

**THE TROPHIC AND SPATIAL ECOLOGY OF
JUVENILE PORCUPINE RAYS *UROGYMNUS*
ASPERRIMUS AT THE REMOTE ST.
JOSEPH ATOLL**

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Abstract

Little information exists for the widely occurring but rare porcupine ray *Urogymnus asperrimus*. This is a concern given that it is a vulnerable species and likely plays an important ecological role in tropical atoll ecosystems. The aims of this thesis were to investigate the trophic and spatial ecology of juvenile porcupine rays within the St. Joseph Atoll, which is hypothesized to be functioning as a nursery for this species.

Specific objectives were to determine i) the dietary composition and resource selectivity displayed by juvenile porcupine rays, ii) residency to the atoll, space use, and seasonality in movements, and iii) whether environmental factors affect short-term movements.

Gastric lavage was used to collect stomach contents from 55 juveniles and sediment samples were collected. Thirteen juveniles were implanted with acoustic transmitters and monitored for a year by an array of 88 acoustic receivers situated in and around the St. Joseph Atoll.

Porcupine rays appeared to be generalist and opportunistic feeders, foraging predominantly on annelids with the highest environmental availability. Polychaetes of the family Capitellidae were the most important prey item (Index of Importance = 35%). Rays only fed on deep infaunal prey, likely because of their foraging behaviour, suggesting they may influence this community. There was a size-related shift in the crustacean families consumed.

The tagged rays displayed high residency to the atoll (mean residency index of

64%) and restricted movements, with small core use and activity space areas (mean of 0.5km² and 3km² respectively) and the majority of detections were recorded within 1km of their tagging locations. The rays favoured the sand flats where 88% of detections occurred. Transient use of the lagoon and fringe reef peaked in the north-west monsoon season, indicating a seasonal usage of these habitats. The effects of temperature and water depth on movements were manifested as diel and tidal cyclical patterns in presence.

Evidence illustrates that the St. Joseph Atoll constitutes an important nursery for this species, which has been declared a Marine Protected Area. A major determinant behind the dependence of this nursery habitat is related to predator avoidance. Thermoregulatory behaviours were identified, suggesting that this species is vulnerable to climate change.

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Chapter 1

Introduction



The chondrichthyans or cartilaginous fishes (consisting of sharks, batoids, and chimaeras) are a primitive, evolutionarily conserved class that have survived in diverse ecosystems for over 400 million years (Fowler, 2005; Last & Stevens, 2009; Tilley, 2011). Batoids (i.e. rays, skates and sawfish) in particular are considered to be the most successful chondrichthyan order in terms of number of species (making up roughly 630 of the approximate 1170 chondrichthyan species) (Aschliman *et al.*, 2012) as well as morphological variability (Rosenberger, 2001; Aschliman *et al.*, 2012; Franklin *et al.*, 2014). Batoids are extremely widely distributed and occupy multiple habitats ranging from polar latitudes to the tropics, from the shoreline to depths of about 3000 meters, in pelagic, coastal, abyssal and freshwater ecosystems (McEachran & Aschliman, 2004; Fowler, 2005; Last & Stevens, 2009; Tilley, 2011).

Despite the wide-ranging habitats of batoids, rays specifically are most commonly found in shallow coastal and shelf regions (Fowler, 2005) where they often make up a significant portion of the fish community biomass (O'Shea, 2012). Within these ecosystems, rays are hypothesized to play important ecological roles. Many species are benthic predators (Smith & Merriner, 1985; Wetherbee & Cortés, 2004; Navia *et al.*, 2007) and they have been shown to regulate the size and dynamics of their prey communities (VanBlaricom, 1982; Thrush *et al.*, 1994; Wetherbee & Cortés, 2004; Navia *et al.*, 2007; O'Shea *et al.*, 2013). This is well illustrated by the widespread loss of shellfish in Chesapeake Bay, which was attributed to predation by schooling cownose rays *Rhinoptera bonasus* (Smith & Merriner, 1985; Peterson *et al.*, 2001; Myers *et al.*, 2007). Rays are also understood to be mesopredators, providing critical links between higher and lower trophic levels (Wetherbee & Cortés, 2004; Vaudo & Heithaus, 2011; O'Shea *et al.*, 2013). Given their position in the food web, they mediate changes brought about by apex predator loss (Myers *et al.*, 2007; Heithaus *et al.*, 2008; Baum & Worm, 2009; Vaudo & Heithaus, 2011). Lastly, rays are known to be agents of bioturbation and through their feeding behaviour they modify the physical, biological, and chemical conditions of the substrate over which they occur (Howard *et al.*, 1977; O'Shea *et al.*, 2012). The process of bioturbation has been implicated in damage done to eelgrass and turtlegrass beds through the physical disturbance of the sediment (Orth, 1975; Ogden, 1980; Zieman, 1982; Valentine *et al.*, 1994; Nelson & Brown, 2009), and it alters the geochemistry of the substrate

by increasing the amount of oxygenated water passing deeper into the sediment and the amount of inorganic nutrients being flushed out (Lohrer *et al.*, 2004).

Given these ecological roles, the increasing evidence of declines in chondrichthyan populations globally and across diversity habitats (Friedlander & DeMartini, 2002; Myers & Worm, 2003; Baum & Myers, 2004; Shepherd & Myers, 2005; Robbins *et al.*, 2006; Cortés *et al.*, 2007; Baum & Worm, 2009; Dulvy *et al.*, 2014) is a cause for concern. Stingrays belonging to the family Dasyatidae are considered the fifth most vulnerable chondrichthyan family (Dulvy *et al.*, 2014) and population declines have mainly been attributed to fishing pressure given their conservative life history strategies (Camhi, 1998; Fowler, 2005; Frisk, 2010). Rays are a common by-catch species in various fisheries (White *et al.*, 2006; Piovano *et al.*, 2010; Clarke *et al.*, 2014) and are targeted by a number of artisanal fisheries, for example in Mexico (Smith *et al.*, 2007, 2008), the Gulf of California (Bizzarro *et al.*, 2009), and in Bangladesh (Jit *et al.*, 2012). Rays are also vulnerable to other extrinsic threats including climate change (Chin *et al.*, 2010), habitat destruction (Camhi, 1998; Lotze *et al.*, 2006), and pollution (including the bioaccumulation of heavy metals (Escobar-Sánchez *et al.*, 2014)).

These population declines have resulted in calls for management action and conservation planning (Kinney & Simpfendorfer, 2009). When devising a management plan, it is important to consider all life-cycle stages of a species (Heupel *et al.*, 2007), but it has been suggested that these plans should target first the most vulnerable life-stages (Kinney & Simpfendorfer, 2009). There has been emphasis placed on identifying and protecting "essential fish habitats" (NOAA, 1996), and for sharks in particular, this has been centered around inshore nursery areas (Kinney & Simpfendorfer, 2009).

Nurseries are defined as areas where gravid females give birth and where the young spend their first weeks, months or years (Castro, 1993; Garla *et al.*, 2006). Despite the knowledge of the existence of these habitats, there were originally no methods to identify and delineate a nursery area within an aquatic system until Beck *et al.* (2001) put forward a practical definition. They defined a nursery as an area where juvenile fish occur at high densities, avoid predation more successfully, grow at a faster rate compared to other habitats and thereby provide a relatively greater con-

tribution to adult recruitment. It was subsequently noted that the strict application of this definition was difficult and thus a more easily applied one was suggested for elasmobranch research (Heupel *et al.*, 2007). It was proposed that in order to delineate a nursery area, higher abundances of juveniles less than 1 year old should be found within that area and that juveniles should display a high degree of residency to the area for several years.

Many shark species are known to use such nursery areas and these span across multiple habitats. For example lemon sharks *Negaprion brevirostris* have been seen to utilise isolated habitats as nursery areas such as the Bimini Islands in the Bahamas (Chapman *et al.*, 2009) and an offshore atoll in Brazil (Ach   De Freitas *et al.*, 2009). Coastal bays across the globe are also known to serve as nursery habitats to a number of shark species (Castro, 1993; Simpfendorfer & Milward, 1993; Yokota & Lessa, 2006; Grubbs *et al.*, 2007). Conversely there are relatively few studies that show this phenomenon in rays (with the few examples including Yokota & Lessa, 2006, Dale *et al.*, 2011, Cerutti-Pereyra *et al.*, 2014, Davy *et al.*, 2015). Given the low fecundity of rays, survival in juvenile stages is likely to be vital to population persistence (Cortes, 2002; Kinney & Simpfendorfer, 2009; Pierce & Bennett, 2011; Cerutti-Pereyra *et al.*, 2014) and thus potential nursery areas should be identified.

The St. Joseph Atoll, Republic of Seychelles, is a remote atoll that plays host to an abundance of juvenile porcupine rays *Urogymnus asperrimus* (Bloch and Schneider 1801) with estimates between 1000 - 2000 individuals (von Brandis, 2014). Despite the fact that this species belongs to the Dasyatidae (whiptail stingray) family, it has a short tail that lacks spines and it is an easily identifiable oval-shaped ray with a dorsal surface that is covered with short thorns (Last & Stevens, 2009). The porcupine ray has a wide-ranging distribution in the Indian Ocean and Indo-West Pacific (Compagno, 2005). It occurs from the east coast of South Africa to the Gilbert Islands and Fiji, north to the Phillippines and south to Ningaloo Reef in Australia (Last & Stevens, 2009). It is also reported in the tropical eastern Atlantic off central Africa (Compagno, 2005; Last & Stevens, 2009). Porcupine rays are most commonly found on sand and coral rubble substrate near reefs (Theiss *et al.*, 2010; Chin, 2014).

Despite their wide-spread distribution they are not regularly reported, are uncommon compared to sympatric species of *Himantura*, *Dasyatis*, *Pastinachus*, and *Taeniura* (Compagno, 2005) and are thus considered rare (Theiss *et al.*, 2010; Chin, 2014). In fact, an extensive search through museum and written records in Australia dating back to 1770 only yielded 25 records of the species with limited accompanying data (Theiss *et al.*, 2010). The dearth of information for this species was bolstered by a citizen science project, called the "Porcupine Ray Hunt" (Chin, 2014), which more than doubled the number of records for the species in the Great Barrier Reef. It also provided information on their depth range (1-30m which might be a product of safe diving depths) and identified potential hotspots of occurrence. In terms of biology, the only life-history traits are reported by Last & Stevens (2009) who state that porcupine rays are thought to reach a disc width of up to 147cm, with males and females maturing at approximately 90cm and 100cm respectively. Ecologically, porcupine rays are known to "plough up" sandy substrates, expelling large and observable plumes of sand when feeding (Last & Stevens, 2009; Theiss *et al.*, 2010). The only study that has investigated the diet of this species took place at Ningaloo Reef (Australia), where stomach contents of adults were dominated by annelids and prawns (items occurring in 100% and 36% of individuals respectively) (O'Shea *et al.*, 2013). Their potential predators have not been identified in literature, but it is assumed that larger sharks will prey on juveniles as with other ray species (Davy *et al.*, 2015).

The porcupine ray is listed as Vulnerable by the IUCN given its rarity and apparent decrease in abundance over the last three decades (Compagno, 2005). This species is taken largely as by-catch in unregulated fisheries and is commonly caught in South East Asia where its meat, cartilage and skin are of particularly high value (Compagno, 2005; Theiss *et al.*, 2010). Given its rarity, inshore habitat and large size it has been suggested that this species is unlikely to sustain prolonged targeted fishing (Theiss *et al.*, 2010). In addition, human modification and degradation of critical habitats are thought to be occurring in the higher populated and polluted coastal areas of this ray's range (Compagno, 2005). The porcupine ray is also hypothesized to be one of the two most vulnerable elasmobranch species in the Great Barrier Reef in terms of climate change because of its rarity, immobility and high habitat

dependency (Chin *et al.*, 2010).

Given both the rarity and vulnerability of porcupine rays, the St. Joseph Atoll provides a unique opportunity to study aspects of the ecology of the juvenile life stage of this species. Consequently, the aims of this study were to investigate the trophic and spatial ecology of juvenile porcupine rays at the St. Joseph Atoll.

The specific objectives were to:

- Identify the dietary composition of juvenile porcupine rays and to determine their levels of resource selectivity
- Investigate the residency, extent of movements and habitat use patterns of juvenile porcupine rays to elucidate the nursery role of this habitat
- Investigate the effects of abiotic factors such as diel and tidal cycles, temperature and other environmental variables on the short-term movement patterns of juvenile porcupine rays

Thesis structure

This thesis is divided into six chapters:

Chapter 2 provides an overview of the study site, including a description of the geographic location, habitat types, climatic conditions, and tidal regime. The research approaches used to determine the objectives are also discussed.

Chapter 3 is an assessment of the dietary composition of juvenile porcupine rays through the analysis of stomach contents. Resource selectivity by porcupine rays was also assessed through the collection of sediment samples. Lastly, potential effects of size and sex on dietary composition were investigated.

Chapter 4 investigated the residency and space use of juvenile porcupine rays within the St. Joseph Atoll. Acoustic monitoring data was used to determine long-term residency to provide evidence for the hypothesized nursery role of the atoll. In addition, geographic space use (i.e. core use and activity space areas) as well as en-

vironmental space use (i.e. habitat selection) was determined. Finally, the potential effect of seasonality on movement patterns was assessed.

Chapter 5 deals with the short-term movements of juvenile porcupine rays within the St. Joseph Atoll, and the potential environmental influences on these movement patterns. The data from the acoustic monitoring was used to investigate whether presence within the atoll followed diel or tidal cycles, and whether temperature and/or wind speeds had any significant influences on presence of porcupine rays.

In Chapter 6, the results of the study are synthesized by means of a general discussion. These findings are discussed in relation to their ecological importance and conservation implications.

Chapter 2

Methods and Materials



2.1 Study Site

2.1.1 Geographic location, topography and habitat type

The St. Joseph Atoll and the neighbouring D'Arros Island (5.43° S, 53.35° E) are part of a small chain of islands known as the Amirantes Group located on the Amirantes Bank, Republic of Seychelles in the Western Indian Ocean (Figure 2.1). The Amirantes Bank is a submerged plateau roughly 3220km² in size that is characterised by relatively shallow depths mostly less than 40m, and is surrounded by open ocean with depths in excess of 2000m. D'Arros Island and St. Joseph Atoll are situated in the northern regions of this bank and are separated by a 1.1km wide channel that has a maximum depth of 72m. D'Arros Island is an oval shaped sand cay with an approximate terrestrial area of 1.7km² and roughly 1km² intertidal reef flat. The St. Joseph Atoll has a total approximate area of 22.53km² and comprises of a central lagoon (4.8km²) that is enclosed by a large oval shaped reef flat (17.7km²) which is topped with several small unpopulated islands (1.4km²) (Stoddart *et al.*, 1979). These two systems have recently been declared as the D'Arros and St. Joseph Special Reserve (SeyLII, 2014). The special reserve status means that it is a no-take zone and access to the area, which measures one kilometer from the outer reef flat, is denied to any sea vessel unless they are in duress.

The Cambridge Coastal Research Unit, Cambridge University, collected detailed habitat data for D'Arros Island and St. Joseph Atoll which was used by Spencer *et al.* (2008) to produce a high resolution habitat map that was later ground-truthed and corrected by the Save Our Seas Foundation - D'Arros Research Centre (Figure 2.2). The reef flats are the dominant feature of the atoll, contributing 79% of its total area (Stoddart *et al.*, 1979). This habitat is made up of large areas of sand flats, seagrass beds (predominantly *Thalassia hemprichii* and *Thalassodendron ciliatum*) and unconsolidated coral rubble. In general, the substrate of the inner reaches of the atoll is dominated by sand while the outer edges comprise mostly coral rubble (Figure 2.2). On the north-eastern side of the atoll, the outer edge is characterized by steep sloping coral reef and consolidated coral rubble that rapidly descends to

depths greater than 2000m within 4km offshore. The slope along the southern and eastern edges is more gradual comprising of platform reefs and consolidated coral rubble that descends to the Amirantes Bank between 30 and 60m (Filmlalter, 2011). The lagoon contributes 21% to the total area of the atoll and has a maximum depth of 6.4m (Stoddart *et al.*, 1979). The atoll lacks tidal channels, rather water spills in and out over the entire expanse of the reef flat as the tide rises and ebbs (Filmlalter, 2011). The lagoon comprises mostly of soft sandy sediment scattered with large coral outcrops, generally poriid and flaviid corals (von Brandis, 2014). It is divided into a series of basins by flat-topped reef ridges or “ribbon-reefs” (Stoddart *et al.*, 1979). These ribbon-reefs are often exposed at low tide and are covered by thick sea grass beds. Much of the lagoon edges are also fringed by these ribbon-reefs. The water within the lagoon is mostly turbid with poor visibility (Filmlalter, 2011) and sea temperature varies between 21.8 and 39.3°C (von Brandis, 2014).

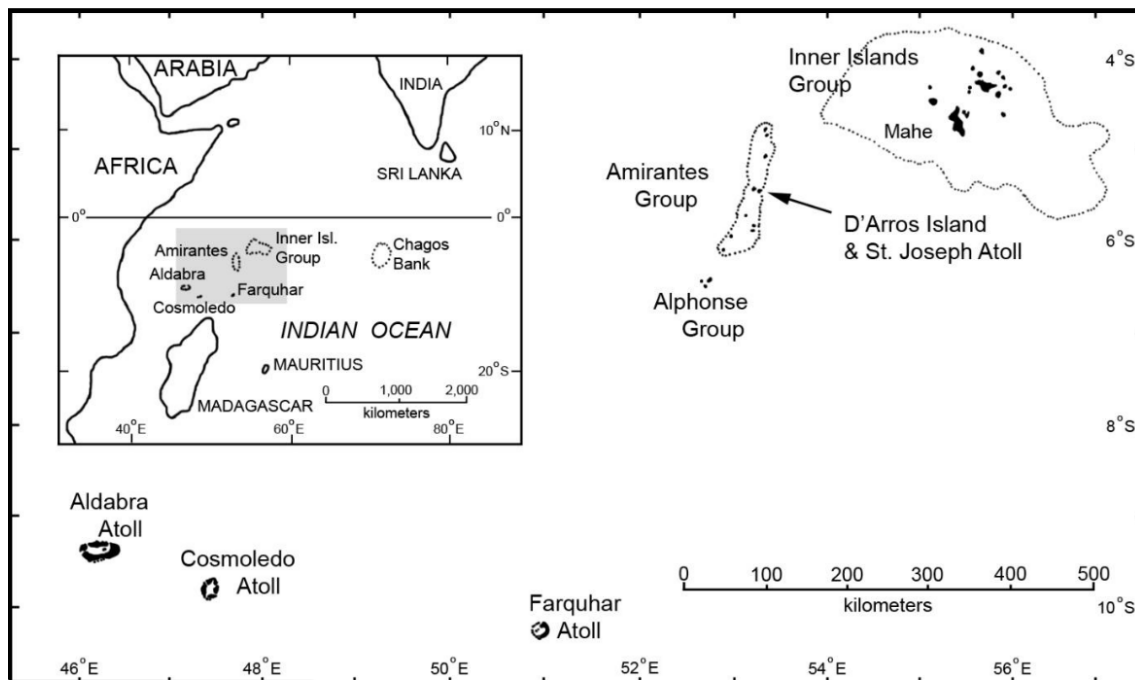


Figure 2.1: Geographic location of D'Arros Island and the St. Joseph Atoll in the Republic of Seychelles, western Indian Ocean (after Filmlalter (2011))

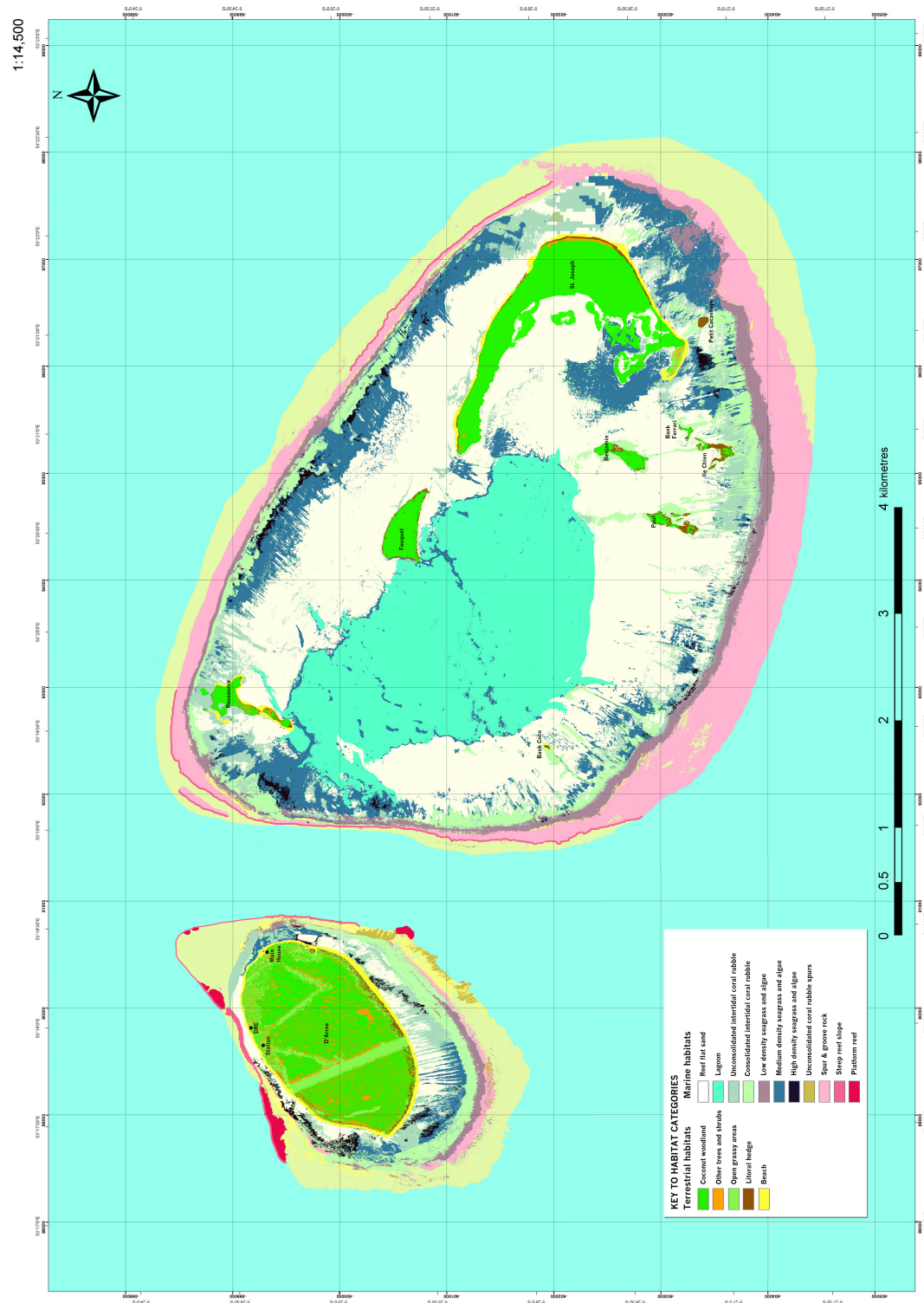


Figure 2.2: Detailed habitat map of D'Arros Island and St. Joseph Atoll. Data collected by the Cambridge Coastal Research Unit and produced by Spencer *et al.* (2008).

