ($p < 0.05$). The full table of all 64 candidate models is available in Appendix 4.6.1.

Rank	**Presence**			**Movement**		
	Model	***df***	**AICc**	**Model**	***df***	**AICc**
1	pa ~ tide	3	277.5*	*Rom* ~ press	3	1575.4*
2	pa ~ press + tide	4	277.9*	*Rom* ~ press + SVL	4	1575.9*
3	pa ~ SVL + tide	4	278.0*	*Rom* ~ press + tide	4	1576.1*
4	pa ~ rain + tide	4	278.6*	*Rom* ~ press + rain	4	1576.6
5	pa ~ press + SVL + tide	5	278.8*	*Rom* ~ press + SVL + tide	5	1576.7
6	pa ~ press	3	279.0*	*Rom* ~ press + wind	4	1576.8
7	pa ~ rain + SVL + tide	5	279.1*	*Rom* ~ 1	2	1576.9
8	pa ~ tide + temp	4	279.3*	*Rom* ~ SVL	3	1576.9
9	pa ~ press + tide + temp	5	279.4*	*Rom* ~ temp	3	1577.1
10	pa ~ tide + wind	4	279.5*	*Rom* ~ press + SVL + wind	5	1577.1
11	pa ~ 1	2	279.7	*Rom* ~ press + rain + SVL	5	1577.2
12	pa ~ press + rain + tide	5	279.7*	*Rom* ~ SVL + temp	4	1577.2
13	pa ~ SVL + tide + temp	5	279.9*	*Rom* ~ press + rain + tide	5	1577.4
14	pa ~ press + tide + wind	5	279.9*	*Rom* ~ press + temp	4	1577.4
15	pa ~ SVL + tide + wind	5	280.0*	*Rom* ~ press + tide + wind	5	1577.7

Table 4.3. Top fifteen models exploring the effect of biological and environmental drivers on presence and movement of monitored ***Hydrophis elegans*** over a **daily** temporal scale. A Generalised Linear Mixed Model (GLMM) framework was used with individuals treated as a random factor (1|ID). Candidate models were compared to a null model [M_O:~ 1 + (1|ID)] and significant differences were evaluated with maximum likelihood ratio tests (χ^2, $p < 0.05$). *Rom*: roaming index, pa: presenceſabsence, SVL: snout–vent length (mm), temp: water temperature (˚C), press: atmospheric pressure (hPa), rain: accumulated rainfall (mm), wind: wind speed (km.hr^{-1}), tide: daily tidal range (mm); *: models that significantly differed from null model ($p < 0.05$). The full table of all 64 candidate models is available in Appendix 4.6.2.

Rank	Presence			Movement		
	Model	***df***	**AICc**	**Model**	***df***	**AICc**
1	pa ~ press + SVL + wind	5	112.7	*Rom* ~ wind	3	372.6*
2	pa ~ press + wind	4	113.1	*Rom* ~ rain + wind	4	372.6*
3	pa ~ 1	2	113.1	*Rom* ~ rain + SVL + wind	5	374.0*
4	pa ~ press	3	113.4	*Rom* ~ SVL + wind	4	374.1*
5	pa ~ SVL	3	113.4	*Rom* ~ press + wind	4	374.4*
6	pa ~ press + SVL	4	113.9	*Rom* ~ press + rain + wind	5	374.5*
7	pa ~ temp	3	114.5	*Rom* ~ temp + wind	4	374.7*
8	pa ~ SVL + wind	4	114.7	*Rom* ~ tide + wind	4	374.7*
9	pa ~ SVL + temp	4	114.7	*Rom* ~ rain + tide + wind	5	374.7*
10	pa ~ press + rain + SVL + wind	6	114.7	*Rom* ~ rain + temp + wind	5	374.7*
11	pa ~ wind	3	114.8	*Rom* ~ rain	3	374.9*
12	pa ~ press + SVL + temp + wind	6	114.8	*Rom* ~ rain + SVL	4	375.7
13	pa ~ press + SVL + tide + wind	6	114.9	*Rom* ~ press + rain + SVL + wind	6	375.9
14	pa ~ press + temp + wind	5	115.0	*Rom* ~ press + SVL + wind	5	375.9
15	pa ~ press + rain + wind	5	115.1	*Rom* ~ rain + SVL + temp + wind	6	376.1

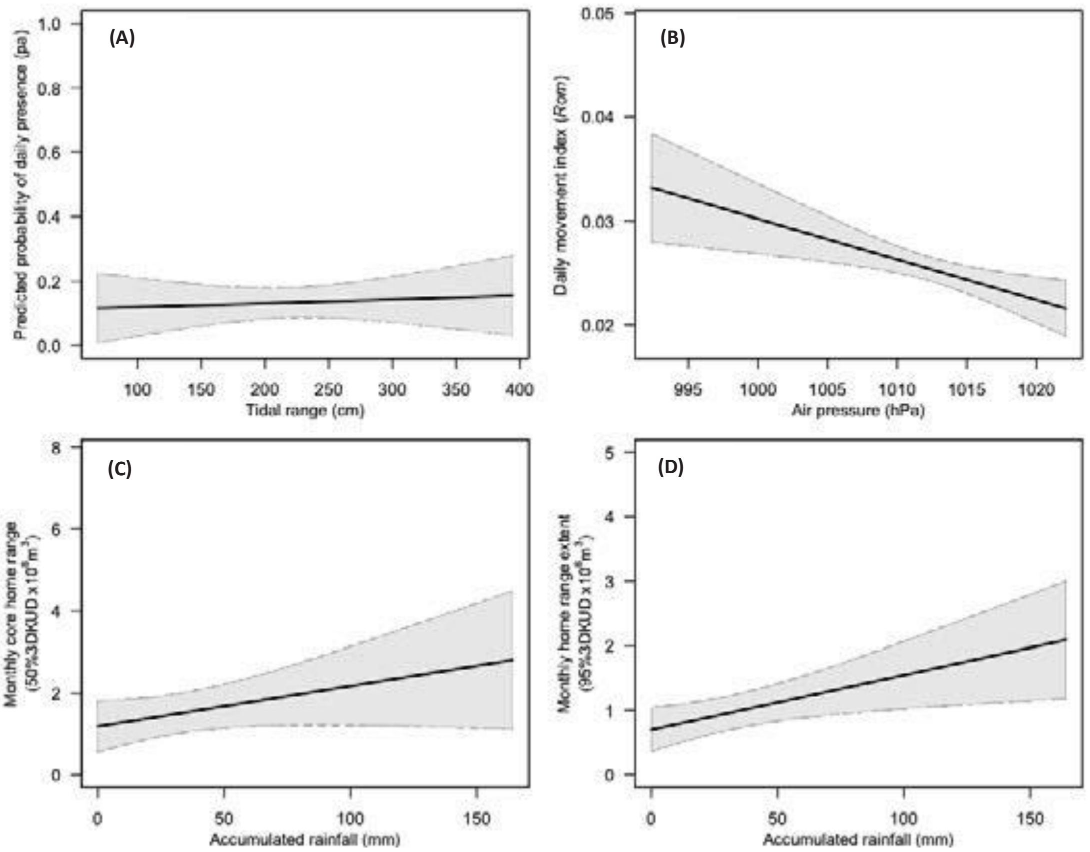

Figure 4.7. Correlation plots of most parsimonious models examining the influence of measured environmental variables on the presence, movement and home range of tagged *Hydrophis curtus*. (A) Probability of daily presence against tidal range, (B) daily movement index (*Rom*) against measured air pressure, (C) monthly core home range (50% 3DKUD) and (D) monthly extent of home range (95% 3DKUD) against accumulated rainfall. Confidence intervals are presented within shaded grey areas.

different to the null model. Correlation plots showed a similar weak relationship between wind speed (Figure 4.8A) and air pressure (Figure 4.8B).

Candidate models showed that daily movements (*Rom*) of *H. curtus* were most influenced by air pressure, which was included in the most parsimonious model (AICc = 1575.4; Table 4.2, Appendix 4.6.1), which was significantly better than the null model. The top six ranked models also included air pressure as an explanatory variable, with tidal range, accumulated rainfall, wind speed and snout− vent length represented. In the case of *Rom*, only the top three models were significantly different from the null model. The daily movements of tagged *H. curtus* (*Rom*) were higher on days with lower air pressures (Figure 4.7B). Wind speed and accumulated rainfall were the two measured environmental variables that had a significant influence on the daily movements (*Rom*) of *H. elegans* and were included in the two top models (Table 4.3, Appendix 4.6.2). These models were significantly different from the null model, however were not significantly different from each other, suggesting that both variables had a combined affect on daily movements in *H. elegans*. The correlation plots showed that daily movements increased with increased wind speed and increased rainfall (Figure 4.8C,D).

Monthly time scale analysis of *Rom*, and core (50% 3DKUD) and the extent (95% 3DKUD) of three−dimensional home range each resulted in 32 candidate models for both species (*Hydrophis curtus*: Table 4.4, Appendix 4.7.1; *H. elegans*: Table 4.5, Appendix 4.7.2). The analyses showed that for both species the null model was the most parsimonious in relation to monthly movements of tagged individuals (Table 4.4,Table 4.5), with none of the other tested models significantly different from the null model. This indicated that the chosen environmental and biological variables were poor predictors of monthly movements of sea snakes.

The 3DKUD analyses showed variability in the three−dimensional home range of tagged *H.curtus* between months (Figure 4.9, 3D model for individual S9 is supplied in Appendix 4.8.1) [two more individuals are represented in Appendix 4.8.2 (S15) and Appendix 4.8.3 (S16)]. The regression analysis for *H. curtus* revealed monthly−accumulated rainfall was the most influential environmental variable (50% 3DKUD AICc = 918.3, 95% 3DKUD AICc = 989.8; Table 4.4, Appendix 4.7.2) with volumes of 50% 3DKUD and 95% 3DKUD larger in months with higher accumulated rainfall

(Figure 4.7C,D). Wind speed and air pressure were also represented in the top five ranked models of 50% 3DKUD volumes, which were all significantly different from the null model. The top four models examining the volumes of 95% 3DKUD also included air pressure, water temperature and wind speed as influential environmental variables (Table 4.4) and were significantly different from the null model. In the case of monthly three−dimensional home range of *H. elegans* the null models were the most parsimonious models with none of the other tested models significantly different from the null model (Table 4.5). The low correlation between monthly metrics and environmental variables were most likely due to the low numbers of detections from the tagged *H. elegans*.

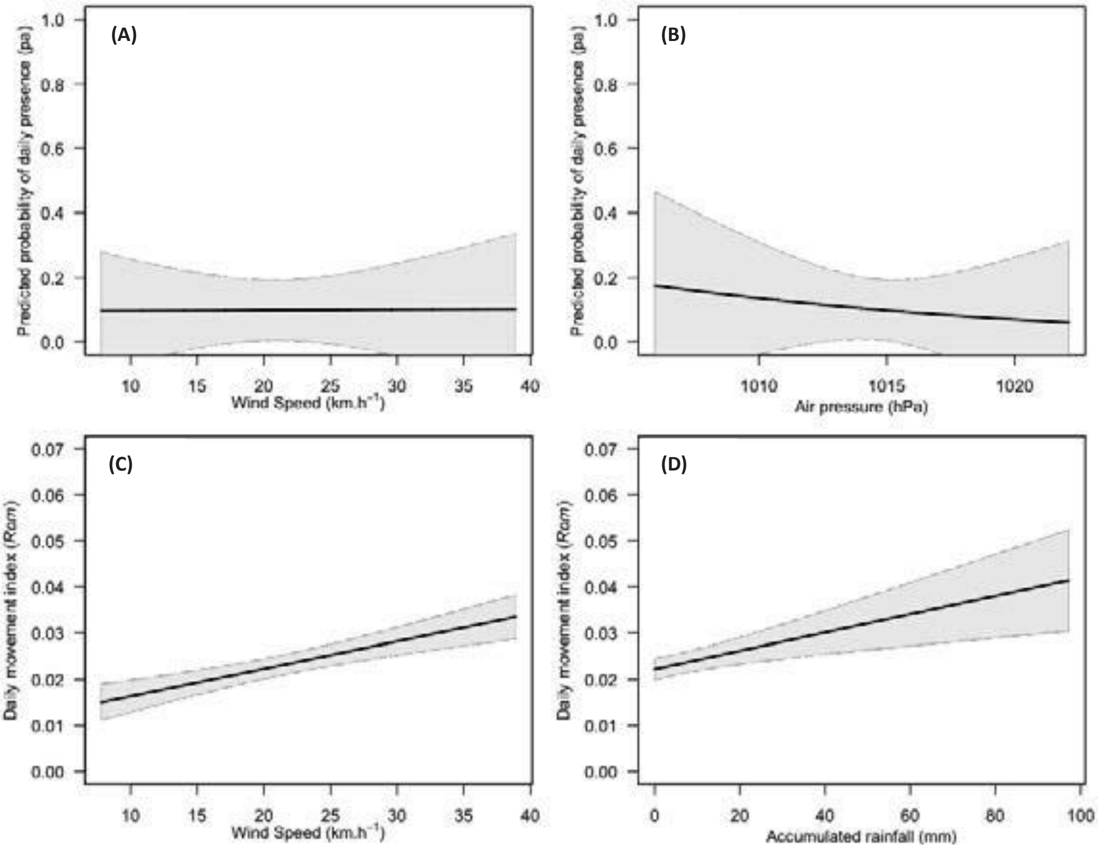

Figure 4.8. Correlation plots of the most influencial measured environmental variables on the daily presence and daily movements of tagged *Hydrophis elegans*. Influence of (A) wind speed and (B) air pressure on the probability of daily presence. Influence of (C) wind speed and (D) accumulated rainfall on the daily movements (*Rom*) of tagged individuals. Confidence intervals are presented within shaded grey areas.

Table 4.4. Effects of environmental and biological drivers on the movement and three–dimensional home range of ***Hydrophis curtus*** over a **monthly** temporal scale. A Generalised Linear Mixed Model (GLMM) framework was used with individuals treated as a random factor (1|ID). Candidate models were compared to a null model [M_O:~ 1 + (1|Tag)] and significant differences were evaluated with maximum likelihood ratio tests (χ^2, $p < 0.05$). *Rom*: roaming index, KUD50: 50%3DKUD (m^3), KUD95: 95%3DKUD (m^3), SVL: snout–vent length (mm), temp: water temperature (˚C), press: atmospheric pressure (hPa), rain: rainfall (mm), wind: wind speed ($km.hr^{-1}$); *: models that significantly differed from null model ($p < 0.05$). The full table of all 32 candidate models is available in Appendix 4.7.1.

Rank	**Movement**			**Three-dimensional home range**					
	Model	***df***	**AICc**	**Model**	***df***	**AICc**	**Model**	***df***	**AICc**
1	*Rom* ~ 1	2	124.7	KUD50 ~ rain	4	918.3*	KUD95 ~ rain	4	989.8*
2	*Rom* ~ SVL	3	126.1	KUD50 ~ wind	4	919.0*	KUD95 ~ press + rain	5	991.2*
3	*Rom* ~ rain	3	126.4	KUD50 ~ rain + wind	5	919.1*	KUD95 ~ rain + temp	5	992.7*
4	*Rom* ~ press	3	126.7	KUD50 ~ press + wind	5	919.4*	KUD95 ~ rain + wind	5	992.9*
5	*Rom* ~ temp	3	127.0	KUD50 ~ press	4	919.7*	KUD95 ~ rain + SVL	5	992.9*
6	*Rom* ~ wind	3	127.3	KUD50 ~ 1	3	920.2	KUD95 ~ press + rain + temp	6	994.4*
7	*Rom* ~ rain + SVL	4	128.4	KUD50 ~ temp + wind	5	920.3*	KUD95 ~ press + rain + wind	6	994.7*
8	*Rom* ~ press + SVL	4	128.5	KUD50 ~ temp	4	921.0*	KUD95 ~ press + rain + SVL	6	994.7*
9	*Rom* ~ SVL + temp	4	128.7	KUD50 ~ rain + SVL	5	921.4*	KUD95 ~ rain + temp + wind	6	996.2*
10	*Rom* ~ SVL + wind	4	128.9	KUD50 ~ rain + temp	5	921.5*	KUD95 ~ rain + SVL + temp	6	996.2*
11	*Rom* ~ rain + temp	4	129.2	KUD50 ~ press + rain	5	921.5*	KUD95 ~ rain + SVL + wind	6	996.4*
12	*Rom* ~ rain + wind	4	129.2	KUD50 ~ SVL + wind	5	922.2*	KUD95 ~ temp	4	996.4*
13	*Rom* ~ press + rain	4	129.3	KUD50 ~ press + temp	5	922.2*	KUD95 ~ press	4	996.6*
14	*Rom* ~ press + temp	4	129.3	KUD50 ~ press + rain + wind	6	922.5*	KUD95 ~ 1	3	997.9
15	*Rom* ~ press + wind	4	129.6	KUD50 ~ rain + SVL + wind	6	922.5*	KUD95 ~ press + rain + temp + wind	7	998.3*

Table 4.5. Effects of environmental and biological drivers on the movement and three−dimensional home range of ***Hydrophis elegans*** over a **monthly** temporal scale. A Generalised Linear Mixed Model (GLMM) framework was used with individuals treated as a random factor (1|ID). Candidate models were compared to a null model [M_O:~ 1 + (1|Tag)] and significant differences were evaluated with maximum likelihood ratio tests (χ^2, $p < 0.05$). *Rom*: roaming index, KUD50: 50%3DKUD (m^3), KUD95: 95%3DKUD (m^3), SVL: snout−vent length (mm), temp: water temperature (˚C), press: atmospheric pressure (hPa), rain: rainfall (mm), wind: wind speed (km.hr^{-1}); *: models that significantly differed from null model ($p < 0.05$). The full table of all 32 candidate models is available in Appendix 4.7.2.

Rank	**Movement**			**Three-dimensional home range**					
	Model	***df***	**AICc**	**Model**	***df***	**AICc**	**Model**	***df***	**AICc**
1	*Rom* ~ 1	2	49.80	KUD50 ~ 1	3	477.0	KUD95 ~ 1	3	495.6
2	*Rom* ~ temp	3	50.97	KUD50 ~ wind	4	480.2	KUD95 ~ wind	4	498.1
3	*Rom* ~ rain	3	51.46	KUD50 ~ SVL	4	480.3	KUD95 ~ SVL	4	498.8
4	*Rom* ~ press	3	51.49	KUD50 ~ press	4	481.0	KUD95 ~ press	4	499.2
5	*Rom* ~ wind	3	52.32	KUD50 ~ rain	4	481.6	KUD95 ~ rain	4	500.2
6	*Rom* ~ SVL	3	52.77	KUD50 ~ temp	4	481.7	KUD95 ~ temp	4	500.3
7	*Rom* ~ rain + wind	4	54.38	KUD50 ~ SVL + wind	5	485.5	KUD95 ~ press + rain	5	502.9
8	*Rom* ~ temp + wind	4	54.42	KUD50 ~ press + wind	5	486.0	KUD95 ~ press + wind	5	503.0
9	*Rom* ~ rain + temp	4	54.54	KUD50 ~ press + SVL	5	486.1	KUD95 ~ SVL + wind	5	503.3
10	*Rom* ~ SVL + temp	4	54.57	KUD50 ~ rain + wind	5	486.1	KUD95 ~ rain + wind	5	503.6
11	*Rom* ~ press + temp	4	54.60	KUD50 ~ temp + wind	5	486.3	KUD95 ~ temp + wind	5	503.9
12	*Rom* ~ press + wind	4	54.83	KUD50 ~ press + rain	5	486.4	KUD95 ~ press + SVL	5	504.6
13	*Rom* ~ rain + SVL	4	54.93	KUD50 ~ rain + SVL	5	486.6	KUD95 ~ press + temp	5	504.6
14	*Rom* ~ press + rain	4	55.03	KUD50 ~ SVL + temp	5	486.6	KUD95 ~ SVL + temp	5	505.0
15	*Rom* ~ press + SVL	4	55.04	KUD50 ~ press + temp	5	486.8	KUD95 ~ rain + SVL	5	505.0

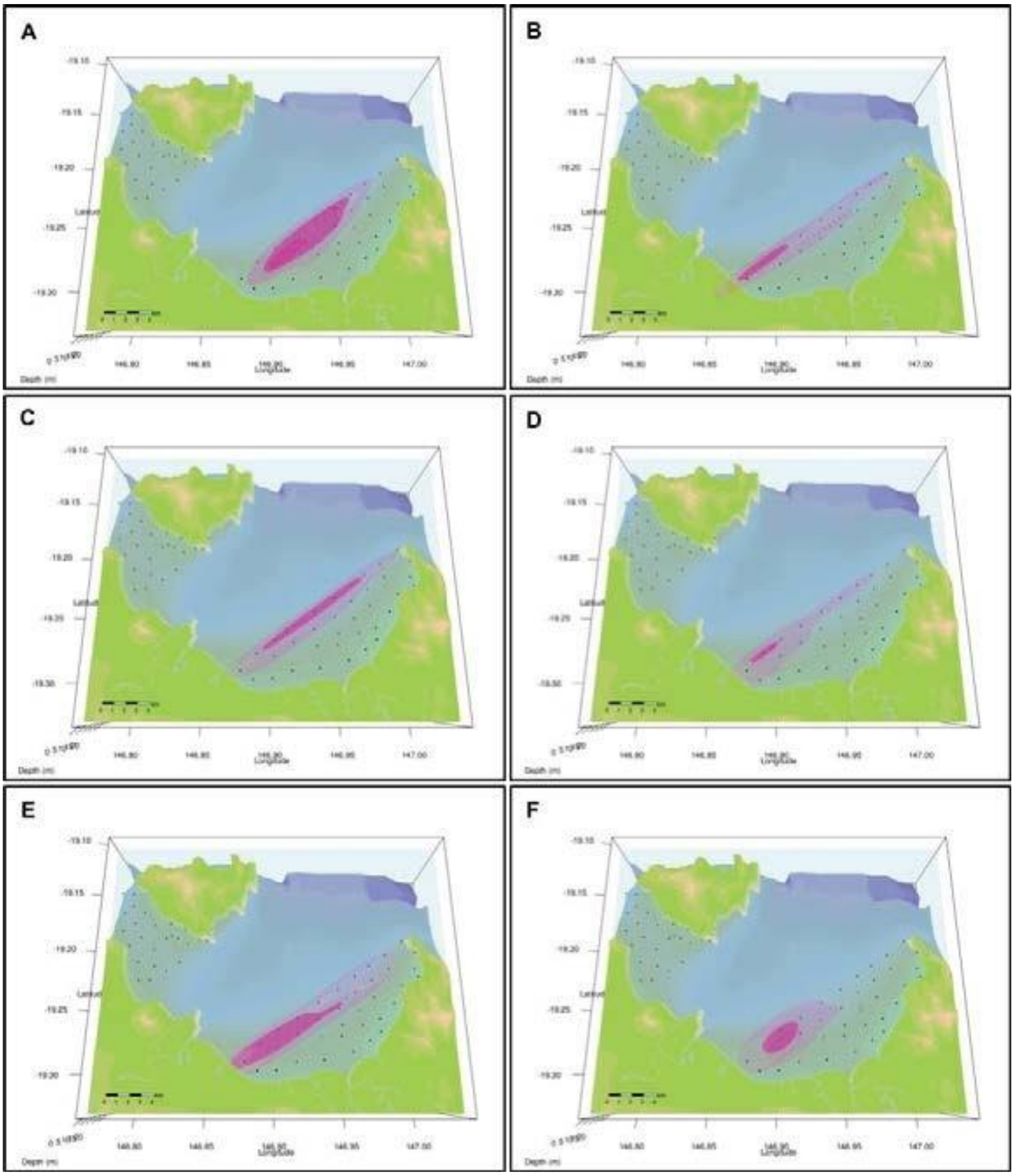

Figure 4.9. Monthly three−dimensional space use (3DKUD) of a representative tagged *Hydrophis curtus* (S9). Screenshots showing monthly 3DKUD for (A) March, (B) April, (C) May, (D) June, (E) July and (F) August. Dark pink shapes represent core home range (50% 3DKUD) and light pink shapes represent extent of home range (95% 3DKUD). Surrounding bathymetry and sea surface are also rendered for context. Black points represent the locations of acoustic receivers. Close up, interactive, three−dimensional versions of 3DKUD models are available in the appendices for this individual (Appendix 4.8.1) and two other tagged individuals (S15: Appendix 4.8.2 and S16: Appendix 4.8.3), please refer to the Note for a list of suitable desktop and mobile browsers.

4.4. Discussion

4.4.1. Patterns in short-term diel movements

The representation of space used by sea snakes in their natural environment requires the integration of their diving capabilities. Here we show that the use of new techniques in three−dimensional spatial analyses are appropriate when considering how sea snakes use space and facilitate detection of diel changes in movement. Previous attempts at understanding sea snake movements and their use of space by Rubinoff *et al.* (Rubinoff et al. 1986, Rubinoff et al. 1988) and Burns and Heatwole (1998) utilised ultrasonic transmitters to reveal short−term movements of the pelagic yellow−bellied sea snake, *Hydrophis* (*Pelamis*) *platura*, and the reef−associated olive sea snake, *Aipysurus laevis,* respectively. These studies were very useful in defining movement; however, as the vertical and horizontal patterns of movement were examined separately (e.g. Rubinoff et al. 1986, Rubinoff et al. 1988), the interpretation of the movements and use of space of these species was limited. The present study demonstrates that with the current advances in statistical analyses, the integration of vertical and horizontal axes will allow for a more accurate interpretation of the patterns of movement and of the use of space in sea snakes.

The use of short−term centre of activities (COA) to calculate mean positions at fixed time intervals accounts for temporal variation in detection patterns and is required when investigating movements and calculating home ranges of individuals using fixed, non−overlapping reciever arrays (Simpfendorfer et al. 2002). When incorporating depth use in this method for long−term monitoring, the resulting home ranges provide information on how individuals use the water column. The COAs position for individuals within the water column were heavily weighted on how often/long the individual surfaced and how often/long the individual stayed at the bottom. Observations from previous studies of diving sea snakes (e.g. Brischoux et al. 2007a, Cook & Brischoux 2014) display patterns of depth use where individuals spend a significant time either at the surface breathing or at depth when foraging or inactive. In the present study a diel pattern was observed in the dive patterns of monitored sea snakes. Individuals were active at the surface at night displaying larger 3D KUD close to the surface, whereas during the day, displaying smaller 3D KUDs at greater depths.

The results in the present study indicate a clear diel change in diving patterns, use of space and habitat by both species of sea snakes within Cleveland Bay. The drivers of change are potentially numerous, but one factor that most likely has an important influence on diurnal and nocturnal behaviour is the abundance and activity of prey. *Hydrophis elegans* almost exclusively prey on snake eels (Family Ophichthidae) (Voris & Voris 1983, Kerford 2005), which are abundant within the shallow mud−flat benthos of Cleveland Bay. This may not only restrict the use of space by *H. elegans* to mud flats close to the mouths of creeks within Cleveland Bay, but might also drive some of their movements at night. The movements and activity patterns of eels within coastal habitats are closely related to diel patterns, with greater activity and movement at night (Helfman 1986, Dutil et al. 1988). Increased activity of prey species at night may explain the greater use of space by *H. elegans* at night and the low proportion of overlap between core areas between day and night. On the other hand, the diet of *H. curtus* is varied and includes a wide range of prey species (Voris &

Voris 1983) suggesting *H. curtus* are not restricted to a particular habitat within the bay. This may explain the larger volumes and increased overlap between spaces used between day and night. The results also indicate that different species of sea snakes likely display different patterns in diel movements, and therefore susceptibility to natural and anthropogenic threats will vary.

One aspect of the present study that needs to be considered is that the majority of individuals that were monitored were juvenile. The few adults that were monitored displayed similar patterns of diel movements to juvenile conspecifics. However, previous studies have shown that movement patterns in adult sea snakes can vary seasonally, with increased movements displayed by males during breeding season related to mate−searching behaviours (Heatwole 1999, Lynch 2000). This is an additional factor that needs to be considered when exploring diving and movement patterns of sea snakes over multiple seasons. In the present study, low numbers of tagged adults and limitations in tag life restricted the ability to explore such seasonal changes in three−dimensional movement patterns related to breeding cycles. Additionally, ontogenic shifts in habitat use and diets in sea snakes during different life stages may also alter movement patterns. Presently, very little information is available on ontogenic changes in diet or habitat use in sea snakes. Further long−term studies are required to investigate if dietary preference and use of habitat changes with life stages in sea snakes, which can potentially influence how individuals move within the environment and use space.

4.4.2. Environmental drivers of daily and monthly patterns of movement

Different environmental variables have varying degrees of influence on the presence, movement and home range of sea snakes. In particular, individual environmental variables may be more influential at different time−scales. On a daily time−scale tidal reach and air pressure had the greatest influence on the presence and movement of tagged sea snakes, respectively. Whereas, on a monthly timescale, accumulated rainfall played a significant role in influencing the size of home ranges. These variables are likely affecting the location, distribution and movement patterns of spine−bellied sea snakes in Cleveland Bay, explaining some of the daily and monthly movement patterns observed for this species.

Tidal cycles can be an important factor with respect to diurnal and nocturnal activity patterns of sea snakes (Ineich & Laboute 2002). In the present study tidal range had considerable influence on daily presence of tagged spine−bellied sea snakes, with a higher probability of presence on days with larger tidal reach. Studies in Shark Bay, Western Australia, have reported coastal species like *Hydrophis elegans* and *H. major* (previously *Disteira major*) use the tidal cycle as a cue to move in and out of shallow seagrass habitats to avoid predation by tiger sharks (*Galeocerdo cuvier*) on high tides (Kerford et al. 2008, Wirsing & Heithaus 2009). The influence of tidal currents has also been noted in other species of sea snakes such as the beaked sea snake (*Hydrophis zweifeli*, previously *Enhydrina schistosa*), where activity was inhibited during strong tidal currents (Heatwole 1999). In the case of tagged spine−bellied sea snakes in Cleveland Bay, an increased probability of presence during periods of increased tidal range suggests that individuals moved more broadly during periods with larger tidal reach (during full and new moon phases). One explanation for such a link may be the availability and activity of prey species. Spine−bellied sea snakes prey on a large range of coastal fish species from elongated anguilliform eels and gobies to fusiform sand whiting and spinous catfish (Voris & Voris 1983) that are all abundant within Cleveland Bay. Fish movements and activity in intertidal areas is often closely related to tidal movements (Palmer 1995), therefore increased activity of prey species may be directly influencing the activity of spine−bellied sea snakes within Cleveland Bay.

Conversely, the presence of sea snakes in shallower waters of the bay during periods of larger tidal reach may be an attempt to avoid predators that inhabit deeper water as noted for closely related *H. elegans* and *H. major* by Kerford et al. (2008). Previous studies on coastal sharks within the study site have identified several species present within Cleveland Bay (i.e. *Galeocerdo cuvier*, Simpfendorfer 1992, *C. amboinensis*, Knip et al. 2011, *C. sorrah*, Knip et al. 2012, *Carcharhinus melanopterus*, Chin et al. 2013, *Rhizoprionodon taylori*, Munroe et al. 2014). However, with the exception of *C. melanopterus* (Lyle & Timms 1987) and *G. cuvier* (Simpfendorfer et al. 2001, Ineich & Laboute 2002) most of the species present within the bay are not known predators of sea snakes. Use of tidal cycles as cues for feeding or predator avoidance behaviours may explain why the tidal range was a significant environmental variable not only for daily presence of tagged sea snakes but also to a lesser extent for daily movements. Another possibility is that exploitation of shallow water decreases energetic demands associated with diving behaviour (Shine 1988).

Therefore, use of shallow coastal areas could provide multiple benefits for sea snakes ranging from shelter from predation to feeding and energetic benefits.

The daily movements of tagged sea snakes in the present study were strongly influenced by changes in atmospheric pressure with increased movements on days with low pressure. Air pressure, rainfall and wind are often correlated during periods prior to extreme weather events however changes in atmospheric pressure may likely be a key indicator and driver of behaviours in a range of marine organisms (e.g. Heupel et al. 2003, Liu et al. 2010, Udyawer et al. 2013). Previously, Liu et al. (2010) reported sea kraits (*Laticauda* spp.) using changes in atmospheric pressure related to typhoon Marakot (2009) on Orchid Island, Taiwan, as a cue to anticipate rough weather. Liu et al. (2010) observed a significant decrease in the presence and abundance of sea kraits a day prior to the onset of the typhoon that was closely related to the drop in atmospheric pressure. Similar behaviours have also been observed within Cleveland Bay and other shallow coastal habitats by other coastal marine organisms prior to large storm events (Heupel et al. 2003, Udyawer et al. 2013). In the present study, cyclonic conditions were not experienced during the monitored period, but significant drops in atmospheric pressure were measured on two occasions (January 2013 and April 2014, Figure 4.2) prior to periods of increased rainfall. There are likely combinations of environmental factors that influence movements of individuals at a daily time−scale, however, here the drop in atmospheric pressure are a key factor that triggered an increase in movements of sea snakes within the bay. Biological mechanisms for sensing atmospheric pressure are not well understood in sea snakes, but previous studies on *Hydrophis curtus*

(Westhoff et al. 2005) and closely related file snakes (Acrochordidae; Povel & Van Der Kooij 1996) have identified cutaneous scale sensillae and inner ear hair cells as structures that are sensitive to hydrodynamic stimuli. Further study is required to understand how sea snakes are affected by changes in pressure, however the present data suggest atmospheric pressure is an important environmental variable influencing sea snake activity on a daily timescale.

Environmental factors appeared to be less influential on the movements of tagged sea snakes over a monthly timescale. Previous studies on marine ectotherms have reported water temperature as a key cue for seasonal occurrence and movements (e.g. Heupel 2007, Froeschke et al. 2010). Sea surface temperature has a significant effect on abundance and distribution of sea snakes on a global scale (Heatwole et al. 2012). In the present study, average monthly temperatures seemed to have little effect on the movements of tagged individuals within the study site. The regression analyses in the present study however, did not consider extreme temperature fluctuations (maximum and minimum daily or monthly temperatures) within the environment during the monitored period. Temperature extremes can potentially affect behaviours of individuals, increasing or decreasing movements if temperatures exceed the tolerance levels of sea snakes for a period of time. The upper limit of thermal tolerance in sea snakes generally ranges between 39 − 40˚C, with the upper lethal limit of *H. curtus* measured at 37.8 ˚C (Heatwole et al. 2012). As environmental temperatures fall below 18 – 20˚C survival rates of sea snakes decrease. Temperatures during the present study ranged between 21.4 and 30.6˚C, well within the thermal tolerances of sea snakes. The results of this analysis therefore, cannot define the effects of temperature extremes on the behaviour of sea snakes. Longer−term or more focused research is required to assess how changes in water temperature may effect sea snake physiology and as a consequence their behaviour, movements and use of space.

Previous data on movements and home range in sea snakes are scarce and have focused on short−term movement of reef−associated species like the olive sea snake (*Aipysurus laevis*; Burns & Heatwole 1998) or longer term movements of the turtle−headed sea snake (*Emydocephalus annulatus*; Lukoschek & Shine 2012). For example, a mark−recapture study revealed movement patterns in male olive sea snakes were more extensive during the mating season as males searched for potential mates (Lynch 2000). However, these patterns were not associated with any environmental cue. As the majority of individuals tagged in the present study were juveniles, mate−searching behaviours would not be part of the observed movements and use of space. Individuals in Cleveland Bay also displayed home ranges within the bay throughout the eleven−month monitoring period suggesting site attachment to shallow habitats for at least part of the year. Older, sexually mature individuals, however, did not stay within the detection range of the array for the full monitoring period and had to be excluded from the regression analyses. This may have masked any influence of reproductive activity within the data set. Therefore, exploring environmental cues related to adult movements or reproductive behaviours was not possible. Further investigation is required to assess possible environmental cue for longer−term seasonal movements by adult sea snakes that inhabit coastal areas like Cleveland Bay.

Salinity, and indirectly precipitation, is an environmental variable that greatly affects the health and diversity of marine snakes (e.g. Lillywhite & Tu 2011, Brischoux et al. 2012a, Brischoux et al. 2012b). Extensive work has investigated potential solutions used by pelagic and reef associated sea snakes to maintain water balance in areas away from fresh water sources (Lillywhite et al. 2008, Lillywhite et al. 2014b). In the present study, tagged individuals had year round access to freshwater sources and were detected in close proximity to freshwater sources. Therefore individuals should not have had a problem maintaining internal water balance. Monthly−accumulated rainfall was a significant predictor of the volume of spaces used (both 50% 3DKUD and 95% 3DKUD), with individuals displaying larger home ranges in months with higher precipitation. This suggests that changes in salinity indirectly brought about by increased precipitation (i.e. increased flow rate from rivers and creeks) may be an important factor in how these animals use space within shallow coastal areas. Increased precipitation and freshwater input possibly allows snakes to occupy more space and move farther during the wet season by reducing the need to remain near freshwater sources. As freshwater runoffs were not directly measured in the present study, a direct correlation was not possible. However, changes in the size of home range depending on rates of freshwater input within Cleveland Bay has previously been observed in other mobile intertidal fauna (i.e. coastal sharks; Knip et al. 2011) and is key in influencing the structure and ecology of coastal habitats.

4.5. Implications for management and conservation

Globally, the primary anthropogenic threat marine snakes face is capture in coastal trawl fisheries (Elfes et al. 2013). Trawl fisheries target a range of commercially valuable species (e.g. *Penaeus esculentus, Penaeus longistylus, Amusium balloti*) that are fished during different times of the year and at different times of the day (Courtney et al. 2010). The diel patterns observed in the present chapter, with increased space used in the water column at night suggest that these species of sea snakes have an elevated susceptibility to nocturnal trawling activity; however, this may vary for other species and differ among life stages. In Australia, bycatch in the trawl fishery is effectively managed by mandatory use of bycatch−reduction devices (BRD) as well as spatial and temporal restrictions to fishing. The combination of BRDs and fishing restrictions have been shown to be effective in reducing landings of sea snakes in Australia (Milton et al. 2009). These management practices however, may not be practical or enforceable in other parts of the world where coastal fisheries overlap with sea snake populations. Monitoring the movements of sea snakes and understanding how they use space within heavily trawled areas can help identify areas of spatial or temporal overlap that can be more effectively mitigated using targeted management policy.

4.6. Conclusions

The inclusion of the vertical axis (i.e. depth, altitude, height) in the visualisation and analysis of spatial data clearly enhances our understanding of how sea snakes occupy space and move. This may ultimately allow for more accurate identify spatial and temporal overlaps with anthropogenic threats (e.g. trawling, dredging), and allow managers to develop targeted policy designed to mitigate any adverse effects to vulnerable populations of sea snakes. Similar techniques can greatly benefit future studies on the spatial ecology of aquatic, aerial and arboreal animals in their natural habitat and refine their susceptibility to natural and anthropogenic threats that operate in the same three−dimensional environment. Here, we also emphasises the importance of temporal scale when considering the influence of environmental conditions on the behaviour of animals that inhabit highly varied ecosystems like coastal embayments. Unfortunately, the bias towards juveniles in the present study made it difficult to examine influences of reproductive state on the movements and the use of space by individuals, however is an important aspect of sea snake ecology and should be explored further in future studies. With the current technology, the movements of these animals were observed for a full seasonal cycle however, longer−term, multi−year studies are still required to assess the influence of shifting climate conditions on the behaviour, movement and home range of sea snakes. A better understanding of how localised environmental changes and anthropogenic threats affect populations of sea snakes is key to successful management and conservation of this unique taxon (Elfes et al. 2013).

Chapter 5

Selection of habitat by sea snakes and notes on dietary composition within nearshore environments

5.1. Introduction

Nearshore environments are highly productive areas often associated with important foraging and nursery grounds for a range of animals (Simpfendorfer & Milward 1993, Heupel et al. 2007, Bonnet et al. 2014, Cerutti–Pereyra et al. 2014). Unfortunately, coastal habitats and the animals that occupy them are under increasing pressure around the world and are highly vulnerable to degradation from anthropogenic and natural changes (Beck et al. 2001, Halpern et al. 2008). The degradation of these habitats can affect the resources they provide (e.g. prey, shelter) and ultimately impact the health of animal populations. Therefore, understanding the spatial and habitat requirements of animals that use these environments is essential when developing targeted adaptive management and conservation strategies under changing environmental conditions.

True sea snakes are marine elapid snakes (Elapidae, Hydrophiinae) commonly found in shallow tropical and sub–tropical 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). Most species of sea snake have highly specialised diets that are often associated with specific habitat types (Glodek & Voris 1982). Any degradation of preferred habitat or prey abundance may have significant consequences to the health of sea snake populations if they are unable to use different habitats.

Despite frequent encounters as bycatch in trawl fisheries worldwide, little ecological information is available about how sea snakes use space and select suitable habitats (Elfes et al. 2013). Studying movements and selection of habitats by sea snakes in nearshore areas can be challenging as using visual survey techniques is often difficult in turbid environments and research trawling is not possible in habitats that are usually inaccessible to trawl vessels (e.g. fringing reefs, shallow estuarine areas). The present chapter used passive acoustic telemetry data reported in the previous chapter (Chapter 4) to assess the habitat use patterns of sea snakes in coastal habitats and address the second aim of the overall thesis (Aim 2:). The main objective of this chapter was to explore how sea snakes select habitats within this system based on type of habitat, depth of habitat and proximity to sources of freshwater. Composition of sea snake diet was also examined using regurgitate from captured individuals.

5.2. Methods

5.2.1. Study site and field methods

This part of the project used acoustic telemetry data from twenty−five individuals from two species of sea snakes (19 Spine−bellied sea snakes, *Hydrophis curtus* and six Elegant sea snakes; *H. elegans*) examined in the previous chapter (Chapter 4).

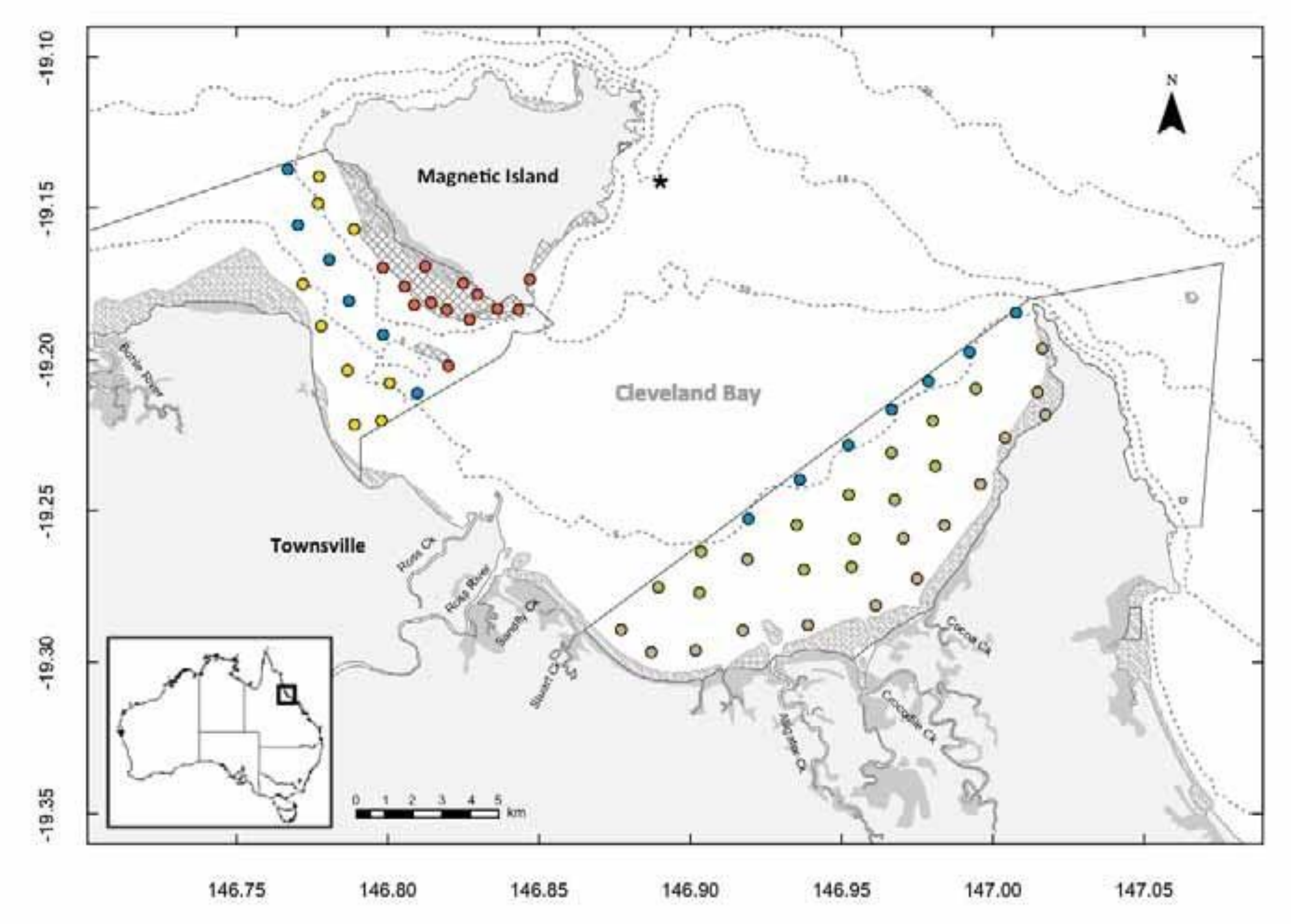

Figure 5.1. Map of study site within Cleveland Bay, Queensland. Points represent locations of acoustic receiver stations deployed on the east and western side of Cleveland Bay divided by a port area. The major habitat types are represented at each station; deep mud habitat (HT1; blue points ●), intertidal mudflat habitat (HT2; brown points ●), fringing reef habitat (HT3; red points ●), inshore sandy habitat (HT4; yellow points ●) and seagrass habitat (HT5; green points ●). Broken grey lines indicate bathymetry and solid lines are boundaries of Conservation Park zones (no trawling or netting). 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. The location of the weather buoy operated by the Australian Institute of Marine Science within the study site is displayed as an asterix (*).

Detection data was obtained using an array of 63 acoustic recievers previously described in Chapter 4.2. (Figure 5.1). 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 (Figure 5.1). The bay consists of multiple habitat types including extensive seagrass meadows, small patches of coral reef, sand and mud flats. Recievers were deployed within the bay to cover the major habitat types represented in the bay (Figure 5.1). The southern shore is lined with mudflats and mangroves with several sources of freshwater entering the bay and provides the majority of freshwater input. Field methods to capture and surgically implant acoustic transmitters (V9P−2H, Venco Ltd.) have been previously described in Chapter 4.2.2.

5.2.2. Data analysis

Use of different habitats within Cleveland Bay by monitored sea snakes was examined using Bayesian random−effects discrete−choice models previously formulated by Thomas et al. (2006). The models examined how tagged individuals selected habitats based on relocations from passive acoustic telemetry on a population−level and individual−level, incorporating individuals 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 (Figure 5.1) to investigate 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) five categorical habitat types determined from their location in the bay and the habitat at the point of anchorage of each station. Habitat types included deep mud substrate (deep, HT1), intertidal mudflat (mudflat, HT2), fringing reef (reef, HT3), inshore sandy substrate (sand, HT4) and seagrass meadows (seagrass, HT5; Figure 5.1).

The model contained three components, a data (likelihood) model, a parameter model and a hyperparameter model. The data model calculated the probability of use of each receiver 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):

(Eq: 5.1)
$$w_i(s) = \frac{e^{\beta_i x(s)} a_i(s)}{\sum_{s \in S} e^{\beta_i x(s)} a_i(s)}$$

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 animal *I,* and β_i ($\beta_{i1}, \beta_{i2}, \ldots, \beta_{ik}$) is a k−dimensional vector of parameters for animal *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 $a_i(s)$ = 1f63, which reduced the model to a discrete−choice model:

(Eq: 5.2)
$$w_i(s) = \frac{e^{\beta_i x(s)}}{\sum_{s \in S} e^{\beta_i x(s)}}$$

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:

(Eq: 5.3)

$$\beta_{il} \sim \text{Normal}(\beta^{*}_{l}, \sigma^{2}_{l})$$

where l = 1, 2, …, k using hyperparameters of β^{*}_{l} and σ^{2}_{l}. 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^{2}_{l}; 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 such:

(Eq: 5.4)

$$\beta^{*}_{l} \sim \text{Normal}(\text{[illegible]})$$

(Eq: 5.5)

$$\sigma^{2}_{l} \sim \text{[illegible]}\,\text{Gamma}(\text{[illegible]})$$

5.2.2.1. *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 three Markov chains with 10,000 iterations per chain, with the first 1,000 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 two levels. First, 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 four global models with all measured covariates formulated as such:

Global model 1 (full model): A model with population−level effects and individual random effects with covariates [$x(s)$] pFW, hDep and the five 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 ($\beta_l^* = 0$). 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 $\beta_{il} = \beta_l^*$ for all animals (i) and $\sigma_l^2 = 0$.

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 ($\beta_{il} = 0$; $\beta_l^* = 0$). Thus, the probability of use of every station is the same as its availability. For this model, there are no parameters to estimate, with $p_i(s)$ = 1ƒ63.

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.

5.2.2.2. *Depth preferences and proximity to freshwater sources*

The Bayesian models described above provided 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 were compared to those available within the study site using Chesson's α (Chesson 1978):

(Eq: 5.6) [illegible]

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 >1ƒ(number of intervals) indicating electivity for, and values <1ƒ(number of intervals) indicating avoidance of the habitat attribute. To highlight this, electivity values were standardised by subtracting 1ƒ(number of intervals) with the resulting deviations >0 indicating electivity and deviations <0 indicating avoidance.

5.2.3. Notes on sea snake diet

Since individuals captured in the present study were tagged and released in healthy condition, complete 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. Regurgitate were at different stages of digestion, but in most cases, prey were fresh. Regurgitate from individuals was collected and identified where possible to provide information on the diet of the two species. The prey composition in regurgitate was compared to data from previous studies, with prey not previously recorded in the literature noted.

5.3. Results

Movements of 19 *Hydrophis curtus* and six *H. elegans* were monitored within Cleveland Bay between January 2013 and March 2014. Initial tagging trips focused within the full extent of the bay, however no sea snakes were captured in the western section, 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 individuals of both species were predominantly detected in this area. However, some individuals were detected on the western side revealing short excursions to fringing reef near Magnetic Island (Figure 5.1) before returning to the eastern side of Cleveland Bay. Monitored *H. curtus* were predominantly detected on stations within seagrass habitat (12430 detections, 86%) followed by deeper mudflat habitats (1494 detections, 10.3%; Table 5.1). *Hydrophis curtus* were detected in all but one habitat type (inshore sandy habitat) and only detected twice within fringing reef habitat (Table 5.1). In contrast *H. elegans* were detected in all habitat types, predominantly in seagrass (3820 detections, 79.5%) and intertidal mudflat habitats (902 detections, 18.1%; Table 5.1).

Table 5.1. Number of detections of *Hydrophis curtus* and *H. elegans* in representative habitat types within Cleveland Bay during monitored period (January 2013 − March 2014). Percentages of detections are presented in parenthesis.

	Deep outer bay mud habitat	**Intertidal mudflat habitat**	**Fringing reef habitat**	**Inshore sandy habitat**	**Seagrass habitat**
	HT1	**HT2**	**HT3**	**HT4**	**HT5**
Hydrophis curtus	1494 (10.3%)	514 (3.6%)	2 (<0.1%)	0 (0%)	12430 (86.1%)
Hydrophis elegans	229 (4.6%)	902 (18.1%)	34 (0.7%)	6 (0.1%)	3820 (76.5%)

Analysis of habitat selection using Bayesian random−effects discreet−choice models revealed the full global model (including both population−level and individual random effects) was most parsimonious for both species (Table 5.2). The best−fitting model was also ranked higher than the no selection model (global model 4; Table 5.2), 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 5.3). The best−fitting models showed that population−level parameter estimates closely matched those of individual−level estimates for both species (Table 5.2). The influence of covariates on overall habitat selection (both at 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

Table 5.2. 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).

	Hydrophis curtus			***Hydrophis elegans***		
Global model	**DIC**	**ΔDIC**	**Rank**	**DIC**	**ΔDIC**	**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

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 depth (hDep) were significant covariates to habitat selection for both species (Figure 5.2A, C). Deep mud (HT1) and seagrass habitats (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 sandy (HT4) habitats were selected against by both species, with significant avoidance by *H. curtus* (Figure 5.2A). 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 (Figure 5.3). Parameter estimates for each station showed that in both species, habitats on the south eastern side of Cleveland Bay were selected preferentially. Overall habitat selection in *H. curtus* indicated deep water and habitats close to freshwater sources in the south east of the bay were used significantly more than random, with

Table 5.3. Model selection to estimate the contribution of covariates in population effects for the most parsimonious global model (see **Table 5.2**). 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).

Model	*Hydrophis curtus*			*Hydrophis elegans*		
	DIC	**ΔDIC**	**Rank**	**DIC**	**ΔDIC**	**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

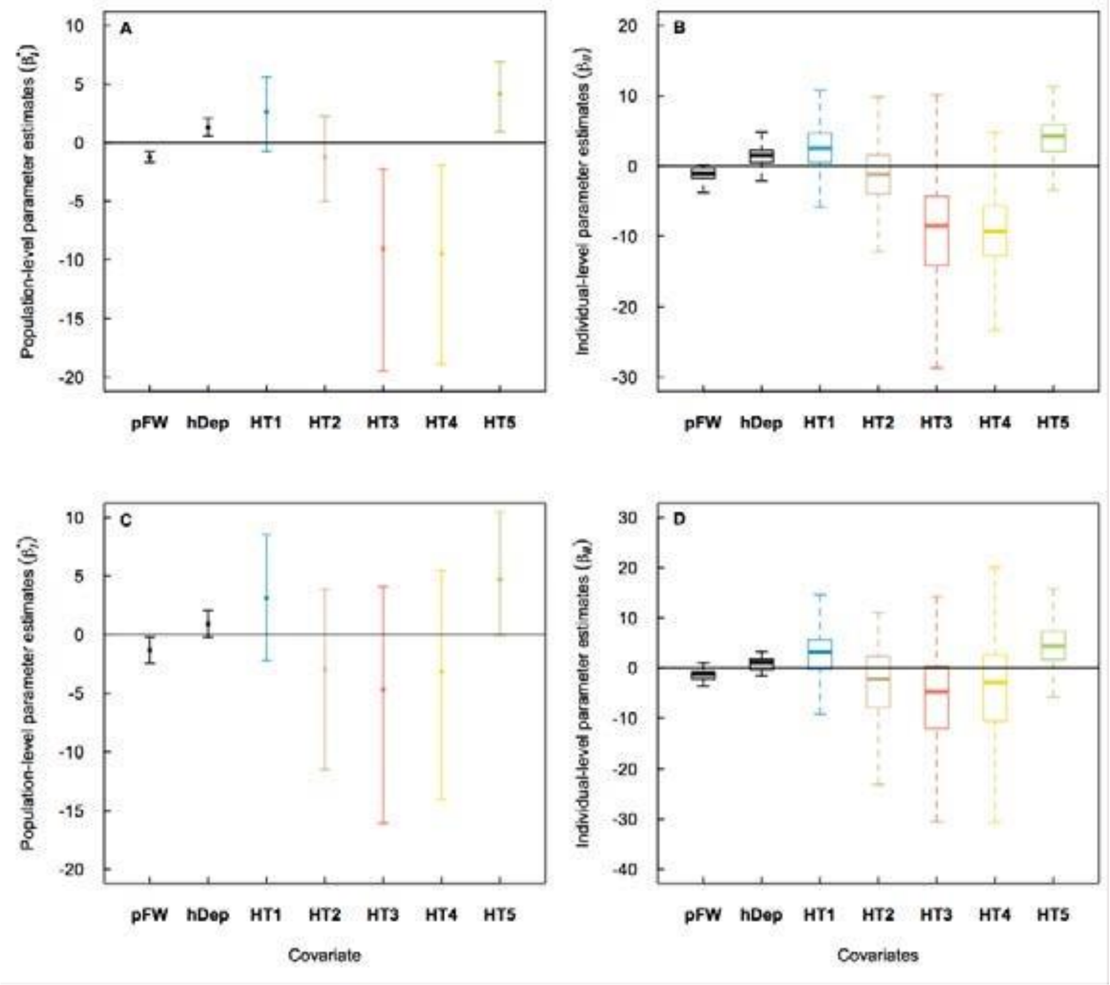

Figure 5.2. Posterior distribution parameters from the most parsimonious Bayesian model (see **Table 5.3**) for *Hydrophis curtus* (A, B) and *H. elegans* (C, D). (A, C) Population−level Bayes estimates (β_i^*) with bounds representing 95% credible intervals. (B, D) Boxplots of distribution of individual−level parameter estimates (β_{il}) for each covariate in the fitted model. 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 and HT5; seagrass habitat.

detections restricted to the eastern side of the bay (Figure 5.3A). However, *H. elegans* displayed more extensive movements and were detected on reef and sandy habitats near Magnetic Island (Figure 5.3B). 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 (Figure 5.3B).