2.1.2 Climate and tidal regime

The St. Joseph Atoll experiences two major seasons namely the south-east monsoon (April to November) and the north-west monsoon (December to March). The south-east monsoon season is characterised by strong persistent south-easterly winds, lower rainfall and lower temperatures. Conversely, the north-west monsoon is dominated by light north-westerly winds, higher rainfall and warmer temperatures (Filmalter, 2011; von Brandis, 2014). A weather station (Davis Vantage Pro2) was deployed on D'Arros Island at the end of May 2014 which recorded a variety of environmental variables. Monthly air temperatures, wind speeds, and rainfall are summarised in Table 2.1 for the period June 2014 - March 2015. In addition, 88 sea temperature loggers (HOBO U22-001) were coupled with the acoustic receiver array (see details below) and the water temperature data recorded from a logger situated in the lagoon is also summarised (Table 2.1).

The Amirantes region experiences a mixed semi-diurnal tidal cycle where there are two high tides and two low tides of different heights every lunar day. Due to the variation in time between a lunar and solar day, this translates to just slightly less than two tidal cycles per solar day and each successive high and low tide occurs later in every 24 hour cycle (Figure 2.3). There is a maximum tidal range of approximately 2.2m at spring tides and a minimum tidal range of about 1.6m during neap tides. The tides are an important factor when considering the depths and currents of the St. Joseph Atoll sand flats; for example at spring low tide large portions of the sand flats become exposed or are covered by very shallow water (10-30cm depth) while at spring high tide these flats can be covered by up to 2m of water (Filmalter, 2011). There is a tidal delay within the lagoon because of the time it takes for the water to “spill over” the reef flats into the lagoon. A tidal level logger (HOBO U20-001-01-TI) was deployed in the lagoon for the duration of the study to account for this and to obtain high accuracy tidal level data.

Table 2.1: Summary of weather variables for D'Arros Island and the St. Joseph Atoll from June 2014 to March 2015

		Air temperature (°C)	Wind speed (km/hr)	Rain (mm)	Lagoon temperature (°C)
June	Min	23,30	1,60	0,00	26,38
	Max	29,40	19,30	5,59	28,44
	Mean	26,72	9,92	0,02	27,43
	St.Dev	1,05	2,87	0,21	0,37
July	Min	22,60	0,00	0,00	25,55
	Max	28,00	19,30	8,89	28,12
	Mean	25,64	9,08	0,04	26,76
	St.Dev	1,00	2,82	0,36	0,55
August	Min	22,30	0,00	0,00	25,21
	Max	28,20	19,30	2,29	28,47
	Mean	25,54	9,16	0,01	26,53
	St.Dev	1,05	3,45	0,10	0,60
September	Min	24,00	0,00	0,00	25,62
	Max	29,10	17,70	2,40	27,88
	Mean	26,24	10,64	0,02	26,84
	St.Dev	1,02	3,09	0,13	0,43
October	Min	23,60	0,00	0,00	26,79
	Max	30,60	16,10	5,40	30,17
	Mean	27,32	6,96	0,03	28,59
	St.Dev	1,31	3,16	0,28	0,71
November	Min	23,40	0,00	0,00	27,97
	Max	31,60	12,90	16,60	30,65
	Mean	27,49	4,18	0,11	29,46
	St.Dev	1,82	2,81	0,80	0,46
December	Min	23,30	0,00	0,00	27,75
	Max	31,80	14,50	32,00	31,08
	Mean	27,36	2,96	0,14	29,53
	St.Dev	1,76	2,25	1,11	0,64
January	Min	22,70	0,00	0,00	27,04
	Max	31,40	24,10	35,40	29,89
	Mean	27,85	10,28	0,09	28,48
	St.Dev	1,24	5,00	1,08	0,57
February	Min	23,60	0,00	0,00	27,55
	Max	30,70	17,70	13,60	30,75
	Mean	27,70	7,87	0,06	28,98
	St.Dev	1,12	3,51	0,67	0,65
March	Min	24,60	0,00	0,00	28,35
	Max	32,10	11,30	1,40	31,36
	Mean	28,41	3,21	0,01	29,58
	St.Dev	1,71	2,42	0,09	0,63

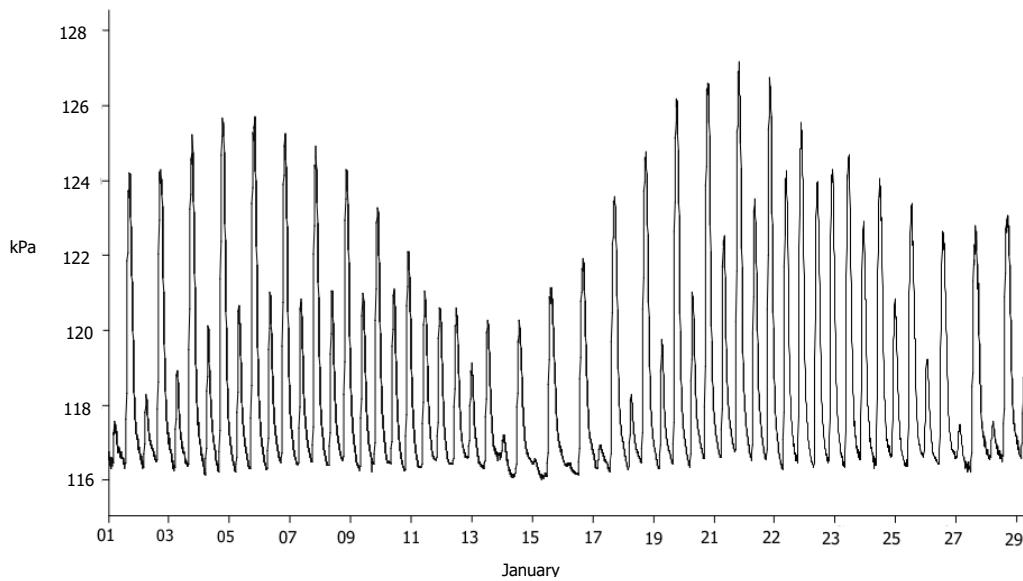


Figure 2.3: Tidal regime within the St. Joseph Atoll from 01/01/2015 to 31/01/2015 illustrating the mixed semi-diurnal tidal cycle as well as two spring tides with a larger tidal range and a neap tide with a smaller tidal range

2.2 Diet Analysis

2.2.1 Research approach

Previous diet determination studies often involved lethal sampling to obtain stomach contents (for e.g. Platell *et al.*, 1998, Kyne & Bennett, 2002, White *et al.*, 2004, Flores-Ortega *et al.*, 2011, and O'Shea *et al.*, 2013). Given the recent concerns over the conservation status of elasmobranchs there have been calls for reliable non-lethal sampling methods (Hammerschlag & Sulikowski, 2011; Bangley *et al.*, 2013). There are two classes of non-lethal diet determination - extracting stomach contents using non-lethal techniques or obtaining animal tissue for stable isotope analyses. Stable isotopes are beneficial in that they provide a longer-term view of an animal's diet as opposed to the "snapshot" view obtained from stomach content samples (Pinnegar & Polunin, 1999; Pinnegar *et al.*, 2001; MacNeil *et al.*, 2005; Kim *et al.*, 2012). However the drawback of stable isotope analyses is the limited ability to obtain fine-scale taxonomic resolution of prey items (Blanco-Parra *et al.*, 2012; Schiffman *et al.*, 2012). Given that the dietary information on the porcupine ray is limited to a single study, which yielded stomach contents from only 13 individuals (O'Shea *et al.*,

2013), it was necessary to obtain fine-scale taxonomic resolution of stomach contents from a representative sample to understand the trophic ecology of this species. Thus, stomach contents were collected from porcupine rays using a non-lethal approach.

There are various non-lethal techniques to obtain stomach contents from elasmobranchs. Stomach eversion has been performed either by direct application of forceps or by inducement through injection of an emetic (Schurdak & Gruber, 1988; Cortés & Gruber, 1990; Andrews *et al.*, 1998; Webber & Cech, 1998; Sims *et al.*, 2000). Both these techniques generally involve holding the animal in an enclosure, either for recovery from anaesthetisation (which is often used in conjunction with forceps) (Cortés & Gruber, 1990) or until the animal has everted its stomach, which can take up to 10 minutes to occur after the injection of the emetic (Andrews *et al.*, 1998; Sims *et al.*, 2000). Gastric lavage or stomach flushing is an easy diet sampling method that requires minimal equipment (Bangley *et al.*, 2013) as it involves the pumping of water into the stomach via a tube until food items are expelled via the mouth (Barnett *et al.*, 2010). Gastric lavage has been performed on a variety of animals including marine mammals (Antonelis Jr. *et al.*, 1987), turtles (Eckert *et al.*, 1999; von Brandis *et al.*, 2015), teleost fishes (Hartleb & Moring, 1995) and to a much lesser extent elasmobranchs. Given the relatively short alimentary canal between the mouth and stomach in rays (Sims *et al.*, 2000) and evidence of a relatively hardy gut (rays are able to evert their stomachs with no apparent harm (Schurdak & Gruber, 1988; Sims *et al.*, 2000; Brunnschweiler *et al.*, 2005)), gastric lavage was deemed an appropriate method to collect stomach contents from porcupine rays.

2.3 Movement Patterns

2.3.1 Research approach

Data on the presence, location and movement patterns of animals have historically been collected through mark-recapture studies (Heupel *et al.*, 2006b). In recent years, acoustic tracking has become increasingly popular throughout scientific literature as it makes use of low-cost acoustic receivers that are able to record the

presence of marine animals over varying spatial (Heupel *et al.*, 2006a) and temporal scales (e.g. from days (Childs *et al.*, 2008) to years (Chin *et al.*, 2013)). Acoustic tracking has been utilised in a variety of environments to answer a multitude of different questions on an assortment of different species including teleosts, chondrichthyans, crustaceans, and cephalopods (Heupel *et al.*, 2006a). Passive acoustic tracking in particular is advantageous over actively tracking an animal as it is much less labour-intensive, multiple individuals can be monitored simultaneously, it removes the bias of closely following the animal and potentially altering behaviour, and it reduces the risk of recording unusual behaviour as a result of the tagging procedure (Heupel *et al.*, 2006a).

During this study, passive acoustic telemetry was used to monitor the movements of juvenile porcupine rays in the St. Joseph Atoll over a one year period (March 2014 - March 2015) to elucidate site fidelity to the St. Joseph Atoll, area use within the atoll, and changes in movement in response to environmental variables. Porcupine rays were surgically implanted with uniquely coded acoustic transmitters and were monitored using an array of omni-directional automated acoustic receivers.

2.3.2 Acoustic receiver array

The acoustic receivers (Vemco VR2W's, Vemco ©Ltd.,Halifax, Canada) used in this study are fully submergible units that automatically collect and store long-term data by continuously monitoring the environment on a single frequency of 69kHz for the presence of uniquely coded transmitter signals (Heupel *et al.*, 2006a). The receivers use non-volatile flash memory to log and store the date, time, and identity of the acoustic transmitter when in reception range (Filmlalter *et al.*, 2013). An array of 88 VR2W receivers exists on the Amirantes Bank with the highest concentration of receivers ($n = 48$) occurring within the D'Arros and St. Joseph Special Reserve (Figure 2.4). Receivers are moored with concrete blocks and are attached to a rope held afloat with a buoy. The array is currently used to monitor the movements of three stingray species, manta rays, seven shark species, two teleost species and two turtle species. Seventy of these receivers were deployed in Phase 1 between August

and November 2012, prior to the start of this study. The remaining receivers were deployed in Phase 2 during the course of this study: 11 were deployed on 27 August 2014, four were deployed during September 2014, and the final three were deployed during November 2014. The data from the receivers are downloaded at six month intervals using a netbook computer and the batteries are replaced annually. Each receiver is paired with a temperature logger (HOBO U22-001) that is set to record the water temperature every 10 minutes.

2.3.3 Transmitter specifications

Two different types of acoustic transmitters were used in this study. V13-1L (Vemco ©Ltd.,Halifax, Canada) transmitters were used for porcupine rays that had a disc width of less than 60cm. These transmitters were 13mm in diameter and 36mm in length. They weighed 6g in water, power output was 153dB, they transmitted individually coded pulses randomly at 80 - 160 second intervals and they were estimated to have a battery life of 1118 days. V16-4H (Vemco ©Ltd.,Halifax, Canada) transmitters were used with porcupine rays that had a disc width greater than 60cm. The tags were 16mm in diameter and 68mm in length. They weighed 8,1g in water, power output was 158dB, they transmitted individually coded pulses randomly at 50 - 130 second intervals and they were estimated to have a battery life of 1018 days.

2.3.4 Code collisions

The receivers are only able to positively identify one transmitter at any given point. There is, however, the possibility that more than one transmitter could be in range of the receiver and emit a signal at the same time. If this happens, neither transmitter will be detected, rather a false detection that is a combination of the two will be recorded. If this happens it is unlikely that the next emission will occur at the same time as the transmitters emit signals at random intervals. Any such false detections were excluded from the database.

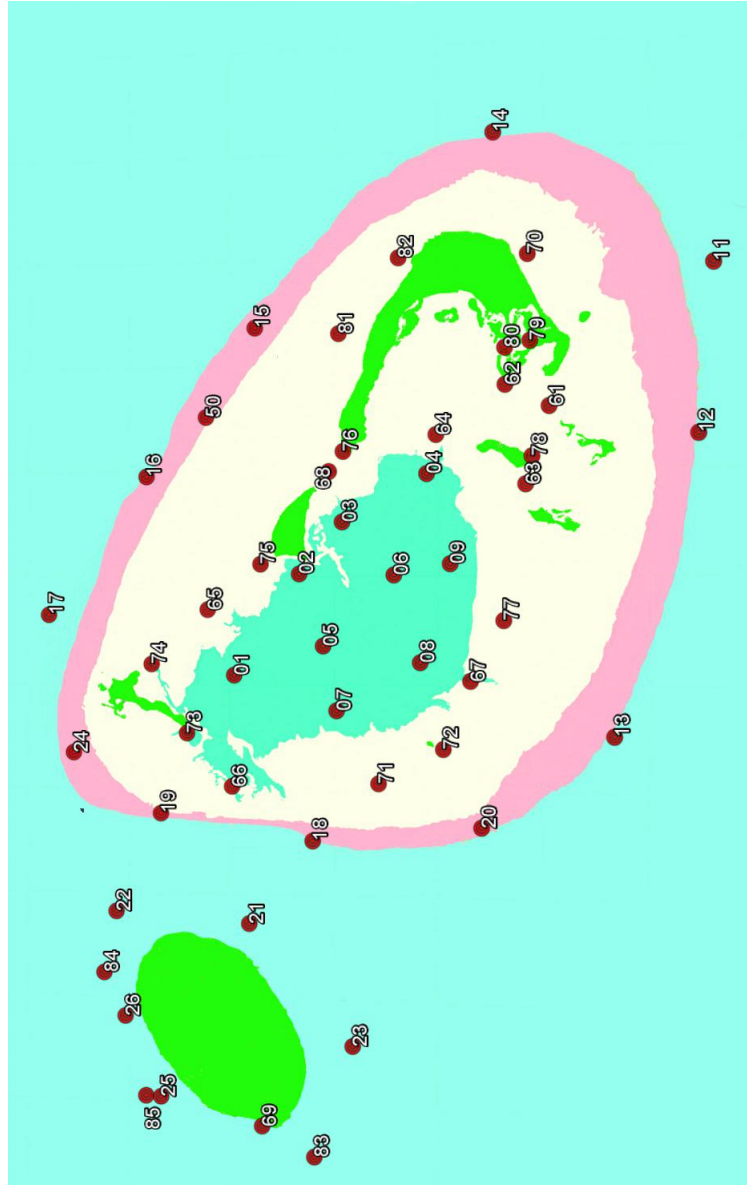


Figure 2.4: Locations of acoustic receivers within and around the immediate vicinity of the St. Joseph Atoll and D'Arros Island. Within the atoll green represents the islands, blue represents the lagoon, beige represents the sand flats, and pink represents the fringe reef. Receiver numbers 71 and upwards were deployed in Phase 2.

2.3.5 Range testing

As the distance between an acoustic transmitter and an acoustic receiver increases, there is a smaller likelihood of the receiver detecting the transmitter's signal (Heupel *et al.*, 2006a; Simpfendorfer *et al.*, 2008). This likelihood of transmission detection is not only affected by distance but by a variety of factors including physical sources

such as wave action (Voegeli & Pincock, 1996; Finstad *et al.*, 2005; Heupel *et al.*, 2006a), current strength, physical obstruction (Heupel *et al.*, 2006a), haloclines and thermoclines (Voegeli & Pincock, 1996; Heupel *et al.*, 2006a), water chemical conditions (Finstad *et al.*, 2005), sediment type (Heupel *et al.*, 2006a), and wind speed (Simpfendorfer *et al.*, 2008); biological sources such as alpheid shrimps; and anthropogenic sources such as vessel noise, fish farms, underwater construction (Heupel *et al.*, 2006a). Some of these factors occur with a diel or tidal frequency and when making inferences about rhythmic cycles in movement patterns, one needs to ensure that they are indeed related to animal behaviour and not to the variability in transmission detection likelihood (Payne *et al.*, 2010). Two separate range tests were conducted in the St. Joseph Atoll to determine the probability of transmission detection on the sand flats and in the deeper lagoon and to determine whether or not this probability is affected by diel or tidal cycles.

A preliminary range test was conducted using two VR2W receivers deployed in the south-eastern section of the atoll, one on the shallow sand flats (min depth = 20cm) and one in the deep lagoon (min depth = 2m). Two V16-4x transmitters (with a 40-80 second nominal delay) were deployed with each receiver, in a straight line in the absence of physical obstacles, at distances 50m and 100m away from the receivers. The test ran from 5 May 2014 - 22 May 2014. One transmitter broke free from its mooring on 10 May, but it was recovered and was redeployed on 11 May.

The mean number of detections for each hour of the day over the test period was calculated for each transmitter (Figure 2.5). A non-parametric Kruskal-Wallis analysis revealed that they were significantly different between the transmitters ($\chi^2 = 41.71$, $p < 0.01$). Post-hoc comparisons showed there was no significant difference in the mean number of hourly detections between the 50m and 100m lagoon transmitters, but the 100m sand flat transmitter recorded a significantly lower number of hourly detections compared to the 50m sand flat transmitter and the 100m lagoon transmitter (Table 2.2). This suggests that the likelihood of detection drops when the distance between the transmitter and receiver reaches 100m on the sand flats, but not in the lagoon. The sand flats are a very shallow environment and the transmitters and receivers are in very close proximity to the surface of the water column.

Wind and wave action on the surface are more pronounced compared to the deeper lagoon, potentially causing this lower probability of transmission detection in this habitat.

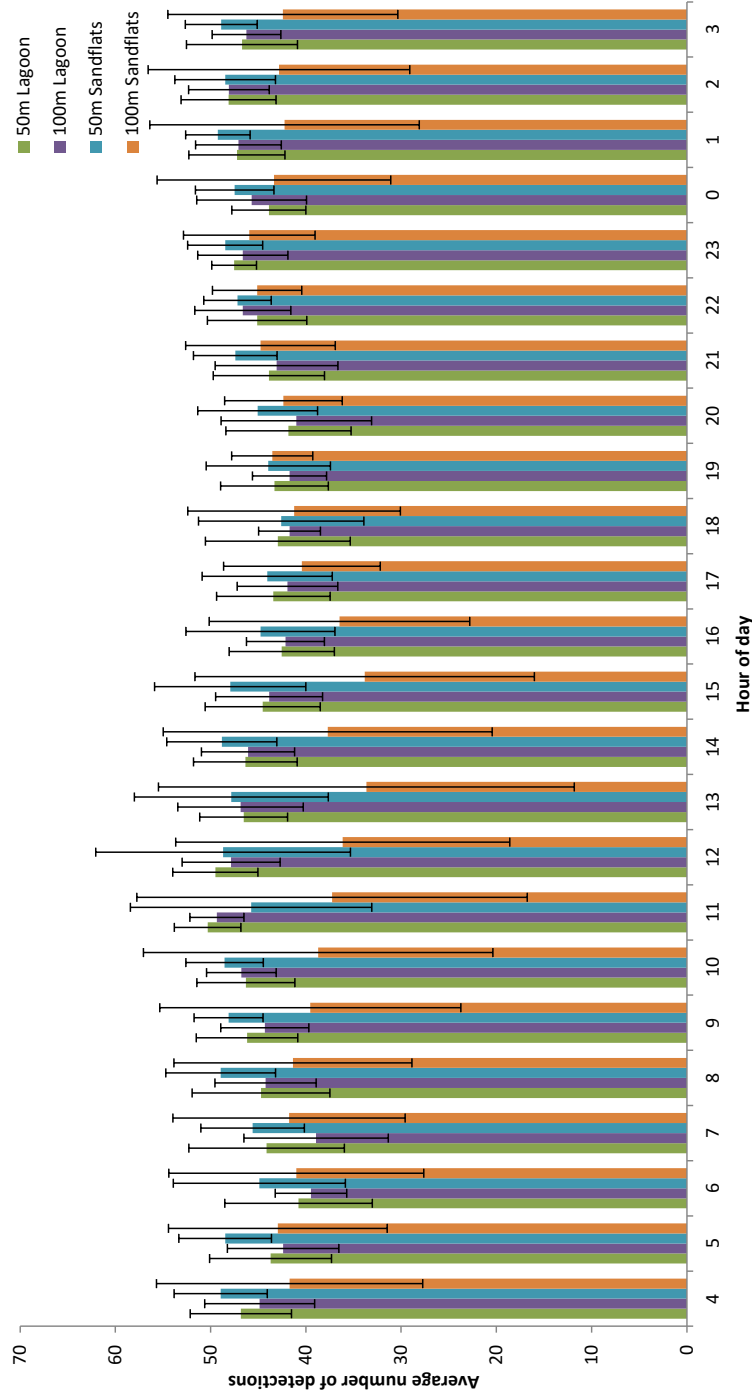


Figure 2.5: Number of detections for each hour of the day averaged over the period of the range test. Error bars denote standard deviation.