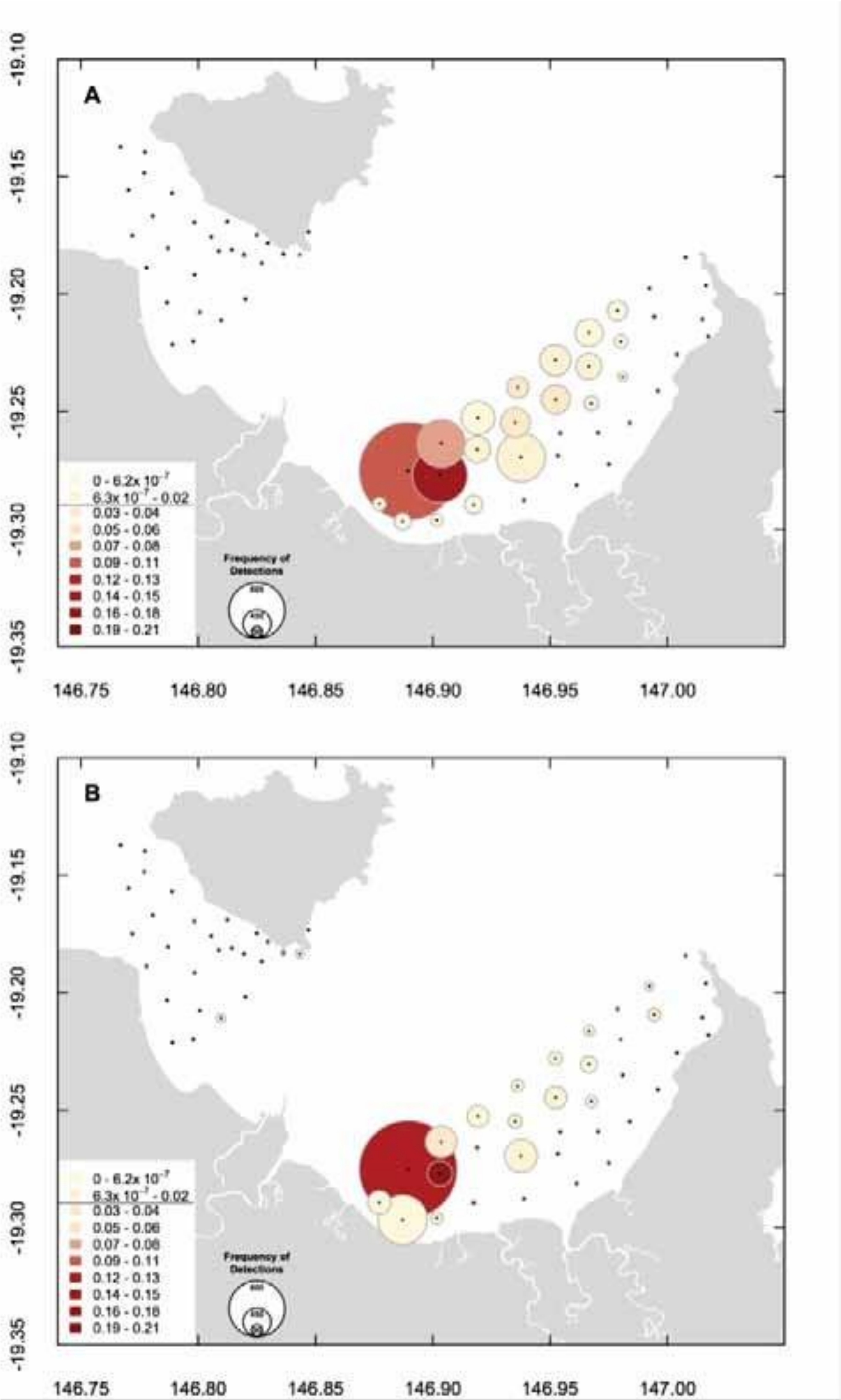

Figure 5.3. Frequency of detections and predicted mean probability of habitat use at each station ($p_i(s)$; see *(Eq: 5.2)* by *Hydrophis curtus* (A) and *H. elegans* (B). Size of circle represents the frequency of detections at each station. Colour of circles represents if individuals selected habitats significantly more/less than random, with darker red circles representing higher estimated probability of selection. Horizontal line in the legend indicates random habitat selection probability.

As the proximity to freshwater sources was used a proxy to the influence of freshwater input from creeks, the results showed that sea snakes prefered habitats close to the mouths of Ross river and secondary creeks in the southeast section of the bay (Figure 5.3). Both species displayed higher detection frequencies in habitats closer to the mouth of Ross river than the smaller secondary creeks in southeast of the bay, which is likely due to the increased flow rate and volume of freshwater input into Cleveland bay.

5.3.1.1. Depth preferences and proximity to freshwater sources

Results of habitat selection models showed that proximity to freshwater (pFW) and habitat depth (hDep) significantly influenced habitat selection (Figure 5.4). Monitored individuals of both species were detected more often on stations close to freshwater sources (Figure 5.4A) and at shallow depths (Figure 5.4B). Individual *H. elegans* displayed an affinity to habitats less than 4 km from sources of freshwater in habitats less than 3 m in depth, while *H. curtus* selected for slightly deeper habitats (1 – 4 m) further from freshwater sources (2 – 5 km; Figure 5.4C, 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.

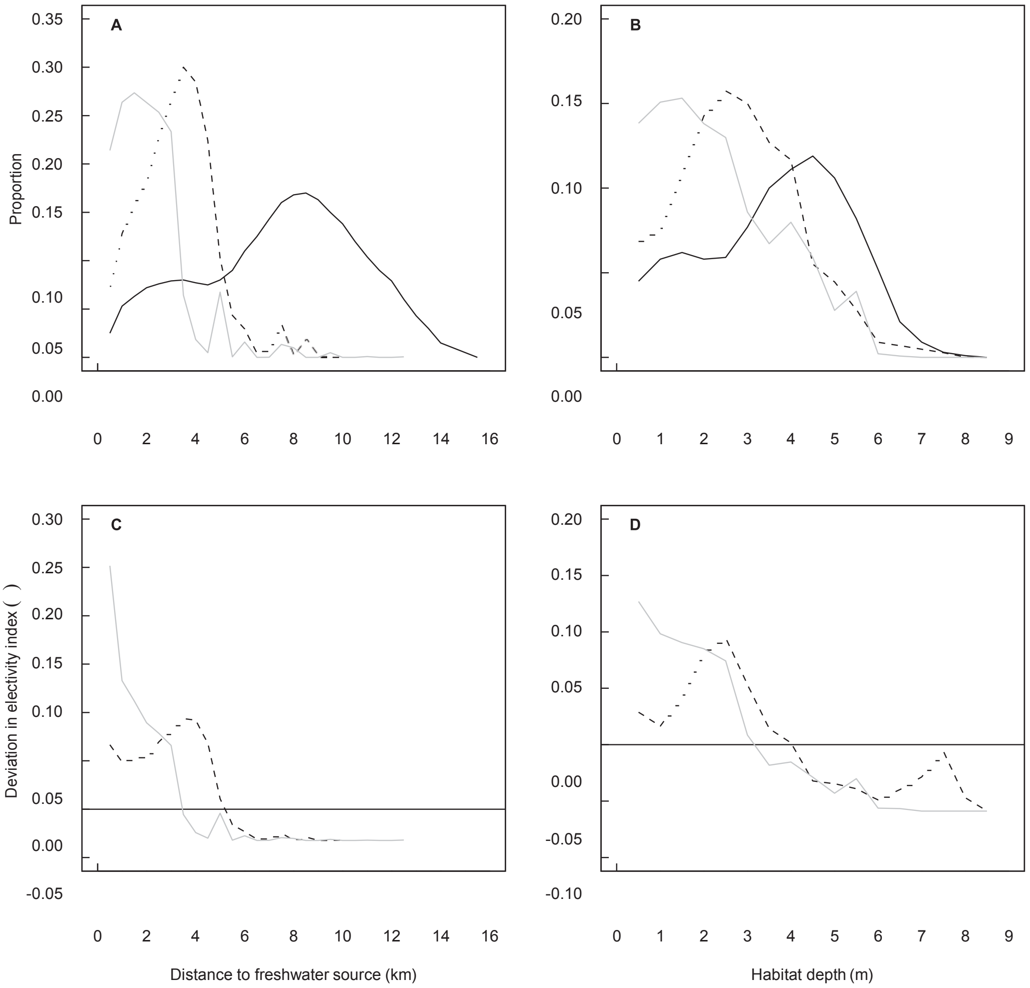

Figure 5.4. Use of habitats in relation to proximity to freshwater and depth. Proportion of available distances to freshwater sources (A) and habitat depths (B) available in Cleveland Bay (solid black lines) and the proportion of detections within the respective habitat attributes by *Hydrophis curtus* (broken black line) and *H. elegans* (solid grey line). Selection for freshwater (C) and depth (D) in *H. curtus* (broken black line) and *H. elegans* (solid grey line) with values >0 indicating affinity.

5.3.2. Diet

Regurgitate of captured individuals showed significantly different prey composition between the two species (Figure 5.5, Figure 5.6). *Hydrophis curtus* regurgitated at least four families of juvenile coastal fishes (Carangidae: *Caranx ignobilis, Parastromateus niger, Agnathadon speciosus*; Triacanthidae: *Tripodichthys* sp.; Leiognathidae: *Leiognathus* sp.; Gobiidae: *Amblygobius* sp.; Figure 5.5B),

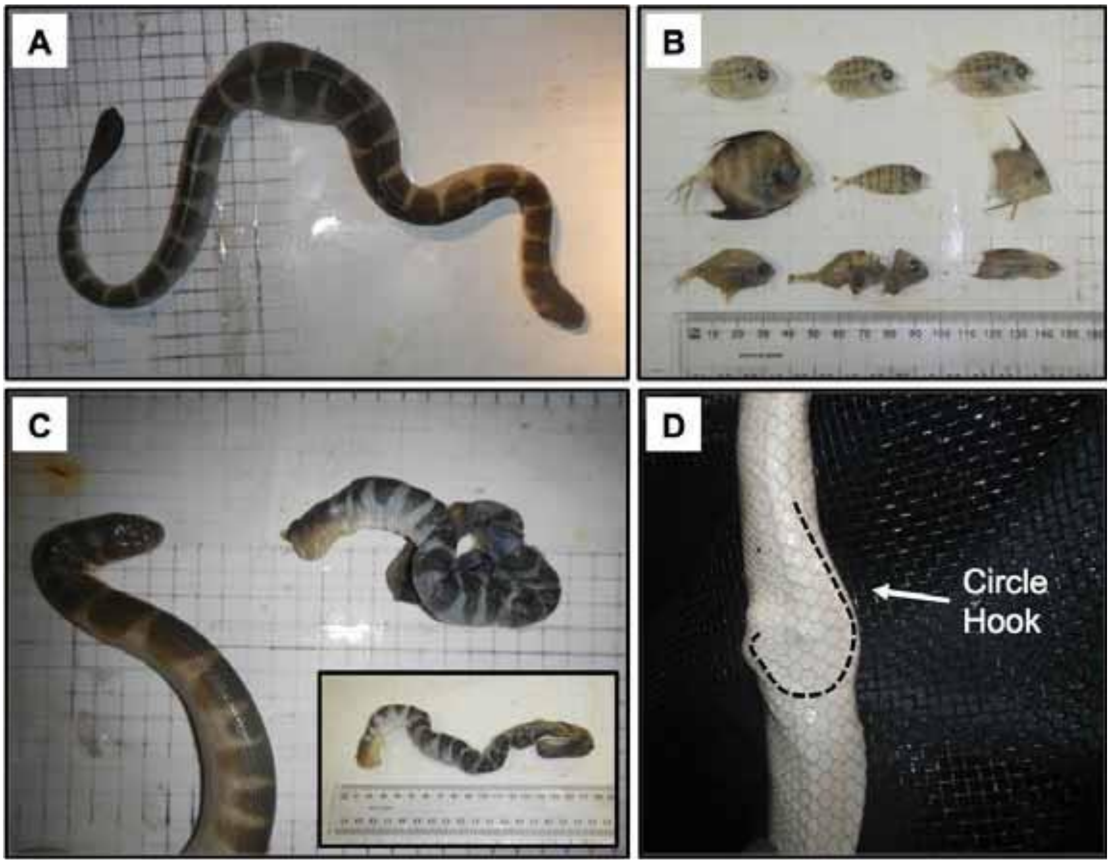

Figure 5.5. Examples of diet of *Hydrophis curtus* from regurgitated specimens from captured snakes. (A) *H. curtus* after capture with freshly caught prey in its stomach. (B) Regurgitated fish representing species targeted by *H. curtus* including *Caranx ignobilis, Parastromateus niger, Agnathadon speciosus, Tripodichthys* sp.*, Leiognathus* sp. and *Amblygobius* sp. (C) A juvenile *H. curtus* and regurgitated conspecific. (D) Example of an individual with a fishing hook in its stomach indicating *H. curtus* opportunistically takes fishing bait.

whereas regurgitate from *H. elegans* solely comprised snake eels (Ophichthidae; Figure 5.6B). A juvenile *H. curtus* (snout–vent length = 640.4 mm; estimated age = 1.27 years) regurgitated a juvenile conspecific (Figure 5.5C), 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 (Figure 5.5D), suggesting an opportunistic generalist diet.

Figure 5.6. (A) Example of diet composition of *Hydrophis elegans* from regurgitated specimens from captured snakes. (B) Examples of snake eels (Family Ophichthidae) regurgitated from *H. elegans* at different stages of digestion.

5.4. Discussion

Passive monitoring 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 on receiver stations on both sides of the bay, however 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 *Hydrophis curtus*, and seagrass and mudflat habitats by *H. elegans* as well as differences in diet suggest that sea snakes use these areas differently. As we have already seen in the previous chapter (Chapter 4.4.2.) this population in Cleveland Bay display a tidal−based pattern in short−term (daily) presence of *H. curtus* with the probability of presence in shallower habitats increasing with increased tidal reach. Kerford et al. (2008) and Wirsing and 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 tide. A similar combination of effects (i.e. predator−avoidance and increased prey abundance) likely governs the selection of seagrass habitats by the individuals examined here. 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 for sea snakes in vulnerable periods of their life (Voris & Jayne 1979, Voris 1985, 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 the most frequently encountered age classes were juveniles, with adults encountered in summer months during parturition periods (see Chapter 7). 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; inshore sandy habitats or HT3; fringing reef 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, Brischoux et al. 2012b, Liu et al. 2012). In Cleveland Bay, access to freshwater is available throughout the year and this may play an important role in why such habitats are important to sea snakes that utilize 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. Unfortunately in the present study, the battery life of tags (215 days) 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 *Hydrophis 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 dietary niche separation may allow the two species of sea snake to use similar habitats with reduced competition.

Previous literature on the diet of *Hydrophis 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 (Figure 5.5D) reflect anecdotal evidence from local recreational fisherman and previous research activity that this species opportunistically consumes bait (S. Moore, personal communication). 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* shortly after capture (Figure 5.5C). Although intraspecific predation is often considered infrequent, it occurs commonly in a range of animals including reptiles (Polis & Myers 1985). 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). Maternal or filial cannibalism has also been observed in a range of snake species, where mothers consume non−viable or underdeveloped offspring as a means of recycling energy to aid in maternal recovery, or increase the fitness of the surviving clutch (Lourdais et al. 2005, Mociño−Deloya et al. 2009). In the present study, the cannibalistic individual observed was a juvenile, therefore maternal cannibalism could be ruled out. A review of intraspecific predation in amphibians and reptiles by Polis and Myers (1985) concluded that cannibalism in reptiles is often a by−product of opportunistic predatory behaviours, especially in environments with a high density of conspecifics. 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. 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

5.5. Conclusions

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 crutial resources (e.g. shelter, prey), therefore any degradation or loss in the availability of this habitat may have dire consequences on the health of the 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). 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 habitats types. 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 the light of increasing natural and anthropogenic disturbances in coastal and nearshore environments (Bonnet et al. 2009, Elfes et al. 2013).

Chapter 6

Effects of seasonal water temperature on oxygen use, dive duration and field metabolic rate in sea snakes

6.1. Introduction

Energetic requirements are fundamental to the spatial ecology of free living animals (Cooke et al. 2004a, Wilson et al. 2015). Differences in energy requirements can produce significant variation in movement patterns and home ranges in reptiles (Carfagno & Weatherhead 2008, Lelievre et al. 2012). One environmental factor that often plays an important role in metabolic processes in reptiles is temperature (Dorcas et al. 2004, Dorcas & Willson 2009), therefore investigating how temperatures influence activity–associated metabolic rates can provide key information on movement ability. Energy expenditure in the form of aerobic metabolism can be indirectly measured in a laboratory setting using measurements of oxygen consumption rates ($\dot{V}o_2$, Nagy et al. 1999). While an understanding of the metabolic rates of animals in their natural environment is vital to gaining insight into patterns of spatial ecology, technical limitations often preclude $\dot{V}o_2$ measurements from free–roaming animals (Wilson et al. 2008).

Several 'proxies' have been employed to examine metabolic requirements of free–living animals including doubly labelled water, heart–rate sensors (electrocardiogram; ECG) and muscle sensors (electromyograms; EMG) (see Butler et al. 2004, Cooke et al. 2004b). Despite its relative simplicity and low cost, the doubly labelled water method only reliably provides a single mean estimate of $\dot{V}o_2$ over a limited temporal period. The ECG method makes use of the direct association between blood flow and oxygen transport and estimates $\dot{V}\mathrm{o}_2$ by measuring the heart rate of individuals (Clark et al. 2010), while the EMG method provides a less−direct proxy and uses measures of voltage in active muscles to estimate $\dot{V}\mathrm{o}_2$ (Cooke et al. 2004b). Both these methods use small implantable data loggers or telemetry devices that can provide long−term data over fine temporal scales. Those techniques, however, often require complex surgical procedures to implant electrodes and data logging devices that typically need to be retrieved on completion of the experiment (Butler et al. 2004). More recently, the use of animal−borne accelerometers to measure body acceleration has been used as an alternative that provides similar long−term, fine scale data on metabolic rates in the wild (Gleiss et al. 2010, Halsey et al. 2011a). Since movement related energy expenditure in animals results in some form of acceleration, measures of body acceleration can serve as a proxy for activity associated metabolic rates (Halsey et al. 2009a). Estimation of field metabolic rates using accelerometry has provided useful information relating to energetic requirements of a range of animals including mammals (Halsey et al. 2008, Shepard et al. 2008, Halsey et al. 2009b), birds (Wilson et al. 2006, Halsey et al. 2011b, Elliott et al. 2013) and fish (Whitney et al. 2007, Gleiss et al. 2009, Murchie et al. 2011, O'Toole et al. 2011, Payne et al. 2011, Wilson et al. 2012), but thus far has not been applied to sea snakes. Body acceleration and metabolic data can also provide useful insights into diving and movement patterns and be used to explore the effect of environmental variables on the spatial ecology of sea snakes.

Air−breathing marine animals often use different diving strategies to minimise predation risk at the surface (Lima & Dill 1990, Heithaus & Frid 2003). These strategies are based on the premise that proximity to the surface increases an individuals' vulnerability to aerial or aquatic predation. Therefore, in theory individuals can minimise predation risk by maximising dive durations, however this would require individuals to remain at the surface for longer periods to replenish the oxygen debt from long dives. A second strategy would involve short, shallow dives with individuals spending the majority of their time at shallower depths, frequently surfacing but for shorter intervals (Heithaus & Frid 2003, Pratt & Franklin 2009). Individuals are likely to shift between these strategies depending on a range of biotic and abiotic factors including water temperature and metabolic requirements to minimise exposure to potential predators. Differences in dive behaviours at different temperatures may suggest that metabolic requirements play a major role in selecting surfacing strategies and diving behaviours to minimise predation risk.

Sea snakes, like many other aquatic reptiles, respire bimodally and have displayed the ability to uptake a large proportion of their oxygen requirements cutaneously (Graham 1974). Increased dive durations in cooler waters may mean that animals deplete oxygen stores within their lungs quickly and may have to rely on cutaneous respiration to compensate (Heatwole & Seymour 1976). Many bimodally respiring diving animals display up−regulation of cutaneous oxygen uptake (up to 100% in the freshwater turtle *Elseya albagula*) to prolong dive durations, either due to environmental conditions or under stress (Mathie & Franklin 2006). The capacity to uptake oxygen cutaneously varies considerably between different species of aquatic snakes (Heatwole & Seymour 1975, Heatwole & Seymore 1978, Pratt & Franklin 2010). For example, file snakes (e.g., *Acrochordus granulatus, A. arafurae*) display very low metabolic rates which potentially allows for long dive times (Heatwole &

Seymour 1975), however the ability to respire cutaneously has been shown to increase dive durations up to 30% (Pratt et al. 2010). Cutaneous respiration in a range of true sea snakes was observed by Heatwole and Seymour (1975) with individuals acquiring up to 22% of their total oxygen via cutaneous means (at 25˚ – 27˚C). Graham (1974) previously recorded higher cutaneous oxygen uptake rates in the pelagic sea snake (*Hydrophis platura*, previously *Pelamis platura*), with individuals meeting up to 33% of their oxygen requirements via cutaneous respiration (at 26˚ – 28˚C). The authors of these studies acknowledged that water temperature played an important role in metabolic and oxygen consumption rates, but did not test how changes in temperature may affect oxygen uptake and energy requirements.

In this chapter, I examined how environmental factors can affect metabolic rates and use animal−borne accelerometer transmitters to estimate field metabolic rates in two sea snake species; addressing the third aim of the overall thesis (Aim 3:). The estimation of field metabolic rates in individuals was completed by first establishing a relationship between body acceleration and $\dot{V}O_2$ using bimodal respirometry. This chapter is divided into laboratory and field components. The laboratory component used respirometry techniques to: (a) explore how water temperature affects diving behaviours, pulmonary and cutaneous oxygen uptake in sea snakes and, (b) use the measured total metabolic rates and acceleration data to establish individual− and species−level calibration relationships between body acceleration and $\dot{V}O_2$. The field component: (a) used the calibration relationships to estimate field metabolic rates in free swimming sea snakes within Cleveland Bay, and (b) examined patterns in estimated field metabolic rates over diel and seasonal scales.

6.2. Methods

6.2.1. Collection, tagging and holding conditions

Two species of sea snake (spine−bellied sea snake, *Hydrophis curtus* and elegant sea snake, *H. elegans*) were collected from wild populations within Cleveland Bay (see Chapter 4.2.1. for description of field site). Individuals were located at night using spotlights and captured from the surface of the water using dip nets. Once captured, the snout−vent length (SVL) and mass of each snake were recorded, and each individual was fitted with a passive integrated transponder (PIT) tag for future identification. Twenty−two individuals (*Hydrophis curtus*, *n* = 12 and *H. elegans*, *n* = 10) in visibly healthy condition and large enough to be implanted with a transmitter were secured within breathable catch bags and transported to the National Sea Simulator facility (SeaSim) at the Australian Institute of Marine Science (AIMS) in Townsville. Once at AIMS, snakes were housed within individual holding tanks supplied with flow−through seawater at ambient temperature (27 ± 2˚C). Lighting within the laboratory was set on a 12:12 h day:night cycle to mimic local conditions at the time of experiments.

Individuals were allowed 3 – 4 days to acclimate to holding tanks and to digest any food they may have eaten prior to capture, after which they were surgically implanted with a tri−axial accelerometer acoustic transmitter (Vemco. Ltd., Model V9AP−2H, 69 kHz). Implantation of transmitters was similar to that previously reported in Chapter 4.2.2. Transmitters were small (3.3 g in water, 46 mm length, 9 mm diameter) and less than 2% of the body mass of the tagged snakes (*mean ± se*; 1.40 ± 0.19%). Each transmitter was uniquely coded, alternately transmitted measurements of depth (m) and acceleration (m s^{-2}), and had a battery life of approximately 38 days. Acceleration data were transmitted on a pseudorandom repeat every 19 – 21 s and were sampled at 5 Hz for a period of 16 s every second transmission cycle. Acceleration data were calculated as an average root mean square (RMS) value representing the vectorial dynamic body acceleration (*V*DBA; Qasem et al. 2012) from all three axes (RMS = [illegible]) over each sampling period and ranged between 0 – 3.465 m s^{-2} (resolution 0.014 m s^{-2}). A high pass filter was used to remove the static contribution to overall acceleration measurements prior to calculations of RMS.

Snakes were given 4 – 5 days to recover in their holding tanks after surgery, during which time they were observed at least once per day. Animals were given access to freshwater daily and were fasted during the recovery period to reduce any influence of digestion on measurements of oxygen consumption rates ($\dot{V}o_2$). The collection and holding of sea snakes were staggered, to only have a maximum of eight individuals at the facility at any one time. Staggered collection ensured that individuals were held for a maximum of three weeks before being released at their location of capture. Acoustic transmitters remained within individuals after release to allow collection of acceleration data from the field.

6.2.2. Respirometer design

Respirometry was conducted in the same room in which snakes were held. Four bimodal respirometer chambers were constructed in an L–shaped arrangement based on designs previously reported by Dabruzzi et al. (2012), which allowed simultaneous measurements of cutaneous and pulmonary oxygen uptake rates of sea snakes ($\dot{V}o_{2cut}$ and $\dot{V}o_{2pul}$, respectively; Figure 6.1). Four L–shaped chambers (height 165 cm, width 80 cm) were constructed using transparent acrylic tubing (150 mm outer diameter) and opaque Polyvinyl chloride connector fittings. Chambers were airtight and held a fixed amount of water (29.73 ± 0.61 L) with a fixed air space (1.05 ± 0.03 L) at the top to capture acceleration movements related to diving and surfacing. Chambers were large enough to allow snakes free movement, but small enough to accurately quantify $\dot{V}\mathrm{o}_{2\mathrm{cut}}$. All four chambers were submerged in a large water bath such that only the top 30 cm extended above the water level, and water temperatures were precisely regulated (± 0.1˚C) by external flow−through systems. Air temperature was also precisely regulated (± 0.1˚C). Both water and air temperatures were monitored continuously (0.5 Hz) with thermocouples (Firesting, PyroScience, Germany). A VR2W acoustic receiver was placed in the water bath adjacent to the chambers to record transmitted signals from acoustic transmitters. Data from acoustic transmitters were also continuously monitored using an omnidirectional hydrophone (VH165, Vemco Ltd.) placed in the water bath to a VR100 acoustic receiver (Vemco Ltd.). Both the VR100 and VR2W systems were used simultaneously to ensure all detection data was recorded from tagged individuals, and as a backup, incase one or the other system failed.

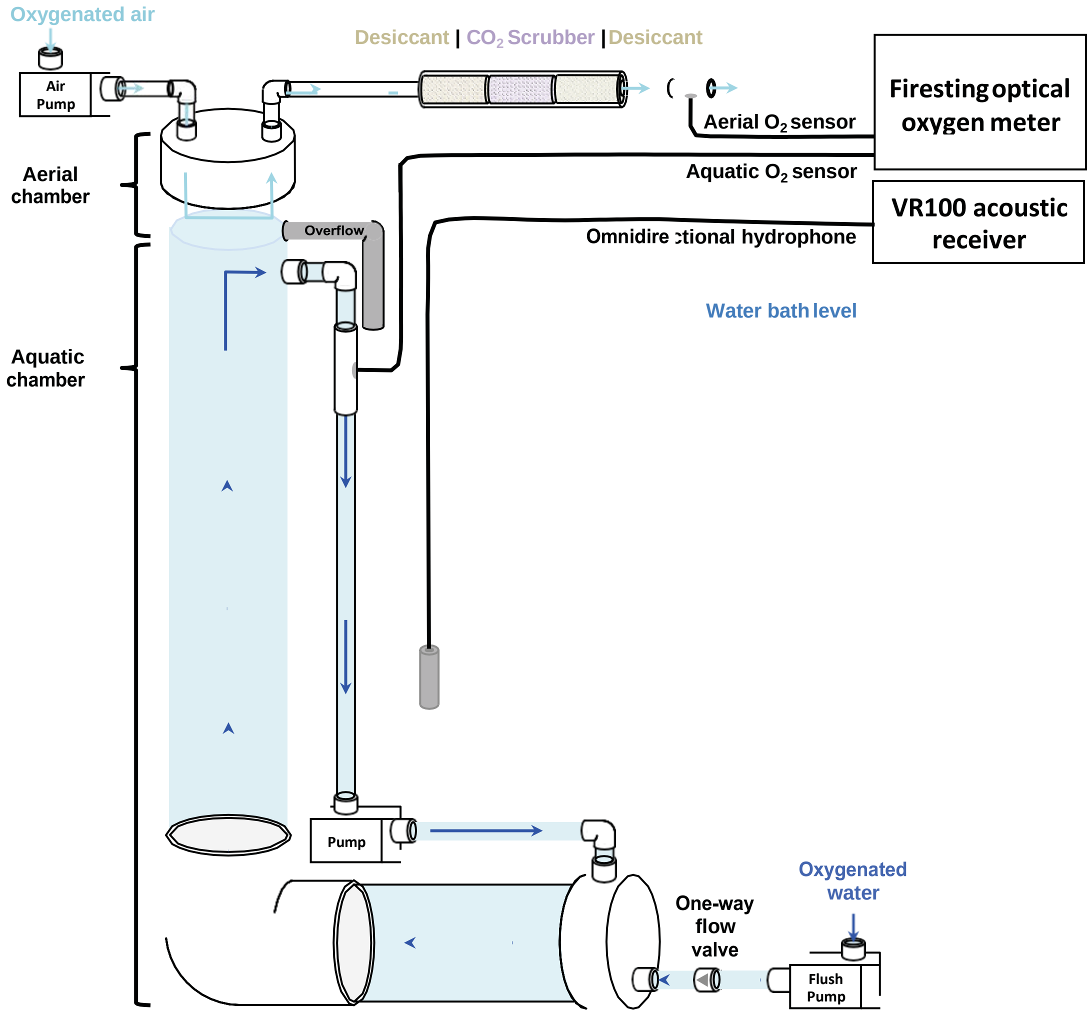

Figure 6.1. Schematic of bimodal respirometry chamber designed to measure oxygen uptake by sea snakes through pulmonary and cutaneous means simultaneously (based on designs previously described by Dabruzzi et al. 2012). Four chambers (height 165 cm, width 80 cm) were constructed using transparent acrylic tubing (150 mm outer diameter) and opaque Polyvinyl chloride connector fittings. Chambers were airtight and held a fixed amount of water (29.73 ± 0.61 L) with a fixed air space (1.05 ± 0.03 L) at the top to capture movements related to diving and surfacing.

Cutaneous oxygen uptake was measured using a static intermittent−flow system, using best practice techniques outlined in Clark et al. (2013). An inline submersible pump recirculated water through a loop in each respirometer to ensure homogeneous oxygen levels throughout the water volume. Temperature−corrected oxygen concentration (mg L^{-1}) was measured continuously (0.5 Hz) in the recirculation loop using optical oxygen sensors and contactless spots (Firesting, PyroScience, Germany; Figure 6.1). An automated flush pump refreshed the water in respirometers for 30 minutes every 60 minutes, with excess water flowing out of an overflow positioned at the air−water interface. $\dot{V}o_{2cut}$ was calculated from the decline in oxygen concentration of respirometer water between flush cycles (Figure 6.2). Gas exchange between the aerial and aquatic media within each chamber was tested before the commencement of experiments by filling respirometers with deoxygenated seawater and measuring any change in oxygen concentration in the air and water over a sealed cycle of approximately 1 h. Oxygen readings in the water during these cycles showed insignificant levels of increase toward ambient levels, indicating that gas exchange across the air−water interface was negligible.

Pulmonary oxygen uptake was measured via the air space at the top of each respirometer using a positive−pressure flow−through system (Figure 6.1). An air pump was used to pump fresh, oxygenated air through the air space of each chamber at a constant flow rate (7.89 ± 0.21 ml s^{-1}). The air subsequently passed through drying columns filled with a chemical desiccant (Drierite®; $CaSO_4$) and an aggressive CO_2 scrubber (Ascarite II®; NaOH) before oxygen concentration

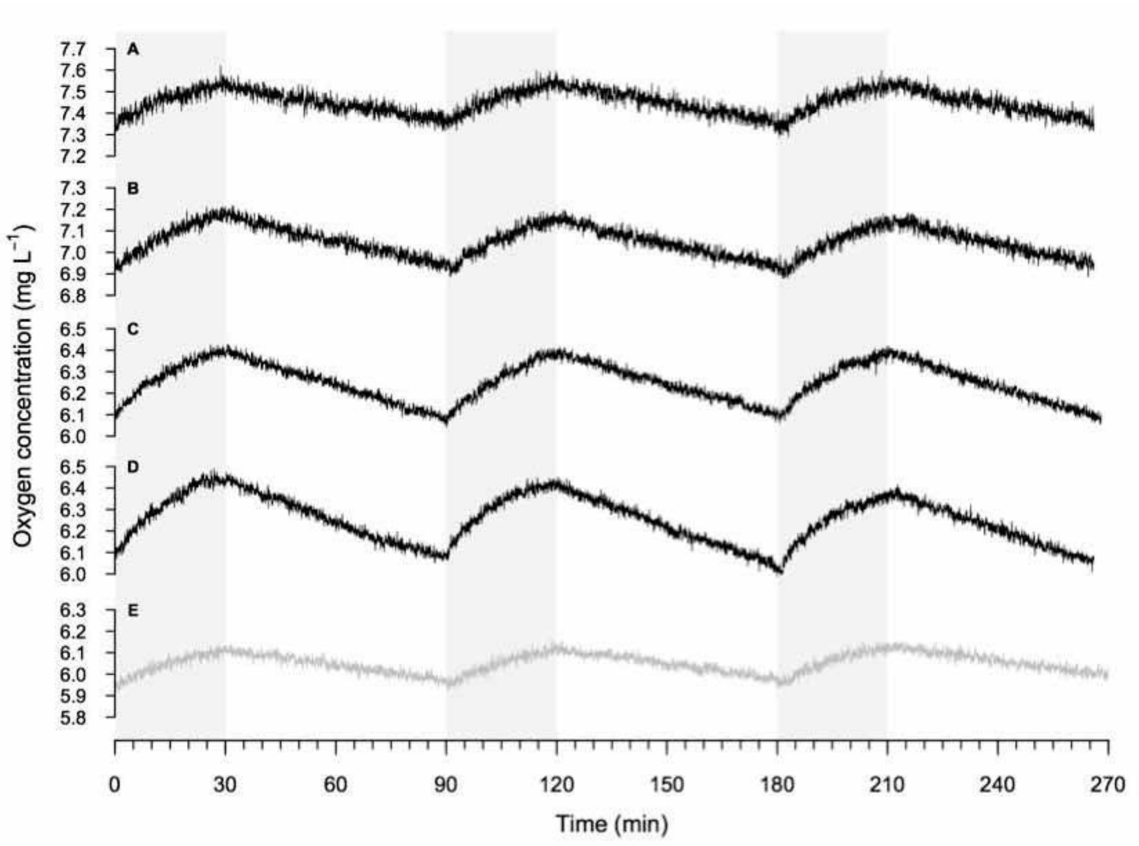

Figure 6.2. Raw oxygen traces for a representative individual testing the cutaneous oxygen consumption of sea snakes at four temperature treatments (A) 21˚, (B) 24˚, (C) 27˚ and (D) 30˚C. A background trace at 30˚C is also represented (E), which was used to account for background metabolic rates due to microbial activity in the seawater. Background measurements were made for all temperature treatments but only the 30˚C trace is represented in this figure. Grey background represents periods when flush pumps were running.

was measured at 0.5 Hz using a second Firesting system. As in Heatwole and Seymour (1975), individual breathing bouts of snakes were clearly identifiable on the recorded trace (Figure 6.3A−D). Fixed volumes (5, 10, 20, 40 ml) of inert gas (N_2) were regularly injected into the air space between breathing bouts to assist with calculating the volume of oxygen consumed by the snake during each breathing bout (Figure 6.3E−H).

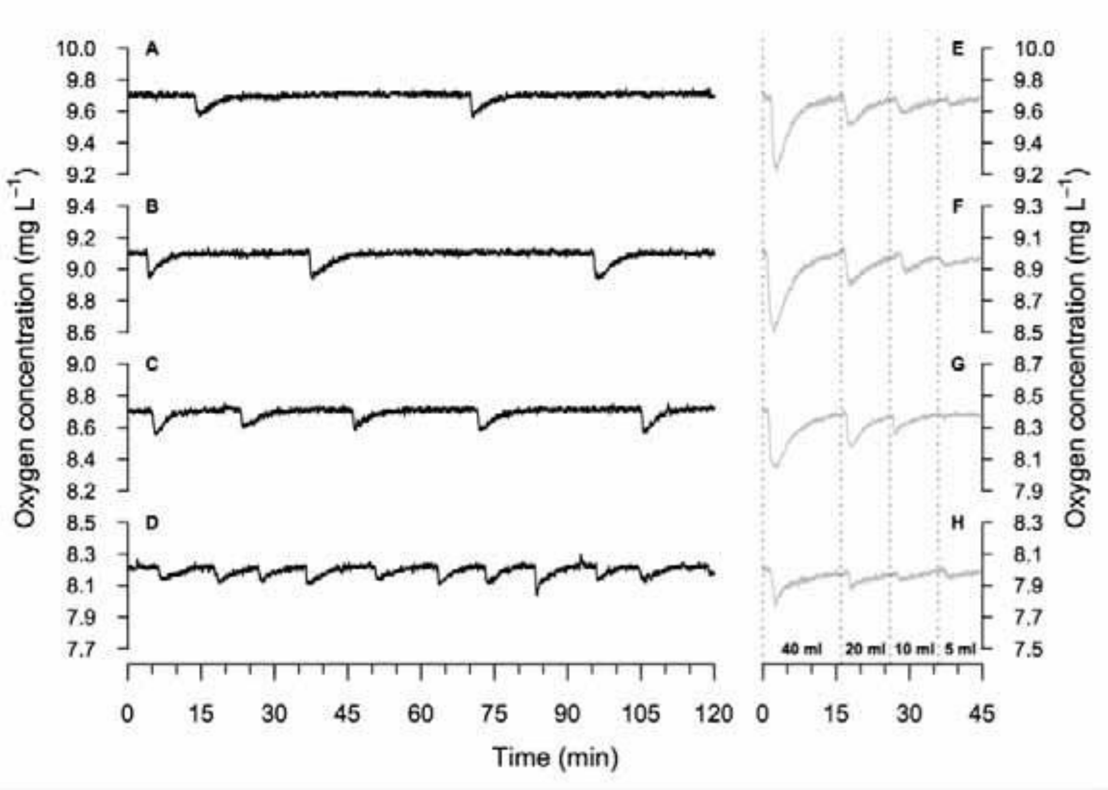

Figure 6.3. Raw oxygen traces for a representative individual testing the pulmonary consumption of oxygen at four temperature treatments; (A) 21˚, (B) 24˚, (C) 27˚ and (D) 30˚C. Each drop in oxygen concentration along the trace represents one breathing bout, with individuals having an increased breathing rate in warmer waters. Fixed volumes of N_2 (40, 20, 10 and 5 ml) were also injected during periods between snake breathing bouts and the associated traces were recorded (E – H). These traces were used to calculate the volume of oxygen consumed during each breathing bout.

6.2.3. Experimental protocol

The pulmonary and cutaneous oxygen uptake from each individual was recorded over four water temperature treatments (21, 24, 27 and 30˚C) that encompassed conditions sea snakes experience in their natural environment. During each treatment, the air temperature was adjusted to 3 – 4˚C below the water temperature to reduce condensation within the flow−through aerial system and avoid saturating the desiccant within the drying columns. Individuals were placed within respirometer chambers for at least 12 hours prior to the start of the experimental trials to acclimate to chambers and water temperature. Measures of oxygen uptake were recorded over a period of 24 hours for each temperature treatment, after which the water temperature was adjusted at a rate of ~2˚C h^{-1} to reach the next treatment temperature. Individuals were allowed an hour to acclimate to the new temperature before recordings commenced to ensure that body temperatures reached equilibrium with water temperature. All individuals from both species were tested over all four water temperature treatments, with temperatures stepped sequentially up or down to avoid extreme changes in temperatures between treatments. Respirometer chambers were run empty once before and once after each batch of snakes to record any background microbial respiration in the water and any potential drift in oxygen sensor probes. Between each batch of experiments, chambers were removed from the water bath, cleaned and flushed with freshwater to reduce excessive microbial growth.

The consumption of oxygen by four of the 22 individuals (three *Hydrophis curtus* and one *H. elegans*) was measured once before, and once after the surgical procedure at all four temperature treatments to test if tag insertion had an effect on oxygen consumption rates and general activity patterns.

6.2.4. Calculation of oxygen consumption metrics

Several metrics related to the consumption of oxygen and diving performance of sea snakes were calculated using the recorded oxygen traces in the experimental setup. The cutaneous oxygen uptake rate ($\dot{V}o_{2cut}$; $mlO_2\ min^{-1}$) was calculated during each sealed cycle of the respirometers according to:

(Eq: 6.1) $$\dot{V}o_{2cut} = [(V_w - V_s) \times \Delta Co_2] \text{ ƒ } \Delta t$$

where V_w is the volume of water within the respirometer, V_s is the volume of the snake (where it was assumed that 1 g of snake displaced 1 ml of water), ΔCo_2 is the change in oxygen concentration in the respirometer water, and Δt is the change in time during which ΔCo_2 is measured.

Pulmonary oxygen uptake ($\dot{V}o_{2pul}$; $mlO_2 \, min^{-1}$) was calculated for each breathing bout according to Frappell et al. (2002) as:

(Eq: 6.2) $$\dot{V}o_{2pul} = flow' \times (F'IO_2 - F'EO_2) \text{ ƒ } (1 - F'IO_2)$$

where $F'IO_2$ and $F'EO_2$ are the fractional oxygen concentrations of incurrent and excurrent air, respectively ($F'IO_2$ was taken immediately prior to the breathing bout, and $F'EO_2$ was calculated as the mean oxygen concentration across the duration of the breathing bout). These data were standardised to the length of the breathing bout, then divided by the time since the last breathing bout to calculate average $\dot{V}o_{2pul}$ per unit time. Measures of $\dot{V}o_{2pul}$ and $\dot{V}o_{2cut}$ were then summed to provide total oxygen consumption values ($\dot{V}o_{2tot}$) for each individual at all four temperature treatments. Temperature coefficients (Q_{10}) were then calculated for each individual using the following equation (Dabruzzi et al. 2012):

(Eq: 6.3) $$Q_{10} = (K_2 \text{ ƒ } K_1)^{10 \text{ ƒ } (T2 - T1)}$$

where K_1 is mean $\dot{V}o_{2tot}$ at the lowest temperature treatment (T1; 21˚C), and K_2 is mean $\dot{V}o_{2tot}$ at the highest temperature treatment (T2; 30˚C).

The time between breathing bouts was used to calculate surfacing rate (S_r; breathing bouts h^{-1}). The volume of air consumed during each breathing bout was calculated using the oxygen traces recorded and comparing them with the traces from the N_2 injections of known volumes (Figure 6.3). Linear models were created to represent the relationship between the known volumes of N_2 injected and the resulting degree of deviation from the baseline trace for each respirometer and at each temperature treatment. The resulting relationship was used to calculate the volume of oxygen consumed at each breathing bout (V_B; ml bout^{-1}) using the recorded oxygen traces of tested sea snakes.

The effects of temperature on oxygen consumption and diving performance of both species were tested using calculated metrics. Values of $\dot{V}\mathrm{o}_{2\mathrm{pul}}$, $\dot{V}\mathrm{o}_{2\mathrm{cut}}$, S_r and V_B were compared between temperature treatments using generalised linear mixed models (GLMMs) with mass of the individual as a covariate to account for its potential influence and the individual ID as a random factor to account for the repeated measures nature of the data. Oxygen consumption values (both $\dot{V}\mathrm{o}_{2\mathrm{cut}}$ and $\dot{V}\mathrm{o}_{2\mathrm{pul}}$) were compared before and after tagging in four individuals to test for potential influence of surgical procedures using *t*−tests ($\alpha = 0.05$).

6.2.5. Laboratory acceleration calibration

Measurements of body acceleration coupled with respiration data from laboratory experiments were used to create individual− and species−level calibration curves relating measured body acceleration with metabolic rates. Measures of body acceleration (m s^{-1}) obtained during respirometry experiments as well as total mass−specific oxygen consumption rate ($\dot{V}\mathrm{o}_{2\mathrm{tot}}$; $\mathrm{mlO_2\ min^{-1}\ kg^{-1}}$) were binned to hourly average values. Linear models were used to explain individual−level relationships between body acceleration and total oxygen uptake at the four temperature treatments for all individuals that provided enough data to formulate robust relationships. Data from these individuals were also pooled to create species−level calibration curves at the four temperature treatments. Species−level calibration curves were used for individuals or temperature treatments where enough acceleration or oxygen consumption data were not available to create accurate individual−level linear models.

6.2.6. Field acceleration measures and estimated metabolic rates

The 22 individuals captured for laboratory experiments were subsequently released back into Cleveland Bay in the location of their capture with acceleration tags still operational. This allowed for collection of acceleration data from sea snakes in their natural environment via acoustic receiver monitoring. Calibration curves formulated for individuals were used to estimate the metabolic rates of sea snakes in the field using acceleration data obtained post−release. In addition to the 22 individuals captured for laboratory measurements, six additional individuals were fitted with accelerometer transmitters in the field following methodology outlined in Chapter 4.2.2. to obtain acceleration data from individuals not kept in captivity. Tag and release procedures for these individuals lasted between 20 – 40 minutes with minimal handling stress. Field acceleration data from individuals captured for laboratory experiments were compared to individuals tagged in the field using a *t*−test to assess if captive holding and experimental procedure had any significant effect on field acceleration values.

Acceleration data from released sea snakes were recorded using an array of 63 acoustic receivers (VR2 and VR2W, Vemco Ltd.) placed within Cleveland Bay (previously described in Chapter 4.2.1.). AIMS weather buoys (described in Chapter 4.2.2.) provided water temperature data within the bay during field measurements that were applied to the appropriate individual−level calibration curve (i.e. closest temperature treatment; ± 1.5˚C) to estimate metabolic rates. Patterns in estimated field metabolic rates were explored: (a) over a diel period to examine changes in metabolic rates between day and night and (b) over the entire monitoring period to examine changes in metabolic rate from the start of the monitoring period (cooler dry season) to the end (warmer wet season).

6.3. Results

6.3.1. Temperature effects on dive behaviours and metabolic rates

Twenty−two individuals from two species (*Hydrophis curtus*, *n* = 12 and *H. elegans*, *n* = 10) were held in captivity and monitored within respirometers (Table 6.1). Measurements of surfacing metrics in the laboratory showed a clear temperature effect on diving behaviours in sea snakes. Individuals of both species displayed reduced surfacing rates at lower temperatures (21˚C; *Hydrophis curtus*: 1.6 breathing bouts h^{-1}; *H. elegans*: 2.7 breathing bouts h^{-1}) with long dive durations (*H. curtus*: 36.8 ± 1.1 min, max = 152.5 min; *H. elegans*: 24.5 ± 0.6 min, max = 93.6 min). In warmer temperatures, individuals of both species displayed higher surfacing rates (30˚C; *H. curtus*: 4.5 breathing bouts h^{-1}; *H. elegans*: 5.6 breathing bouts h^{-1}) with shorter dive durations (*H. curtus*: 10.7 ± 0.1 min, max = 34.7 min; *H. elegans*: 10.4 ± 0.1 min, max = 37.2 min). Surfacing rates of the smaller *H. curtus* (snout−vent length: 470 – 1086 mm; mass: 120 – 940 g) tended to be more frequent than those of the larger *H. elegans* (snout−vent length: 1058 – 1738 mm; mass: 315 – 1755 g) at all four temperature treatments, however not significantly so ($p > 0.05$ for all comparisons, Figure 6.4A). Generalised linear mixed models showed both species had significantly increased surfacing rates with increasing temperature (*H. curtus*: $p < 0.001$; *H. elegans*: $p < 0.001$) when mass was factored into models.

Experimental measurements also showed that the volume of oxygen consumed by individuals at each breathing bout were constant with no significant difference between temperature treatments (Figure 6.4B; GLMM: *H. curtus*: 29.5 ± 15.9 ml bout^{-1}, $p = 0.76$; *H. elegans*: 18.9 ± 9.4 ml bout^{-1}, $p = 0.34$). This suggests that despite displaying more frequent surfacing rates, individuals of *H. curtus* compensate by consuming large volumes of oxygen per breath to maintain longer dive durations than *H. elegans*.

Table 6.1. Summary of morphometrics and detection patterns of sea snakes. Laboratory calibration temperatures for each individual are listed with full individual−level calibration equations presented in Appendix 6.1. Oxygen consumption of four individuals in bold (*) were measured before and after surgical implantation of transmitters. Six individuals in italics (**) fitted with transmitters in the field to assess the effect of captivity on field acceleration measurements. Lab−based oxygen measurements and individual−level calibration curves were not constructed for these individuals therefore; species−level calibration curves were used to estimate oxygen consumption. Estimated mean daily field metabolic rate (± SE) is also provided for individuals where sufficient field acceleration data were available.

Species	**Tag code**	**Snout-vent length (mm)**	**Body mass (g)**	**Laboratory calibration temperatures**	**Temperature coefficient (Q_{10})**	**Number of days detected in Cleveland Bay**	**Total number of detections in Cleveland Bay**	**Estimated mean daily field metabolic rate ($mlO_2\ min^{-1}\ kg^{-1}$)**
Hydrophis curtus (Spine−bellied sea snake)	LC1	523	140	21, 24, 27, 30	2.86	-	-	-
	LC2	531	120	21, 27, 30	1.94	18.6	448	3.91 ± 0.19
	LC3	522	165	21, 24, 27, 30	3.33	-	-	-
	LC4	531	125	21, 27, 30	1.36	-	-	-
	LC5	659	137	21, 27, 30	3.61	0.1	2	3.12
	LC6	501	141	21, 24, 27, 30	3.59	18.7	449	4.31 ± 0.16
	LC7	597	169	21, 24, 27, 30	3.01	-	-	-
	LC8	470	200	21, 24, 30	2.00	-	-	-
	LC9*	636	185	21, 24, 27, 30	2.10	9.1	220	3.76 ± 0.12
	LC10*	559	300	21, 24, 27, 30	2.61	0.1	3	4.10
	LC11	617	175	21, 24, 27, 30	1.86	7.3	177	3.95 ± 0.01
	LC12*	586	230	21, 24, 27, 30	2.09	24.9	598	3.37 ± 0.22
	*LC13***	1086	940	-	-	8.9	215	3.82 ± 0.21
Hydrophis elegans (Elegant sea	HE1	1254	560	21, 27, 30	1.76	-	-	-
	HE2	1265	525	21, 27, 30	1.60	23.2	557	3.04 ± 0.29

snake)	HE3	1291	455	21, 27, 30	3.27	25.0	601	3.16 ± 0.15
	HE4	1090	315	21, 24, 27, 30	2.28	17.1	412	4.54 ± 0.07
	HE5	1210	480	21, 24, 27, 30	3.17	3.5	84	2.77 ± 0.23
	HE6	1128	385	21, 24, 27, 30	2.47	8.0	194	3.36 ± 0.28
	HE7	1738	1755	21, 24, 27, 30	2.59	21.9	526	3.61 ± 0.25
	HE8*	1329	680	21, 24, 27, 30	2.90	6.2	150	3.69 ± 0.23
	HE9	1058	320	21, 24, 27, 30	3.01	0.1	2	3.44
	HE10	1680	1075	21, 24, 27, 30	1.66	1.0	23	3.67 ± 0.21
	*HE11***	1341	755	-		6.3	151	3.42 ± 0.31
	*HE12***	1364	985	-		28.8	692	2.98 ± 0.08
	*HE13***	1227	385	-		11.3	272	3.69 ± 0.49
	*HE14***	1245	490	-		-	-	-
	*HE15***	1435	635	-		9.9	239	2.53 ± 0.09

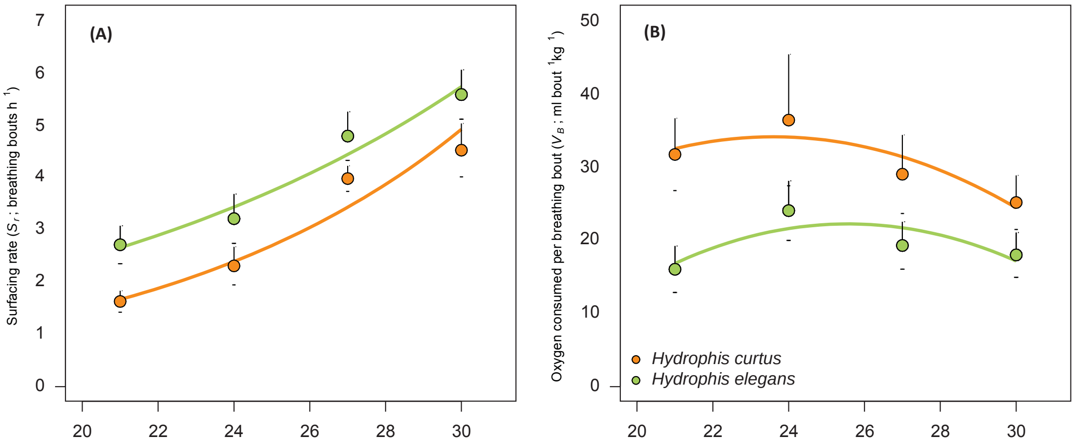

Figure 6.4. Experimental measurements of dive behaviours of *Hydrophis curtus* (orange) and *H. elegans* (green) showing (A) an increased surfacing rate with increased water temperature while (B) relatively constant volumes of oxygen were consumed per breathing bout across temperatures. Mean values displayed with standard error bars.

Laboratory measurements of pulmonary and cutaneous oxygen consumption by sea snakes also showed a clear increasing pattern with temperature (Figure 6.5). Consumption of oxygen though pulmonary means significantly increased with increased water temperature (Figure 6.5; GLMM: *H. curtus*: $p < 0.001$, *H. elegans*: $p < 0.001$). However, the consumption of oxygen though cutaneous means remained relatively constant with no significant difference between temperature treatments (GLMM: *H. curtus*: $p = 0.71$, *H. elegans*: $p = 0.32$) despite reduction in oxygen tension in the water with increasing temperature. Temperature coefficient values (Q_{10}) for both species were similar with total metabolic rates increasing about 2.5 times with every 10˚C increase in water temperature (Q_{10}; *H. cutrus:* 2.51 ± 0.23, *H. elegans*: 2.47 ± 0.19). Consumption of oxygen in four individuals tested before and after tag implantation revealed no significant difference in the rate of oxygen consumption via either pulmonary (*t*–test: $t = -1.65$, $p = 0.09$) or cutaneous means (*t*–test: $t = -1.17$, $p = 0.08$) suggesting acclimation and recovery periods after surgical procedures were

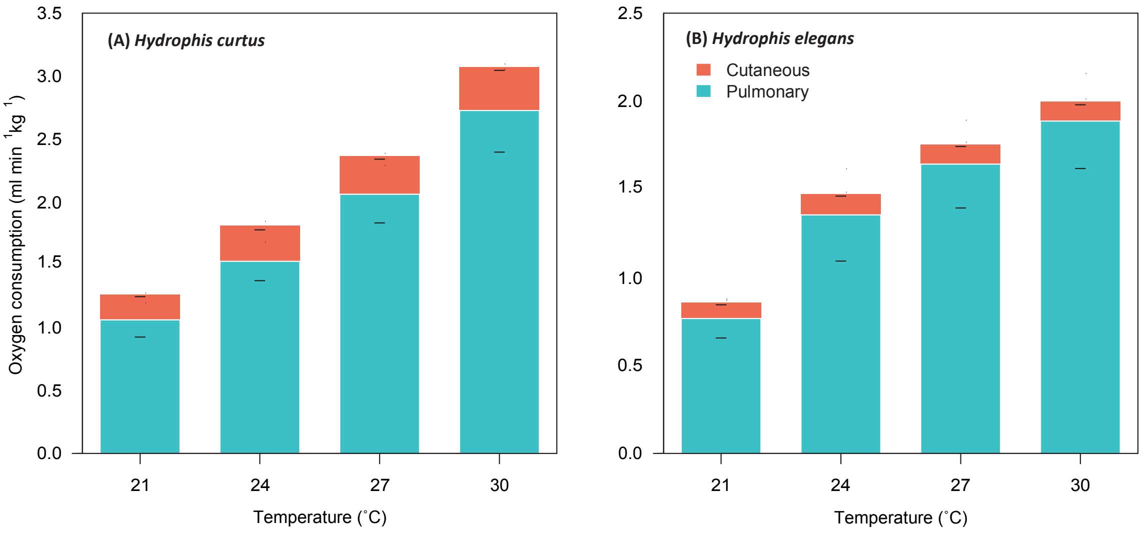

Figure 6.5. Patterns in mean oxygen consumption with standard errors through pulmonary (blue bars) and cutaneous (red bars) means by (A) *Hydrophis curtus* and (B) *H. elegans* across the four temperature treatments.

sufficient for respiratory behaviour to return to normal prior to measurement of oxygen consumption within respirometers.

6.3.2. Laboratory acceleration calibration

Measurements of body acceleration during respirometry experiments showed *Hydrophis curtus* displayed the full range of acceleration values measured by the acceleration tags (0 – 3.5 m s^{-1}), however *H. elegans* displayed lower body acceleration values within respirometers (0 – 1.9 m s^{-1}; Figure 6.6). Despite the range of acceleration values measured in tested individuals, no significant difference was found in laboratory acceleration values between day and night (*H. curtus:* t = −1.6, p = 0.09; *H. elegans:* t = 1.7, p = 0.1). Measurements of mean mass specific metabolic rate in *H. curtus* and *H. elegans* were similar between species and increased with increasing water temperature (*H. curtus*: 21˚C = 1.18, 24˚C = 1.76, 27˚C = 2.33, 30˚C =

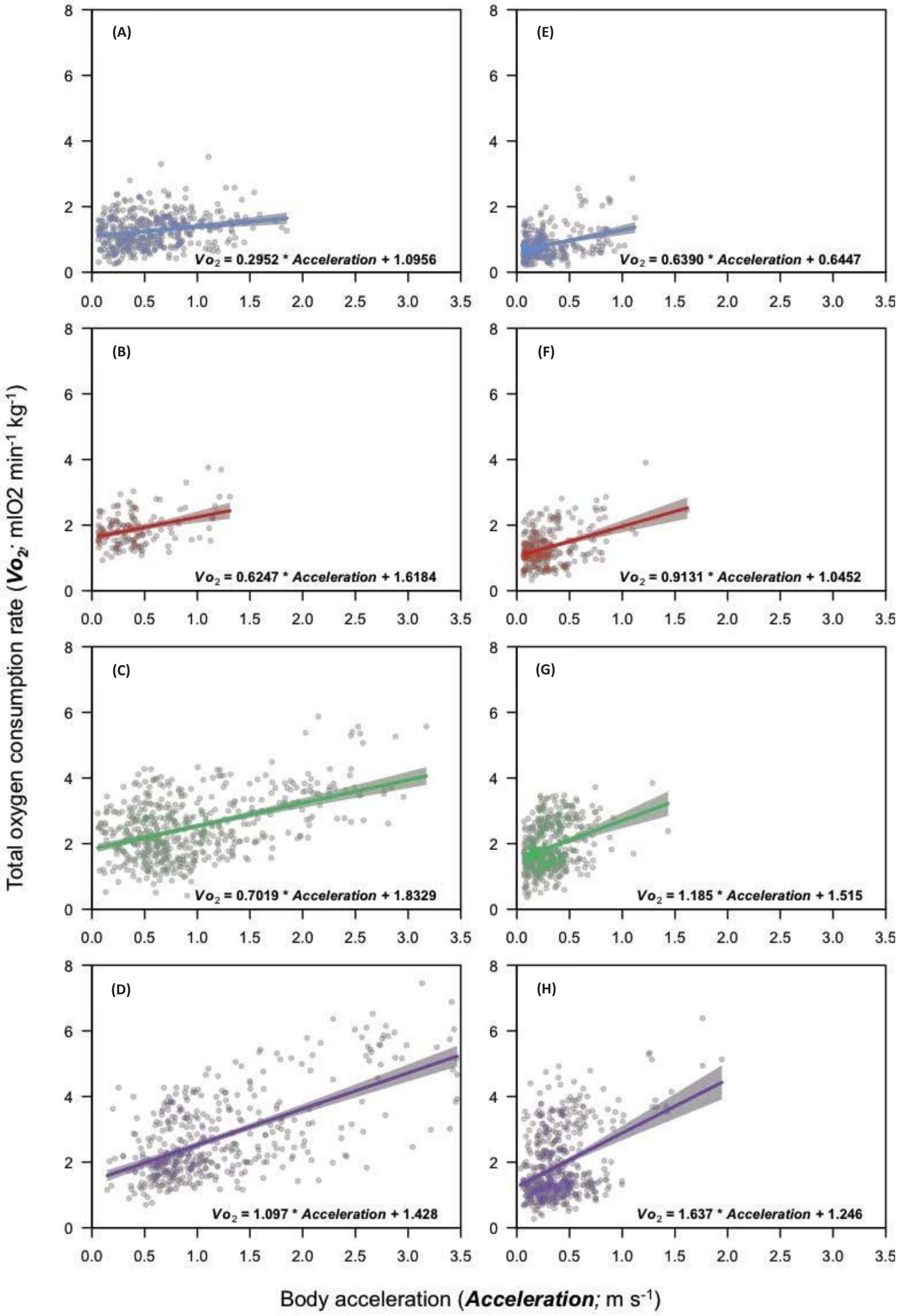

Figure 6.6. Relationship between measured total oxygen consumption rate ($\boldsymbol{\dot{V}\mathrm{o}_2}$) and body acceleration (***Acceleration***) for *Hydrophis curtus* (A–D) and *H. elegans* (E–H) at four temperature treatments (from top to bottom) 21˚, 24˚, 27˚ and 30˚C. Data were pooled for all individuals within each species and provide the basis for the species–level calibration equations (provided within each panel). Individual–level calibration equations are provided in Appendix 6.1.