Table 2.2: Post-hoc analysis on the mean hourly detections for transmitters employed for the initial range test

	50m Lagoon	100m Lagoon	50m Sandflats
100m Lagoon	0.88	-	-
50m Sandflats	0.16	0.02	-
100m Sandflats	<0,01	0.01	<0,01

The second range test was conducted on the sand flats because of the evidence that the detection likelihood was affected more by environmental variables. The purpose of this second test was to determine if the detection likelihood was influenced by diel, tidal cycles or environmental variables. Two VR2W receivers were deployed 100m apart on the sand flats at 20cm depth (at spring low tide). Five V16-4x transmitters (with a nominal delay of 40-80 seconds) were deployed, each 25m apart, starting 100m away from the closest receiver (the same transmitter was therefore 200m from the furthest receiver). This provided detection frequencies from 100m to 300m at 25m intervals. The test ran from 28 May 2015 - 22 June 2015.

The mean number of detections for day hours (06:00 - 17:59) and night hours (18:00 - 05:59) over the test period was calculated for each transmitter. Chi-squared goodness of fit tests found that the mean number of detections did not differ significantly between day and night hours for all the transmitters, with the exception of the transmitter that was at a distance of 225m away from the receiver (Table 2.3). The probability of detection decreased with increasing distance from the receiver but at 300m detections were still being recorded (Figure 2.6). This is an important consideration when looking at acoustic detections between different habitat types of the atoll in Chapter 4. For example, receivers 2, 3, and 4 are situated in the lagoon but are within 150m, 200m and 110m respectively from the shallow sand flats. It is thus possible that detections on these receivers can come from individuals situated on the shallow reef flat and not in the lagoon.

Generalised linear models were used to investigate whether water pressure (kPa) as a proxy for water depth (with the lowest values corresponding to low tide and the highest values corresponding to high tide), water temperature, or wind speed were significant predictors of detection frequency for each transmitter. Constructed models which combined these three environmental factors as predictors failed to

explain much of the variance in detection frequency (between 16 - 34% for the different transmitters), but in every model wind speed was a significant predictor of detection frequency. In addition, for the transmitters located 150m as well as 200m and further from the receivers, water pressure was also found to have significant effects on detection frequency. Lastly the only transmitter for which temperature was a significant predictor was 300m away from the receiver (Table 2.4). These results suggest that detection frequencies do not vary over diel cycles, but they may vary over tidal cycles and in relation to wind speeds in particular.

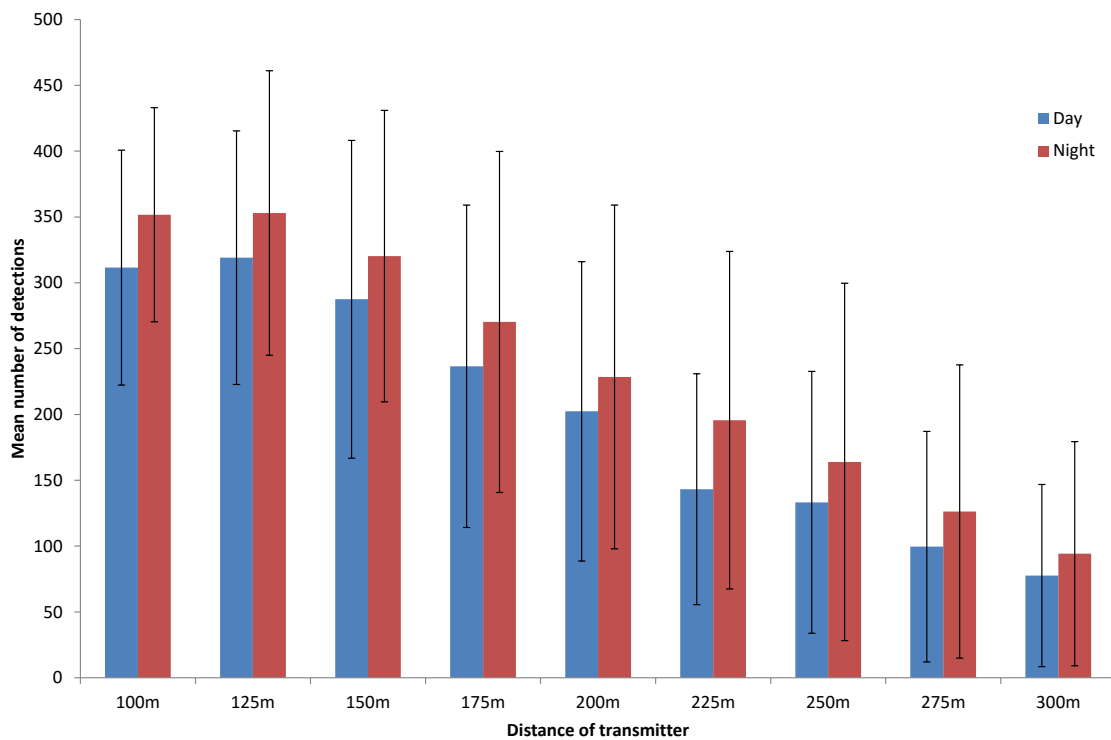


Figure 2.6: Number of detections for day and night averaged over the period of the second range test. Error bars denote standard deviation.

Table 2.3: Chi-squared goodness of fit tests performed on the mean number of detections between day and night for transmitters deployed in the second range test

Distance from receiver	Chi-squared value	DF	p-value
100m	2,43	1	0,12
125m	1,72	1	0,2
150m	1,77	1	0,18
175m	2,23	1	0,14
200m	1,58	1	0,21
225m	8,12	1	<0,01
250m	3,17	1	0,08
275m	3,17	1	0,08
300m	1,6	1	0,21

Table 2.4: Results of generalised linear models performed on the detection frequencies for each transmitter deployed during the second range test. Predictors of detection frequency included wind speed, water pressure and water temperature.

Transmitter	R-squared	p-value for model	Predictor	p-value for predictor
100m	0.16	<0,01	Wind speed	<0,01
			Water pressure	0.16
			Water temperature	0.42
125m	0.16	<0,01	Wind speed	<0,01
			Water pressure	0.12
			Water temperature	0.46
150m	0.25	<0,01	Wind speed	<0,01
			Water pressure	0.01
			Water temperature	0.73
175m	0.31	<0,01	Wind speed	<0,01
			Water pressure	0.08
			Water temperature	0.58
200m	0.34	<0,01	Wind speed	<0,01
			Water pressure	<0,01
			Water temperature	0.39
225m	0.22	<0,01	Wind speed	<0,01
			Water pressure	<0,01
			Water temperature	0.07
250m	0.28	<0,01	Wind speed	<0,01
			Water pressure	<0,01
			Water temperature	0.09
275m	0.26	<0,01	Wind speed	<0,01
			Water pressure	<0,01
			Water temperature	0.12
300m	0.24	<0,01	Wind speed	<0,01
			Water pressure	<0,01
			Water temperature	<0,01

2.4 Field Methods

All porcupine rays were captured on the shallow sand flats of the St. Joseph Atoll. Two methods were employed to catch the porcupine rays. Initially, once an individual was spotted either from a motorised boat or on foot, it was foul-hooked using a weighted treble-hook and line. However, it soon became apparent that the rays could easily be captured by hand. This was deemed less harmful for the rays and, as porcupine rays possess no spine on their tail, it was safe for the person capturing the ray. To hand-capture a porcupine ray, it was approached from behind until the person was close enough to lunge forward and grab the ray around the base of the tail with a gloved hand. If at first unsuccessful, the capturer pursued the ray on foot until it was caught.

Once restrained by the tail, another person approached the ray from the front and used one hand to secure its mouth and the other to support its back as it was lifted out of the water. The animal was placed ventral side up on a water-filled working surface (we employed a sit-on-top recreational kayak with plugged drainage holes) to ensure continued respiration throughout the gastric lavage and the transmitter implantation procedures. Once ventral side up, the rays entered tonic immobility within a couple of seconds. Rays were sexed by the presence or absence of claspers, and disc-width was measured to the nearest cm using a set of callipers. Date, time and locality (using a hand-held GPS) of each capture was also recorded.

Chapter 3

Trophic ecology of *Urogymnus asperrimus*



3.1 Introduction

Rays are commonly reported as abundant in tropical coastal ecosystems such as bays and estuaries (Last & Stevens, 2009) as these habitats generally exhibit high levels of productivity and plentiful prey resources (Beck *et al.*, 2001; Dale *et al.*, 2011; Cerutti-Pereyra *et al.*, 2014; Davy *et al.*, 2015). Rays are also known to occur in oceanic atolls which represent insular areas of high productivity surrounded by open ocean that is otherwise characterised by low primary productivity and levels of dissolved nutrients (Rayner & Drew, 1984). However, most of the dietary studies related to rays have occurred along continental coastlines because of their ease of access (for e.g. Ebert & Cowley, 2003, Ajemian & Powers, 2012, O'Shea *et al.*, 2013, Bornatowski *et al.*, 2014, and Costa *et al.*, 2015), while dietary studies at remote atolls are comparatively few (but see Tilley *et al.*, 2013).

Understanding the trophic ecology of a species is vital when attempting to understand the functions, dynamics, and stability of the ecosystem in which it occurs (Navia *et al.*, 2007; Valls *et al.*, 2011; Yick *et al.*, 2011). Stingrays in particular play important ecological roles as mesopredators, influencing the community structure of their prey organisms (VanBlaricom, 1982; Thrush *et al.*, 1994; Myers *et al.*, 2007) and transferring effects of top predators down the food chain (Myers *et al.*, 2007; Heithaus *et al.*, 2008; Baum & Worm, 2009; Vaudo & Heithaus, 2011). Thus, the diet determination of stingrays increases the knowledge of the roles that they play in the ecosystem, particularly in relation to predation (Bowman *et al.*, 2000; Vaudo & Heithaus, 2011), and is an important area of research in atoll environments. In addition, diet determination is vital when attempting to understand the ecology, community structure (Hyslop, 1980; Johnson, 1980; Bizzarro *et al.*, 2007; Hammer-schlag & Sulikowski, 2011), natural history, and distribution of the species itself (Cortes, 1999; Blanco-Parra *et al.*, 2012). Unfortunately, despite the recognised importance of this information, knowledge on the feeding ecology of elasmobranchs as a whole is scarce (Bizzarro *et al.*, 2007; Ebert & Bizzarro, 2007; Valls *et al.*, 2011; Blanco-Parra *et al.*, 2012), with information on rays in particular lagging behind that of sharks (Bizzarro *et al.*, 2007; Valls *et al.*, 2011; Yick *et al.*, 2011; Tilley & Strindberg, 2013).

Generally coastal rays have been shown to eat epibenthic prey such as crustaceans, molluscs and fish, as well as infauna such as polychaetes and sipunculids (Ebert & Cowley, 2003; Marshall *et al.*, 2008; O'Shea *et al.*, 2013; Tilley & Strindberg, 2013) but various factors have been found to influence their dietary compositions. One of the most important factors is that of size and ontogeny (Smith & Merriner, 1985; Gray *et al.*, 1997; Kyne & Bennett, 2002; Ebert & Cowley, 2003; Marshall *et al.*, 2008; Ajemian *et al.*, 2012). This is not surprising given that as many species of sharks and rays increase in size they change the habitats that they occupy, their movement patterns and swimming speed. The size of their jaws, teeth and stomachs, as well as their energy requirements, experience with prey, and vulnerability to predation all vary with age. All of these factors influence the ability of a shark or ray to obtain prey (Wetherbee & Cortés, 2004). Another factor found to influence a ray's diet is that of geographic location (Tilley, 2011; Ajemian *et al.*, 2012), and there has been some evidence to suggest seasonal shifts in dietary composition as well (Harris *et al.*, 1988; Platell *et al.*, 1998). Lastly, prey availability may affect the specialist or opportunistic nature of a predator (Lucifora *et al.*, 2006). An opportunistic predator will consume prey in the same proportions in which they occur in the environment while a selective predator exhibits resource selectivity and consumes prey in different proportions to those in the environment (Chesson, 1978; Jaksic, 1989; Lucifora *et al.*, 2006). Resource selectivity in elasmobranchs is becoming apparent for a number of species differing widely in morphology and ecology (Harris *et al.*, 1988; Lucifora *et al.*, 2006; Barbini *et al.*, 2011; O'Shea *et al.*, 2013). All of these factors highlight the need for the diet determination of a species throughout its range of occurrence and across different environmental conditions.

The knowledge on the trophic ecology of the porcupine ray is restricted to one article in peer-reviewed literature (O'Shea *et al.*, 2013). Given both the Vulnerable status of the porcupine ray (Compagno, 2005) and the fact that they could potentially play important ecological roles within the St. Joseph Atoll, elucidating the dietary composition of these animals is vital to understanding the ecosystem of the St. Joseph Atoll and for future conservation or management plans for this species. This chapter aims to provide the first detailed assessment on the trophic ecology of juvenile porcupine rays and objectives were to determine:

- The dietary composition of juvenile porcupine rays within the St. Joseph Atoll
- Whether or not juvenile porcupine rays exhibit resource selectivity
- Whether size and/or sex influences the diets of juvenile porcupine rays

3.2 Methods and Materials

3.2.1 Field methods

Juvenile porcupine rays were caught by hand on the sand flats (0.1 - 1.5m depth) of the St. Joseph Atoll using the techniques described in Chapter 2 during the months of May and June 2014. All individuals caught were assumed to be juveniles based on the calcification of the claspers in males and the estimated size at maturity for males and females. Only individuals that were seen actively feeding were caught for the collection of stomach contents. It is unlikely that the same individual was caught twice as sampling locations were different and these rays displayed restricted movements within the atoll (Chapter 4); there was a low number of empty stomachs found; and it is easy to see if an individual has been caught before due to the redness of the ventral side post-capture.

Once the porcupine ray was in tonic immobility on the working surface the anterior end of the ray, inclusive of the spiracles, was placed in a food collection apparatus consisting of an oval mesh basket constructed out of mosquito netting (1mm mesh size) and a flexible wire rim. The posterior end of the stingray was elevated slightly so that the head pointed downward. It was found that placing the ray on top of a piece of shade cloth (which was also covered by mosquito netting in case of stomach content spillage) facilitated this as the two posterior corners of the shade cloth could be lifted to support the animals weight while minimising capture myopathy (Figure 3.1). A clear flexible plastic hose (diameter 14.4mm and wall width 1mm), bevelled on one end, was attached to a bilge pump (Rule Industries, 4160L/hr) that was placed in seawater and connected to a 12 volt battery. The hose was pinched closed to prevent water flow and the bevelled end inserted down the oesophagus of the ray

until resistance was encountered at the gastro-esophageal sphincter. The hose was then gently manipulated a few centimetres into the stomach and opened to allow seawater to flow continuously into the stomach and back out the mouth. Confirmation that the tube had entered the stomach was through the visual expansion of the stomach region. In smaller rays (≤ 50 cm disc width) the hose was slightly pinched to reduce the water pressure entering the stomach. Successful regurgitation of stomach contents only took place if the hose was opened in the stomach and not if the hose was opened while still in the oesophagus. Once regurgitated, the stomach contents were expelled via the mouth or the spiracles, where they were caught by the food collection apparatus. At this time the ray was lifted off our working surface to ensure the stomach contents did not re-enter the spiracles. Occasionally cloacal protrusion of the valvular intestine occurred which sometimes resulted in defecation. The defecated material was not collected as it was too digested for identification. If cloacal protrusion occurred, the hose was immediately withdrawn from the ray and the intestine would revert back to its original position.



Figure 3.1: Gastric lavage technique employed on *Urogymnus asperrimus*. The ray was held with the anterior end pointed downward while the stomach was flushed with seawater pumped through a plastic hose inserted through the mouth.

After being released, the rays were observed for approximately 5 minutes to ascertain immediate post-release survival. The stomach contents were placed into labelled vials, in a solution of 70% ethanol for subsequent analysis in the laboratory.

Sediment samples were collected at the site of each gastric lavage attempt to assess prey availability. A spade was inserted into the sediment (until the entire blade was submerged) at a random location within 5m of the capture location that had not been disturbed by trampling during the capture procedure. The volume of each sediment sample was measured using graduated cylinders after which it was sieved to remove fine particles ($\approx$ 1mm mesh size). Once at the lab, the sediment was systematically sorted using the naked eye to extract all fauna present. The fauna was then transferred to vials containing 70% ethanol.

3.2.2 Sample processing

Each stomach contents sample was weighed to the nearest 0.5g using a digital scale. The prey items from stomach samples and the fauna from the sediment samples were identified to the lowest taxonomic level based on morphological characteristics using a dissecting microscope. If stomach contents were too digested for identification it was placed into an unidentifiable category. This category was excluded from all analyses.

Recording the presence/absence of prey items in stomach contents (%F) has been utilised in dietary studies for decades, but it was also suggested that a more quantitative analysis was needed to understand better the feeding ecology of an animal (Hyslop, 1980). These included bulk measures such as measuring the weight and/or volume of prey categories, and recently these measures have been combined into indices (Baker *et al.*, 2014). There have been concerns over the level of accuracy of data obtained from these bulk measures, for example Baker *et al.* (2014) argued that generally prey items cannot be separated unambiguously and there are unquantifiable factors that affect the gut composition at any given point such as mechanical prey handling as well as the variable digestion and evacuation rates of different prey items. Given that only actively feeding juvenile porcupine rays were caught for the

collection of stomach contents, much of the variability associated with these bulk measures was eliminated. Most of the prey items obtained from stomach contents were relatively undigested and the individual prey components could be separated with a high level of confidence. In addition it was found that porcupine rays do not mechanically handle their prey and almost all of the prey items obtained from stomach contents were intact. In addition the dominance of soft-bodied annelids within the stomach contents provided evidence that the collected stomach contents were indeed recently ingested, avoiding the problem of over-estimating the abundance of harder-to-digest crustaceans.

The data analyses and results are based on the assumption that all prey items stand an equal chance of being evacuated during gastric lavage. This assumption is somewhat supported by the fact that evacuations were mostly sudden i.e. food contents were regurgitated as one large mass comprising of mixed prey items. There is also the chance that gastric lavage may not have resulted in complete stomach evacuation. However, the likelihood of this is small given that other studies have confirmed that gastric lavage removes most, if not all, stomach contents for broadnose sevengill sharks *Notorynchus cepedianus* (Barnett *et al.*, 2010), spiny dogfish *Squalus acanthias* (Bangley *et al.*, 2013) and spotted eagle rays *Aetobatus narinari* (Ajemian *et al.*, 2012). These findings, coupled with the gut morphology of stingrays (i.e. the relatively short distance from the mouth through the oesophagus to the stomach (Sims *et al.*, 2000)), suggests a high probability of complete stomach evacuation for stingrays. In addition, concern about possible incomplete stomach evacuation is counter-balanced by the relatively large sample size obtained (Barnett *et al.*, 2010).

Given these factors, I was confident that a volumetric measure of prey components contained little inaccuracy for this specific case. To measure the volume of the prey items, they were placed onto 1cm x 1cm grid paper at a uniform depth and the area was visually estimated as a proxy for volume (Hyslop, 1980). As this study was not looking at calorific intake, exact volume or weight was not necessary and the technique employed was deemed adequate. The same technique was applied to estimate the volume of the fauna from the sediment samples.

3.2.3 Data analysis

Cumulative prey curves were constructed to determine whether a sufficient number of stomach samples had been analysed to accurately describe the diet of juvenile porcupine rays. The order in which the stomachs were analysed was randomised ten times and the mean number of cumulative prey items found in the stomachs was plotted against the number of stomachs analysed. If the plot reached an asymptote it is assumed that the number of stomachs analysed is sufficient (Ferry *et al.*, 1997). To quantitatively determine if the cumulative prey curve reached an asymptote, methods outlined by Bizzarro *et al.* (2007) were followed. A linear regression was conducted on the mean cumulative number of prey taxa for the final four stomach samples, i.e. endpoints, to determine if the slope of the best fit line through these points were significantly different from a line of slope zero. Slopes were then statistically compared using a Students t-test ($t = (b-0)/S_b$, b = slope of the best fit line and S_b = standard error of the slope).

Prey items were grouped to family level and the contribution of each family to the dietary composition of the porcupine ray was assessed using three indices: the volumetric composition expressed as the percentage of the total volume of ingested prey (%V), the percentage frequency occurrence (%F), i.e. the percentage of stomachs within the sample containing the specific family (Hyslop, 1980; Vaudo & Heithaus, 2011), and these were combined into an Index of Importance expressed as a percentage (%IoI):

$$\%IoI_a = \frac{100 \times (\%F_a + \%V_a)}{\sum_{a=1}^n \%F + \%V}$$

The feeding strategy of the porcupine ray was described by plotting %F against the prey-specific volume (%P), calculated as the percentage volume of a prey item for all stomachs containing that prey item (Amundsen *et al.*, 1996; Ajemian *et al.*, 2012). These plots provide much information, including the importance of a prey item as a component of the diet, whether the animal has a generalist or specialist feeding strategy, as well as assessing inter-individual and intra-individual niche width. If

the prey item is in the upper left of the graph there is specialization by individual predators on the prey item, those in the upper right indicate specialization by the entire population, and prey items in the lower half of the graph are only eaten occasionally. Thus if most prey items fall into the upper right of the diagram, the population has a specialized feeding strategy and a narrow niche width. If all prey items fall along or below the diagonal from the upper left to the lower right, the population is considered to have a generalist diet and a broad niche width (Amundsen *et al.*, 1996). This method is analogous to calculating a niche breadth index, but gives additional information on individual contribution to a population niche (Lucifora *et al.*, 2006).

To assess resource selectivity, the Manly-Chesson index (α) was calculated (Manly, 1974; Chesson, 1978):

$$\alpha_i = \frac{r_i/p_i}{\sum_{i=1}^m r_i/p_i}$$

Where r_i = the proportion of food item i in the diet and p_i = the proportion of food item i in the environment, m = the number of food items in the environment. Values range between 0 (complete avoidance) and 1 (complete preference).

The percentage volumetric composition was used for multivariate analyses to determine if dietary compositions varied significantly between males and females or between size classes for juvenile porcupine rays (Hyslop, 1980; Platell *et al.*, 1998; Marshall *et al.*, 2007). Volume was used because it represents better the relative importance of each dietary category (White *et al.*, 2004) and much of the uncertainty often associated with volume was reduced in this specific study (as discussed above). Application of these multivariate analyses closely followed White *et al.* (2004). Individuals were first grouped together to overcome the problem of limited numbers of prey taxa in their stomachs resulting in a lot of zeroes within the data set. Rays of each sex were randomly assigned to groups of 3, 4 or 5 individuals, forming a dietary sample, depending on the number of individuals for each sex. The mean volumetric composition for each dietary sample was calculated and used in the analyses. Initial comparisons of males and females showed no significant differences between sex so

the data could be pooled for the various size classes and individuals were randomly assigned to groups of 3 or 4 within successive 10cm size classes (40-49cm, 50-59cm, 60-69cm, 70-79cm, and 80-89cm). The size classes are referred to very small, small, medium, large and very large for discussion purposes. Prey items that could not be identified to family level were excluded from the analyses to avoid bias in the results (as they are likely to contain remnants of more than one dietary category).