2.47 $mlO_2 \, min^{-1} \, kg^{-1}$; *H. elegans*: 21˚C = 0.72, 24˚C = 1.19, 27˚C = 1.59, 30˚C = 1.68 $mlO_2 \, min^{-1} \, kg^{-1}$). Linear models best explained individual−level calibration equations (Appendix 6.1) and were also used to create species−level calibration equations (Figure 6.6).

6.3.3. Field acceleration measures and estimated metabolic rates

Field acceleration measurements were obtained for eight of 13 *H. curtus* and 13 of 15 *H. elegans* monitored between the 24th June and 18th November 2014 (Figure 6.7).

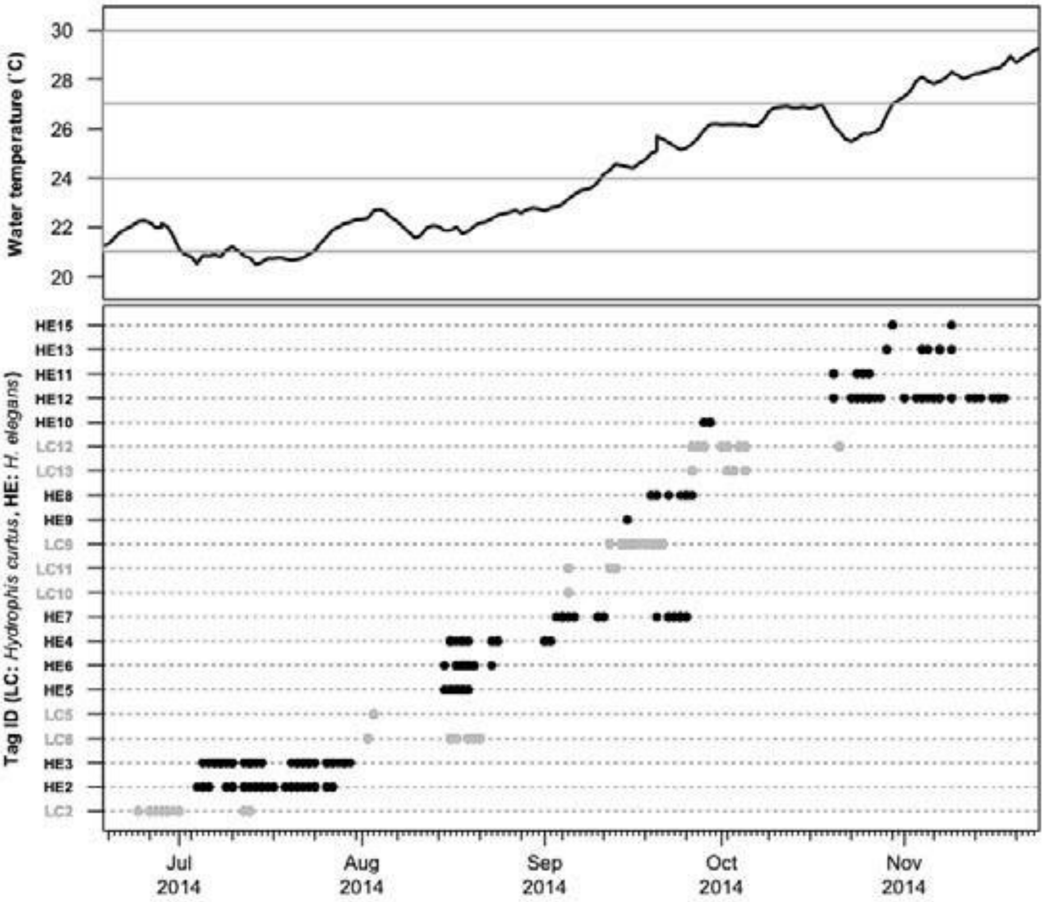

Figure 6.7. Top panel: Water temperature measurements within Cleveland Bay between June and November 2014. Horizontal grey lines indicate the four temperature treatments tested in the lab. Bottom panel: Detection pattern for eight *H. curtus* (grey; Tag ID starting LC) and thirteen *H. elegans* (black; Tag ID starting HE) within Cleveland Bay.

The time individuals were detected within Cleveland Bay ranged from less than a day (LC5, LC10, HE9; Table 6.1, Figure 6.7) to a maximum of 28 days (HE12). The full range of acceleration values (0 – 3.5 m s^{-1}) were measured from individuals in the field. Water temperature measurements within Cleveland Bay ranged from 20.4˚ − 28.9˚C suggesting monitored individuals experienced the full range of temperatures measured in the lab (Figure 6.7). Field measurements of acceleration were not significantly different between individuals used in captive experiments and individuals captured and released in the field (*t*−test: t = 1.7, p = 0.09) suggesting that there was no observable effect of captivity and that snakes returned to normal swimming behaviours post release.

Patterns in estimated metabolic rates were observable at both a diel temporal scale and throughout the monitoring period for both species (Figure 6.8). On a diel scale, both species displayed significantly higher field acceleration measurements and mean metabolic rates at night with lower mean values and larger variation during the day (*t*−test; *H. curtus:* t = −3.5, $p < 0.001$; *H. elegans:* t = −5.2, $p < 0.001$; Figure 6.8A, C). Over the monitoring period, estimated metabolic rates in both species increased over time (Figure 6.8), with the maximum metabolic rates of both species estimated in the months of October and November. Increased metabolic rates toward the end of the year coincided with increased water temperatures and reflected experimental results.

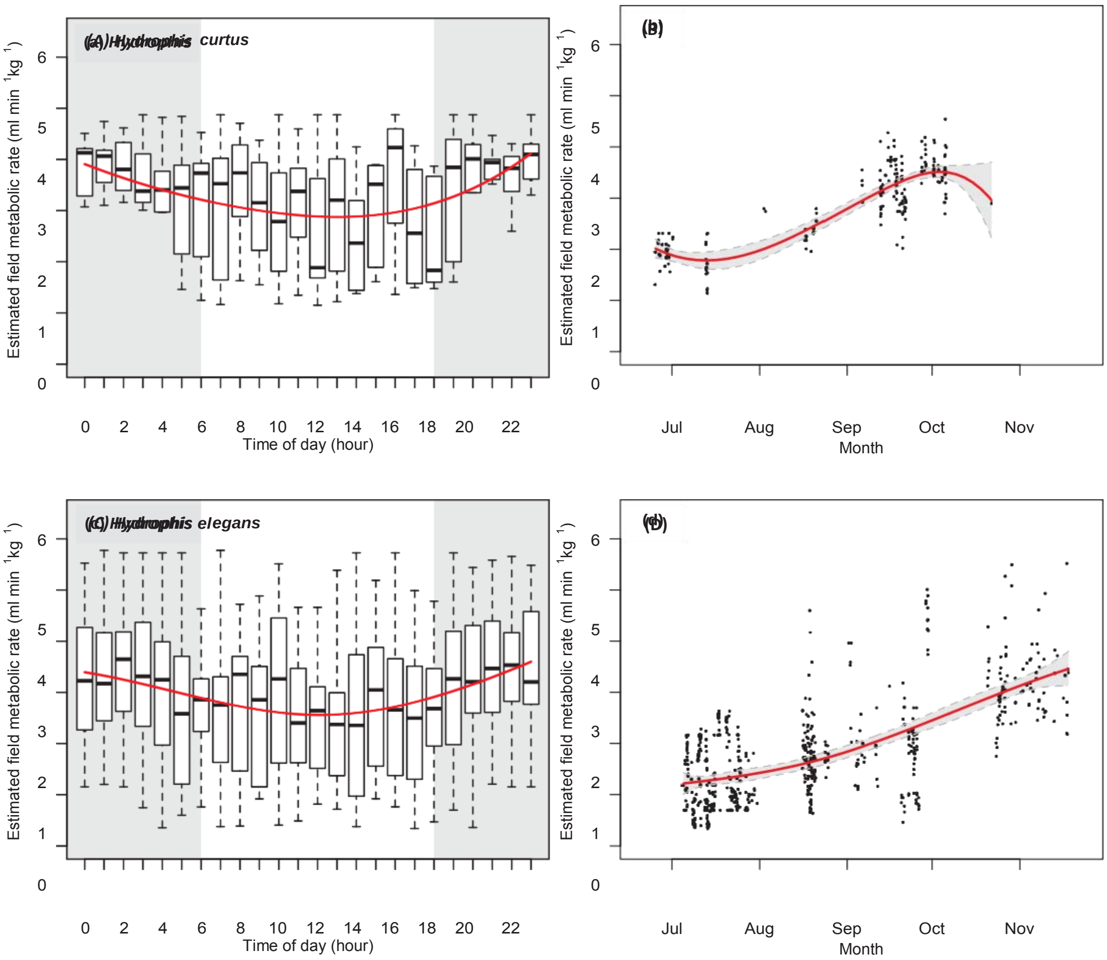

Figure 6.8. Patterns in estimated field metabolic rates for *Hydrophis curtus* (A–B) and *H. elegans* (C–D) over a diel scale (A,C) and over the entire monitoring period (B,D). Boxplots (A,C) represent quartiles for hourly estimated field metabolic rates. Grey background in diel plots represent nighttime hours. Trend lines (red) are based on polynomial B–splines with associated 95% confidence intervals represented in panels B and D.

6.4. Discussion

6.4.1. Temperature effects on dive behaviour and metabolic rates

Respirometry experiments showed that diving behaviours and the rate of oxygen consumption in sea snakes is greatly affected by environmental temperatures. Increased surfacing rates with shorter dive durations suggest that sea snakes would be more active within the water column or occupy space closer to the surface during warmer seasons or at lower latitudes. Previous work on aquatic file snakes

(*Acrochordus arafurae*) showed similar patterns with reduced dive durations and increased metabolic rates in warm waters (Pratt & Franklin 2010). Short, shallow dives were suggested to be related to predation risk from avian predators, which was also observed in the wild (Pratt et al. 2010). In the present study, individuals displayed similar short dives (max duration 37.2 min) during the warmer temperature treatments (27˚ and 30˚C), but exhibited longer dives (max duration 163.2 min) with reduced surfacing rates in cooler temperatures (21˚ and 24˚C), suggesting that individuals may alter diving behaviours depending on water temperatures and metabolic needs.

An increase of 10˚C in ambient temperature is typically associated with a 2−3−fold change in metabolic rate in ectotherms (Schmidt−Nielsen 1997, Gillooly et al. 2001). In the present study, the Q_{10} values for total metabolic rates in both species was approximately 2.5 which is lower than the previously calculated value for closely related sea kraits (*Laticauda colubrina*, Q_{10} = 3.07; Dabruzzi et al. 2012), but similar to file snakes (*Acrocordus arafurae,* Q_{10} = 2.52; Pratt & Franklin 2010). High Q_{10} values are hypothesised to increase metabolic efficiency in sea kraits that are known to experience daily body temperature fluctuations exceeding 15˚C (Pough & Lillywhite 1984). Higher Q_{10} values may mean that sea kraits can maximise digestive performance on land where temperatures are high, while reducing metabolic demand and increasing submergence times in cooler aquatic habitats. The lower Q_{10} values in the present study may reflect the fully aquatic habit of ‘true’ sea snakes, where individuals rarely experience excessive temperature fluctuations between habitats or over a diel period.

The results of the present study also showed that cutaneous respiration was independent of water temperature, and that with decreased water temperature and increased dive duration, cutaneous respiration was not up−regulated. The thermal independence of cutaneous respiration in sea snakes is similar to previous findings in other closely related aquatic snakes (*Acrochordus arafurae*; Pratt & Franklin 2010, *Laticauda colubrina*; Dabruzzi et al. 2012). Apart from changes in water temperature, previous work by Heatwole and Seymour (1975) found that levels of activity in sea snakes can influence the amount of cutaneous respiration measured. In their experiments, Heatwole and Seymour (1975) found that active sea snakes displayed increased cutaneous uptake of oxygen of 14 – 120% higher than inactive levels. The level of stress individuals experienced was also found to greatly influence the cutaneous uptake of marine snakes, with restrained animals displaying higher levels of cutaneous oxygen uptake than free swimming animals (Heatwole & Seymour 1976). In the present study, the consistent cutaneous oxygen uptake over the four temperature treatment suggests that water temperatures alone may not influence the up−regulation of aquatic respiration.

As snakes were relatively unrestrained within respirometers, this study showed that individuals may not have much control over the amount of oxygen they uptake cutaneously. If this were possible, we would expect that individuals would actively increase cutaneous oxygen uptake in warm temperatures to minimise surfacing frequencies. The level of stress of individuals were not tested in the present study, and as suggested by Heatwole and Seymour (1976) may play an important role in the up−regulation of cutaneous respiration in sea snakes. The activity and stress levels of individuals may also have implications when considering anthropogenic threats of dredging and trawl fishing. Potentially, individuals may not have the ability to up−regulate their cutaneous respiration during periods of stress (i.e. trapped in trawl nets), which may play an important role in the survival of sea snakes caught in fishing gear. The effect of stress on cutaneous respiration was not tested in the present study, but is an important mechanism that should be examined in more detail in future work.

Although cutaneous respiration formed a significant proportion of total oxygen uptake in the present study (up to 23%), the expulsion of CO_2 was not measured. Previous work has suggested that CO_2 elimination may be a more significant function of sea snake skin, with studies measuring up to 94% of total CO_2 excretion via cutaneous means (Graham 1974). Overall, sea snakes display a high degree of bimodal respiration with individuals meeting most of their O_2 requirements via pulmonary means, and potentially eliminating CO_2 via cutaneous means (Heatwole & Seymour 1976).

Some sea snakes are known to actively move towards deeper habitats or dive to great depths and remain in cooler waters as potential mechanisms to reduce metabolic rates (Dunson & Ehlert 1971, Cook & Brischoux 2014). However, diving behaviours and dive patterns in air breathing marine animals are often constrained by maximum aerobic limits (Heithaus & Frid 2003). Cook and Brischoux (2014) previously estimated maximum aerobic dive durations in the yellow−bellied sea snake (*Hydrophis platura*) to be 3 h 33 min at 22˚C and 2h 23 min in 28˚C waters. In the present study, values of mass specific metabolic rates ($\dot{V}o_{2tot}$) and volume of oxygen consumed per breathing bout (V_B) were measured and can be used to estimate maximal aerobic dive durations. The amount of oxygen available before a dive can be calculated by adding the maximum breath volume (V_B) and the amount of oxygen dissolved in their blood, assuming negligible levels of O_2 is held in muscle. Using blood volumes and blood−oxygen capacities measured previously by Heatwole and Dunson (1987) & Pough and Lillywhite (1984) the additional volume of O_2 held in snakes at the start of dives in nearly−air saturated blood can be estimated (Rubinoff et al. 1986). As blood−oxygen capacities for *Hydrophis curtus* or *H. elegans* were not measured by Pough and Lillywhite (1984), values for a closely related *Hydrophis coggeri* (identified as *Hydrophis melanocephalus*) can be used [blood volume = 9.85 ± 0.48% body mass; blood−oxygen capacity = 0.108 ± 0.017 mlO_2 (ml blood)$^{-1}$]. Pough and Lillywhite (1984) also found that blood−oxygen capacities for sea snakes in the *Hydrophis* group did not significantly vary between 10˚ – 40˚C. Therefore, applying their measured values to the monitored individuals it is possible to calculate the volume of oxygen available in the blood at the start of dives as 10.6 $mlO_2\,kg^{-1}$. Using the total mass specific metabolic rates measured at the two extreme temperatures tested, maximum aerobic dive durations are estimated as 106 min for *H. curtus* and 104 min for *H. elegans* at 21˚C and 44 min for *H. curtus* and 63 min for *H. elegans* at 30˚C. These estimated values are within the majority of maximum dive durations observed in this study as well as dive times measured previously by Heatwole (1975c)[*H. curtus*: 37 min at 21˚C, *H. elegans*: 47 min at 23˚C]. This indicates that observed diving behaviours in these species are constrained within aerobic limits, but this needs to be tested in the natural environment. The near halving of maximum aerobic dive duration between 21˚ and 30˚C water temperature observed in the present study also illustrates how long−term or seasonal changes in environmental temperature can affect diving and movement patterns in the wild.

6.4.2. Body acceleration as a proxy for field metabolic rates

The present study illustrated that body acceleration can be a suitable proxy for movement−specific field metabolic rates in sea snakes and using field acceleration data can provide key information on activity−associated energy expenditure in the wild. Diel patterns in diving behaviours, acceleration and oxygen consumption rates were not observed during laboratory experiments in the present study, but increased activity and acceleration measurements were recorded post−release. This may have been due to the semi−restrictive nature of the respirometer, especially for the larger specimens of *H. elegans*. Development of bimodal swimming tunnels or flume chambers may provide a better range of values for future work. Nevertheless, individuals displayed a diel activity patterns in the field and in many cases acceleration measurements were larger than that recorded within the respirometers. Increased mean field acceleration values at night and reduced values during the day correlate with previous findings from this thesis (Chapter 4.3.1.) as well as other observations (Heatwole & Seymour 1976, Heatwole et al. 1978). Increased activity at nights in *H. curtus* and *H. elegans* can be correlated with increased nocturnal foraging patterns. Reduced acceleration values during the day may relate to periods of inactivity displayed by individuals and are possibly a strategy for sea snakes to reduce surfacing frequency when avian and aquatic predators are most active (Heithaus & Frid 2003).

Heatwole and Seymour (1975) previously measured metabolic rates of a range of species of sea snakes (*Hydrophis curtus*, *H. belcheri*, *H. elegans*, *Acalyptophis peronii*, *Aipysurus duboisii* and *A. laevis*) and found that some individuals had higher rates of oxygen uptake during the day than at night (almost twice as high for a given species) reflecting diurnal activity patterns, whereas others displayed an opposite pattern reflecting nocturnal patterns. These diel patterns were found to be independent of water temperature and activity, with individuals that were considered ‘inactive’ throughout the testing period still displaying diel patterns in metabolic rates. Elevated metabolic rates independent of activity may mean that individuals have a higher energetic requirement to fulfil other metabolic demands not associated with movement (i.e. digestive or reproductive), but may influence how much energy individuals can partition for activity or diving. In the present study, both species displayed increased field acceleration and estimated field metabolic rates at night, which reflect the nocturnal activity patterns of *H. curtus* and *H. elegans.* Energy requirements related to digestive (e.g. specific dynamic action) or reproductive demands were not measured in the present study, but are presumed to play a critical role in determining daily or seasonal energy budgets in sea snakes.

A seasonal pattern was evident with the estimated field metabolic rates, with metabolic demands increasing with seasonal increases in water temperature. This study illustrates the importance of measuring and incorporating environmental temperatures when estimating field metabolic rates using accelerometry techniques over large temporal/spatial scales. Mean estimated field metabolic rates doubled between the start (July 2014) and end (November 2014) of the monitoring period, illustrating that calibration curves accounting for the range of temperatures need to be established to enable accurate estimates of field metabolic rates. The doubling of metabolic rates and energy requirements can influence not only how individuals move and occupy space within the water column, but can also influence their susceptibility to fishing activities that occur predominantly in summer months (Courtney et al. 2010). The study site was a well−mixed shallow coastal habitat that can experience warmer mean temperatures with a lower degree of variation between depths than deeper, stratified waters offshore. Coastal habitats have often been associated with larger numbers of juvenile snakes and in many populations these areas form important nursery grounds (Voris & Jayne 1979, Bonnet et al. 2014). Shine (1988) hypothesised that juveniles or gravid female snakes may have impaired locomotory ability, and hence may seek out shallower waters to reduce energy costs of deep diving to find prey and subsequently reach the surface to breath. Apart from reducing energy within shallow waters, coastal habitats with higher water temperatures may facilitate raised metabolic rates in juveniles and neonates, allowing them to elevate their development at early life stages.

6.5. Conclusions

Understanding the energy requirements and acceleration patterns in sea snakes can highlight important patterns in their spatial ecology. The use of accelerometry techniques alongside laboratory−based calibrations provided the first estimates of movement−related field metabolic rates in this group of animals that has typically been data poor (Heatwole 1999). This study has outlined concepts that can be expanded in future work, such as exploring the effect of stress or forced submergence on cutaneous respiration which can provide further insight on conditions these animals face in trawl nets. Longer−term studies of this nature are also required to fully understand energy expenditure in relation to other key metabolic activities including reproductive investment and measures of specific dynamic action. The use of biotelemetry acceleration sensors and laboratory respirometry techniques are expanding and these tools can be used to fill fundamental knowledge gaps in the ecology and biology of sea snakes (Elfes et al. 2013).

Chapter 7

Importance of nearshore habitats as refugia from trawl fishing

7.1. Introduction

Sea snakes form a significant component of bycatch in tropical trawl fisheries around the world. The life history traits of sea snakes (late maturity, long lived and low fecundity) make them highly vulnerable to fishing−related mortality (Heatwole 1997). As they are air−breathers and highly venomous, snakes that are caught in trawl nets have high mortality rates through drowning or being killed by the crew (Milton 2001). In some parts of the world (e.g. Gulf of Thailand), snakes caught in trawls or by hand lines are considered a valuable bycatch and are taken as part of a largely unregulated commercial trade (see Van Cao et al. 2014), whereas in other places (e.g. Australia) where snakes are not considered a valuable commodity, the animals are generally discarded alive (Milton 2001). Nevertheless, post−release survival in sea snakes has been shown to vary between species (Wassenberg et al. 2001) and low post−release survival from trawl interactions may have dire consequences for species that are less resilient (Milton 2001).

Spatial closures and restrictions on the activities that can be conducted in some areas have shown to be effective in management of commercially important populations of fishes or for animals of conservation value (Dryden et al. 2008, McCook et al. 2010). Many trawl fisheries around the world have worked to minimise the risk to non−target species by introducing a range of management arrangements, including fitting bycatch reduction devices to the cod end of the trawl net which allows sea snakes to escape the net while not reducing the take of target species. However, a recent global review of the conservation status of sea snakes and the trawl fishery around the Gulf of Thailand found bycatch management in many parts of the world is often inadequate and enforcement virtually non−existent (Elfes et al. 2013, Van Cao et al. 2014). Identification of critical habitats and appropriate spatial management of those areas can help maintain sea snake populations, improve recovery rates of sea snake populations, and improve management of bycatch in highly productive trawl grounds.

Nearshore habitats play an important role in the life stages of many of the sea snake species commonly encountered in trawl fisheries. Indeed, previous research has identified, shallow bays and tidal creeks as areas where sea snakes congregate seasonally and potentially provide habitat to increase survival of vulnerable life stages (Voris 1985, Stuebing & Voris 1990, Hin et al. 1991, Lobo et al. 2005). This chapter provides data to address the final aim of the overall thesis (Aim 4:). To examine the utliity of nearshore environments to sea snakes I surveyed a coastal bay within the Great Barrier Reef Marine Park to: (1) determine the species assemblage of sea snakes present within shallow coastal habitats, (2) identify the age structure of commonly encountered species, and (3) define temporal trends in habitat use. Findings were considered in the context of their potential to inform future management and conservation strategies to mitigate trawling impacts on sea snake populations.

7.2. Methods

7.2.1. Study site

Extensive boat−based surveys were conducted in the south−eastern half of Cleveland Bay (Figure 7.1) between October 2012 and October 2014. The surveyed area within the bay covered an area of approximately 140 km^2 with the habitat consisting mainly of soft sediment substrates with extensive seagrass meadows (Unsworth et al. 2009). Multiple tidal creeks with mudflat and mangrove habitats line the southern shore and provide the majority of freshwater input.

Cleveland Bay includes the large commercial port of Townsville, but the majority of the bay (and survey area) is classed as a Conservation Park Zone under the Great Barrier Reef Marine Park Authority (GBRMPA) zoning scheme (Figure 7.1; yellow zones). Trawling and most netting are not allowed within Conservation Park Zones, making the majority of Cleveland Bay closed to trawl fishing. Trawling occurs in the Townsville port area (Figure 7.1) and areas directly offshore of Townsville. These are productive trawling grounds with a historically high amount of fishing effort from the East Coast Otter Trawl Fishery (ECOTF; Grech & Coles 2011). Previous trawl−based surveys (e.g. Dunson 1975, Courtney et al. 2010) and fisheries−independent video surveys (e.g. Udyawer et al. 2014) have shown that areas offshore from Townsville also have high abundances of sea snakes.

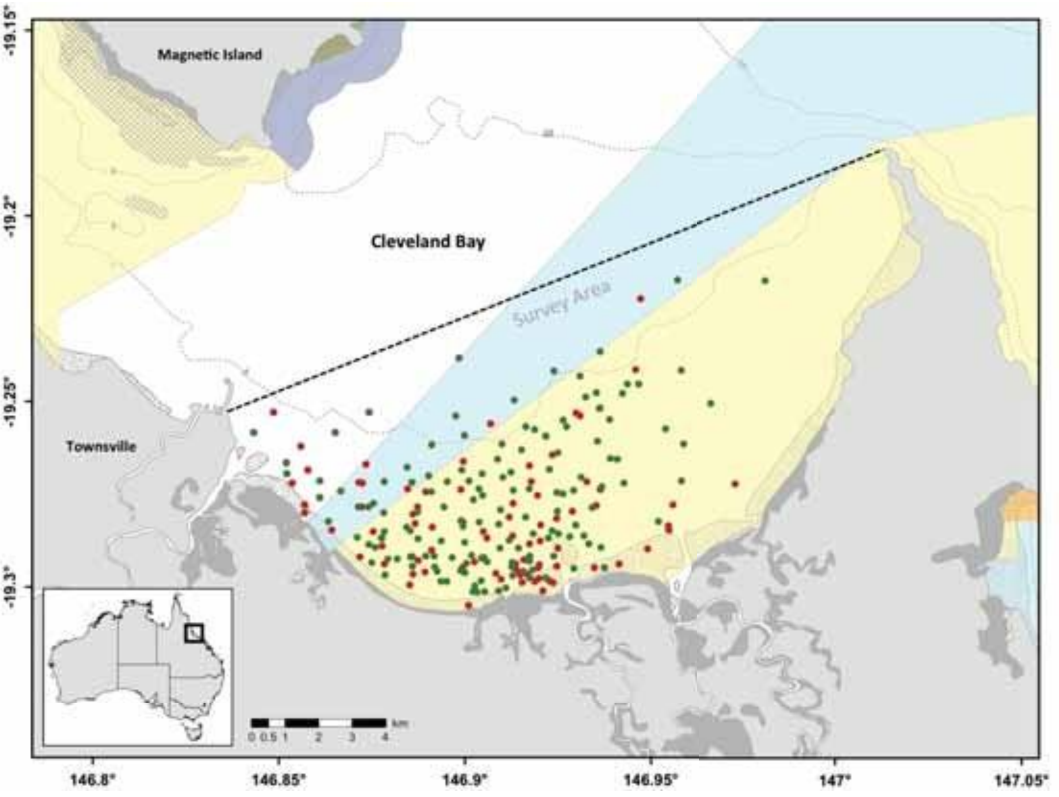

Figure 7.1. Survey location within Cleveland Bay included the area encompassed within the black dashed line and adjacent coastline. Broken grey lines indicate bathymetry within the bay, with light grey stippled areas indicating shallow mud–flat habitat. Dark grey areas indicate mangrove habitats along tidal creeks on the southern border of the bay. Crosshatched areas around Magnetic Island indicate fringing reef habitat within Cleveland Bay. Great Barrier Reef Marine Park zones are represented: conservation zone (yellow), general use zone (light blue), habitat protection zone (dark blue), marine national park zone (green), scientific zone (orange). The shipping lane and area managed by Townsville Port is indicated in white. Capture locations for *Hydrophis curtus* (green points) and *H. elegans* (red points) within survey area are also represented.

7.2.2. Data Collection and Analysis

Sea snakes were located on the water surface within the surveyed area after dark on nights with calm sea conditions (i.e. wind speed < 10 km.h^{-1} and swell < 1 m) using spotlights and captured using dip nets. Surveys within the area were designed to cover as much of the survey area during each trip, or, within periods of calm weather attempts were made to divide the survey effort into manageable−sized 'blocks' that allowed the entire survey area to be surveyed over consecutive nights. The location of each captured individual and the depth at each location was recorded using an on−board GPS and depth sounder. Captured snakes were identified to species and the snout−vent length (SVL, mm), tail length (TL, mm) and mass (g) were recorded and each individual was fitted with a passive integrated transponder (PIT) tag for future identification before release. The determination of sex using external characteristics (by exposing the hemipenes) was unreliable in juvenile sea snakes; therefore sex was excluded from the analysis.

Several aspects of morphology and age structure of sea snakes caught within Cleveland Bay were examined during the two−year survey period. Regression analyses of body length−weight and body length−tail length relationships were conducted to assess any correlation between the different measured metrics. Age of all captured individuals was estimated using von Bertalanffy growth curves and parameters determined by Ward (2001). The age structure of sea snakes caught within the bay were compared to those of snakes caught as incidental bycatch in trawl fisheries in Northern Australia from previously published literature (Ward 2001). Individuals were classed as either juvenile or adults based on measured length and length at sexual maturity estimates reported previously (Hin et al. 1991, Fry et al. 2001, Ward 2001). Temporal patterns in the presence of individuals based on age structure of sea snakes captured within the bay were identified by examining the change in adult–juvenile proportions in the catch throughout the year.

7.3. Results

A total of 130 survey trips were conducted between October 2012 and October 2014 within the survey area in Cleveland Bay, with each survey lasting an average of 4.13 hours (range: 1.75 – 7.25 hrs; Figure 7.2). A total of 251 snakes; including 243 individuals belonging to five species within the genus *Hydrophis* (*Hydrophis curtus* [previously *Lapemis curtus*]*, H. elegans, H. major* [previously *Disteira major*]*, H. kingii* [previously *Disteira kingii*] *and H. zweifeli* [previously *Enhydrina schistosa*]; see Sanders et al. 2013 and Ukuwela et al. 2013 for details of recent phylogenetic restructuring within the *Hydrophis* group) and eight marine file snakes (*Acrochordus granulatus*) were caught (Table 7.1). The most abundant species in the surveys was

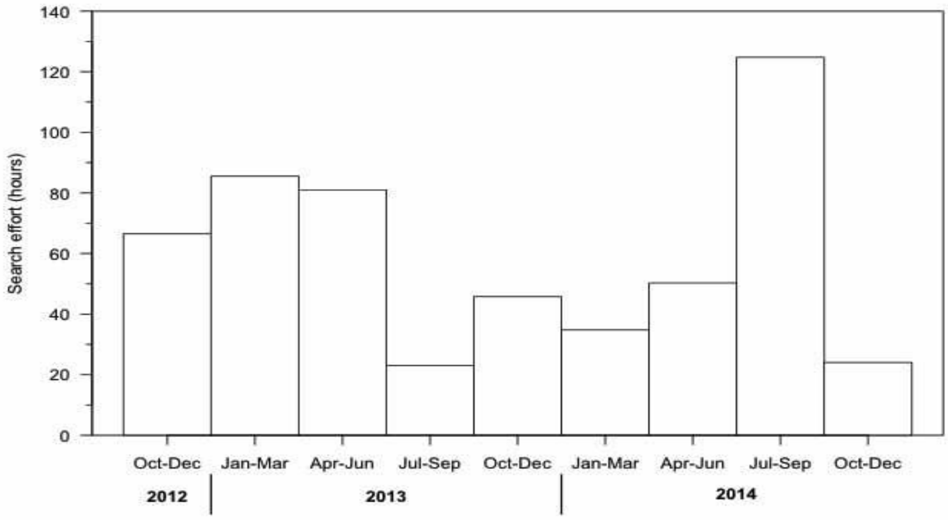

Figure 7.2. Survey effort (130 trips) within Cleveland Bay throughout the two year period. Survey trips consisted of an average of 4.13 hours of search time. Search effort is displayed in three−month periods.

Table 7.1. Summary table of morphometrics of five species of Hydrophid snakes and one Acrochordid marine snake (*****) caught within the survey area of Cleveland Bay between October 2012 and October 2014. Table displays total number of individuals (*n*) captured during the study with mean (X), standard deviation (SD) and range of body length (Snout−Vent length) and mass (Weight) for each species.

Species	***n***	**Snout-Vent Length (mm)**			**Weight (g)**		
		X	**SD**	**Range**	**X**	**SD**	**Range**
Hydrophis curtus	155	490.5	183.9	158–1100	180.6	264.3	10–1560
Hydrophis elegans	81	991.1	291.4	488–1738	351.3	356.5	10–1755
*Acrochordus granulatus**	8	672.0	165.0	435–923	284.4	67.8	200–405
Hydrophis major	3	728.9	283.1	524–1052	133.3	90.2	40–220
Hydrophis kingii	2	542.7	4.4	540–546	53.0	38.2	26–80
Hydrophis zweifeli	2	919.7	232.9	755–1084	909.0	878.2	288–1530

H. curtus, which comprised 62% of the total catch, followed by *H. elegans* at 32%. The remaining species; *H. major*, *H. kingii*, *H. zweifeli* and *A. granulatus* were caught in very low numbers and together comprised 6% of the total catch. These four species were excluded from further detailed analysis.

The distribution pattern for captures of *H. curtus* and *H. elegans* shows most individuals were captured in the south−western quadrant of the survey area, with individuals captured in shallow inter−tidal and sub−tidal habitats on the southern shore of Cleveland Bay and out into more exposed waters (Figure 7.1). For the stocky−bodied *H. curtus,* individuals ranged in SVL from 158 mm neonates to 1100 mm adults that weighed up to 1560 g. Metrics for *H. curtus* indicated body length (SVL) was a strong predictor of body mass ($r^2 = 0.801$) as well as tail length ($r^2 = 0.796$;

Figure 7.3). In comparison, *H. elegans* is a longer bodied snake with individuals caught ranging from 488 mm neonates to adults of 1739 mm. Individuals weighed up to 1755 g and showed a similar relationship between body length and mass ($r^2 = 0.838$) to *H. curtus*, but displayed a weaker relationship between body length and tail length ($r^2 = 0.616$; Figure 7.3).

Length frequency of both species showed that 92% of *H. curtus* (<760mm SVL) and 70% of *H. elegans* (<1200mm SVL) were juveniles (Figure 7.4). Age estimates of individuals caught within the survey area indicate that *H. curtus* were predominantly less than two years of age, with very few individuals caught that were older (Figure 7.5). Similarly, the majority of the catch of *H. elegans* were also aged less than two years, however a larger proportion of individuals aged between 2 to 4 years were

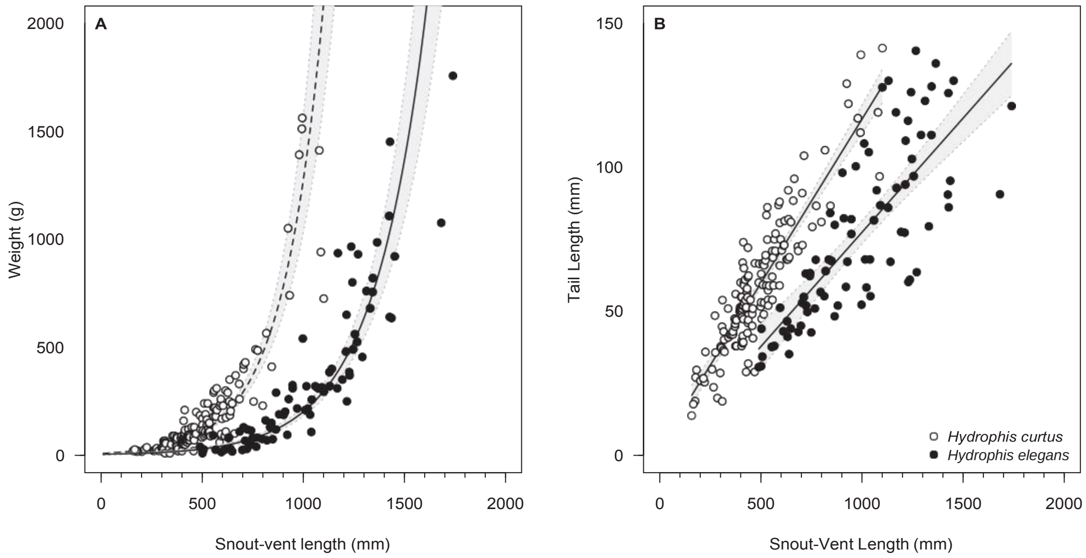

Figure 7.3. Allometric relationships of individuals caught within survey area in Cleveland Bay between October 2012 and October 2014: (A) weight and (B) tail length against snout–vent length of *Hydrophis curtus* (open circles) and *H. elegans* (solid circles) with associated regression lines and 95% confident intervals.

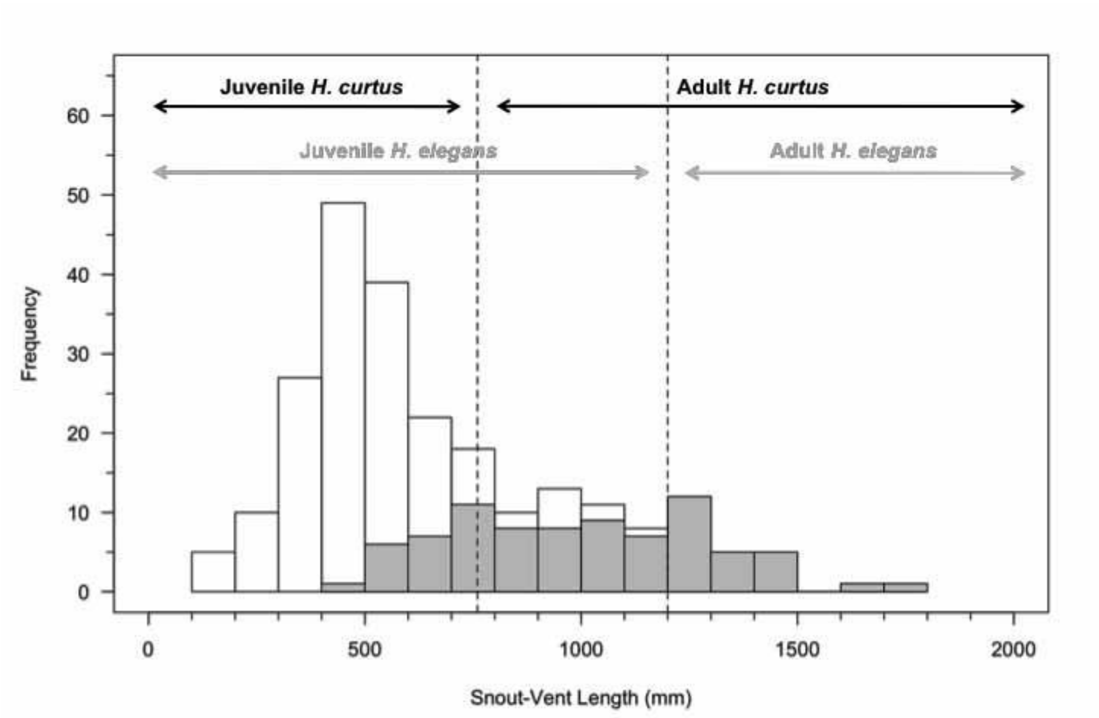

Figure 7.4. Size frequency of *Hydrophis curtus* (white bars) and *H. elegans* (grey bars) captured within the survey area in Cleveland Bay. Vertical broken lines indicate limits between the adult and juvenile age classes based on size at sexual maturity from Ward (2001).

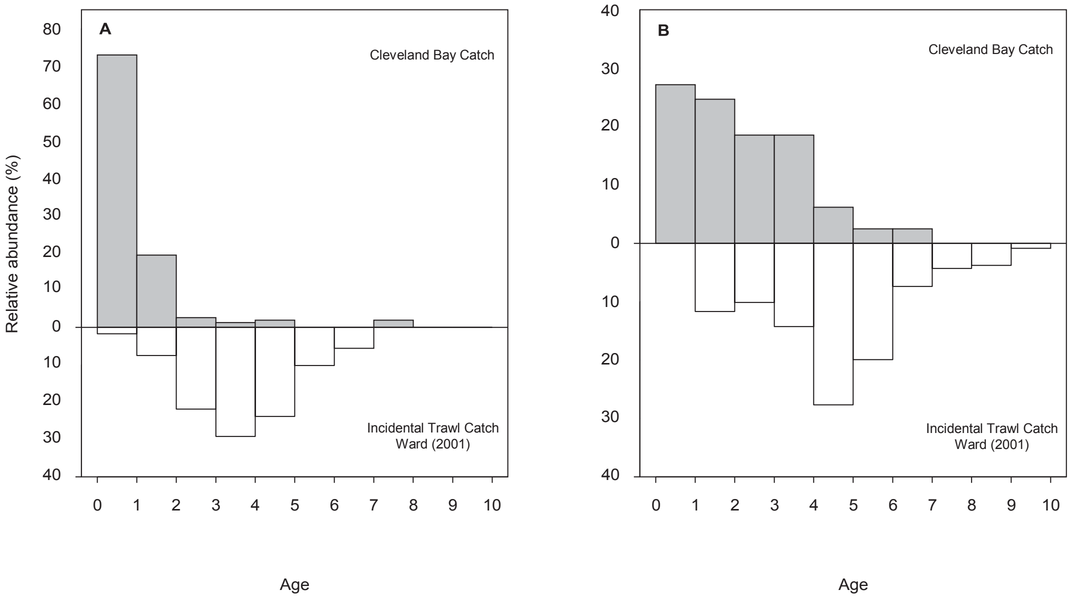

Figure 7.5. Age structures of (A) *Hydrophis curtus* and (B) *H. elegans* caught within the survey area in Cleveland Bay (grey bars) compared to age structures of the same species caught in trawl fisheries from previously published data (white bars; Ward, 2001)

also caught within the survey area (Figure 7.5). Comparing the age structures of snakes caught in this study and previously published trawl data (Ward 2001) show that incidental catches in deeper trawl grounds are comprised of older individuals whereas shallower coastal areas like Cleveland Bay are largely inhabited by younger individuals (Figure 7.5). The temporal pattern of age structures of snakes caught within the survey area indicated a predominantly juvenile *H. curtus* catch year round, with only a few sexually mature individuals encountered during summer (Figure 7.6). The data for *H. elegans* show that although fewer individuals were caught within the bay, the age structure was stable throughout the year with approximately 30% of the population represented as sexually mature age classes during each three−month period (Figure 7.6).

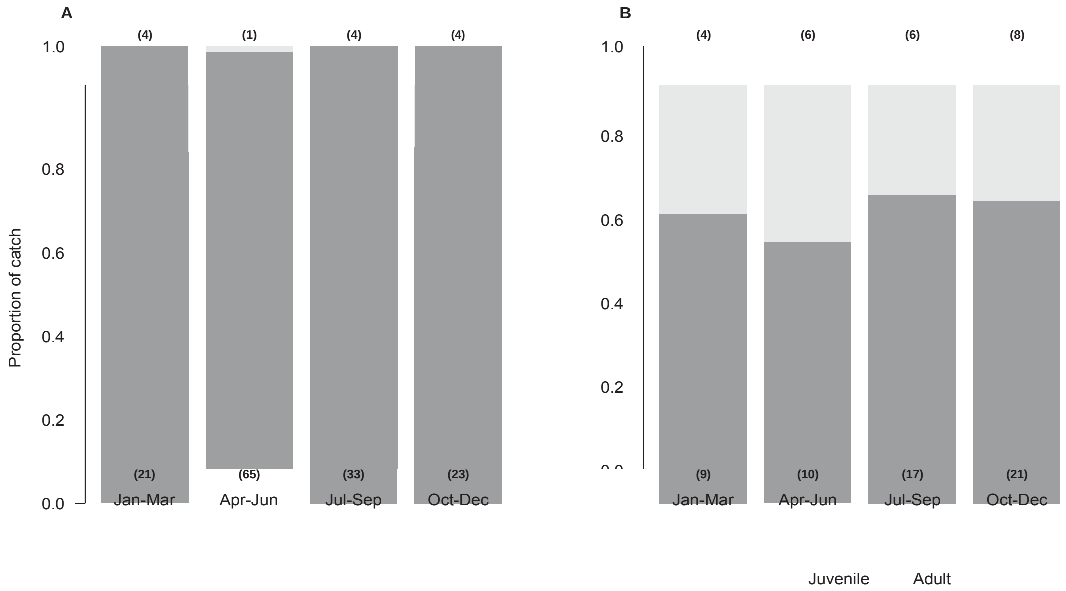

Figure 7.6. Temporal trend in the proportion of juvenile (dark grey) and adult (light grey) (A) *Hydrophis curtus* and (B) *H. elegans* caught within the survey area in Cleveland Bay between October 2012 and October 2014. Catch composition was pooled into three−month periods for both years to display temporal trends over a calendar year. Number of individuals in each age class caught represented in parentheses above (adult) and below (juvenile) plots.

7.4. Discussion

The species composition of sea snakes captured within Cleveland Bay matched that of incidental trawl catches within the ECOTF (Courtney et al. 2010) as well as previous scientific trawl surveys conducted within the region (Dunson 1975), where *H. curtus* was the most commonly encountered species followed by *H. elegans*. Dunson (1975) also recorded larger numbers of *H. major* and *H. kingii* as well as three species that we did not encounter (*Aipysurus laevis, A. duboisii, H. stokesii* [previously *Astrotia stokesii*]). The methodology used by Dunson (1975) included a combination of boat−based surveys as well as short research trawls that were conducted both during day and night time, and included deeper waters outside Cleveland Bay. In comparison we used a single boat−based night time survey technique focusing on shallow inter−tidal and sub−tidal habitats within Cleveland Bay (which would not have been accessible for research trawls) and this difference may explain why the catch composition in the present study was not as varied as previous reports.

As sex of individuals was not reliably determined in the present study, any morphometric traits related to sexual dimorphism were difficult to ascertain. Previous studies on *H. curtus* have shown that this species does not display any noticeable sexual dimorphism and has similar growth rates and morphometric relationships between the sexes (Ward 2001, Lobo et al. 2004). The weaker relationship between body length and tail length in *H. elegans* may suggest that this relationship in larger, sexually mature individuals may vary by sex. Similar observations have been made in other populations of *H. elegans* where females have higher growth rates and show distinctly different allometric relationships between body length, tail length and weight than male counterparts (Ward 2001, Kerford 2005). Previous work by Shine and Shetty (2001) found that tail length relative to body lengths in sea kraits (*Laticauda colubrina*) was a good indicator of growth rate and individual fitness. They found that males kraits had longer relative tail lengths than females, which influenced the probability of survival, locomotory ability and mating success.

Previous accounts of marine snake assemblages in coastal habitats have shown that shallow water habitats support large numbers of juveniles and gravid females (e.g. Voris 1985, Stuebing & Voris 1990, Bonnet et al. 2014). The use of such habitats by juveniles and gravid females may increase survival at these vulnerable life stages (Shine 1988). The predominantly juvenile population of *H. curtus* and *H. elegans* in Cleveland Bay suggests that shallow inter−tidal and sub−tidal habitats within coastal embayments may provide critical nursery habitats for these species. The capture rate of adult *H. elegans* was relatively consistent throughout the year, whereas the capture rate of adult *H. curtus* was elevated in the summer months. This suggests that the two species use Cleveland Bay in different ways: adult *H. curtus* enter coastal bays seasonally to give birth before leaving for deeper waters, while adult *H. elegans* may be present consistently throughout the year.

Reasons for the differing temporal patterns of species caught in our study are unclear, but diet specialisation in *H. elegans* may play a role in their consistent presence in shallow mud−flat habitats. *Hydrophis elegans* almost exclusively preys on snake eels (Family Ophichthidae; Voris & Voris 1983, Kerford 2005), which are abundant within the shallow muddy benthos of Cleveland Bay. Some individuals regurgitated snake eels after capture, confirming that this species forms part of the diet for *H. elegans*. Conversely, *H. curtus* are known dietary generalists (Voris & Voris 1983), therefore individuals may not have been strongly associated with any particular habitat type. Previously, Shine (1988) hypothesised that gravid or egg−bearing female marine snakes may have impaired locomotory ability, and hence may seek out shallower waters to reduce energy costs of deep diving to find prey and then surfacing to breath. This, alongside the potential for increased protection from predators and higher preferred prey density, most likely explains the use of shallow water habitats by juveniles and gravid females of *H. curtus* and *H. elegans* populations within Cleveland Bay and emphasises the importance of these habitats.

7.4.1. Implications for management and conservation

A recent assessment of the risk posed by the ECOTF to sea snakes found an elevated risk for a number of species, including *Hydrophis elegans* (Courtney et al. 2010). Their large body size, low natural mortality and low post−trawl survival rates mean *H. elegans* is at high risk from trawling activities. In fact, a recent ecological risk assessment of the Queensland ECOTF estimated that incidental fishing mortality was high enough to reduce recruitment in this species (Pears et al. 2012). The majority of the surveyed area in the present study is closed to trawl fishing, which may provide juvenile *H. curtus* and *H. elegans* some shelter from the potential negative effects of trawl fishing while they remain within the bay. However, as individuals grow older, their movement to deeper waters exposes them to threats offshore. Further long−term biological information is required to understand the extent of sea snake movements between Cleveland Bay and offshore trawl grounds. However, this study has shown that protected areas, like those within conservation zones in Cleveland Bay, can potentially serve as refugia to populations of sea snakes that are at high risk from trawl fishing.

The mandatory use of Bycatch Reduction Devices (BRDs) has been effective in reducing the landing of sea snakes onboard trawl vessels in the Australian trawl fishery (Milton et al. 2009). The age structures of sea snakes caught in the trawl activities indicate a high catch rate of sexually mature individuals (Figure 7.5; between 2−6 years), therefore BRDs may be an effective tool for reducing fishing pressure on older age classes. However, the mandatory use of BRDs may not be practical, properly implemented or adequately regulated in other parts of the world where sea snakes are among the major trawl bycatch in commercial and artisanal coastal trawl fisheries (e.g. India, Philippines, Thailand). Spatial closures and fishing restrictions within important coastal habitats could be used as a management tool to help further reduce sea snake−trawl interactions and reduce trawl pressures on sea snake populations (Lobo et al. 2005) as well as regulate direct harvest in habitats with high sea snake abundances (Van Cao et al. 2014). The present study provides an example of how coastal bays and shallow water habitats may act as refuge sites for young snakes amongst heavily trawled habitats and potentially allow for increased recruitment in the local area. The identification of refuge habitats, and implementation of fishing restrictions within such habitats, is an important step in effectively mitigating risks to sea snakes and maintaining healthy populations.

Chapter 8

General discussion, application and future directions

8.1. General discussion and application of findings

Information on animal movement patterns and spatial ecology is valuable when examining the effects of natural and anthropogenic threats (Brooks et al. 2006). This information is vital not only to develop our understanding of the natural environment but also when developing management and conservation policy (Roberts et al. 2003). In the case of sea snakes, such information is lacking which severely impedes effective conservation efforts (Elfes et al. 2013, Heatwole & Cogger 2013). This thesis explored several aspects of the movement ecology of sea snakes and attempted to not only examine the natural history of these unique marine reptiles, but also provide information to help develop effective management and conservation policies in the Great Barrier Reef Marine Park (GBRMP) and other parts of the world. Two main research questions (section 1.6.1.) were the focus of this PhD project. In this chapter, I will use the data presented in this thesis to answer the questions posed, discuss the potential application of these data and suggest future directions in this area of research.

1) *What are the movement and space use patterns of sea snakes in coastal ecosystems?*

The space use patterns of sea snakes were explored at multiple spatial and temporal scales. On a geographic scale, the distribution patterns of sea snakes were examined using baited remote underwater video stations (BRUVS) which provided a snapshot view of three species of sea snake (*Aipysurus* laevis, *Hydrophis ocellatus* and *Hydrophis curtus*) over a ten−year period (2000 – 2010). The three species recorded on BRUVS represent species that are frequently encountered in the trawl fishery in Queensland. The distribution patterns varied among the three species with deep offshore habitats preferred by *Hydrophis ocellatus,* shallower inshore areas occupied by *Hydrophis curtus* and *Aipysurus laevis* found in both inshore and offshore areas. Overall, sea snakes displayed 'patchy' geographic distribution patterns in the GBRMP (Figure 8.1A). Inshore waters of the central GBR were one area that all three species occupied, and had high abundances, indicating that this area is particularly favourable for sea snake populations on the GBR.

On a regional scale, the movement patterns, home ranges and habitat selection of sea snakes was examined within a coastal embayment in the central GBRMP. Passive acoustic telemetry was used to monitor movements of two commonly occurring species (*Hydrophis curtus* and *Hydrophis elegans*) with patterns of movement and space use examined over diel (day and night), daily and monthly scales. As diving patterns are important when considering how sea snakes use space, this thesis used a new analytical approach by using data from

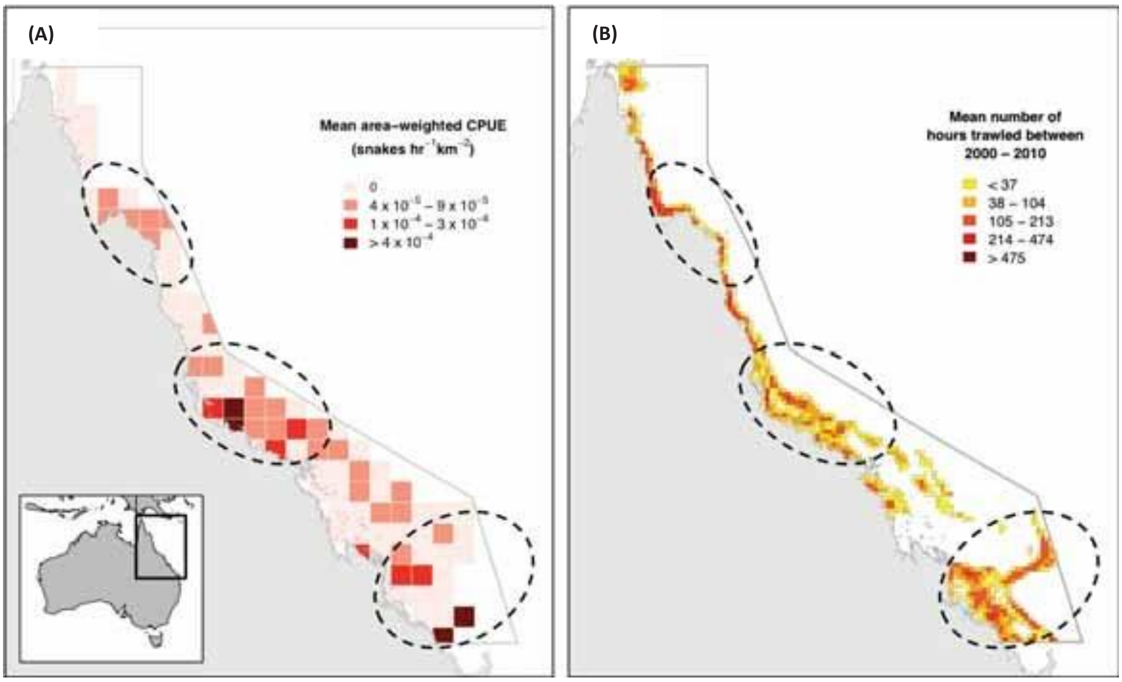

Figure 8.1. Overlap between sea snakes and trawl fishing. (A) Map showing the distribution patterns of sea snakes on the GBR from data gathered in this thesis (Chapter 3). (B) Spatial pattern of trawl fishing effort recorded by the Department of Agriculture and Fisheries Queensland using satelite based vessel−monitoring system. Circles with broken lines outline areas along the GBRMP with high levels of overlap.

all three axes of movement (see section 4.2.3.1.). Definition of three−dimensional home ranges showed that sea snakes displayed clear diel patterns in their movements and use of space. Individual *Hydrophis curtus* and *H. elegans* displayed restricted movements at greater depths during the day and broader movements on the surface at night. The data showed that individuals used different core areas between day and night, but had similar home range extents.

The space use patterns of monitored sea snakes were also evaluated alongside environmental parameters to determine what factors influenced the spatial ecology of sea snakes in nearshore habitats. Since different environmental factors may have varying influence at different temporal scales patterns of presence, movement and home range were tested at a daily and monthly scales. Results indicated that tide and atmospheric pressure played an important role in the daily presence and movements of sea snakes within shallow coastal habitats. Individuals were more likely to be detected within Cleveland Bay on days with higher tidal reach (spring tides) and movement patterns were elevated on days with lower air pressure. Monthly three−dimensional home ranges of sea snakes were highly correlated with precipitation. Sea snakes displaying larger home ranges (core and extent) in months with higher rainfall suggesting increased precipitation and freshwater input possibly allowed snakes to occupy more space and move farther by reducing the need to remain near freshwater sources.