The data were square-root transformed to reduce the influence of prey with high abundances and similarity matrices were produced using the Bray-Curtis similarity co-efficient (Marshall *et al.*, 2007). MDS ordinations were performed on the similarity matrices to provide a visual estimation of the differences in dietary compositions and were considered successful if stress values were ≤ 0.2 (Clarke & Gorley, 2006). One-way analyses of similarities (ANOSIM) were employed to test whether the compositions of the dietary samples differed significantly between sex and between size classes. If a significant difference ($p < 0.05$) was found in the global ANOSIM, pair-wise tests were then examined. These pair-wise tests were not solely interpreted through significance levels because in this context P-values are highly dependent on the number of replicates in the comparison and the smallest and largest size classes only had one replicate. Thus, R-values are considered more reliable for interpretation (Clarke & Gorley, 2006). Values close to 1 indicated the dietary compositions were very different and those close to zero indicate they are very similar. Similarity percentages (SIMPER) were employed to determine which prey items typified the diet of a particular size category and to identify those prey items that contributed most to any differences between the diets of the various size classes. All analyses were done in PRIMER v6 package (Clarke & Gorley, 2006).

3.3 Results

Gastric lavage was conducted on 55 juvenile porcupine rays (23 females and 32 males) each at a different location on the sand flats of the St. Joseph Atoll. Individuals ranged from 43-81cm disc width with a mean ($\pm$ standard deviation) of 62.2 ± 8.3 cm. Only three individuals had empty stomachs yielding a high percentage (94.5%) of

successful gastric lavage attempts. Lavage duration (from hose entering mouth till hose exited mouth) ranged from 32 seconds to 2 minutes 38 seconds. Short-term post-release survival was 100% with no observed shark predation/encounters and no obvious signs of distress. Defecation after the cloacal protrusion of the intestine occurred in 21.4% of all individuals caught. This phenomenon occurred throughout the size range of captured rays.

3.3.1 Diet composition

The cumulative prey curve reached an asymptote as the slope of the best fit line through the endpoints was not statistically different from 0 ($t=2.38$, $p=0.11$). This indicates the sample size was sufficiently large enough to accurately determine the dietary composition of this species (Figure 3.2).

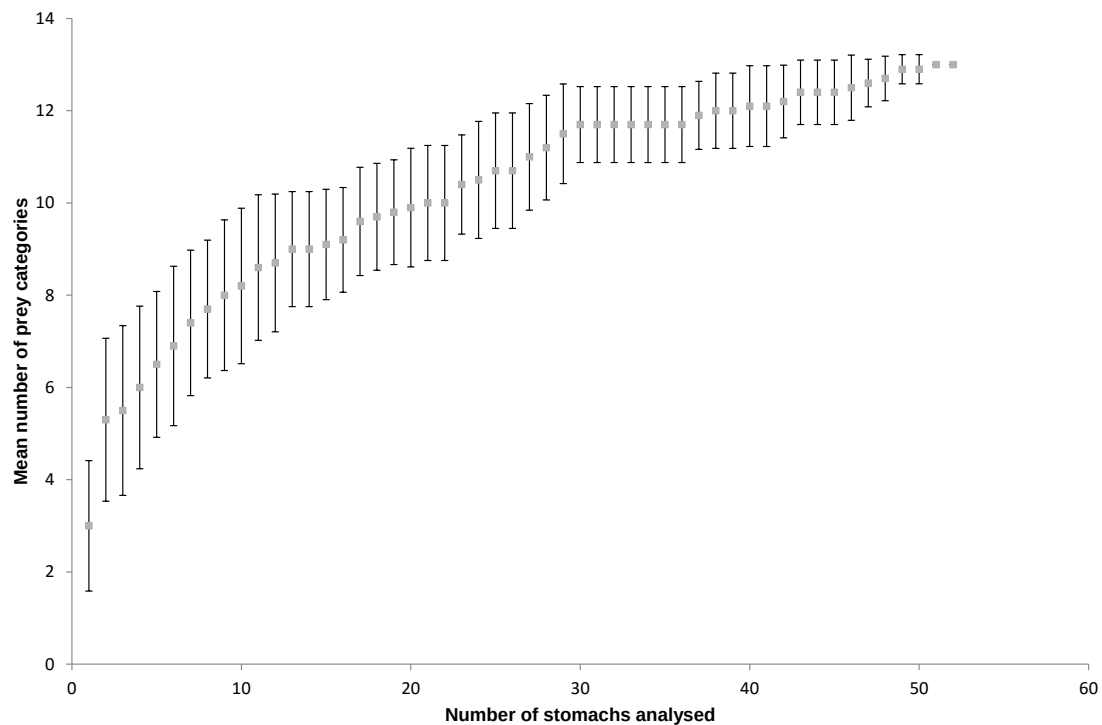


Figure 3.2: Cumulative prey curve for *U. asperrimus*. Error bars denote standard deviation.

The weight of the stomach samples was highly variable and ranged between 0.5g and 61.5g with a mean of 15g. Morphological analysis identified two prey categories to phyla level, sipuncula and nemertea, and eleven categories to family level (six polychaete and 5 crustacean families) (Table 3.1).

Table 3.1: Percentage frequency (%F), percentage volume (%V) and percentage index of importance (%IoI) of prey items collected from stomach contents of *U. asperrimus* as well as from sediment samples. α represents Manly–Chesson index used to assess resource selectivity.

Stomach samples					Sediment samples			
	%F	%V	%IoI	%F	%V	%IoI	α	
ANNELIDA								
Polychaeta	sum	67.2	78.1	74.180.0				
Capitellidae	98.1	50.0	34.5	73.1	38.9	35.9	0.22	
Lumbrineridae	59.6	7.5	15.7	7.7	5.2	4.1	0.25	
Glyceridae	48.1	2.3	11.8	21.1	7.9	9.3	0.05	
Serpulidae	25.0	0.8	6.0	0.0	0.0	0.0	-	
Maldanidae	17.3	1.4	4.4	7.7	1.1	2.8	0.21	
Unidentified family	15.4	1.6	4.0	15.4	2.5	5.7	0.11	
Eunicidae	3.9	3.6	1.7	48.1	17.9	21.2	0.03	
Orbiniidae	0.0	0.0	0.0	1.9	0.7	0.8	0.00	
SIPUNCULA	5.8	7.0	3.0	19.2	13.8	10.6	0.09	
NEMERTEA	1.9	5.8	1.8	0.0	0.0	0.0	-	
CRUSTACEA	sum	19.9	17.0	3.02.8				
Stomatopoda								
Protosquillidae	7.7	0.9	2.0	0.0	0.0	0.0	-	
Squillidae	5.8	3.4	2.1	0.0	0.0	0.0	-	
Unidentified family	1.9	1.5	0.8	0.0	0.0	0.0	-	
Brachyura								
Uca tetragonon	1.9	1.5	0.8	0.0	0.0	0.0	-	
Thalassanidae								
Callianassidae	17.3	10.4	6.5	0.0	0.0	0.0	-	
Caridea								
Alpheidae	9.6	104.0	2.6	0.0	0.0	0.0	-	
Unidentified family	7.8	0.6	1.9	5.8	3.0	2.8	0.04	
Dendrobranchiata								
Sergestidae	1.9	0.4	0.5	0.0	0.0	0.0	-	
CEPHALOCHORDATA	0.0	0.0	0.0	3.9	0.9	1.5	0.00	
HEMICHORDATA	0.0	0.0	0.0	5.8	2.8	2.7	0.00	
MOLLUSCA								
Gastropoda								
Naticidae	0.0	0.0	0.0	1.9	5.4	2.3	0.00	
Total	328.9	100.0	100.0	211.5	100.0	100.0	1.0	

Polychaetes dominated the stomach samples with an IoI of 78%, were identified in all of the stomach samples, and accounted for 67% of the total prey volume on average. The most prevalent polychaete was the family Capitellidae with the highest IoI (34,5%). Capitellidae was found in 98.1% of all stomachs and 9.6% of stomachs only contained Capitellidae. The feeding strategy plot confirmed the importance of Capitellidae as it was the only prey item to fall in the upper right quadrant of the plot, indicating specialisation by the entire population on this burrowing sediment dweller. The polychaete families Glyceridae and Lumbrineridae were consumed in low densities but occurred in a high proportion of individuals (Figure 3.3). Cumulatively, crustaceans were also an important prey item (IoI of 17%) with the burrowing families of the ghost shrimp (Callianissidae), snapping shrimp (Alpheidae) and mantis shrimps (Stomatopoda) contributing most to the diet (IoI of 6.5%, 2.6% and 5% respectively). Burrowing sipuncula were also found in low proportions (IoI of 3.0%). The feeding strategy plot revealed that individual crustacean families, the sipuncula and the various other polychaete families identified contributed little to the overall diet as they were eaten rarely and in low proportions (Figure 3.3). A single individual of the free-living nemertea and of the semi-terrestrial fiddler crab (*Uca tetragonan*) were found and were most likely ingested accidentally, not forming an important part of the porcupine rays diet (Table 3.1).

3.3.2 Resource selectivity

Polychaetes were the most abundant in the sediment samples making up 74.2% of the volume on average. The most abundant polychaete was Capitellidae (with an average volume of 38.9%) and despite the specialisation on Capitellidae by porcupine rays, the Manly-Chesson index reveals there is only a moderate preference for Capitellidae ($\alpha = 0.22$) when compared with this high environmental availability. There is also moderate preference for the polychaetes Lumbrineridae and Maldanidae ($\alpha = 0.25$ and 0.21 respectively) while other polychaetes, Glyceridae, Eunicidae and Orbiniidae are avoided ($\alpha = 0.05$, 0.03 , and 0 respectively). Despite the fact that crustaceans were common in stomach samples, only three individual crustaceans (belonging to Caridea) were found in the sediment samples. Sediment-

dwelling lancelets (cephalochordata), burrowing acorn worms (hemichordata), and epifaunal moon snails (naticidae) were present in low densities in the sediment samples but were not found in stomach samples, indicating avoidance. However given the small sizes and soft bodies of Cephalochordata, it is likely that individuals are digested very quickly which may explain why none were found in stomach samples. Sipuncula was abundant in the sediment samples (14% of the total volume on average) and porcupine rays seem to avoid these worms ($\alpha = 0.09$) (Table 3.1).

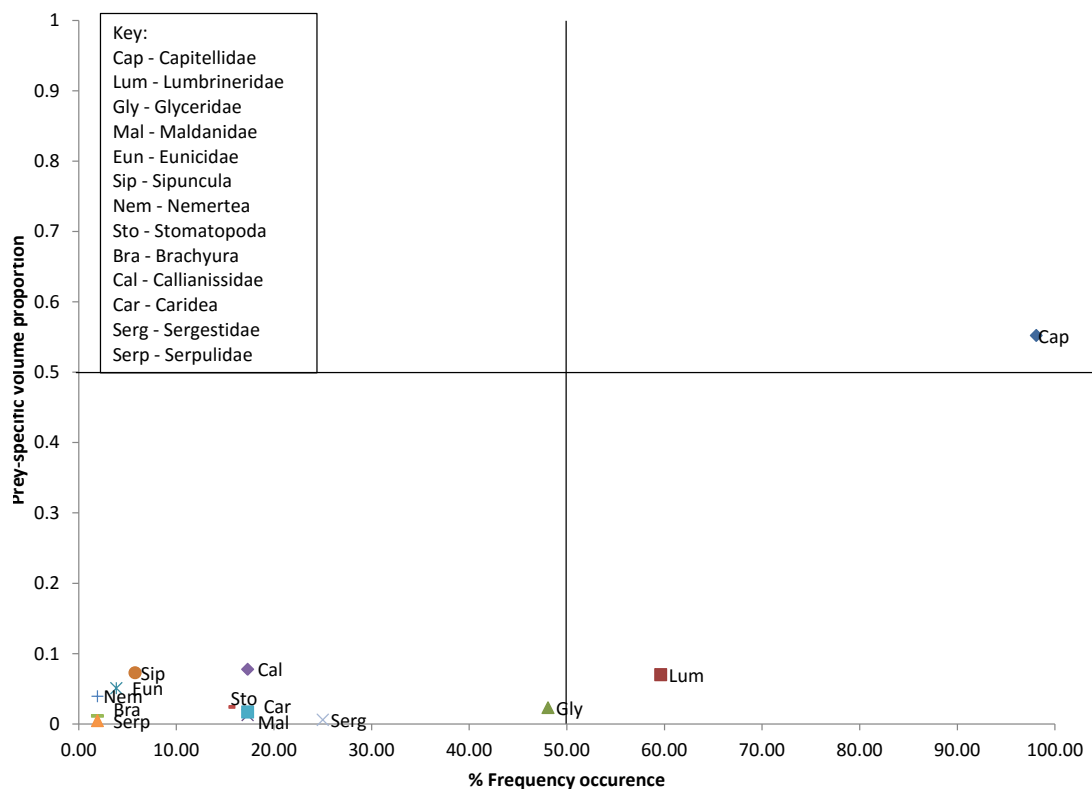


Figure 3.3: Feeding strategy plot for *U. asperrimus*. Upper quadrants represent prey items that are eaten in large quantities, while those in the lower quadrants are eaten in small amounts. The right quadrants represent prey items that are eaten by a large portion of the population, while those in the left are eaten by few individuals in the population.

3.3.3 Size and sex related shifts in dietary composition

The global ANOSIM revealed no significant differences in dietary composition between males and females (Global $R = -0.03$, $p = 0.61$). The SIMPER analysis revealed that Capitellidae contributed most to the stomach samples for all size groups

(74.4%; 76.5%; 65.4% for the small, medium and large size groups respectively, note that this could not be calculated for the very small and very large size groups because they only contained one sample), but the ANOSIM still revealed significant differences in the dietary composition between size classes (Global $R = 0.3$, $p = 0.02$). The pair-wise comparisons within the ANOSIM highlighted that the only significant differences occurred between the small and large size groups as well as between the medium and large size group (Table 3.2). The MDS plot further verified these results with the large size class lying mostly separate from the overlapping small and medium size classes (Figure 3.4). Upon examining the SIMPER results, it was found that an increase in Callianissidae contributed most to the dissimilarity between these size groups (27.9% between the small and large size groups and 30.9% between the medium and large size groups).

It must be noted that the very small and very large size groups had very small sample sizes, which is known to affect statistical significance for this particular analysis. Thus, even though the pair-wise comparisons found no significant differences in any comparisons involving these size classes, the high R values for all comparisons (except between the small and medium size classes) as well as the similar SIMPER percentage dissimilarity values (Table 3.2) suggests that the differences between all size classes may be relevant. The SIMPER showed that the families Lumbrineridae, Callianissidae, Caridea, and Glyceridae consistently contributed large amounts to the percentage dissimilarities between size classes. A plot of IoI for these groups across different size classes illustrates the changes in these prey items; the IoI of Lumbrineridae increases slightly as size increases, the change in Glyceridae is variable, but the most striking changes occur with the two crustacean families. The IoI of Caridea decreases while that for Callianissidae increases as size increases. The importance of Capitellidae is likely over-estimated in the very small and very large size class as small sample sizes reduces the chance of obtaining less dominant prey items (Figure 3.5).

Table 3.2: Top values in each cell represents R-statistics and corresponding p-values for the ANOSIM pair-wise comparisons between the different size-classes of *U. asperrimus*. Stars denote those that are considered statistically significant. Bottom values in each cell represent percentage dissimilarity values between the various size classes of *U. asperrimus*.

	40-49	50-59	60-69	70-79
50-59	0.44 (p = 0.33) 22.62			
60-69	0.22 (p = 0.29) 29.37	0.01 (p = 0.47) 23		
70-79	1.00 (p = 0.20) 34.48	0.64 (p = 0.02)* 25.04	0.30 (p = 0.04)* 26.55	
80-89	- 15.29	0.64 (p = 0.17) 26.14	0.24 (p = 0.29) 31.22	0.92 (p = 0.2) 22.55

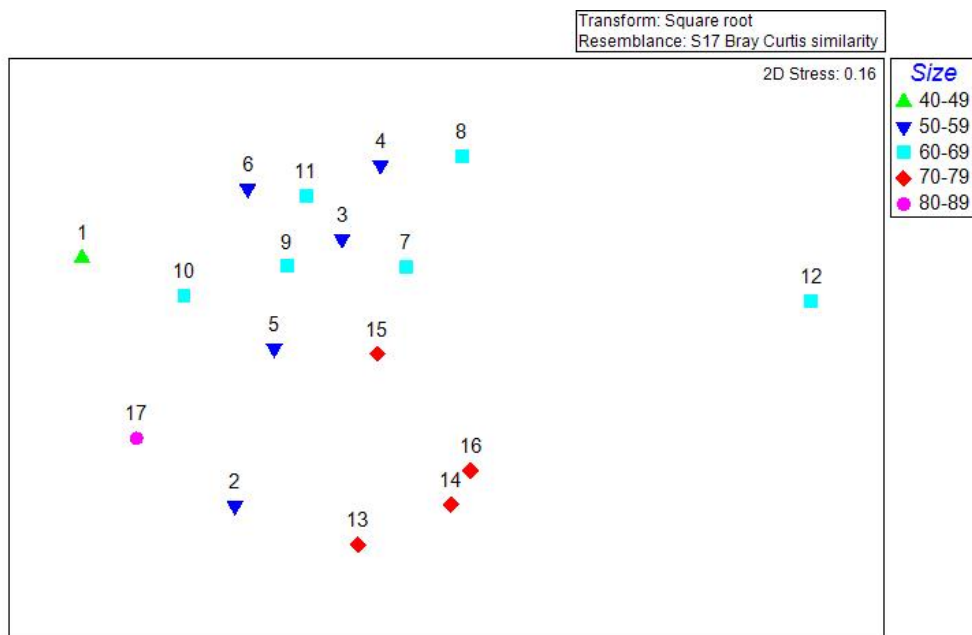


Figure 3.4: MDS plot of dietary sample collected from *U. asperrimus* grouped by size class

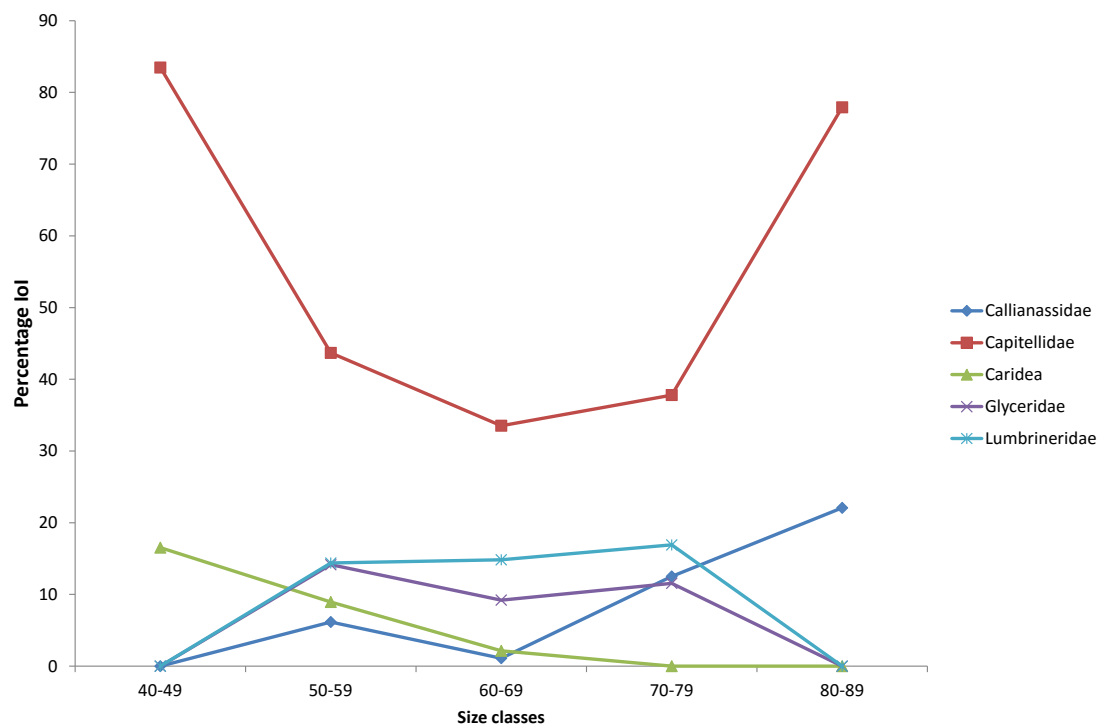


Figure 3.5: Percentage IoI of the most important prey items within the dietary samples of the various size classes of *U. asperrimus*.

3.4 Discussion

This chapter investigated the trophic ecology of juvenile porcupine rays and found that these animals are generalist predators within the St. Joseph Atoll, consuming a variety of infaunal polychaetes and crustaceans. The sample size was large enough to accurately describe their diet and it was found that the polychaete family Capitellidae was an important prey item for porcupine rays as most stomach contents contained high proportions of this prey item. Despite the apparent specialisation by porcupine rays on Capitellidae, it was consumed with only a moderate preference given its high environmental availability. Other polychaete families were consumed with moderate or low levels of preference. These results are similar to those obtained by O'Shea *et al.* (2013) who examined the diet of adult porcupine rays in a reef environment. These rays were found to consume mostly annelids and prawns, also with a moderate preference given their abundance within the environment. This study, in combination with that of O'Shea *et al.* (2013), suggests that porcupine rays are opportunistic predators, feeding predominantly on the prey items that have the highest environmental availability.

Stingrays are often quoted to play the important ecological role of mediating prey communities (Navia *et al.*, 2007; Vaudo & Heithaus, 2011; O'Shea, 2012). Within tropical marine ecosystems there are generally high levels of trophic complexity and there are both strong and weak predator-prey interactions present (Connell *et al.*, 1978; OGorman *et al.*, 2010). The strength of an interaction is a measure of influence over one another (Tilley, 2011) and only if a ray displays a strong predator-prey interaction can it potentially have strong influences over the prey species. As porcupine rays were found to be generally non-selective in their prey consumption, it suggests weak predator-prey interactions and thus a low potential influence over invertebrate communities. However, given that they feed on the organisms that were most plentiful within the substrate, porcupine rays could be functioning to keep these abundant prey groups suppressed and to prevent them from out competing other biota and becoming completely dominant within the system. Top-down effects by predators on prey populations have been controversial, but studies have noted its importance as a structuring element in ecosystems (Johnson *et al.*, 2007; Ripple & Beschta, 2012), as well as more specifically in batoid communities (VanBlaricom, 1982; Peterson *et al.*, 2001; Myers *et al.*, 2007).

It is important to note the absence of crustaceans in the sediment samples despite the presence in the stomach samples. This could indicate a relatively high degree of selectivity for crustaceans. However this is difficult to say with any level of confidence as it could have been an effect of sampling protocol. There may have been a smaller chance of sampling potentially deeper and more mobile crustaceans, but highly mobile burrowing worms (such as Capitellidae) were sampled in this manner. This suggests that the lack of crustaceans might not have been due to sampling protocol. There have been certain instances where batoids have been found to feed selectively, for example *Himantura uarnak* was found to feed selectively on brachyurans in Ningaloo Reef, Australia (O'Shea *et al.*, 2013), *Rhinoptera bonasus* appeared to select for amphipods and bivalves under certain circumstances (Ajemian & Powers, 2012), and *Aetobatus narinari* seems to be a hard-prey specialist both in Taiwan and Australia (Schluessel *et al.*, 2010). Thus selective feeding on crustaceans by porcupine rays cannot be ruled out, but future sediment sampling with a variety of sampling techniques would be needed to confirm this.

Even though it is difficult to say whether juvenile porcupine rays are selectively feeding on certain prey items, there does seem to be some indication that they select for deep-burrowing infauna as opposed to surface-dwelling epifauna. Almost all the prey items identified in the stomach contents were that of burrowing infauna, despite the presence of epifauna on the sand flats of the atoll. This apparent selection for deep infaunal prey is likely linked to their foraging behaviour. It has been noted that porcupine rays feed in a slightly different manner to other benthic species of rays by strongly ploughing up the benthos, expelling large plumes of sand from their spiracles (Last & Stevens, 2009; Theiss *et al.*, 2010). This feeding behaviour was observed by porcupine rays at the St. Joseph Atoll whereas the other two common stingray species (*Himantura granulata* and *Pastinachus sephen*) were not seen to excavate the sediment to such an extent.

The foraging behaviour and apparent selection for deep infaunal prey may suggest potential resource partitioning by porcupine rays. Theory predicts that where there are similar species in the same ecosystem, their co-existence should be facilitated by resource partitioning along some ecological axis in order to minimise competitive effects (Schoener, 1974; Schlosser, 1982). Thus, given the high abundances of the three stingray species (von Brandis, 2014), partitioning of resources is likely necessary for the co-existence of these individuals within the St. Joseph Atoll. Variability in mouth morphology and the manner in which prey items are excavated from the substratum may contribute to differences in foraging behaviour, which can facilitate resource partitioning in benthic batoids (Platell *et al.*, 1998; Platell & Potter, 2001; Marshall *et al.*, 2008). The partitioning of prey items has been evident in certain elasmobranch communities (White *et al.*, 2004; Marshall *et al.*, 2008; Sommerville *et al.*, 2011; Yick *et al.*, 2011) but to confirm resource partitioning by the sympatric species of St. Joseph Atoll, the dietary composition and habitat utilisation of *H. granulata* and *P. sephen* would need to be investigated.

There were no differences in dietary compositions between males and females, a trend that is common in batoid dietary studies (Platell *et al.*, 1998; Ebert, 2002; White *et al.*, 2004; Marshall *et al.*, 2007; O'Shea *et al.*, 2013). Also, given that these individuals were juveniles, potential segregation in habitat and diet would only occur

at the onset of sexual maturity (Dale *et al.*, 2011). There is some evidence to suggest size-related changes in diet. Although Capitellidae was the most abundant prey item in all size classes, the larger juveniles appeared to favour the ghost shrimps (Callinassidae) as opposed to the snapping shrimps (Caridea) which were more common in the smaller size classes. These ghost shrimps were larger in size and could be providing the necessary increase in energy for the larger porcupine rays. Size-related shifts in diets are common in batoids (Smith & Merriner, 1985; Gray *et al.*, 1997; Kyne & Bennett, 2002; Ebert & Cowley, 2003; Marshall *et al.*, 2008; Ajemian *et al.*, 2012) and given the evidence of the phenomenon in this study as well as the fact that only juveniles are abundant in the atoll (young-of-the-year have never been seen and adults only encountered on rare occasions), it is likely that this species changes both their habitat and diet throughout ontogeny.

As for the technique itself, gastric lavage has not often been used in the dietary studies of batoids. It was, however, found to be a simple, effective and rapid non-lethal technique. On average, the rays were held captive for less than three minutes, while the gastric lavage procedure took just over a minute to perform. In addition the high percentage of stomachs that were found to contain food (94.5%) and the 100% immediate post-release survival confirms that it was appropriate method to collect stomach contents from these rays. Why cloacal protrusion sometimes occurs during gastric lavage is unknown, but it has previously been observed in captive elasmobranchs, as well as in a wild manta ray *Manta birostris*, and it has been suggested that it may be a natural response to flush out undigested material or parasites from the digestive tract (Crow *et al.*, 1990; Sims *et al.*, 2000; Henningsen *et al.*, 2005; Clark *et al.*, 2008). In addition, cloacal protrusion was observed in individuals that were caught but not lavaged, providing evidence that the phenomenon is not directly caused by the lavage process, but could be a stress response.

Porcupine rays are considered as rare and infrequent throughout much of their range (Theiss *et al.*, 2010; Chin, 2014) and thus most populations are not likely to play major roles in structuring benthic communities and altering the benthos through bioturbation. The opposite is true for the St. Joseph Atoll which hosts an abundance of these juvenile porcupine rays (von Brandis, 2014). Given their high density and

the fact that they seem to selectively consume burrowing infaunal organisms, they have the potential to mediate these prey communities. In addition, given that they excavate the sediment to a seemingly greater extent than co-occurring rays, the affects of bioturbation through this feeding behaviour is likely emphasized. The porcupine ray is thus considered to be an ecologically important species in the St. Joseph Atoll ecosystem.

Chapter 4

Residency and space use of *Urogymnus asperrimus*



4.1 Introduction

Identifying habitats that are important to a species is crucial to conservation and management efforts (Dale *et al.*, 2011; Filmlalter, 2011; Davy *et al.*, 2015). For elasmobranchs these important habitats include areas where reproduction and parturition takes place (Springer, 1967), aggregation sites (Speed *et al.*, 2011), and juvenile nurseries (Simpfendorfer & Milward, 1993; Heupel & Hueter, 2002; Garla *et al.*, 2006; Heupel *et al.*, 2007; Knip *et al.*, 2010). Nurseries in particular are considered critical habitats because juvenile survival is thought to be an important factor in regulating the population size of elasmobranchs, given their low fecundity and slow growth rates (Cortes, 2002; Heupel *et al.*, 2007; Kinney & Simpfendorfer, 2009; Dale *et al.*, 2011; Davy *et al.*, 2015).

Information regarding fidelity and residency to a habitat as well as the finer-scale space use is needed when trying to understand the relative importance of a habitat to a species (Filmlalter, 2011). Advances in acoustic tracking technology and the increasing recognition that identifying critical habitats is important to conservation, has made obtaining this information easier and more popular (Heupel *et al.*, 2006b). Habitat selection is the process whereby an individual chooses a specific habitat type from a set of available habitat types and it is based upon the animal's preference and the variation in the possible choices (Van Moorter *et al.*, 2015). Literature suggests that animals select habitats according to a variety of influences including habitat quality (Papastamatiou *et al.*, 2010; Boyce *et al.*, 2015), which in itself is affected by multiple biotic and abiotic factors, particularly in nurseries (Beck *et al.*, 2001). Other influences include the feeding strategy of a species and the relative abundance and availability of prey (Sims, 2003), as well as intra and interspecific interactions, including competition and predation (Heupel & Hueter, 2002; Papastamatiou *et al.*, 2010). Ultimately, the preference for a set of environmental variables should be related to its effects on individual fitness (Van Moorter *et al.*, 2015) and selecting the correct habitat will determine the success of the animal in obtaining food, potential mates, and safety from predation (Papastamatiou *et al.*, 2010).

A multitude of studies have provided evidence that sharks use areas such as coastal bays, estuaries and/or offshore atolls as nurseries (Castro, 1993; Simpfendorfer & Milward, 1993; Heupel & Hueter, 2002; White & Potter, 2004; Grubbs *et al.*, 2007; Wetherbee *et al.*, 2007; Deangelis *et al.*, 2008; Aché De Freitas *et al.*, 2009; Chapman *et al.*, 2009). It has been hypothesized that these areas provide an abundance of prey resources given their high levels of productivity as well as refuge from predation given their typically shallow habitats (Branstetter, 1990; Castro, 1993; Simpfendorfer & Milward, 1993; Heupel & Hueter, 2002; Dale *et al.*, 2011; Cerutti-Pereyra *et al.*, 2014). Comparatively few studies have provided evidence for batoids using such nurseries (but see Yokota & Lessa, 2006, Aguiar *et al.*, 2009, Vaudo & Heithaus, 2009, Dale *et al.*, 2011, Cerutti-Pereyra *et al.*, 2014, Davy *et al.*, 2015), but given the under-researched nature of batoids (Tilley, 2011; Vaudo & Heithaus, 2012), this phenomenon is likely to be more common than what is represented in scientific literature.

If nursery habitats are important to juvenile stingrays, restricted movement patterns and residency that spans months to years within a defined habitat is expected (Cerutti-Pereyra *et al.*, 2014). Literature on the movement of juvenile rays is scarce, particularly for the porcupine ray. Only one study has investigated the movements of four juvenile porcupine rays and the authors suggested that they were making use of a coastal nursery habitat (Cerutti-Pereyra *et al.*, 2014). This gave a basis to the hypothesis that the remote St. Joseph Atoll is a potential nursery habitat to the abundant juvenile porcupine rays that occur there (von Brandis, 2014). As long-term information was required to support this hypothesis, passive acoustic telemetry was used to gain a year-long data set on the movements of juvenile porcupine rays. The St. Joseph Atoll has very recently (in 2015) been gazetted as a marine protected area (MPA) and could thus provide important conservation benefits if these Vulnerable (Compagno, 2005) juveniles utilise this habitat as a nursery. Specific objectives for this chapter were to determine:

- The degree of residency to the St. Joseph Atoll
- Geographical space use within and around the atoll

- Environmental space use (i.e. habitat utilisation)
- Whether space use is affected by seasonality

4.2 Methods and Materials

4.2.1 Field methods

The residency and space use of acoustically tagged porcupine rays was assessed using an acoustic receiver array within and around the St. Joseph Atoll (see Chapter 2 for details). Detection data was collected for a one-year period (March 2014 to March 2015). To acoustically tag the porcupine rays, juveniles were caught using the methods described in Chapter 2 at various locations on the shallow sand flats (0.1–1.5m depth) of the St. Joseph Atoll (Figure 4.1). All captured individuals were assumed to be juveniles based on the lack of calcification of the claspers in males as well as size, which was below the estimated size at maturity for males (90cm DW) and females (100cm DW) (Last & Stevens, 2009). Once a captured porcupine ray was in tonic immobility, an acoustic transmitter was surgically implanted into its abdominal cavity. A small incision, about 3cm in length, was made through the lining of the abdominal cavity with a sharp scalpel blade. The transmitter was first soaked in ethanol and then inserted into the abdominal cavity through the incision. Two or three independent sutures (SupraMed), depending on the size of the cut, were then used to close the incision. The ray was released as close as possible to the capture location and monitored for approximately 5 minutes to determine immediate post-release health. All individuals appeared healthy post-surgery and no predation events were witnessed. The average surgery time was 3 minutes and 21 seconds (see Table 4.1).

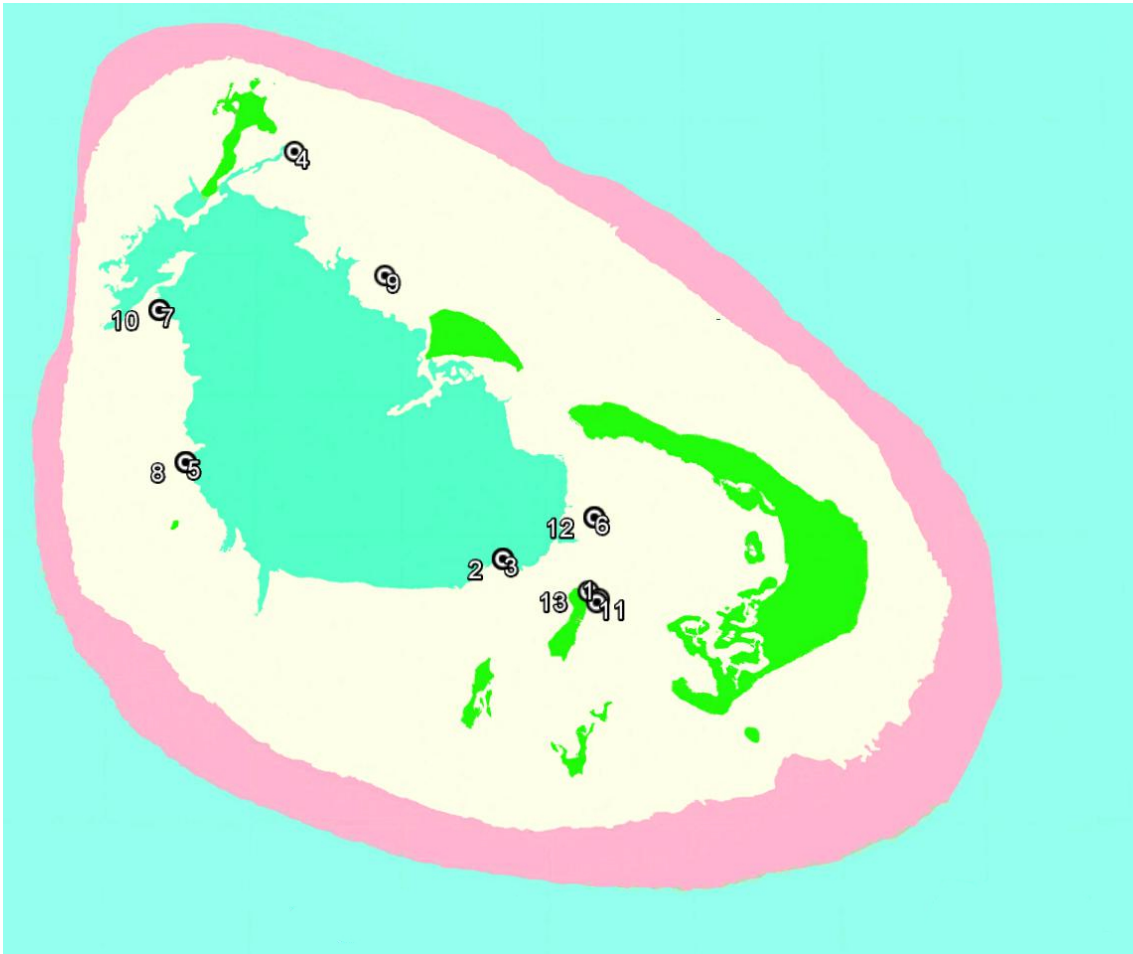


Figure 4.1: Tagging locations of *U. asperrimus* within the St. Joseph Atoll. Colours represent different habitat types. Green represents the islands, blue within the atoll represents the lagoon, beige represents the sand flats, pink represents the fringe reef, and blue surrounding the atoll represents the offshore habitat.

4.2.2 Data analysis

Data from the receivers were analysed in the R environment (R Development Core Team: www.r-project.org) in two parts because of changes made to the receiver array during the monitoring period (see Chapter 2 for details). The Phase 1 receiver array comprised 70 receivers (18 within the atoll) that were moored from the date that rays were tagged. The Phase 2 array included an extra 38 receivers (resulting in 30 receivers located within the atoll), that were deployed from 28 August 2014 to 20 March 2015. During Phase 2 certain receivers were deployed in September and November, however these receivers recorded very few detections (see habitat utilisation results), and their different deployment dates were not taken into consideration when analysing the data.

Table 4.1: Details of acoustically tagged *U. asperrimus* individuals within the St. Joseph Atoll

Individual	Transmitter type	Date tagged	Disc width (cm)	Sex	Surgery time
1	V13-1x	10/03/2014	58	m	3:05
2	V13-1x	11/03/2014	59	f	2:27
3	V13-1x	11/03/2014	59	m	2:14
4	V13-1x	14/03/2014	59	m	2:38
5	V16-4x	11/03/2014	60	f	2:52
6	V16-4x	10/03/2014	61	f	3:59
7	V16-4x	11/03/2014	62	m	3:58
8	V16-4x	11/03/2014	63	m	3:48
9	V16-4x	10/03/2014	63	m	4:43
10	V16-4x	11/03/2014	63	f	2:51
11	V16-4x	10/03/2014	66	m	3:11
12	V16-4x	10/03/2014	69	m	3:45
13	V16-4x	10/03/2014	73	f	4:02

Residency to the atoll

Residency of the juvenile porcupine rays to the St. Joseph Atoll was assessed on a monthly and daily scale. At the monthly scale, the number of days in each month that each ray was present in the atoll was calculated. An individual was considered present if it was detected two or more times per day (this was done to exclude any potential false detections) on a receiver that was located within the atoll or on the fringing reef of the atoll. At a daily scale, a residency index (RI) was calculated for each individual:

$$\text{RI} = \text{number of days present within the array} / \text{number of days monitored}$$

where RI is the residency index, and the number of days monitored is from the date tagged to the date of last detection (as it was impossible to determine if an individual had permanently left the array). The index ranges from 0 to 1 indicating low and high residency respectively.

The residency indices were not normally distributed so non-parametric tests were used to determine if there were significant differences in RI between Phase 1 and Phase 2 of the receiver deployment (Wilcoxon signed rank test), between sexes (Mann-Whitney U test), and to determine if there was any correlation in RI with the size of the individual (using Spearman's rank correlation).

Geographical space use

The extent of geographical space use by juvenile porcupine rays was assessed by two different means. Firstly, the size of core use and activity space areas were calculated. The location of each individual was estimated for every 30 minute interval it was present in the array using a mean position algorithm, providing its centre of activity (COA) (Simpfendorfer *et al.*, 2002). This algorithm relies on multiple detections from multiple receivers so only individuals that were detected by two or more receivers for more than five days per month were analysed. COA locations were then used to calculate individual monthly activity spaces and core use areas. The *adehabitatHR* package in R (Calenge, 2006) was used to calculate the 50% kernel utilisation distributions (KUDs) as a proxy for core use areas and 95% KUDs as a proxy for activity space areas. The rule-based ad hoc method was used to determine the smoothing parameter (h) in the KUD analysis (Kie, 2013). The monthly 50% KUDs and 95% KUDs were not normally distributed and could not be transformed so non-parametric tests were used to test for significant differences between sexes (Mann-Whitney U test), between Phase 1 and Phase 2 of receiver deployment (Wilcoxon signed rank test), and to determine if there was any correlation with the size of the individual tagged (Spearman's rank correlation).

Secondly, the relationship between the proportions of detections at each receiver and the distance from the tagging site was used to further elucidate the extent of movements made by porcupine rays (this analysis was restricted to Phase 2 given the addition of new receivers). The distance from an individual's tagging site to each receiver that recorded detections for the individual was calculated and the mean of these distances was determined as a proxy for average movement range. A Mann-Whitney U test was performed to determine if the mean distances were significantly different between males and females and Spearman's rank correlation was used to determine if there was any correlation with size. The distances traveled to each receiver were then averaged across individuals and plotted against the proportion of detections at each of the receivers to determine if there was a relationship between the distance traveled and the proportion of detections recorded.

Environmental space use

Environmental space use was assessed by delineating distinct broad habitat types within and around the atoll. The habitat types identified were sand flats, lagoon, fringe reef and offshore (outside of the atoll). The extent of these habitat types are shown in Figure 4.1. The proportions of detections on each receiver were then calculated and assigned to each habitat type to determine high use areas and thus which habitat type was most important to the juvenile porcupine rays.

Seasonality

It could not be determined if there was any seasonality effects on movements on the sand flats of the atoll because of the two different receiver arrays used for the duration of this study. However, the receivers located within the lagoon and fringe reef habitats remained unchanged throughout the year long monitoring period and thus potential seasonality in the usage of these habitats could be assessed. The mean number of days per month that detections were recorded on receivers in the lagoon and on the fringe reef were calculated and plotted. Chi-square goodness of fit tests were performed to determine if these were significantly different from an even distribution.

4.3 Results

A total of 13 juvenile porcupine rays were caught and released with surgically implanted acoustic transmitters at various locations within the St. Joseph Atoll in March 2014. The tagged individuals (8 males and 5 females), ranged in size from 59 to 73cm disc width. These rays were monitored for a year and a total of 146342 detections were recorded. One individual (transmitter ID 7) only had a single detection one month after tagging and was excluded from all analyses. It could not be determined why there were no more detections for this ray but the likeliest scenario is that the ray died after the single detection, either through predation or some other

event.

4.3.1 Residency to the atoll

The monitoring periods for the remaining twelve porcupine rays ranged from 110 to 375 days. The rays displayed a high degree of fidelity to the atoll and seven of them were still present at the end of the monitoring period in March 2015. The other five individuals were last detected on various dates between June 2014 and February 2015 (Table 4.3). Three of these rays were last detected within the atoll, one individual was last detected on the fringing reef of the atoll, while the final individual (ID # 9) was last detected on receiver 40 situated on the northern plateau, about 7km NW of the atoll. The latter might be related to a predation event as this was the only time a detection occurred outside the atoll or its fringing reef. At a monthly scale, only two individuals were detected in every month ($n=13$) of the study period, but 10 individuals were detected in more than half of the months. The months with the highest rays being undetected were May, June and July 2014, with no detections from 8, 5 and 6 individuals respectively (Table 4.2).

Residency indices were generally high but variable across individuals during both Phase 1 and Phase 2 of receiver deployments, with some individuals not detected at all and others detected for up to 93% of the total monitoring days (Table 4.3). The mean ($\pm$ standard deviation) residency indices for Phase 1 and Phase 2 were 0.26 ± 0.27 and 0.64 ± 0.32 respectively, and they were significantly different (Wilcoxon signed rank test: $v = 7$, $p = 0.009$). The number of individuals that were detected for more than 50% of the monitoring days increased from 3 to 9 in Phase 2. There were no significant differences in the residency indices between sexes ($W = 22$, $p = 0.53$ and $W = 21$, $p = 0.64$ for Phase 1 and Phase 2 respectively) and they were not significantly correlated to disc width (Spearman's rank correlation $\rho = 0.52$, $s = 137.65$, $p = 0.084$ and $\rho = 0.51$, $s = 139.68$, $p = 0.089$ Phase 1 and Phase 2 respectively).