Data obtained from passive acoustic telemetry was also used to assess how sea snakes selected habitats within Cleveland Bay. Despite access to several habitat types within the bay, overall, sea snakes displayed a high preference toward seagrass and mudflat habitats. *Hydrophis elegans* displayed an affinity to seagrass meadows and mudflat habitats less than 4 km from sources of freshwater and depths less than 3 m. Whereas, *Hydrophis curtus* selected slightly deeper habitats (1 – 4 m) further from freshwater sources (2 – 5 km). Affinity to seagrass and mudflat habitats within Cleveland bay indicates that these habitats provide key resources (i.e. prey, shelter from predators) to sea snakes. Therefore, degradation or loss of these habitats may have significant consequences for local sea snake population health.

2) *How do movement and space use patterns affect the vulnerability of sea snakes to anthropogenic activities?*

As mentioned previously, sea snakes are a significant component of bycatch in coastal trawl fisheries, and are vulnerable to fishing−related mortality (Heatwole 1999). Distribution patterns, movement and home range data can provide valuable information on the exposure of sea snakes to anthropogenic threats. The distribution patterns presented in this thesis show sea snakes are abundant in inshore waters of the central GBR, with the highest abundances in inshore habitats (Figure 8.1). The inshore waters of the GBR are highly productive trawl grounds that are fished heavily during each season (Figure 8.1B, Grech & Coles 2011). As sea snake distribution patterns varied among the species examined, the spatial overlap between distributions and trawl fisheries may vary as well. Of the three species examined, two (*Aipysurus laevis* and *Hydrophis curtus*) displayed higher abundances in inshore habitats, potentially elevating their vulnerability to trawl fishing and coastal human activity. The geographic−scale distribution patterns observed here can be used to identify certain areas within the GBRMP where there is a high degree of overlap between sea snake abundance and fishing activity (Figure 8.1) that can guide development of more targeted management policy.

On a regional scale, *Hydrophis curtus* and *Hydrophis elegans* displayed a strong diel pattern in their use of space and movements. Increased nocturnal movements within the water column potentially make these species more likely to be caught in trawl fishing activities which generally operate at night. To understand how environmental factors effect sea snake dive patterns and movements within the water column, these species were also observed in a laboratory setting. Laboratory observations showed that sea snakes displayed shorter dive durations and surfaced more frequently as water temperature increased. The energy requirements of sea snakes were also estimated in the field and showed a doubling of metabolic rate from the cooler dry season to the warmer wet season (section 6.3.3.), which potentially increases their susceptibility to fishing activities that occur in summer months. In many bimodally respiring animals, individuals have the ability to up−regulate cutaneous respiration during periods of stress to prolong dive durations (e.g. Mathie & Franklin 2006). This mechanism is important to understand and can potentially allow sea snakes to prolong their dive durations when caught in trawl nets to increase their chances of survival. Results showed that sea snakes may not have much control over the amount of oxygen they uptake cutaneously, which may severely impede their chances of survival once caught in fishing gear.

The distribution and movement patterns of sea snakes outlined their high degree of exposure to inshore trawl fishing activities (Figure 8.1). The central GBR was highlighted as an area of high sea snake abundance as well as heavily fished trawl grounds. The use of spatial closures (e.g. Marine Protected Areas; MPAs) is effective in reducing the exposure of bycatch species to fishing activities on the GBR (Dryden et al. 2008, McCook et al. 2010), and may be useful in managing fishing−related mortality in sea snakes. However, identifying important habitats for sea snakes is critical to ensure that MPAs function effectively. Here shallow coastal habitats were identified as important habitats for juvenile and gravid sea snakes. Cleveland Bay in particular, is an embayment in the central GBR that is closed to trawling activity and is adjacent to a highly productive trawl ground (Figure 8.2). This area potentially provides juvenile and gravid sea snakes shelter from the potential negative effects of trawl fishing while they remain within the bay. Further long–term data is still required to understand the extent of sea snake movements between shallow protected areas and offshore trawl grounds. However, this study has shown that protected areas, like those within conservation zones in Cleveland Bay, can potentially serve as refugia to populations of sea snakes that are at high risk from trawl fishing.

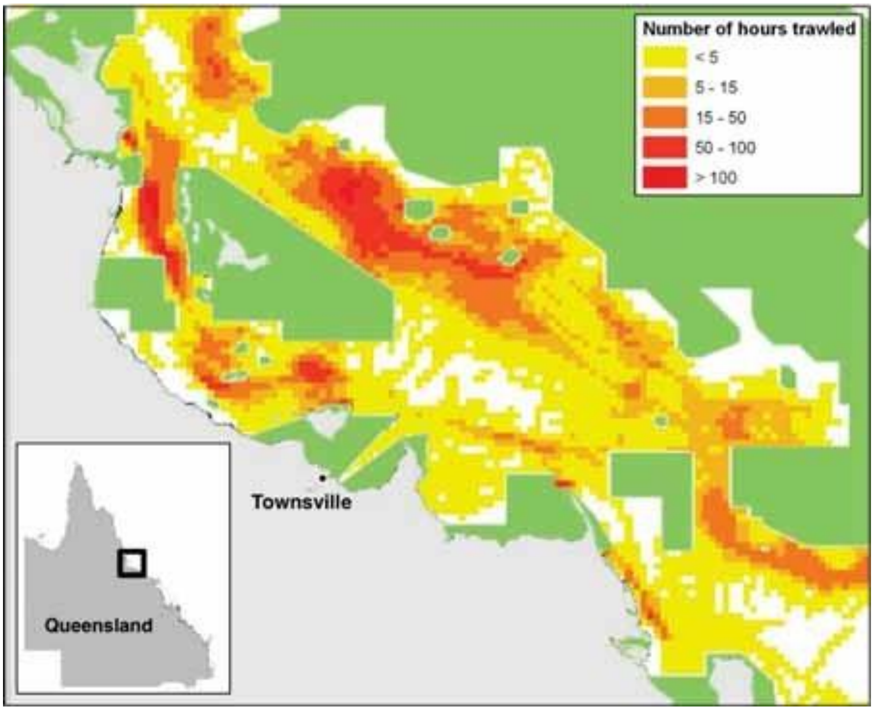

Figure 8.2. Coastal habitats closed to trawl fishing within the GBRMP (green zones) that are adjacent to heavily fished grounds can potentially act as refuge sites for bycatch species like sea snakes. Cleveland Bay, adjacent to Townsville is one such potential refuge habitat (adapted from Grech & Coles 2011).

With increased urbanisation and industrialisation of coastal areas, additional threats like dredging and marine pollution can influence the health of sea snake populations that occupy coastal environments. During the course of this PhD, a sea snake (*Hydrophis elegans*) was encountered entrapped in marine debris (Figure 8.3; see Appendix 8.1 for full record). Entanglement in derelict fishing gear (e.g. ghost nets) and marine flotsam is being recognised globally as a growing cause of strandings or deaths in large marine wildlife (Laist 1997, Derraik 2002). However, there is little known about how smaller, and often less frequently observed animals like sea snakes are impacted by marine debris. The movements and use of urbanised coastal environments by sea snakes may increase their exposure to marine debris causing increased entanglements and strandings. However, as human interactions with sea snakes are less frequent, few instances are reported.

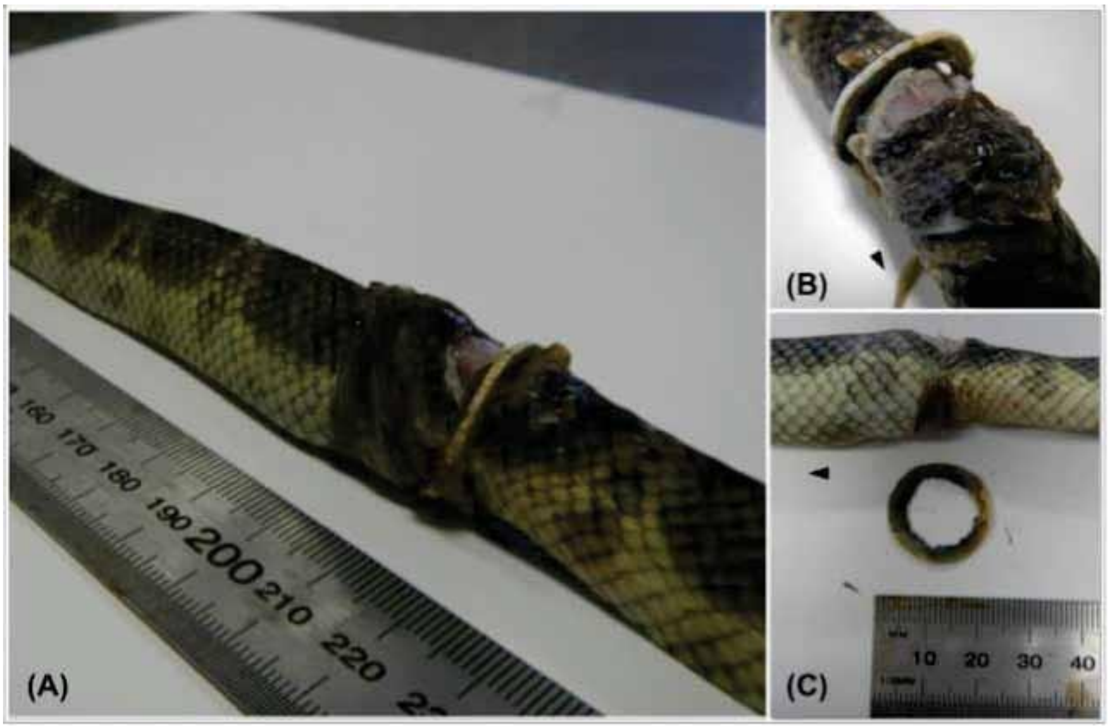

Figure 8.3. (A) *Hydrophis elegans* caught on the coast of Queensland. A ceramic washer was found surrounded in the slough approximately 210mm from the snout. (B) Dorsal view of the severe damage to the vertebral column caused by the ceramic washer. (C) Dramatic difference in the size of the snake posterior and anterior of the wound. Constriction of the body caused by the washer resulted in a major blockage for the passage of food down the oesophagus. Black arrows denotes direction of the head of the snake. See Appendix 8.1 for full details.

8.2. Future directions

This thesis applied new techniques in underwater visual surveys and field and lab based biotelemetry to address fundamental questions around the distribution, spatial ecology and physiology of sea snakes. Although the BRUVS data presented in the present thesis displayed the utility of such methods in assessing ecosystem−scale distribution patterns, one finding from this data was the low diversity of species encountered. Previous work using diver based visual surveys have revealed similar patchy reef−scale distributions on the GBR (Heatwole 1975b, Limpus 1975, Lukoschek et al. 2007), other parts of Australia (Western Australia; Guinea 2012a, Lukoschek et al. 2013) and other sea snake 'hotspots' around the world (New Caledonia; Lukoschek & Shine 2012, Goiran & Shine 2013). These studies were part of larger long−term monitoring projects that used diver based transect surveys which covered small areas. Further large−scale surveys are needed to fully understand the current distribution patterns of sea snakes on the GBR and in other parts of the world, with the highest success of accurate data pooled from a range of sources (e.g. researchƒcommercial fisher trawl surveys, visual surveys, BRUVS). The quality of such large−scale distribution patterns is critical as inaccurate distribution patterns can over− or under−estimate the global conservation status of threatened species (Heatwole & Cogger 2013). New techniques are constantly being developed to allow researchers to gain valuable data covering large spatial scales while still retaining data quality and reducing costs (e.g. Underwater Autonomous Vehicle surveys, drone based aerial visual surveys, etc.). Perhaps these new techniques can be used in future studies to provide high quality data to develop accurate baseline distribution patterns and assess the health of sea snake populations. The establishment of good baseline data will allow future studies to examine how sea snake populations react to environmental conditions in the light of climate change.

This thesis also explored regional scale movement ecology of sea snakes and identified certain habitats as important environment for these animals. The use of biotelemetry to monitor movements of sea snakes has allowed us to gain an in−depth understanding of how individual movement patterns are affected by diel and seasonal environmental conditions. This thesis provides the first data where sea snakes have been monitored for an extended period of time using passive acoustic telemetry (215 day monitoring period), and the first time biotelemetry acceleration sensors have been used to estimate field metabolic rates in this group. The development of smaller power sources and miniaturisation of sensors has allowed for longer term tracking and monitoring of other biological processes (i.e. body temperature, acceleration, heart−rate) in a range of marine animals (Cooke et al. 2004a, Hussey et al. 2015, Wilson et al. 2015). These techniques can be used further in future studies to gain insight on fundamental aspects of sea snake biology that have been difficult to measure in the past. Such data can be used to develop management policies to mitigate threats and conserve sea snake populations where sea snakes are exposed to natural and anthropogenic threats.

Currently, six species of sea snake (9% of total) have been identified by the IUCN Red List assessment as having a high risk of extinction (Elfes et al. 2013). Two species (*Aipysurus apraefrontalis* and *A. foliosquama*), both endemic to Australia, are classified as Critically Endangered (Livingstone 2009). These species are found in protected, healthy reef ecosystems in Western Australia and causes for their declines are not well understood (Guinea 2012a, Lukoschek et al. 2013). There is a need to understand what is causing these declines within protected reef systems and should be a focus for future research. One third of sea snake species (34%; 23 species) assessed by the IUCN are classified as data deficient (Livingstone 2009, Elfes et al. 2013). Basic biological data is urgently required to accurately assess the status of these species. As most species of sea snake occupy muddy coastal waters they are infrequently encountered, and in many cases data deficient species are only known from a few specimens collected as fisheries bycatch with many species not being sighted in 50 years (Livingstone 2009). With little biological data available, the population health and any affects from anthropogenic threats (i.e. trawling, skin trade) are unknown. Despite large annual harvest rates of sea snakes in many regions of Asia (Punay 1975, Van Cao et al. 2014), no species of sea snake are presently protected under the Convention on International Trade in Endangered Species of Flora and Fauna (CITES). For quotas to be set under CITES, non−detrimental findings studies (NDFs) must be completed to estimate the sustainable take for any given species or population (Elfes et al. 2013). Unfortunately, at present, sufficient species−specific information is not available for most species of sea snake to complete NDFs. This highlights a critical need for future species−specific research to better understand the fundamental ecology, fill critical knowledge gaps, implement management and set quotas to determine sustainable harvest of this unique group of marine reptiles.

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Appendices

Appendix 4.5.

The following appendices provide URLs to explore the diel patterns in three−dimensional space use of tagged sea snakes reported in Chapter 4.3.1. These models coincide with figures in the body of the thesis which are listed in parenthases below. These models are provided for readers to be abe to interact with the 3D model and better visualise diel patterns of volumetric space use in individuals monitored in the study. Please refer to Note at the end of the appendicies for a full list of suitable desktop and mobile internet browsers

Appendix 4.5.1.

Three−dimensional model of study site in Cleveland Bay ***(Figure 4.1)***. *Black points* represent locations of acoustic receivers. Depth has been exaggerated for ease of viewing bathymetry. Sea surface represented at highest astronomical tide at Townsville Port. For the interactive version of this data please visit: https:ffdl.dropboxusercontent.comfuf31456301f3DSSfSM1findex.html

Appendix 4.5.2.

Three−dimensional space use by a representative *Hydrophis curtus* within the study site ***(Figure 4.5 A)***. Day−time core (50% 3DKUD; dark red) and extent (95% 3DKUD; light red) 3DKUD as well as night−time core (50% 3DKUD; dark blue) and extent (95% 3DKUD; light blue) 3DKUD are represented. Surrounding bathymetry and sea surface are also rendered to provide context. Black points represent the locations of acoustic receivers within the study site. Close up version of this model is available in Appendix 4.5.3. For the interactive version of this data please visit: https:ffdl.dropboxusercontent.comfuf31456301f3DSSfSM2findex.html

Appendix 4.5.3.

Close up three−dimensional model of diel pattern in space use of a representative *Hydrophis curtus* within Cleveland Bay ***(Figure 4.5 B)***. Day−time core (50% 3DKUD; dark red) and extent (95% 3DKUD; light red) 3DKUD as well as night−time core (50% 3DKUD; dark blue) and extent (95% 3DKUD; light blue) 3DKUD are represented.Depth has been exaggerated for ease of viewing bathymetry. Sea surface represented at highest astronomical tide at Townsville Port. Overall version of this model is available in Appendix 4.5.2. For the interactive version of this data please visit: https:ffdl.dropboxusercontent.comfuf31456301f3DSSfSM3findex.html

Appendix 4.5.4.

Three−dimensional space use by a representative *Hydrophis elegans* within the study site ***(Figure 4.5 C)***. Day−time core (50% 3DKUD; dark red) and extent (95% 3DKUD; light red) 3DKUD as well as night−time core (50% 3DKUD; dark blue) and extent (95% 3DKUD; light blue) 3DKUD are represented. Surrounding bathymetry and sea surface are also rendered to provide context. Black points represent the locations of acoustic receivers within the study site. Close up version of this model is available in Appendix 4.5.5. For the interactive version of this data please visit: https:ffdl.dropboxusercontent.comfuf31456301f3DSSfSM4findex.html

Appendix 4.5.5.

Close up three−dimensional model of diel pattern in space use of a representative Hydrophis elegans within Cleveland Bay ***(Figure 4.5 D)***. Day−time core (50%−3DKUD; dark red) and extent (95%−3DKUD; light red) 3DKUD as well as night−time core (50%−3DKUD; dark blue) and extent (95%−3DKUD; light blue) 3DKUD are represented.Depth has been exaggerated for ease of viewing bathymetry. Sea surface represented at highest astronomical tide at Townsville Port. Overall version of this model is available in Appendix 4.5.4. For the interactive version of this data please visit: https:ffdl.dropboxusercontent.comfuf31456301f3DSSfSM5findex.html

Appendix 4.6.

The following appendices provide all candidate models resulting from Genral Linear Mixed Models (GLMM) reported in Chapter 4.3.2. Models explore the effect of biological and environmental drivers on presence and movement patterns of two species of sea snakes (*Hydrophis curtus* and *H. elegans*) over a **daily** temporal scale. These tables are full versions of the tables provided in the body of the thesis which are listed in the table captions below.

Appendix 4.6.1. Model selection table exploring the effect of biological and environmental drivers on presence/absence and movement (roaming index) of ***Hydrophis curtus*** over a **daily** temporal scale. This table is a full version of Table 4.2. Response variables; SVL: snout–vent length, temp: water temperature, press: air pressure, rain: rainfall, wind: wind speed, tide: daily tidal range. A Generalised Linear Mixed Model (GLMM) framework was used with individuals treated as a random factor (1|ID). The most parsimonious model in each category is represented in bold font.

Model		**df**	**Roaming Index**			**Presence/absence**		
			AICc	**ΔAICc**	***w*AICc**	**AICc**	**ΔAICc**	***w*AICc**
M1	~ 1	2	1576.87	1.4467	0.0327	279.6591	2.1452	0.0256
M2	~ press	3	**1575.42**	**0**	**0.0673**	279.0373	1.5234	0.0350
M3	~ rain	3	1578.78	3.3592	0.0126	280.2823	2.7684	0.0188
M4	~ press + rain	4	1576.60	1.1767	0.0374	280.6645	3.1506	0.0155
M5	~ SVL	3	1576.90	1.4791	0.0321	280.2755	2.7616	0.0188
M6	~ press + SVL	4	1575.92	0.4921	0.0526	280.1214	2.6075	0.0203
M7	~ rain + SVL	4	1578.86	3.4388	0.0121	280.7998	3.2859	0.0145
M8	~ press + rain + SVL	5	1577.24	1.8133	0.0272	281.6301	4.1162	0.0096
M9	~ tide	3	1578.21	2.7824	0.0167	**277.5139**	**0**	**0.0749**
M10	~ press + tide	4	1576.09	0.6645	0.0483	277.9346	0.4207	0.0607
M11	~ rain + tide	4	1580.18	4.7563	0.0062	278.6381	1.1242	0.0427
M12	~ press + rain + tide	5	1577.43	2.0007	0.0248	279.6952	2.1813	0.0252
M13	~ SVL + tide	4	1578.31	2.8811	0.0159	278.0156	0.5017	0.0583
M14	~ press + SVL + tide	5	1576.70	1.2797	0.0355	278.8253	1.3114	0.0389
M15	~ rain + SVL + tide	5	1580.31	4.8882	0.0058	279.0939	1.5800	0.0340

M16	~ press + rain + SVL + tide	6	1578.16	2.7401	0.0171	280.4964	2.9825	0.0169
M17	~ temp	3	1577.05	1.6287	0.0298	281.3027	3.7888	0.0113
M18	~ press + temp	4	1577.44	2.0115	0.0246	280.3810	2.8671	0.0179
M19	~ rain + temp	4	1578.82	3.3911	0.0124	282.1562	4.6423	0.0074
M20	~ press + rain + temp	5	1578.63	3.2093	0.0135	282.1184	4.6045	0.0075
M21	~ SVL + temp	4	1577.24	1.8192	0.0271	282.0316	4.5177	0.0078
M22	~ press + SVL + temp	5	1577.93	2.5086	0.0192	281.4709	3.9570	0.0104
M23	~ rain + SVL + temp	5	1579.06	3.6397	0.0109	282.7576	5.2437	0.0054
M24	~ press + rain + SVL + temp	6	1579.28	3.8512	0.0098	283.1070	5.5931	0.0046
M25	~ tide + temp	4	1578.23	2.8097	0.0165	279.3400	1.8261	0.0301
M26	~ press + tide + temp	5	1578.12	2.6963	0.0175	279.4133	1.8994	0.0290
M27	~ rain + tide + temp	5	1580.10	4.6753	0.0065	280.6063	3.0924	0.0160
M28	~ press + rain + tide + temp	6	1579.47	4.0423	0.0089	281.2569	3.7430	0.0115
M29	~ SVL + tide + temp	5	1578.50	3.0734	0.0145	279.9149	2.4010	0.0226
M30	~ press + SVL + tide + temp	6	1578.74	3.3178	0.0128	280.3559	2.8420	0.0181
M31	~ rain + SVL + tide + temp	6	1580.41	4.9845	0.0056	281.1100	3.5961	0.0124
M32	~ press + rain + SVL + tide + temp	7	1580.21	4.7889	0.0061	282.1208	4.6069	0.0075
M33	~ wind	3	1578.79	3.3696	0.0125	281.4871	3.9732	0.0103
M34	~ press + wind	4	1576.84	1.4146	0.0332	281.0471	3.5332	0.0128
M35	~ rain + wind	4	1580.70	5.2707	0.0048	281.9851	4.4712	0.0080
M36	~ press + rain + wind	5	1577.73	2.3101	0.0212	282.6295	5.1156	0.0058
M37	~ SVL + wind	4	1578.70	3.2742	0.0131	282.2192	4.7053	0.0071
M38	~ press + SVL + wind	5	1577.14	1.7142	0.0286	282.1555	4.6416	0.0074
M39	~ rain + SVL + wind	5	1580.65	5.2212	0.0049	282.6692	5.1553	0.0057
M40	~ press + rain + SVL + wind	6	1578.18	2.7535	0.0170	283.6469	6.1330	0.0035
M41	~ tide + wind	4	1580.19	4.7695	0.0062	279.5345	2.0205	0.0273
M42	~ press + tide + wind	5	1577.69	2.2623	0.0217	279.9428	2.4289	0.0222
M43	~ rain + tide + wind	5	1582.16	6.7399	0.0023	280.6349	3.1210	0.0157
M44	~ press + rain + tide + wind	6	1578.79	3.3687	0.0125	281.7340	4.2201	0.0091
M45	~ SVL + tide + wind	5	1580.20	4.7754	0.0062	280.0445	2.5306	0.0211
M46	~ press + SVL + tide + wind	6	1578.13	2.7097	0.0174	280.7839	3.2700	0.0146
M47	~ rain + SVL + tide + wind	6	1582.20	6.7767	0.0023	281.1353	3.6214	0.0123
M48	~ press + rain + SVL + tide + wind	7	1579.36	3.9340	0.0094	282.5149	5.0010	0.0061
M49	~ temp + wind	4	1578.97	3.5420	0.0115	283.1364	5.6225	0.0045

M50	~ press + temp + wind	5	1578.87	3.4484	0.0120	282.4150	4.9011	0.0065
M51	~ rain + temp + wind	5	1580.70	5.2803	0.0048	283.8772	6.3633	0.0031
M52	~ press + rain + temp + wind	6	1579.75	4.3235	0.0077	284.1502	6.6363	0.0027
M53	~ SVL + temp + wind	5	1579.03	3.6035	0.0111	283.9799	6.4660	0.0030
M54	~ press + SVL + temp + wind	6	1579.18	3.7532	0.0103	283.4913	5.9774	0.0038
M55	~ rain + SVL + temp + wind	6	1580.82	5.3937	0.0045	284.6378	7.1239	0.0021
M56	~ press + rain + SVL + temp + wind	7	1580.19	4.7693	0.0062	285.1559	7.6420	0.0016
M57	~ tide + temp + wind	5	1580.23	4.8007	0.0061	281.3698	3.8559	0.0109
M58	~ press + tide + temp + wind	6	1579.72	4.2980	0.0078	281.3667	3.8528	0.0109
M59	~ rain + tide + temp + wind	6	1582.08	6.6537	0.0024	282.6156	5.1017	0.0058
M60	~ press + rain + tide + temp + wind	7	1580.80	5.3772	0.0046	283.2672	5.7533	0.0042
M61	~ SVL + tide + temp + wind	6	1580.40	4.9742	0.0056	281.9488	4.4349	0.0082
M62	~ press + SVL + tide + temp + wind	7	1580.17	4.7487	0.0063	282.2280	4.7141	0.0071
M63	~ rain + SVL + tide + temp + wind	7	1582.29	6.8643	0.0022	283.1588	5.6449	0.0045
M64	~ press + rain + SVL + tide + temp + wind	8	1581.37	5.9442	0.0034	284.0812	6.5673	0.0028

Appendix 4.6.2. Model selection table exploring the effect of biological and environmental drivers on presenceʃabsence and movement (Roaming index) of ***Hydrophis elegans*** over a **daily** temporal scale. This table is a full version of Table 4.3. Response variables; SVL: snout−vent length, temp: water temperature, press: air pressure, rain: rainfall, wind: wind speed, tide: daily tidal range. A Generalised Linear Mixed Model (GLMM) framework was used with individuals treated as a random factor (1|ID). The most parsimonious model in each category is represented in bold font.