Table 4.2: The number of days per month that tagged *U. asperrimus* individuals were detected within the St. Joseph Atoll

Individual	Month												
	Mar	Apr	May	June	July	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar
1	5	1	0	0	0	0	0	6	10	7	15	0	1
2	17	1	0	1	0	0	0	0	0	0	0	0	0
3	1	0	0	0	0	0	0	8	2	2	2	2	6
4	2	0	0	3	0	5	27	4	0	0	0	0	0
5	2	0	0	0	0	4	7	15	23	25	19	16	14
6	21	27	20	14	12	20	29	29	30	22	26	24	19
8	2	2	0	0	0	3	4	27	15	23	23	21	20
9	16	14	19	17	25	14	22	23	18	0	1	0	0
10	5	4	0	13	28	24	23	29	30	30	28	28	19
11	2	3	0	0	2	6	14	21	19	27	29	12	0
12	12	20	20	13	30	24	26	28	25	26	22	20	19
13	17	27	8	3	15	11	14	17	22	0	0	0	0

Table 4.3: Calculated residency indices for tagged *U. asperrimus* within the St. Joseph Atoll. TMD = Total Monitoring Days, DD = Days Detected, RI = Residency Index

Individual	First detection	Last detection	TMD (Phase 1)	TMD (Phase 2)	DD (Phase 1)	DD (Phase 2)	RI (Phase 1)	RI (Phase 2)
1	12-03-14	15-03-15	169	199	6	39	0,04	0,2
2	12-03-14	29-06-14	110	-	19	-	0,17	-
3	11-03-14	20-03-15	168	204	1	22	0,01	0,11
4	26-03-14	07-10-14	165	40	5	36	0,03	0,9
5	23-03-14	19-03-15	168	203	2	122	0,01	0,6
6	10-03-14	20-03-15	169	204	109	183	0,64	0,9
8	24-03-14	20-03-15	168	204	4	135	0,02	0,66
9	10-03-14	12-01-15	169	137	102	66	0,6	0,48
10	11-03-14	20-03-15	168	204	70	190	0,42	0,93
11	15-03-14	18-02-15	169	173	11	124	0,07	0,72
12	10-03-14	20-03-15	169	204	114	170	0,67	0,83
13	10-03-14	30-11-14	169	75	77	56	0,46	0,75

4.3.2 Geographic space use

Activity spaces could not be estimated for four of the porcupine rays due to the low frequency of total detections (0.31%, 0.35%, 0.34% and 1.36% for individuals #1, 2, 3, and 4 respectively). The remaining 8 porcupine rays predominantly stayed in the areas where they were caught and exhibited both small core use areas (50%KUDs) and activity spaces (95% KUDs). The monthly 50% KUDs ranged from 0.002km² to 2.4km² (mean of 0.5km²) and the monthly 95% KUDs ranged from 0.01km² to 17.7km² (mean of 3.2km²). The activity spaces were not significantly different

between sexes ($W = 483.5$, $p = 0.3$ and $W = 481$, $p = 0.4$ for 95% and 50% KUDs respectively) and there was no significant relationship with disc width (Spearman's rank correlation $\rho = 0.04$, $s = 31$, $p = 0.75$ and $\rho = 0.03$, $s = 31603$, $p = 0.84$ for 95% KUDs and 50% KUDs respectively). There was however a significant increase in calculated activity space during Phase 2 receiver deployment ($V = 19$, $p = 0.009$ and $V = 26$, $p = 0.03$ for 95% and 50% KUDs respectively) (Figure 4.2). This increase in activity space was not only due to detections on the newly added receivers but all individuals, except one, were detected on more of the pre-existing receivers on the sand flats during Phase 2.

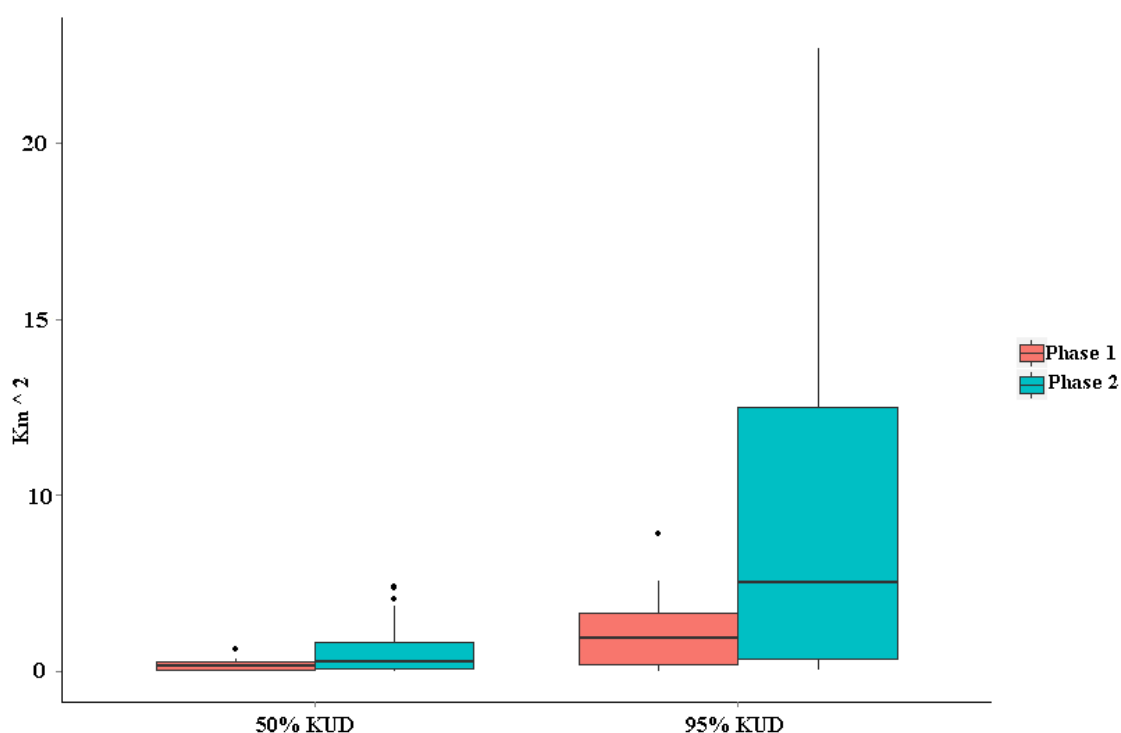


Figure 4.2: Boxplot illustrating 50% and 95% KUDs of *U. asperimus* for Phase 1 and Phase 2 receiver deployment. Circles represent outliers

The furthest an individual was detected from its tagging location was 9.1km, but the mean distances traveled by individuals ranged from 0.4km to 2.2km (Table 4.4). The mean distances were not significantly different between sexes ($W = 18$, $p = 1$) but were significantly correlated to disc width (Spearman's rank correlation $\rho = 0.76$, $s = 68.36$, $p = 0.004$). When these distances were averaged across individuals, they were strongly related to the proportions of detections on the receivers. Receivers located within 1km of the tagging locations accounted for 52.2% of all detections,

while receivers located further away recorded fewer detections (with each receiver accounting for less than 3%) (Figure 4.3).

Table 4.4: Minimum, maximum, and mean distances that *U. asperrimus* traveled from their tagging locations to the various receivers that they were detected on.

Individual	Min distance (km)	Max distance (km)	Mean distance (km)
1	0.4	1.5	0.78
2	0.6	1.7	1.15
3	0.7	1.2	0.90
4	0.1	0.7	0.40
5	0.5	3.8	1.95
6	0.1	2.6	1.34
8	0.5	3.4	1.96
9	0.3	9.1	1.87
10	0.5	3.5	1.94
11	0.5	4.2	2.22
12	0.1	4.5	2.18
13	0.4	4.6	1.95

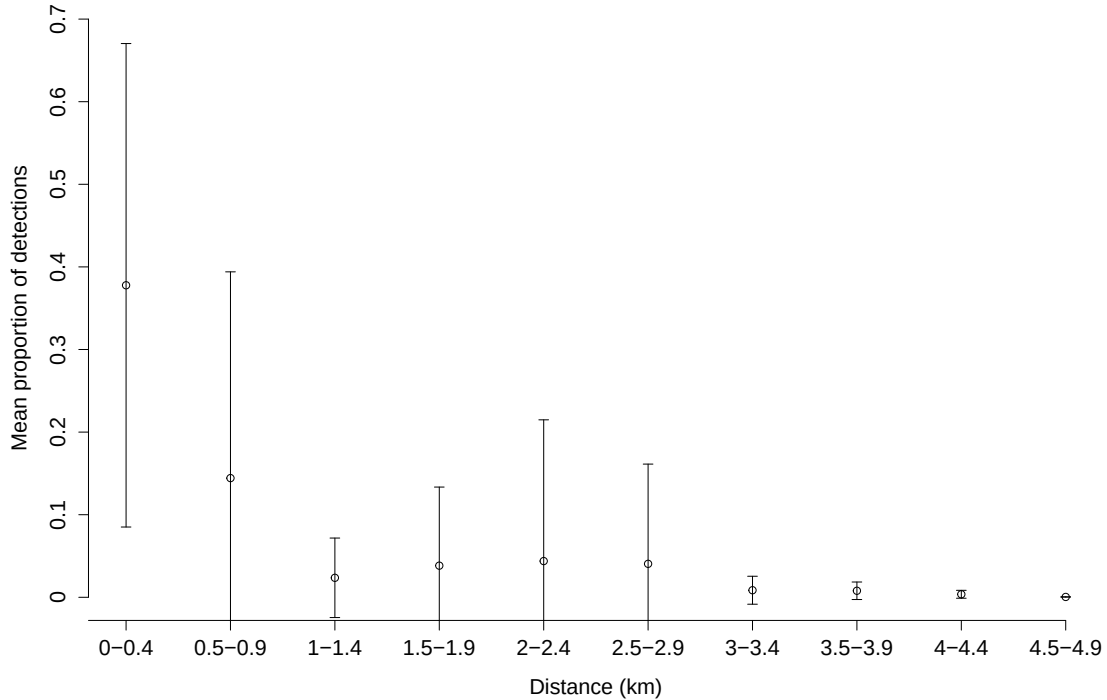


Figure 4.3: The mean proportions of detections that receivers recorded plotted against the distance of those receivers from each individuals tagging location. Error bars denote standard deviation.

4.3.3 Environmental space use

Detections from tagged porcupine rays were recorded on 35 of the 88 receivers deployed within the St. Joseph Atoll and along the Amirantes Bank. The proportion of the detections was skewed across the receiver array, according to habitat type (Figure 4.4). Receiver #40 was the only receiver not located within the atoll or its fringe reef to record detections; it recorded two detections for individual ID #9 and it is unclear whether this was related to a predation event as mentioned above or whether the individual left the atoll. Few detections (0.07%) were recorded on receivers on the fringe reef (these detections were from the three largest porcupine rays (ID # 11, 12, 13)). A large portion of detections (12.1%) came from receivers located within the lagoon but it is important to note that some receivers may be located within detection range of the sand flats (Chapter 2). The majority of detections (87.8%) were from receivers located on the sand flats. During Phase 1 receivers #64, 65, and 67 each recorded high proportions of the detections and collectively accounted for 72.8% of all detections on the sand flats. Receivers #2, 4, and 62 also recorded a considerable number of detections, and when included these six receivers accounted for 93.6% of all detections on the sand flats during Phase 1. In Phase 2, receivers #64, 67, and 4 still recorded a high percentage of the detections but new receivers #75, 77 and 78 each recorded a large proportion of the detections. Collectively these 6 receivers accounted for 82.8% of all detections on the flats in Phase 2.

4.3.4 Seasonality

The mean number of days per month on which detections were recorded were not significantly different from an even distribution in the fringe reef habitat (X-squared = 9.52, df = 12, p = 0.66) but were so in the lagoon habitat (X-squared = 37.01, df = 12, p = 0.0002). The only time detections were recorded in the fringe reef was in the North-West monsoon season (Nov 2014 to Feb 2015) and with the majority of detections in the lagoon occurred at the same time (Figure 4.5). The sand flats habitat was excluded from this analysis given the variable number of receivers.

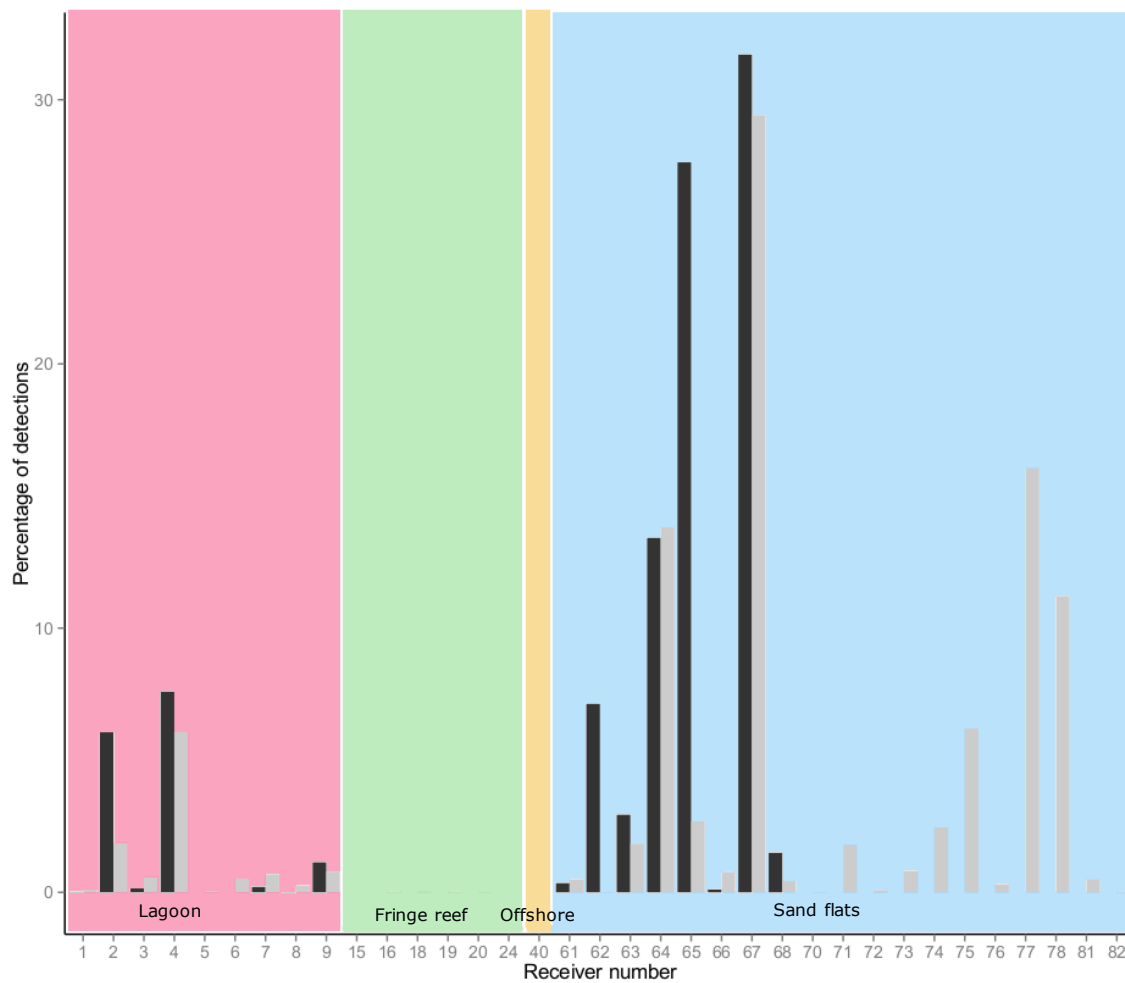


Figure 4.4: Detections recorded by receivers (%) in Phase 1 (black bars) and Phase 2 (grey bars). Receivers 1 - 9 occur in the lagoon, receivers 15 - 24 occur in the fringe reef, receiver 40 occurs offshore, and receivers 61 - 82 occur on the flats of the St. Joseph Atoll.

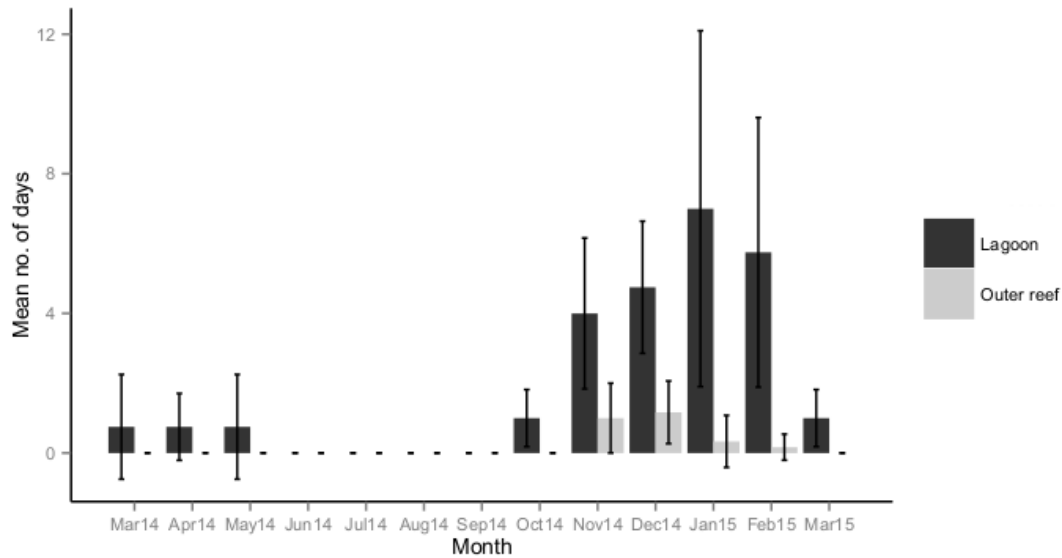


Figure 4.5: Mean number of days per month that tagged *U. asperrimus* were detected within the lagoon and outer fringe reef habitats of the St. Joseph Atoll. Error bars denote SD.

4.4 Discussion

The passive acoustic monitoring of juvenile porcupine rays over a year-long period indicates that they may be utilising the isolated St. Joseph Atoll as a nursery. One of the suggested criteria when delineating a nursery area is that individuals should display a high degree of long-term residency to the area in question (Heupel *et al.*, 2007). In this case, long-term fidelity, high degrees of residency, as well as restricted space use within the atoll by juvenile porcupine rays provide testimony of their dependance on this habitat as a nursery area. Temporally, more than half of the tagged individuals were still present in the atoll after a year and 83% of individuals were detected in more than half of the months. The mean residency index of 64% for juvenile porcupine rays in the St. Joseph Atoll falls between the values calculated for other studies. Juveniles of four stingray species were detected for 51% of monitoring days on average in an identified nursery within Ningaloo Reef, Australia (Cerutti-Pereyra *et al.*, 2014), while juveniles of *Himantura uarnak* were detected for an average of 81% of the monitoring period in their identified nursery in Pioneer Bay, Australia (Davy *et al.*, 2015). There was no effect of sex on residency or space use, presumably because habitat segregation would occur as individuals

become sexually mature (Dale *et al.*, 2011).

Residency was higher in Phase 2, as the data revealed an apparent absence of a number of tagged porcupine rays in the months of May, June and July. This could be a result of the individuals leaving the atoll at the onset of the cooler and windier South-East monsoon period. However, this is unlikely as no detections were recorded on the receivers surrounding the atoll or D'Arros Island. Alternatively, the limited number of detections might not be related to the absence of porcupine rays, but rather other factors. For example, the tagged individuals might have restricted their movement patterns in these cooler months, making them less detectable on the receivers. Another factor to consider is that the reception range of the receivers may have been compromised over this period. Strong winds are known to influence receiver performance, particularly in shallow waters (Payne *et al.*, 2010; Cerutti-Pereyra *et al.*, 2014; Kessel *et al.*, 2014) and range tests performed on the sand flats of the atoll confirmed that wind speed had the greatest potential to affect receiver performance (Chapter 2). However, strong winds persisted through to September (Chapter 2), thus not fully explaining why these lower detection frequencies were isolated to three months only. The final factor to take into consideration is the receiver array itself. Prior to August there were fewer receivers within the array and thus less listening power while after the deployment of extra receivers in August, there was a higher probability of rays being detected. Therefore it is likely that tagged porcupine rays were present in the atoll prior to August however, they were simply not detected on the smaller receiver array.

Porcupine rays displayed limited geographical movement patterns as they exhibited both small core use and activity space areas. The furthest distance an individual traveled from its tagging site to a receiver was 9km, but the majority of detections occurred within 1km of each individual's tagging location. When considering these limited movements in an environmental sense i.e. in terms of habitat usage, they were mainly restricted to the sand flats of the atoll, where the majority of detections occurred. Theoretically, the link between an animal's activity space and its habitat selection is the animal's movement (Van Moorter *et al.*, 2015). Movement has been defined as a change in geographic space, but is driven by changes in environmental

space (Van Moorter *et al.*, 2013) as an animal tries to satisfy its requirements in terms of gaining energy, seeking refuge, learning and reproducing (Nathan *et al.*, 2008). It has been hypothetically and empirically illustrated that animals exploit more favourable environments by displaying smaller core use areas and increased residency within the area (Van Moorter *et al.*, 2015). Given the limited space use and high degrees of residency to the sand flats by juvenile porcupine rays, this habitat type likely provides the most preferable conditions for them.

When considering habitat selection specifically related to nursery choice in elasmobranchs, an abundance of prey as well as safety from predation has commonly been cited as the reasons behind the selection (Branstetter, 1990; Castro, 1993; Simpfendorfer & Milward, 1993; Heupel & Hueter, 2002; Dale *et al.*, 2011; Cerutti-Pereyra *et al.*, 2014). However, cases of high juvenile mortality due to starvation (Duncan & Holland, 2006) and a lack of correlation with prey abundance (Heupel & Hueter, 2002) has resulted in doubt cast over the first hypothesis. Furthermore, a study within an atoll system found that shallow sand flats are relatively depauperate compared to the deeper habitats (Tilley, 2011), which puts into question whether juvenile porcupine rays selected the sand flats for prey resources.

A more probable hypothesis for the selection of this shallow habitat is that it provides a measure of safety from predation. Within the atoll the deeper lagoon is frequented by sicklefin lemon sharks and to a lesser extent bull sharks (Filmatler *et al.*, 2013, James Lea, Plymouth University, unpublished data) and thus this habitat represents an area with an increased risk of predation. Different organisms select habitats based on their unique set of defences that have evolved through millennia, such as cryptic coloration, swimming speed, burial, and grouping behaviour (Lima & Dill, 1990). Although porcupine rays were seen in groups occasionally, the majority of individuals were alone suggesting that grouping behaviour is not a defence mechanism for this species. They were also rarely seen buried, but given their cryptic colouration this was presumably not needed. However, when considering their dorsoventrally flattened bodies that can access shallower waters compared to top predators, the selection of shallow water can be viewed as one of their best defence mechanisms and provides a likely cause behind the high degree of selection for the

shallow sand flats. A similar result was found within Glovers Reef Atoll where juvenile southern stingrays *Dasyatis americana* were abundant on the depauperate shallow sand flats, indicating that predation risk most likely had a strong influence over their behaviour, causing a trade-off of energy for safety (Tilley, 2011).

It must be mentioned that this result should be treated with caution. All of the individuals were caught and tagged on the sand flats. Given their apparent small range of movements, it is not surprising that the majority of detections occurred on the flats. The limitation in this study is that no individuals were caught within the lagoon and acoustically monitored (see Figure 4.1 for distinct habitat types). Thus while the tagged individuals used the lagoon on rare occasions, there is the possibility that resident individuals live in this deeper habitat. Nonetheless, the latter is somewhat unlikely given the evidence that juvenile rays are known to avoid areas with high predation risk (Tilley, 2011; Cerutti-Pereyra *et al.*, 2014; Davy *et al.*, 2015).

Certain shark species have been known to utilise nursery habitats seasonally (Simpfendorfer & Milward, 1993; Yokota & Lessa, 2006), as warmer inshore waters in the summer months are thought to provide increased metabolic and growth rates for elasmobranchs (Economakis & Lobel, 1998; Knip *et al.*, 2010). Conversely for rays, seasonal nursery use has often been overlooked in studies. The few studies that did take seasonality into account found no or limited evidence for it (Yokota & Lessa, 2006; Vaudo & Heithaus, 2009; Cerutti-Pereyra *et al.*, 2014) while only a single study found direct evidence for it in bat rays *Myliobatus californica* (Gray *et al.*, 1997). At the St. Joseph Atoll, tagged porcupine rays were detected within the atoll throughout the year-long monitoring period (despite lower detections prior to August), suggesting that the use of this nursery habitat is not seasonal. Given the proximity of the study site to the equator, there is limited seasonal variability in temperature, reducing any benefits that a seasonal usage in this habitat would offer.

Having said this, there is some indication of seasonal microhabitat usage in the St. Joseph Atoll. There was a significant increase in the core use and activity space areas of juvenile porcupine rays within Phase 2, which coincides with the warmer North-West monsoon season (November to February). This apparent range expansion is

probably related to the observed seasonal usage of the deeper lagoon and fringe reef habitats. The only time detections were recorded on the fringing reef of the atoll was between November and February and there were more detections within the lagoon during this time. It should be noted here that a reduction in wind speed might be a factor in this trend, with lower wind speeds in the North-West monsoon season potentially increasing receiver efficiency, but the receivers in the deeper lagoon and in the deeper waters of the fringing reef are not likely to be as affected by wind speeds. Both seasonal shifts in microhabitat use (Vaudo & Heithaus, 2009) and an increase in the range of movements in warmer months (Cerutti-Pereyra *et al.*, 2014) have been noted in rays before. In this case, seasonal microhabitat usage is likely related to thermal tolerance. During the warmer months the waters on the flats can reach extremely high temperatures, up to 40°C, and these individuals may be using the cooler, deeper waters of the lagoon or fringe reef to escape these high temperatures (see Chapter 5 for details regarding movement behaviour and temperature).

There is also some evidence to suggest an effect of size on movement. Even though calculated activity spaces were not correlated to size, the mean distances traveled from tagging locations to receivers were. In addition, the only individuals to be detected on the fringing reef were the largest individuals tagged. It has been well documented that increasing body size leads to an increase in home range size (Kramer & Chapman, 1999), and this pattern has been observed to hold true for sharks (Speed *et al.*, 2010) and stingrays (Tilley, 2011). Intuitively as animals increase in size they require more space to provide enough resources to meet their growing energetic demands. There are also reduced risks of predation at the onset of maturity that will increase home range sizes (Speed *et al.*, 2010). It is thus plausible to suggest that as porcupine rays grow, they may not rely as heavily on the safety of the shallow sand flats and may expand their range to the fringe reef of the atoll and perhaps even further along the Amirantes Bank. This is additionally evidenced by the general absence of adults within the atoll (Elston unpub. data.).

The results in this chapter provide further evidence that the elasmobranch populations who utilise the St. Joseph Atoll will benefit from its status as an MPA.

Filmalter *et al.* (2013) highlighted that this atoll is an important area to sub-adult sicklefin lemon sharks, and this study illustrates that the atoll is an important area for juvenile porcupine rays. Also, the atoll is unique in that throughout most of the porcupine ray's range they occur rarely, making the high abundances of juveniles here noteworthy. Given the evidence that juvenile porcupine rays utilise a small shallow embayment within the lagoon of Ningaloo Reef, Australia as a potential nursery area (Cerutti-Pereyra *et al.*, 2014), this species may make use of nurseries throughout a range of habitats, including both coastal coral reef environments and offshore atolls. Identifying these nurseries has important implications for management and conservation efforts (Cerutti-Pereyra *et al.*, 2014) and the protection of these areas is likely to result in a high conservation benefit for this species.

Chapter 5

Environmental influences on short-term movements



5.1 Introduction

Habitat selection is an important aspect in the lives of mobile organisms and in itself has important consequences for ecological dynamics at multiple scales (Morris, 2003). It is important to quantify the habitat selection of an animal as well as the reasons behind these selections (Sims, 2003; Speed *et al.*, 2010) to gain a better understanding of an animal's ecology. Habitat selection is dependent on the interplay between an animal's internal biological factors and the external biotic and abiotic factors of their environment, for example, an animal's physiology may be constrained by an environmental factor, such as salinity, restricting access to some habitats or modifying the costs and benefits of others (Vaudo & Heithaus, 2013). As such, various environmental factors have been found to influence the movement patterns of aquatic animals (Matern *et al.*, 2000; Childs *et al.*, 2008; Sakabe & Lyle, 2010; Heupel & Simpfendorfer, 2014).

For ectothermic organisms in particular, temperature is one of the most important environmental factors to affect movement patterns given that it interacts with physiological performance (Dunham *et al.*, 1989). Both terrestrial and aquatic ectothermic species have been known to exhibit behavioural thermo-regulation whereby they select habitats within a thermally heterogeneous environment to maintain their body temperatures within an optimal range (Adolph, 1990; Speed *et al.*, 2012). Given that the majority of elasmobranchs are ectothermic (Hopkins & Cech, 2003), many species have been shown to select different habitats in response to water temperatures (Matern *et al.*, 2000; Hopkins & Cech, 2003; Sims *et al.*, 2006; Vaudo & Lowe, 2006; DiGirolamo *et al.*, 2012; Speed *et al.*, 2012). The selection of certain water temperatures is probably linked to optimising energetic gains given that water temperature affects growth, reproductive factors including embryonic development and parturition, and feeding factors such as the rate of digestion in elasmobranchs (Economakis & Lobel, 1998; Fangue & Bennett, 2003; Hight & Lowe, 2007; DiGirolamo *et al.*, 2012).

The active selection and movement between habitats of different temperatures occurs at different temporal scales but is often manifested in diel patterns. For example,

for some species of elasmobranchs the peak usage of certain habitats coincides with the warmest temperatures during the day (Cerutti-Pereyra *et al.*, 2014), or there is movement between warmer and cooler parts of a habitat at different times throughout the day (Matern *et al.*, 2000). However, diel patterns in activity are not only the manifestation of a response to temperature, but some species may favour nocturnal movement patterns to avoid visual predators or to optimise foraging opportunities (Cartamil *et al.*, 2003), whereas other species may display different diel patterns as a means of habitat partitioning (Speed *et al.*, 2011).

In shallow environments including atolls, estuaries, bays and lagoons, the tidal heights and currents have also been found to be an important factor regulating habitat choice of elasmobranchs (Medved & Marshall, 1983; Ackerman *et al.*, 2000; Wetherbee *et al.*, 2007; Papastamatiou *et al.*, 2009; Cerutti-Pereyra *et al.*, 2014). Differences in tidal height can i) change the availability of both habitats and prey, ii) cause variability in currents, and iii) alter the physical characteristics such as temperature and salinity of the water (Carlisle & Starr, 2010). For top predators, such as sharks, tidal movements have generally been attributed to foraging choices (Medved & Marshall, 1983). For example, in shallow coastal habitats certain shark species use the incoming tide to exploit areas with an abundance of benthic prey which are inaccessible at low tide (Ackerman *et al.*, 2000; Campos *et al.*, 2009; Carlisle & Starr, 2010). For smaller mesopredators where predation is a threat, such as juvenile sharks and rays, there is increasing evidence to suggest that their movement behaviour in response to changing tides seems to be governed more by predation risk rather than foraging potential. The selection of shallow water seems to be a priority in juvenile rays (Tilley, 2011; Davy *et al.*, 2015) and sharks (Wetherbee *et al.*, 2007).

As numerous factors may influence habitat selection, there may be trade-offs associated with the selection and they may have contradicting effects. For example, three species of rays were found to select for a shallow nearshore microhabitat at low tides, which may serve as refuge from predation, although they likely incur metabolic costs due to very high temperatures (Vaudo & Heithaus, 2013). Understanding how these biotic and abiotic factors influence habitat selection, and their relative importance, is vital in understanding ecosystem dynamics as habitat use patterns and

interspecific interactions are influenced by each other (Wiederholm, 1987; Eklöv, 1997). This knowledge is particularly relevant today as it can assist in predicting consequences and population responses to global changes resulting from phenomena such as climate change or habitat degradation (Sakabe & Lyle, 2010; Speed *et al.*, 2012; Vaudo & Heithaus, 2013). Lastly, understanding why individuals choose specific habitats provides essential information for management by identifying critical habitats (Filmlalter, 2011).

The St. Joseph Atoll was found to be an important habitat for juvenile porcupine rays as they displayed long-term residency to the atoll (see Chapter 4). Acoustically tagged juveniles were found to spend the majority of their time on the shallow flats of the atoll but occasionally moved into the deeper lagoon, which is an area of high predation risk (Chapter 4). The conditions on the flats of the atoll are highly variable, both in terms of water temperature and water depth as the tides change. Given the evidence that elasmobranchs may seek out or avoid a specific set of environmental conditions, this chapter aims to address whether certain abiotic factors affect the habitat selection of juvenile porcupine rays. Specifically the objectives for this chapter included determining:

- Whether the daily presence of these animals within the atoll is affected by temperature
- Whether hourly presence within the atoll as well as within the lagoon micro-habitat occurs in relation to diel and/or tidal cycles and whether these are driven by temperature or other factors

5.2 Methods and Materials

In this chapter, data collected from the passive acoustic monitoring of 11 porcupine rays within the St. Joseph Atoll was used. Details regarding the acoustic receiver array and the tagging of porcupine rays with acoustic transmitters can be found in Chapters 2 and 4 respectively. Only data from Phase 2 of the receiver deployment (28/08/2014 to 19/03/2015) was used due to the improved data collection of

this period. In addition, as range tests highlighted the potential for environmental conditions to affect the detection frequency of receivers (see Chapter 2), presence of individuals (as opposed to number of detections) was used to minimise these confounding effects.

5.2.1 Daily presence in the St. Joseph Atoll

To investigate whether environmental effects influence the daily presence of porcupine rays to the St. Joseph Atoll, a set of 13 candidate generalised linear mixed models were constructed with different combinations of the chosen environmental factors. The GLMMs were considered as an appropriate statistical analysis given that they are able to cope with non-independent data by the incorporation of variables as random effects. In this case, the individual porcupine rays were treated as random factors within the models to account for the repeated nature of the data (Kock *et al.*, 2013; Heupel & Simpfendorfer, 2014). Environmental factors used in the GLMMs included mean daily air temperatures obtained from the weather station on D'Arros Island, mean daily water temperatures on the flats which were obtained from a temperature logger attached to one of the receivers on the flats (receiver 77), and the mean daily water temperatures in the lagoon which were obtained from a temperature logger attached to a receiver located within the lagoon (receiver 5). Mean daily wind speeds, also obtained from the weather station, were included given the evidence that wind speed has the greatest effect on receiver detection efficiency (see Chapter 2). Models were tested against the daily presence or absence (which was coded as a binary factor) of 11 porcupine rays to the St. Joseph Atoll using a logistic regression approach. The candidate models were compared using the Akaike information criterion (AIC) and the model with the lowest AIC value was taken as the best fit model (Heupel & Simpfendorfer, 2014). The factors in the best fit model were considered to have the most significant influence on occurrence. If the null model had the lowest AIC value then the data were considered to be random relative to the tested factors. Likelihood ratio tests were conducted to determine if the AIC values of the candidate models were significantly different to the AIC value of the null model. Models were implemented and run using the lme4 package (Bates

et al., 2012) in the R environment (R Development Core Team: www.r-project.org).

5.2.2 Hourly presence in the St. Joseph atoll and lagoon microhabitat

To determine if the presence of juvenile porcupine rays within the St. Joseph Atoll occurred with diel or tidal periodicity, cyclical patterns in the movements of eight juvenile porcupine rays were investigated using Fast Fourier Transforms (FFT) (there was insufficient data to run the analyses on three individuals). The FFT decomposes time series data and searches for cyclical patterns which are identified as visual peaks in the produced spectral density plot (Papastamatiou *et al.*, 2015). A time series for the data was developed whereby the number of detections recorded on all receivers within the atoll (including the sand flats and lagoon habitats) was binned for every hour of the study, on an individual basis (Filmlalter *et al.*, 2013). The same was done for the receivers within the deeper lagoon only to determine if use of this deeper habitat followed temporal patterns. No smoothing factor was applied to the FFT as the spectral peaks could be easily identified from the surrounding noise in the data series.

A water level logger was deployed in the St. Joseph Atoll on the 23/12/2014 which provided accurate tidal height data from this date. Therefore the following analyses were applied to data collected between 23/12/2014 and 19/03/2015. To determine if environmental variables effected the hourly presence of porcupine rays in both the atoll as a whole and in the lagoon microhabitat only, the same approach for determining environmental drivers on daily presence (as discussed above) was used. Factors in the 24 candidate models included diel effects (day hours were between 6:00am to 5:59pm and night hours were between 6:00pm to 5:59am), tidal effects which was obtained from mean hourly water pressure records; temperature effects which included the mean hourly air, flats and lagoon temperatures; and lastly the effect of wind using mean hourly wind speeds. The models were tested against the hourly presence or absence of eight individuals based on detections from all the receivers within the atoll, and the presence or absence of six individuals based

on detections from receivers in the lagoon only. There was no data for the other individuals.

To visualize the effects of environmental factors on hourly presence within the atoll, various graphs were constructed. Diel changes in the number of detections was visualized by plotting the percentage of detections recorded for each hour of all the monitoring days, averaged across all individuals. Effects of tidal height was visualized by working out the mean water pressure (as a proxy for water depth which is related to tidal height) for every hour of the monitoring period and this was matched to every hour that an individual was detected by a receiver. The mean percentages of hourly detections were then plotted for every 1 increment of water pressure, averaged across all individuals. The hourly air, flats, and lagoon temperatures and wind speeds were averaged across the monitoring period and were plotted. Lastly to determine if temperature extremes affected presence, for each individual's primary receiver (i.e. the receiver on the flats that recorded the most detections for that individual), hourly temperatures were matched to every hour that an individual was detected on the primary receiver to compare temperatures recorded at the receiver to temperatures recorded when individuals were present at their primary receivers.

5.3 Results

5.3.1 Daily presence in the St. Joseph Atoll

Analysis of the 13 candidate models revealed that only five of the models produced results that were significantly better than the null model. Every one of these five models included wind speed as a factor and the best fit model with the lowest AIC value included water temperature in the lagoon and wind speed as factors (Table 5.1). When further investigating the effects of wind speed, a boxplot revealed that the mean wind speed when the porcupine rays were present was slightly lower than the mean wind speed for when they were absent (Figure 5.1).

Table 5.1: Details of generalised linear models constructed to determine whether environmental factors influence daily presence (p) of juvenile *U. asperrimus* in the St. Joseph Atoll. Stars denote those that are significantly different from null and bold model indicates that of best fit

Model	Description	AIC value
M1	$p \sim 1$	2130
M2	$p \sim \text{flats temp}$	2130,7
M3	$p \sim \text{lagoon temp}$	2131,8
M4	$p \sim \text{air temp}$	2132
M5	$p \sim \text{wind speed}$	2122,7*
M6	$p \sim \text{flats temp} + \text{lagoon temp}$	2131,7
M7	$p \sim \text{flats temp} + \text{air temp}$	2131,3
M8	$p \sim \text{flats temp} + \text{wind speed}$	2123,4*
M9	$p \sim \text{lagoon temp} + \text{air temp}$	2133,6
M10	$p \sim \text{lagoon temp} + \text{wind speed}$	2119,7*
M11	$p \sim \text{air temp} + \text{wind speed}$	2124,2*
M12	$p \sim \text{flats temp} + \text{lagoon temp} + \text{air temp}$	2132,1
M13	$p \sim \text{flats temp} + \text{lagoon temp} + \text{air temp} + \text{wind speed}$	2123*

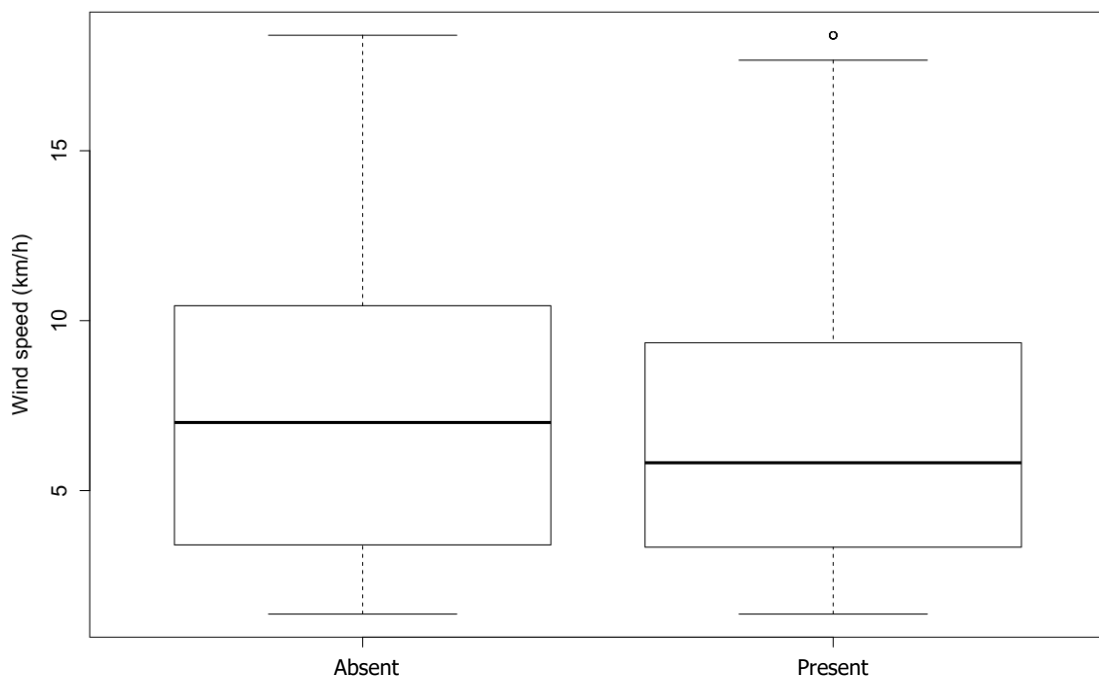


Figure 5.1: Boxplot illustrating wind speeds for when *U. asperrimus* were either present or absent on a daily basis in the St. Joseph Atoll. Circle represents an outlier

5.3.2 Hourly presence in the St. Joseph Atoll and lagoon microhabitat

The FFT spectral analyses conducted on the detection frequency of all the receivers in the array revealed evidence of strong cyclic patterns for most individuals. Diel peaks (at a period of 24 hours) were observed in seven out of the eight tagged porcupine rays (Figure 5.3). The FFT's also revealed spectral peaks around a period of 12.5 hours for six of the eight individuals, which most likely corresponded to tidal fluctuations. This tidal peak was stronger than the diel peak for two individuals (Figure 5.3). The FFT's performed on the detections from the receivers in the lagoon only revealed no spectral peaks.

Analysis of the 24 candidate GLMMs for hourly presence within both the atoll as a whole and the lagoon microhabitat only revealed that most models produced results that were better than the null model. The models for hourly presence within the whole atoll suggested that diel and tidal fluctuations influenced the presence of the porcupine rays in the atoll. However, models highlighted that temperature also played a significant role on their presence both within the atoll as a whole and within the lagoon microhabitat only. The models of best fit for presence within the whole atoll included day/night, temperature on the flats and air temperature, while the model for best fit for presence in the lagoon included only air temperature and temperature on the flats as factors. However, all factors were included in various models that performed better than the null (see Tables 5.2 and 5.3).