Model		**df**	**Roaming Index**			**Presence/absence**		
			AICc	**ΔAICc**	***w*AICc**	**AICc**	**ΔAICc**	***w*AICc**
M1	~ 1	2	377.3	4.6735	0.0101	113.1	0.3959	0.0588
M2	~ press	3	378.5	5.9403	0.0054	113.4	0.6459	0.0519
M3	~ rain	3	374.9	2.2493	0.0340	115.2	2.4740	0.0208
M4	~ press + rain	4	376.6	3.9687	0.0144	115.5	2.7576	0.0181
M5	~ SVL	3	378.1	5.4890	0.0067	113.4	0.6758	0.0511
M6	~ press + SVL	4	379.5	6.9149	0.0033	113.9	1.2031	0.0393
M7	~ rain + SVL	4	375.7	3.1357	0.0219	115.5	2.7788	0.0179
M8	~ press + rain + SVL	5	377.6	4.9738	0.0087	116.1	3.3462	0.0135
M9	~ tide	3	378.8	6.2221	0.0047	115.2	2.4740	0.0208
M10	~ press + tide	4	380.4	7.7561	0.0022	115.4	2.6992	0.0186
M11	~ rain + tide	4	376.4	3.8045	0.0156	117.3	4.5814	0.0073
M12	~ press + rain + tide	5	378.3	5.7206	0.0060	117.6	4.8393	0.0064
M13	~ SVL + tide	4	379.6	7.0309	0.0031	115.5	2.7905	0.0178
M14	~ press + SVL + tide	5	381.3	8.7143	0.0013	116.0	3.2626	0.0140
M15	~ rain + SVL + tide	5	377.3	4.6748	0.0101	117.7	4.9236	0.0061
M16	~ press + rain + SVL + tide	6	379.3	6.6956	0.0037	118.2	5.4351	0.0047
M17	~ temp	3	379.4	6.7522	0.0036	114.5	1.7850	0.0294
M18	~ press + temp	4	380.4	7.8325	0.0021	115.4	2.7097	0.0185
M19	~ rain + temp	4	377.0	4.3639	0.0118	116.6	3.8934	0.0102
M20	~ press + rain + temp	5	378.6	5.9617	0.0053	117.6	4.8528	0.0063
M21	~ SVL + temp	4	380.2	7.5951	0.0024	114.7	1.9773	0.0267
M22	~ press + SVL + temp	5	381.3	8.6809	0.0014	116.0	3.2330	0.0142
M23	~ rain + SVL + temp	5	377.8	5.2486	0.0076	116.8	4.1121	0.0092
M24	~ press + rain + SVL + temp	6	379.4	6.8475	0.0034	118.1	5.4083	0.0048

M25	~ tide + temp	4	380.9	8.3347	0.0016	116.6	3.8967	0.0102
M26	~ press + tide + temp	5	382.3	9.7194	0.0008	117.5	4.8031	0.0065
M27	~ rain + tide + temp	5	378.5	5.9488	0.0054	118.8	6.0350	0.0035
M28	~ press + rain + tide + temp	6	380.4	7.7851	0.0021	119.7	6.9755	0.0022
M29	~ SVL + tide + temp	5	381.8	9.1568	0.0011	116.8	4.1155	0.0092
M30	~ press + SVL + tide + temp	6	383.2	10.5574	0.0005	118.1	5.3295	0.0050
M31	~ rain + SVL + tide + temp	6	379.4	6.8013	0.0035	119.0	6.2816	0.0031
M32	~ press + rain + SVL + tide + temp	7	381.3	8.6500	0.0014	120.3	7.5353	0.0017
M33	~ wind	3	**372.6**	**0**	**0.1048**	114.8	2.0693	0.0255
M34	~ press + wind	4	374.4	1.7839	0.0430	113.1	0.3337	0.0607
M35	~ rain + wind	4	372.6	0.0271	0.1034	116.9	4.1260	0.0091
M36	~ press + rain + wind	5	374.5	1.8685	0.0412	115.1	2.3830	0.0218
M37	~ SVL + wind	4	374.1	1.4561	0.0506	114.7	1.9735	0.0267
M38	~ press + SVL + wind	5	375.9	3.2671	0.0205	**112.7**	**0**	**0.0717**
M39	~ rain + SVL + wind	5	374.0	1.4051	0.0519	116.7	3.9981	0.0097
M40	~ press + rain + SVL + wind	6	375.9	3.2665	0.0205	114.7	2.0176	0.0261
M41	~ tide + wind	4	374.7	2.0876	0.0369	116.9	4.1270	0.0091
M42	~ press + tide + wind	5	376.5	3.8783	0.0151	115.2	2.4718	0.0208
M43	~ rain + tide + wind	5	374.7	2.1040	0.0366	118.9	6.2029	0.0032
M44	~ press + rain + tide + wind	6	376.5	3.9453	0.0146	117.3	4.5565	0.0073
M45	~ SVL + tide + wind	5	376.2	3.5599	0.0177	116.8	4.0764	0.0093
M46	~ press + SVL + tide + wind	6	378.0	5.3735	0.0071	114.9	2.1589	0.0244
M47	~ rain + SVL + tide + wind	6	376.1	3.4864	0.0183	118.8	6.1183	0.0034
M48	~ press + rain + SVL + tide + wind	7	377.9	5.3424	0.0073	116.9	4.2175	0.0087
M49	~ temp + wind	4	374.7	2.0732	0.0372	116.2	3.5055	0.0124
M50	~ press + temp + wind	5	376.5	3.9126	0.0148	115.0	2.3180	0.0225
M51	~ rain + temp + wind	5	374.7	2.1239	0.0362	118.3	5.5976	0.0044
M52	~ press + rain + temp + wind	6	376.6	4.0350	0.0139	117.1	4.3822	0.0080
M53	~ SVL + temp + wind	5	376.1	3.5186	0.0180	116.0	3.2586	0.0141
M54	~ press + SVL + temp + wind	6	378.0	5.4417	0.0069	114.8	2.0858	0.0253
M55	~ rain + SVL + temp + wind	6	376.1	3.4745	0.0184	118.0	5.3193	0.0050
M56	~ press + rain + SVL + temp + wind	7	378.1	5.4733	0.0068	116.9	4.1245	0.0091
M57	~ tide + temp + wind	5	376.8	4.1897	0.0129	118.3	5.6067	0.0043
M58	~ press + tide + temp + wind	6	378.6	6.0354	0.0051	117.2	4.4779	0.0076

M59	~ rain + tide + temp + wind	6	376.8	4.2299	0.0126	120.4	7.7186	0.0015
M60	~ press + rain + tide + temp + wind	7	378.7	6.1405	0.0049	119.3	6.5812	0.0027
M61	~ SVL + tide + temp + wind	6	378.3	5.6492	0.0062	118.1	5.4196	0.0048
M62	~ press + SVL + tide + temp + wind	7	380.2	7.5792	0.0024	117.0	4.2729	0.0085
M63	~ rain + SVL + tide + temp + wind	7	378.2	5.5803	0.0064	120.2	7.5018	0.0017
M64	~ press + rain + SVL + tide + temp + wind	8	380.2	7.5817	0.0024	119.1	6.3544	0.0030

Appendix 4.7.

The following appendices provide all candidate models resulting from Genral Linear Mixed Models (GLMM) reported in Chapter 4.3.2. Models explore the effect of biological and environmental drivers on the movement patterns (Roaming index) and three−dimensional home range of two species of sea snakes (*Hydrophis curtus* and *H. elegans*) over a **monthly** temporal scale. These tables are full versions of the tables provided in the body of the thesis which are listed in the table captions below.

Appendix 4.7.1. Model selection table examining the effects of environmental and biological drivers on the movement (Roaming index) and three−dimensional home range (50%3DKUD: core home range; 95%3DKUD: extent of home range) of ***Hydrophis curtus*** over a **monthly** temporal scale. This table is a full version of Table 4.4. Response variables; SVL: snout−vent length, temp: water temperature, press: air pressure, rain: rainfall, wind: wind speed. A Generalised Linear Mixed Model (GLMM) framework was used with individuals treated as a random factor (1|ID). The most parsimonious model in each category is represented in bold font.

Model		**df**	**Roaming Index**			**df**	**50%3DKUD**			**95%3DKUD**		
			AICc	**ΔAICc**	***w*AICc**		**AICc**	**ΔAICc**	***w*AICc**	**AICc**	**ΔAICc**	***w*AICc**
M1	~ 1	2	**124.694**	**0**	**0.2322**	3	920.162	1.8454	0.0605	997.933	8.1414	0.0062
M2	~ press	3	126.703	2.0085	0.0851	4	919.680	1.3635	0.0770	996.606	6.8137	0.0121
M3	~ rain	3	126.418	1.7238	0.0981	4	**918.316**	**0**	**0.1523**	**989.792**	**0**	**0.3657**
M4	~ press + rain	4	129.274	4.5797	0.0235	5	921.474	3.1578	0.0314	991.240	1.4475	0.1773
M5	~ SVL	3	126.067	1.3733	0.1169	4	923.019	4.7024	0.0145	1000.177	10.3846	0.0020
M6	~ press + SVL	4	128.486	3.7920	0.0349	5	922.837	4.5202	0.0159	999.381	9.5891	0.0030
M7	~ rain + SVL	4	128.437	3.7425	0.0357	5	921.370	3.0538	0.0331	992.944	3.1520	0.0756
M8	~ press + rain + SVL	5	131.577	6.8830	0.0074	6	924.869	6.5523	0.0058	994.738	4.9456	0.0308
M9	~ temp	3	127.033	2.3392	0.0721	4	920.951	2.6347	0.0408	996.418	6.6262	0.0133
M10	~ press + temp	4	129.295	4.6004	0.0233	5	922.187	3.8706	0.0220	999.347	9.5553	0.0031
M11	~ rain + temp	4	129.245	4.5505	0.0239	5	921.465	3.1491	0.0315	992.680	2.8884	0.0863
M12	~ press + rain + temp	5	132.339	7.6451	0.0051	6	924.938	6.6216	0.0056	994.396	4.6042	0.0366
M13	~ SVL + temp	4	128.679	3.9847	0.0317	5	924.089	5.7729	0.0085	999.045	9.2526	0.0036
M14	~ press + SVL + temp	5	131.546	6.8517	0.0076	6	925.670	7.3540	0.0039	1002.394	12.6023	0.0007
M15	~ rain + SVL + temp	5	131.594	6.9003	0.0074	6	924.841	6.5250	0.0058	996.189	6.3969	0.0149

M16	~ press + rain + SVL + temp	6	135.036	10.3420	0.0013	7	928.731	10.4148	0.0008	998.315	8.5234	0.0052
M17	~ wind	3	127.282	2.5882	0.0637	4	918.996	0.6796	0.1084	1000.228	10.4356	0.0020
M18	~ press + wind	4	129.560	4.8656	0.0204	5	919.385	1.0682	0.0893	998.970	9.1779	0.0037
M19	~ rain + wind	4	129.249	4.5552	0.0238	5	919.094	0.7779	0.1032	992.878	3.0864	0.0781
M20	~ press + rain + wind	5	132.402	7.7082	0.0049	6	922.491	4.1749	0.0189	994.682	4.8904	0.0317
M21	~ SVL + wind	4	128.923	4.2288	0.0280	5	922.151	3.8347	0.0224	1002.799	13.0070	0.0005
M22	~ press + SVL + wind	5	131.642	6.9481	0.0072	6	922.893	4.5769	0.0154	1002.132	12.3398	0.0008
M23	~ rain + SVL + wind	5	131.571	6.8765	0.0075	6	922.511	4.1946	0.0187	996.381	6.5894	0.0136
M24	~ press + rain + SVL + wind	6	135.069	10.3748	0.0013	7	926.366	8.0492	0.0027	998.591	8.7995	0.0045
M25	~ temp + wind	4	129.887	5.1928	0.0173	5	920.290	1.9737	0.0568	998.900	9.1081	0.0038
M26	~ press + temp + wind	5	132.450	7.7559	0.0048	6	922.557	4.2403	0.0183	1002.104	12.3118	0.0008
M27	~ rain + temp + wind	5	132.366	7.6717	0.0050	6	922.568	4.2518	0.0182	996.174	6.3815	0.0150
M28	~ press + rain + temp + wind	6	135.823	11.1289	0.0009	7	926.329	8.0131	0.0028	998.256	8.4639	0.0053
M29	~ SVL + temp + wind	5	131.837	7.1426	0.0065	6	923.790	5.4740	0.0099	1001.905	12.1127	0.0009
M30	~ press + SVL + temp + wind	6	135.049	10.3552	0.0013	7	926.456	8.1400	0.0026	1005.603	15.8113	0.0001
M31	~ rain + SVL + temp + wind	6	135.079	10.3850	0.0013	7	926.422	8.1057	0.0026	1000.095	10.3030	0.0021
M32	~ press + rain + SVL + temp + wind	7	138.943	14.2492	0.0002	8	930.682	12.3658	0.0003	1002.664	12.8722	0.0006

Appendix 4.7.2. Model selection table examining the effects of environmental and biological drivers on the movement (Roaming index) and three−dimensional home range (50%3DKUD: core home range; 95%3DKUD: extent of home range) of ***Hydrophis elegans*** over a **monthly** temporal scale. This table is a full version of Table 4.5. Response variables; SVL: snout−vent length, temp: water temperature, press: air pressure, rain: rainfall, wind: wind speed. A Generalised Linear Mixed Model (GLMM) framework was used with individuals treated as a random factor (1|ID). The most parsimonious model in each category is represented in bold font.

Model		**df**	**Roaming Index**			**df**	**50%3DKUD**			**95%3DKUD**		
			AICc	**ΔAICc**	***w*AICc**		**AICc**	**ΔAICc**	***w*AICc**	**AICc**	**ΔAICc**	***w*AICc**
M1	~ 1	2	**49.80**	**0**	**0.2578**	3	**477.0**	**0**	**0.5527**	**495.6**	**0**	**0.5014**
M2	~ press	3	51.49	1.6883	0.1108	4	481.0	4.0258	0.0738	499.2	3.6570	0.0806
M3	~ rain	3	51.46	1.6571	0.1126	4	481.6	4.6232	0.0548	500.2	4.6246	0.0497
M4	~ press + rain	4	55.03	5.2273	0.0189	5	486.4	9.4875	0.0048	502.9	7.3537	0.0127
M5	~ SVL	3	52.77	2.9685	0.0584	4	480.3	3.3529	0.1034	498.8	3.1936	0.1016
M6	~ press + SVL	4	55.04	5.2344	0.0188	5	486.1	9.1202	0.0058	504.6	9.0274	0.0055
M7	~ rain + SVL	4	54.93	5.1327	0.0198	5	486.6	9.6001	0.0045	505.0	9.4763	0.0044
M8	~ press + rain + SVL	5	59.26	9.4608	0.0023	6	493.3	16.3289	0.0002	510.9	15.3583	0.0002
M9	~ temp	3	50.97	1.1656	0.1439	4	481.7	4.7128	0.0524	500.3	4.7128	0.0475
M10	~ press + temp	4	54.60	4.7991	0.0234	5	486.8	9.8971	0.0039	504.6	9.0559	0.0054
M11	~ rain + temp	4	54.54	4.7395	0.0241	5	487.7	10.7075	0.0026	506.2	10.6538	0.0024
M12	~ press + rain + temp	5	58.79	8.9899	0.0029	6	495.2	18.2847	0.0001	511.6	16.0254	0.0002
M13	~ SVL + temp	4	54.57	4.7678	0.0238	5	486.6	9.6363	0.0045	505.0	9.3830	0.0046
M14	~ press + SVL + temp	5	58.93	9.1305	0.0027	6	494.2	17.2614	0.0001	512.4	16.8424	0.0001
M15	~ rain + SVL + temp	5	58.85	9.0477	0.0028	6	495.2	18.2120	0.0001	513.6	18.0323	0.0001
M16	~ press + rain + SVL + temp	6	64.07	14.2656	0.0002	7	506.5	29.5031	0.0000	524.0	28.4692	0.0000
M17	~ wind	3	52.32	2.5217	0.0731	4	480.2	3.2107	0.1110	498.1	2.5145	0.1426
M18	~ press + wind	4	54.83	5.0295	0.0209	5	486.0	9.0002	0.0061	503.0	7.3853	0.0125
M19	~ rain + wind	4	54.38	4.5786	0.0261	5	486.1	9.1910	0.0056	503.6	8.0677	0.0089
M20	~ press + rain + wind	5	58.68	8.8743	0.0030	6	494.7	17.7521	0.0001	511.2	15.6137	0.0002
M21	~ SVL + wind	4	55.86	6.0584	0.0125	5	485.5	8.4993	0.0079	503.3	7.6823	0.0108
M22	~ press + SVL + wind	5	59.11	9.3060	0.0025	6	493.8	16.8544	0.0001	511.3	15.7126	0.0002
M23	~ rain + SVL + wind	5	58.59	8.7902	0.0032	6	494.1	17.1215	0.0001	511.8	16.2632	0.0001
M24	~ press + rain + SVL + wind	6	63.80	14.0001	0.0002	7	506.4	29.4525	0.0000	523.8	28.2167	0.0000

M25	~ temp + wind	4	54.42	4.6156	0.0256	5	486.3	9.3377	0.0052	503.9	8.2885	0.0080
M26	~ press + temp + wind	5	58.78	8.9770	0.0029	6	494.8	17.7986	0.0001	511.8	16.1786	0.0002
M27	~ rain + temp + wind	5	58.57	8.7714	0.0032	6	494.9	17.9903	0.0001	512.4	16.8603	0.0001
M28	~ press + rain + temp + wind	6	63.48	13.6797	0.0003	7	507.9	30.9371	0.0000	524.2	28.5962	0.0000
M29	~ SVL + temp + wind	5	58.74	8.9429	0.0029	6	494.2	17.2015	0.0001	511.9	16.3670	0.0001
M30	~ press + SVL + temp + wind	6	64.08	14.2757	0.0002	7	506.9	29.9541	0.0000	524.5	28.8787	0.0000
M31	~ rain + SVL + temp + wind	6	63.82	14.0181	0.0002	7	507.3	30.3125	0.0000	525.0	29.4632	0.0000
M32	~ press + rain + SVL + temp + wind	7	70.04	20.2353	0.0000	8	528.4	51.4212	0.0000	545.6	50.0511	0.0000

Appendix 4.8.

The following appendices provide URLs to explore the monthly patterns in three−dimensional space use of tagged *Hydrophis curtus* sea snakes reported in Chapter 4.3.2. The first model (Appendix 4.8.1) coincides with Figure 4.9 in the body of the thesis. The other two appendicies supply data from two additional individuals. These models are provided for readers to be abe to interact with the 3D model and better visualise monthly patterns of volumetric space use in individuals monitored in the study. Please refer to Note at the end of the appendices for a full list of suitable desktop and mobile internet browsers.

Appendix 4.8.1. Three−dimensional model of a tagged *Hydrophis curtus* (T9) with the extent of home range (95% 3DKUD) represented for each month (February – September) over the monitored period. Depth has been exaggerated for ease of viewing bathymetry. Sea surface represented at highest astronomical tide at Townsville Port. Screenshots of this model are presented in Figure 4.9. For the interactive version of this data please visit: https:ƒƒdl.dropboxusercontent.comƒuƒ31456301ƒEnvDriversƒS3-6740ƒindex.html

Appendix 4.8.2. Three−dimensional model of a tagged *Hydrophis curtus* (T15) with the extent of home range (95% 3DKUD) represented for each month (April – October) over the monitored period. Depth has been exaggerated for ease of viewing bathymetry. Sea surface represented at highest astronomical tide at Townsville Port. For the interactive version of this data please visit: https:ƒƒdl.dropboxusercontent.comƒuƒ31456301ƒEnvDriversƒS4-6746ƒindex.html

Appendix 4.8.3. Three−dimensional model of a tagged *Hydrophis curtus* (T16) with the extent of home range (95%3DKUD) represented for each month (April – November) over the monitored period. Depth has been exaggerated for ease of viewing bathymetry. Sea surface represented at highest astronomical tide at Townsville Port. For the interactive version of this data please visit: https:ƒƒdl.dropboxusercontent.comƒuƒ31456301ƒEnvDriversƒS5-8866ƒindex.html

Appendix 6.1.

The following appendix table provides individual–level calibration equations for twenty individuals in two species of sea snakes (*Hydrophis curtus* and *H. elegans*) that defind the relationship between body acceleration (x) and total oxygen consumption (y) at four different temperature treatments (21, 24, 27 and 30˚C). Linear relationships were described for all models. Species–level relationships (reported in Figure 6.6, Chapter 6.3.2. were used where sufficient data was not available to produce robust individual–level relationships (denoted as '–' in the table below). Morphometric data for each individual presented here is also available in Table 6.1.

Species	**ID**	**Temperature treatment (˚C)**	**Individual-level calibration equations (y = total oxygen consumption; x = body acceleration)**	**Coefficient of determination (R-squared value)**
Spine–bellied sea snake (*Hydrophis curtus*)	LC10	21	y = −0.0197x + 1.3629	0.00021
		24	y = 0.6464x + 1.6742	0.13798
		27	y = 0.5005x + 2.7365	0.22438
		30	y = 0.0867x + 3.102	0.00283
	LC11	21	y = 0.6955x + 1.246	0.18218
		24	y = 0.5253x + 1.7117	0.10131
		27	-	-
		30	y = 0.1671x + 2.3513	0.00264
	LC12	21	y = 0.5617x + 1.5556	0.22665
		24	y = 1.0526x + 1.7643	0.34511
		27	y = 0.4745x + 2.5563	0.23179
		30	y = 0.8228x + 2.8732	0.033574
	LC13	21	-	-
		24	-	-
		27	y = 0.9642x + 1.2033	0.52933
		30	y = 0.55x + 1.7124	0.28384
	LC2	21	y = 0.4582x + 0.7193	0.10688
		24	-	-
		27	y = 1.0383x + 0.5779	0.55544
		30	y = 0.4321x + 1.3935	0.05419
	LC4	21	y = 0.1993x + 1.1491	0.02134
		24	-	-
		27	y = 1.0489x + 0.6567	0.70765
		30	y = 0.2885x + 1.4412	0.09476

	LC5	21	y = 0.3362x + 0.7992	0.07496
		24	-	-
		27	-	-
		30	-	-
	LC6	21	y = 0.6897x + 0.3968	0.48785
		24	-	-
		27	y = 1.0332x + 1.3565	0.45688
		30	y = 0.6077x + 2.7789	0.11676
	LC7	21	y = 0.0868x + 1.3017	0.00704
		24	-	-
		27	y = 0.8214x + 2.6167	0.33912
		30	y = 1.1925x + 2.4478	0.45335
	LC8	21	y = 0.4065x + 1.294	0.08431
		24	-	-
		27	y = 0.5927x + 1.4494	0.20591
		30	y = 0.3572x + 2.6181	0.02598
	LC9	21	y = 1.0574x + 0.7433	0.17579
		24	y = 0.8723x + 1.274	0.18166
		27	y = 0.4482x + 1.8498	0.11154
		30	y = 0.1858x + 2.0626	0.02605
Elegant sea snake (*Hydrophis elegans*)	HE1	21	y = 0.5621x + 0.4577	0.31275
		24	-	-
		27	y = 1.2413x + 1.0669	0.27586
		30	y = 0.3891x + 0.8968	0.07314
	HE10	21	-	-
		24	y = −0.2309x + 2.1335	0.02296
		27	y = 1.2089x + 2.26	0.21249
		30	y = 1.9501x + 2.1074	0.32035
	HE3	21	y = 0.4384x + 0.3024	0.24429
		24	-	-
		27	y = 0.5847x + 0.6964	0.08461
		30	y = −0.0324x + 1.2098	0.00014
	HE4	21	y = 0.5704x + 0.3785	0.28222
		24	y = 1.0248x + 0.3999	0.62914
		27	-	-
		30	y = 0.0298x + 1.3315	0.00239

HE5	21	$y = 1.0658x + 0.9045$	0.22391
	24	$y = 0.7769x + 1.157$	0.09096
	27	$y = 1.2359x + 1.5879$	0.13938
	30	$y = 1.6433x + 2.5105$	0.41838
HE6	21	$y = 0.5737x + 0.5662$	0.11715
	24	$y = 0.4072x + 0.7726$	0.05919
	27	$y = 0.6874x + 1.1599$	0.19687
	30	$y = 0.2771x + 1.3669$	0.0512
HE7	21	$y = 0.1065x + 0.7015$	0.00654
	24	$y = 0.4858x + 1.003$	0.08872
	27	$y = 0.47x + 1.3754$	0.0387
	30	-	-
HE8	21	$y = 0.6402x + 0.6432$	0.14412
	24	$y = -0.3105x + 1.4774$	0.00968
	27	$y = 0.458x + 1.6591$	0.04034
	30	$y = -0.3111x + 2.1389$	0.01943
HE9	21	$y = 1.4156x + 0.738$	0.50277
	24	$y = 0.846x + 1.641$	0.21525
	27	$y = 1.0576x + 2.3405$	0.2348
	30	$y = 0.7199x + 2.9606$	0.12709

Appendix 8.1.

The following appendix presents data illustrating the effects of the emerging anthropogenic threat of marine debris on sea snakes. This is a record of a sea snake (*Hydrophis elegans*) entrapped in maine debris which was encountered during the field component of my PhD.

Udyawer, V., Read, M. A., Hamann, M., Simpfendorfer, C. A. & Heupel, M. R. (2013). First record of sea snake (*Hydrophis elegans*, Hydrophiinae) entrapped in marine debris. *Marine Pollution Bulletin,* ***73***(1), 336−338.

First record of sea snake (*Hydrophis elegans*, Hydrophiinae) entrapped in marine debris.

Abstract:

Entanglement in derelict fishing gear and other marine debris is a major threat to the survival of large marine wildlife like cetaceans, sea birds and sea turtles. However, no previous reports of entanglement or entrapment have been recorded in sea snakes (Hydrophiinae). We report here on a sea snake (*Hydrophis elegans*) found with a ceramic washer encircling its body captured from the north−east coast of Queensland, Australia. The ring had constricted the body and over time caused extensive damage to the underlying tissues. A post−mortem examination showed the snake was severely emaciated as the ring restricted the passage of food to the stomach and intestine. This is the first record of mortality due to marine debris entrapment in sea snakes.

Keywords: Sea snake, Marine Debris, Entanglement

With the ever−increasing accumulation of derelict fishing gear and marine debris in the world's oceans, it is evident that entanglement and entrapment pose a great threat to the survival of marine wildlife (Laist 1997, Katsanevakis 2008, Gregory 2009). Large marine wildlife like cetaceans, pinnipeds, dugongs, sea turtles and seabirds are prone to entanglement in derelict fishing gear as well as marine debris. Entanglement in derelict fishing gear (e.g. ghost nets) and marine flotsam is a growing cause of strandings or deaths in large marine wildlife reported along the coast of Queensland, Australia (Kiessling 2003, Verlis et al. 2013, Wilcox et al. 2013). However, little is known about how smaller, and often less frequently observed animals like sea snakes are impacted by marine debris. Sea snakes, that may initially be thought to have little interaction with marine debris, may be just as badly affected by this problem, yet as human interactions with sea snakes are less frequent, few instances are reported.

In the past there have been isolated reports of terrestrial and semi−aquatic snakes being entangled or entrapped in mesh netting and other plastic debris (Herrington 1985, Fauth & Welter 1994, Kapfer & Paloski 2011). Ortega and Zaidan III (2009) found 13 individuals of *Nerodia rhombifer* entrapped in ring−shaped flotsam over a three−year tagging project in one location in North America. They concluded that these instances of entrapment significantly increased the mortality of these individuals in an otherwise highly productive environment. In the marine environment, there have been no reports, thus far, of sea snake or other aquatic snake entanglement in marine debris.

An adult elegant sea snake (*Hydrophis elegans*; Male, snout−vent length: 1130mm) was encountered during a field trip as part of a long−term movement study of sea snakes in Cleveland Bay (19.15’11’’S, 146.55’47’’W), off Townsville, Queensland, Australia. When found, the snake was swimming weakly at the surface and was caught using a dipnet from the survey vessel. The poor condition of the snake was noted, as the small girth of the snake was disproportionate to its length. The snake also showed signs of recent shedding, as a large amount of slough was found around parts of the body. It was also noted that there was an unusual ‘ring’ of sloughed tissue tightly encircling the body of the snake. A decision was made to transport the snake back to James Cook University, Townsville, with the intention to allow it to recover overnight and then to remove the ring of sloughed tissue, tag and process the animal and release it the following evening. However, the snake did not survive the transport back to the facilities.

A necropsy was conducted the next day to determine the cause of death. On closer inspection, the ‘ring’ of accumulated slough around the anterior end of the torso concealed a ceramic washer, which completely encircled the body of the animal (Fig. 1). Once the slough was removed, it became evident that the internal diameter of the ceramic washer was smaller than the diameter of the snake and the constriction had caused abrasion of the skin to expose the underlying muscle and severe damage to tissue around the wound site and the vertebral column (Fig. 2). The position of the washer was anterior to the stomach and the constriction had restricted the passage of food. The stomach and intestines were found to be empty. A small blockage of the oesophagus was found just anterior to the ceramic washer

Fig. 1. *Hydrophis elegans* caught on the coast of Queensland. A ceramic washer was found surrounded in the slough approximately 210mm from the snout.

Fig. 2. Dorsal view of the severe damage to the vertebral column caused by the ceramic washer. Black arrow denotes direction of the head of the snake.

Fig. 3. Lateral view of damage caused by the ceramic washer. Dorsally, damage to the skin and vertebral column, and ventrally, tissue damage and lacerations caused by the constriction. Black arrow denotes direction of the head of the snake.

Fig. 4. Dramatic difference in the size of the snake posterior and anterior of the wound. Constriction of the body caused by the washer resulted in a major blockage for the passage of food down the oesophagus. Black arrow denotes direction of the head of the snake.

(Fig. 3). Once the washer was removed, a marked difference in the size of the snake was observed posterior and anterior to the site of the wound (Fig. 4).

The source of the washer is unknown, however as it is ceramic, and denser than water, it would have been lying on the seabed. Coastal sea snakes like *H. elegans* forage by burrowing into hollows and feed on small fish and eel like prey (Voris & Voris 1983). This may explain how the snake would have initially been entrapped within the washer. As the snake would have tried to escape out of the washer by rubbing its body on surrounding surfaces, the washer would have been forced further back along the body and become lodged, held in place by the backward–facing scales, from where it would not have been able to remove it on its own. Given the internal diameter of the ring and the size of the snake, it would appear that the snake had grown substantially since becoming entrapped, with much of the tissue damage resulting from this growth. Similar damage has been reported to sharks that swim into plastic straps from bait boxes (Cliff et al. 2002).

This is the first record of sea snakes (Hydrophiinae) being entrapped in marine debris. A recent global assessment of the conservation status of sea snakes has concluded just how poorly this group of animals is understood and the need for improved understanding of threats acting on their populations (Elfes et al. 2013). This incident highlights how little is known about the effects of marine debris on marine snakes, and the need for better reporting of strandings and entanglements of marine snakes.

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Note on viewing interactive 3D plots

Interactive three–dimensional plots provided in the appendices (appendix 4.1 & 4.4) can be viewed by opening the provided URLs using desktop or mobile internet browsers that support WebGL. The following browsers can be used:

Desktop browsers:

- Google Chrome (> version 9) [*Recommended*]
- Safari (> version 5.1; disabled by default) – to enable open the Safari menu and select Preferences. Then, click the Advanced tab in the Preferences window. Then, at the bottom of the window, check the Show Develop menu in menu bar checkbox. Then, open the Develop menu in the menu bar and select Enable WebGL.
- Internet Explorer – partially supported in Internet Explorer 11. WebGL support can also be manually added to earlier versions of Internet Explorer using third–party plugins such as IEWebGL.
- Mozilla Firefox (> version 4.0), Opera (version 11 & 12; disabled by default)

Mobile browsers:

- Google Chrome mobile browser (> version 25) [*Recommended*]
- iOS – supported through mobile Safari browser in iOS 8
- Android – supported though Google Chrome browser
- Internet Explorer – supported on Windows Phone 8.1
- BlackBerry PlayBook – supported via WebWorks and browser in PlayBook OS 2.00
- Firefox for mobile (> version 4) and Firefox OS
- Maemo (> PR1.2 firmware update), Opera Mobile 12, Tizen, Wbuntu Touch, WebOS