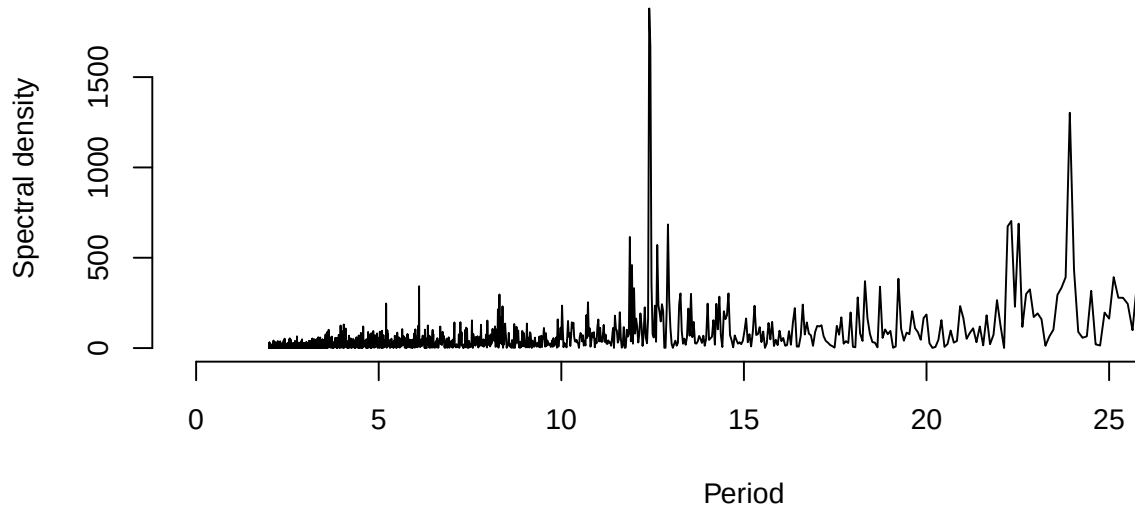


Figure 5.2: Spectral density plot illustrating a strong tidal peak (at 12.5 hours) and a secondary diel peak (at 24 hours) for individual #12

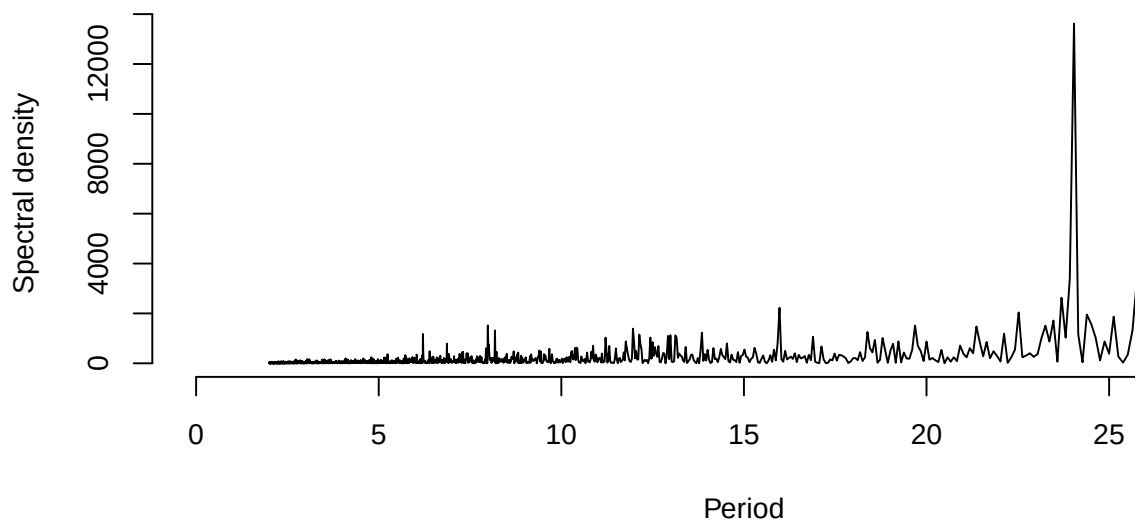


Figure 5.3: Spectral density plot illustrating a strong diel peak (at 24 hours) and no tidal peak for individual #10

Table 5.2: Details of generalised linear models constructed to determine whether environmental factors drive hourly presence (p) of juvenile *U. asperrimus* within the St. Joseph Atoll. Stars denote those that are significantly different from null and bold model indicates that of best fit

Model	Description	AIC
M1	$p \sim 1$	7268,9
M2	$p \sim \text{Day/night}$	7270,7
M3	$p \sim \text{Water pressure}$	7270,6
M4	$p \sim \text{Flats temp}$	7220,6*
M5	$p \sim \text{Lagoon temp}$	7253,7*
M6	$p \sim \text{Air temp}$	7270,6
M7	$p \sim \text{Wind speed}$	7242,5*
M8	$p \sim \text{Day/night} + \text{water pressure}$	7272,5
M9	$p \sim \text{Day/night} + \text{flats temp}$	7189,9*
M10	$p \sim \text{Day/night} + \text{lagoon temp}$	7255,7*
M11	$p \sim \text{Day/night} + \text{air temp}$	7272,5
M12	$p \sim \text{Day/night} + \text{wind speed}$	7243,7*
M13	$p \sim \text{Water pressure} + \text{flats temp}$	7220,4*
M14	$p \sim \text{Water pressure} + \text{lagoon temp}$	7255*
M15	$p \sim \text{Water pressure} + \text{air temp}$	7272,4
M16	$p \sim \text{Water pressure} + \text{wind speed}$	7243,6*
M17	$p \sim \text{Flats temp} + \text{lagoon temp}$	7220,9*
M18	$p \sim \text{Flats temp} + \text{air temp}$	7189,8*
M19	$p \sim \text{Flats temp} + \text{wind speed}$	7202,2*
M20	$p \sim \text{Lagoon temp} + \text{air temp}$	7255,7*
M21	$p \sim \text{Lagoon temp} + \text{wind speed}$	7239,8*
M22	$p \sim \text{Air temp} + \text{wind speed}$	7243,1*
M23	$p \sim \text{Day/night} + \text{water pressure} + \text{flats temp} + \text{lagoon temp}$	7193,6*
M24	$p \sim \text{Day/night} + \text{water pressure} + \text{air temp} + \text{wind speed}$	7246,7*

Table 5.3: Details of generalised linear models constructed to determine whether environmental factors drive hourly presence (p) of juvenile *U. asperrimus* within the lagoon of St. Joseph Atoll. Stars denote those that are significantly different from null and bold model indicates that of best fit

Model	Description	AIC value
M1	$p \sim 1$	-14419,4
M2	$p \sim \text{Day/night}$	-14417,4
M3	$p \sim \text{Water pressure}$	-14429*
M4	$p \sim \text{Flats temp}$	-14426*
M5	$p \sim \text{Lagoon temp}$	-14424*
M6	$p \sim \text{Air temp}$	-14419,6
M7	$p \sim \text{Wind speed}$	-14417,6
M8	$p \sim \text{Day/night} + \text{water pressure}$	-14430,9*
M9	$p \sim \text{Day/night} + \text{flats temp}$	-14423,1*
M10	$p \sim \text{Day/night} + \text{lagoon temp}$	-14421,1
M11	$p \sim \text{Day/night} + \text{air temp}$	-14421,9*
M12	$p \sim \text{Day/night} + \text{wind speed}$	-14415,7
M13	$p \sim \text{Water pressure} + \text{flats temp}$	-14442,8*
M14	$p \sim \text{Water pressure} + \text{lagoon temp}$	-14431,7*
M15	$p \sim \text{Water pressure} + \text{air temp}$	-14427,2*
M16	$p \sim \text{Water pressure} + \text{wind speed}$	-14427*
M17	$p \sim \text{Flats temp} + \text{lagoon temp}$	-14426,1*
M18	$p \sim \text{Flats temp} + \text{air temp}$	-14444,3*
M19	$p \sim \text{Flats temp} + \text{wind speed}$	-14424*
M20	$p \sim \text{Lagoon temp} + \text{air temp}$	-14424,9*
M21	$p \sim \text{Lagoon temp} + \text{wind speed}$	-14422,9*
M22	$p \sim \text{Air temp} + \text{wind speed}$	-14417,6
M23	$p \sim \text{Day/night} + \text{water pressure} + \text{flats temp} + \text{lagoon temp}$	-14437*
M24	$p \sim \text{Day/night} + \text{water pressure} + \text{air temp} + \text{wind speed}$	-14430,6*

The mean proportion of detections within the atoll peaked at 15:00 (Figure 5.4) which corresponds to the peak in mean water temperature on the flats of the atoll (≈ 32 degrees). In contrast, there was very little variation in the water temperature of the lagoon (Figure 5.4). No individual was detected throughout the entire temperature range recorded at their primary receivers. They were absent at both very low temperatures (with only one individual detected at a temperature below 25°C , even though every receiver except one recorded temperatures of 23°C) and very high temperatures (with only two individuals being detected at temperatures above 36°C , even though most receivers recorded temperatures up to 40°C) (Table 5.4). Wind speeds peaked during the day (Figure 5.4) and the majority of detections within the atoll and the lagoon occurred at low tide (below the median water pressure of 122kPa) with no detections recorded at times with the highest water pressure (127 to 128.5 kPa) (Figure 5.5).

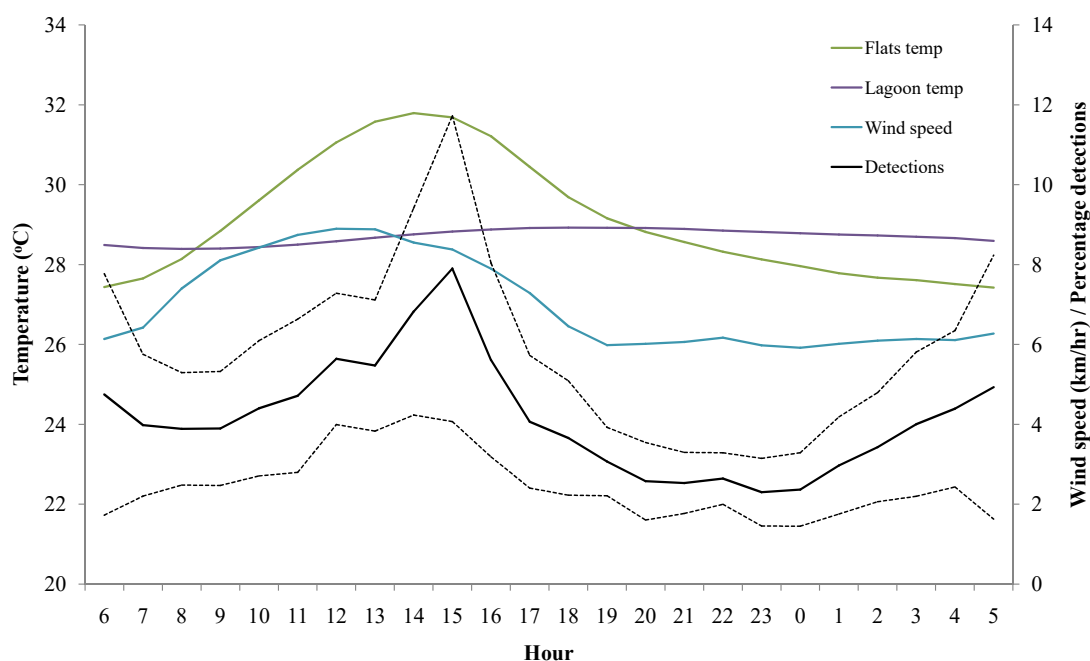


Figure 5.4: Averaged hourly detections (%) for tagged *U. asperimus* (black line) and environmental conditions within the St. Joseph Atoll from 23/12/2014 to 19/03/2015. Conditions include temperatures of the sand flats (green line) and lagoon (purple line), as well as wind speed (blue line). Dashed lines represent 95% confidence intervals.

Table 5.4: Hourly temperature ranges recorded at the primary receivers of each tagged *U. asperrimus* and the temperature range when each ray was present at it's primary receiver

Individual	Primary Receiver	Receiver range (°C)	Presence range (°C)
4	74	23 - 36	25 - 32
5	77	23 - 39	26 - 36
6	64	23 - 38	27 - 38
8	78	23 - 40	25 - 36
9	75	23 - 37	24 - 33
10	67	23 - 34	25 - 33
11	78	23 - 40	25 - 37
12	4	24 - 33	25 - 33
13	78	23 - 40	26 - 35

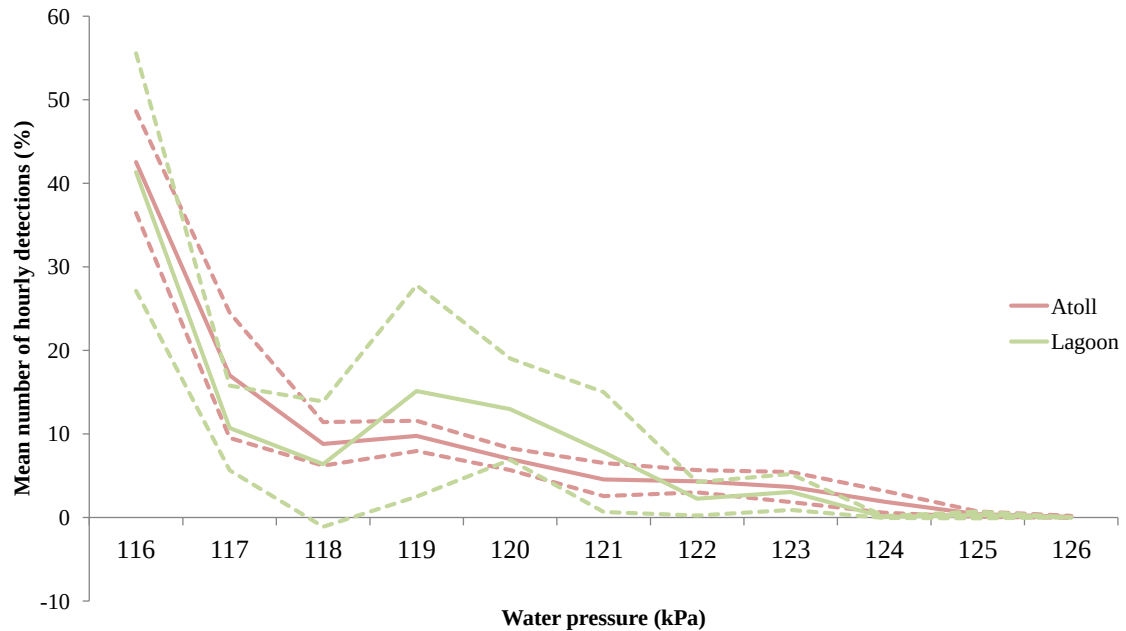


Figure 5.5: Proportion of detections (%) recorded on all the receivers in the St. Joseph Atoll (red line) and on the receivers in the lagoon microhabitat only (green line) averaged for each water pressure increment (as a proxy for water depth and thus tidal height). Dashed lines represent 95% confidence intervals. Vertical line represents median water pressure.

5.4 Discussion

Given that the biotic factors of sex and size had no effect on the daily presence of juvenile porcupine rays to the St. Joseph Atoll (Chapter 4), the first aim of this chapter was to determine whether environmental factors influenced the daily presence of porcupine rays to the atoll. Constructed models revealed that wind speed had the most significant influence on daily presence to the atoll however, this is most likely related to the detection efficiency of the receivers rather than wind speeds having an effect on the movements of these rays. The mean wind speed at which rays were present in the atoll was lower than the mean wind speeds for when they were absent. This is most likely due to the fact that higher wind speeds reduce the detection efficiency of the receivers, particularly on the shallow flats of the atoll (see range testing section in Chapter 2), causing a reduction in the detections of the porcupine rays. At this coarse temporal scale, temperature did not affect the daily presence of these rays within the atoll. This is most likely because mean daily temperatures were relatively consistent, only varying by approximately 4.5 degrees between August and March.

The second aim of this chapter was to determine whether environmental factors affected the presence of porcupine rays on a finer temporal scale. Analyses were conducted on hourly presence within the St. Joseph Atoll as a whole (which includes detections from the sand flats, lagoon, and fringe reef habitats) to try and elucidate the potential influences on the movement patterns within the atoll. Secondary analyses were conducted on the hourly presence of porcupine rays in the smaller lagoon microhabitat only to determine why individuals were utilising this deeper and presumably more dangerous (Chapter 4) microhabitat.

The results revealed that abiotic variables appear to be significant influences on hourly presence, both within the atoll as a whole and in the smaller lagoon microhabitat. The FFT spectral analyses and the GLMMs revealed that the hourly presence within the atoll varied with both diel and tidal cycles for the majority of tagged porcupine rays. In addition, the spectral density plots showed that the diel signal was stronger in four of the six individuals that exhibited both cyclic patterns.

This indicates that although the presence of individuals in the atoll is indeed affected by both diel and tidal cycles, the strength of the impact that these two cycles have on presence is somewhat variable.

Upon further investigation into the effects of the tidal cycle on presence of the porcupine rays in the atoll, it was found that the vast majority of detections occurred at low tide, with only 6% of detections occurring above the median height of the water column (122kPa). This suggests that porcupine rays were absent from the atoll at high tides, but this is unlikely given that the rays were never recorded outside the atoll and they displayed high degrees of residency and site fidelity to the atoll (Chapter 4). An alternative suggestion is that at high tides, porcupine rays may be utilising shallower microhabitats on the flats (potentially shallow banks or island fringes), which then become too shallow or dry at low tide. Given the dorsoventrally flattened nature of rays, they can move easily in very shallow conditions. Conversely acoustic receivers cannot operate in these shallow waters and there are none located in the shallow microhabitats, serving as an explanation behind the apparent absence of these rays at high tide. The use of shallow marginal habitats at high tide was supported by visual observations on numerous occasions, with small groups of stationary individuals encountered on island fringes.

It is hypothesized that juvenile porcupine rays utilise this sheltered marginal microhabitat at high tide to avoid predation. In the atoll, the deeper sections of the flats become accessible to larger predatory sharks at high tide given the increased depth of the water column, up to 2m in certain cases. Indeed, a previous study highlighted that resident sicklefin lemon sharks within the St. Joseph Atoll utilised the flats at high tides (Filmlalter *et al.*, 2013). This increases the risk of predation on the sand flats at these times, which is presumably why porcupine rays sought out shallower and safer water. Predation risk has often been overlooked as an influence on microhabitat choice by elasmobranchs (Vaudo & Heithaus, 2013) but recent studies have highlighted the potential for it to be a significant influence on microhabitat use in rays. Davy *et al.* (2015) found that juvenile mangrove rays *Himantura granulata* actively sought out shallow habitats with the changing tides, presumably to avoid predators; three ray species in Shark Bay, Australia utilised a shallow nearshore

environment as a refuge from predation even though it was thermally disadvantageous (Vaudo & Heithaus, 2013); and juvenile southern stingrays were abundant on the safe and shallow sandflats even though prey resources were more abundant in deeper waters within Glovers Reef Atoll, Belize (Tilley, 2011). It is doubtful that the hypothesized selection of shallower microhabitats is related to better foraging opportunities, as it has been shown that within an atoll environment prey abundances increase at greater depths (Tilley, 2011). Also, individuals encountered on the island fringes were visually observed to be resting as opposed to moving and foraging.

The fine-scale movements of these porcupine rays are not only related to tidal cycles and presumably predator avoidance behaviour, but individuals also responded to diel cycles with the majority of detections occurring in daylight hours. Given that porcupine rays prey on infaunal organisms (Chapter 3), the preference of daylight hours is unlikely linked to the visual foraging for prey. Rather, the major driver behind the diel pattern of hourly presence appears to be related to temperature and behavioural thermoregulation. The GLMMs highlighted that temperature, in particular the water temperature on the flats, had the most significant influence on hourly presence within the atoll. The flats are a relatively shallow habitat compared to that of the lagoon, making it the more thermally heterogeneous microhabitat. In fact, the temperatures on the flats ranged from roughly 23°C to 40°C, whereas the temperatures within the lagoon only varied between 27°C to 29°C. The diel peak in detections occurred in the late afternoon at the same time that water temperature on the flats peaked. It is important to note here that the wind speeds generally remained high throughout the day, illustrating that the peak in detections in the late afternoon was not due wind speed affecting receiver detection efficiency.

Rays are ectothermic and as such microhabitat choice as a means of behavioural thermoregulation has been documented in a variety of studies (Economakis & Lobel, 1998; Hight & Lowe, 2007; DiGirolamo *et al.*, 2012; Cerutti-Pereyra *et al.*, 2014)). Behavioural thermoregulation is often linked to physiological processes. For example, experimental data confirm the hypothesis that is energetically beneficial for rays to feed in warm waters and rest in cool waters as cooler temperatures reduce

the standard metabolic rate and the digestive process slows down, conserving energetic resources (Di Santo & Bennett, 2011). This thermoregulatory behaviour has been observed in bat rays *Myliobatus californica* and dogfish *Scyliorhinus canicula* (Matern *et al.*, 2000; Sims *et al.*, 2006) and could serve to explain the peak in detections of porcupine rays at the warmest part of the day. Within the St. Joseph Atoll, the waters in the shallow microhabitats of the flats (where there are no receivers or temperature loggers) will presumably warm up more than the deeper microhabitats (with receivers). Thus it could be suggested that the rays might be seeking out these cooler and deeper sections of the flats at the warmest part of the day to slow down digestion. However, porcupine rays were observed feeding throughout the day (Elston unpubl data), thus not fully explaining the increased use of the deeper microhabitats in the late afternoon.

A more likely hypothesis to explain this diel peak in detections is the avoidance of lethal temperature extremes. Lab work conducted on atlantic stingrays *Dasyatis sabina* revealed that individuals which were acclimatized to diel thermoperiods of 34.0°C to 37.3°C had a critical thermal maxima of 43.1°C (Fangue & Bennett, 2003). Given that the waters in the deeper sections of the flats can reach up to 40°C where the temperature loggers are situated, the temperatures in the shallower microhabitats of the flats likely reach even higher temperatures and may represent the thermal limits of the porcupine rays. Thus as temperatures peak during the day, these rays avoid the shallowest and warmest water and instead seek out the relatively cooler and deeper refuges on the flats, causing this peak in detections. Further evidence for the avoidance of temperature extremes comes from the fact that no individuals were detected at their primary receivers when their corresponding temperature loggers recorded temperatures above 38°C.

It is interesting that both diel and tidal effects influenced the presence of tagged porcupine rays within the atoll. Given that the time of high and low tide shifts every day, if tides were the only influence over microhabitat selection then there would not be a strong peak in detections at a specific time of the day. However, this was the case with the porcupine rays, despite the fact that the vast majority of detections only occurred at low tide. This highlights interplay between these

two cycles and between two behaviours, that of predator avoidance and extreme temperature avoidance. In this case, it seems that predator avoidance is the major influence on their microhabitat selection, however under specific thermal conditions the need to avoid certain temperature extremes will override the need to avoid predators. This is evidenced by the fact that the vast majority of detections occurred at low tide, suggesting that the utilisation of these deeper sections of the flats is highly constrained to the low tide. However, the peak in detections in the late afternoon reveals that individuals utilise these deeper waters when temperatures on the flats reach their maximums, regardless of tidal height.

Another facet to consider is that individuals were found to utilise the deeper lagoon on a small number of occasions, which is presumably the habitat with the highest risk of predation (Chapter 4). The detections within the lagoon followed no diel or tidal pattern but temperature, particularly the water temperature on the flats, was found to have the most significant influence on the use of this microhabitat. This suggests that porcupine rays could be utilising the more thermally stable environment of the lagoon as a thermal refuge when temperatures on the flats become too high.

Chin *et al.* (2010) proposed that the porcupine ray was one of two most vulnerable shark and ray species within the Great Barrier Reef to climate change. This was due to its rarity and immobility given its high habitat dependency. As temperature appears to be a significant driver of micro-habitat selection, it adds to the evidence that this species is highly vulnerable to climate change. As sea water temperatures rise due to anthropogenic activities (Rahmstorf *et al.*, 2007), porcupine rays at the St. Joseph Atoll will likely be driven out of the safety of the shallow waters more often as they attempt to avoid their lethal thermal maxima. This in turn could lead to increased rates of predation on these juveniles as they spend more time in cooler, deeper waters. It is thus beneficial that the St. Joseph Atoll has recently been declared as a no-take marine protected area, to avoid any further threats to this population through anthropogenic activities.

Chapter 6

General discussion



Given the limited information available on stingrays, particularly for the rare porcupine ray, this study aimed to address some of the knowledge gaps on the trophic and spatial ecology of this species. The investigation into their diet highlighted that juvenile porcupine rays were generalist and opportunistic predators consuming that which was most common in the environment, but evidence suggested a foraging specialisation on deep infaunal organisms. The acoustic telemetry revealed high degrees of residency and site fidelity to the St. Joseph Atoll as well as limited movement ranges and potential seasonal shifts in microhabitat usage within the atoll. Finally the presence of porcupine rays within the atoll was found to fluctuate with diel and tidal patterns, providing evidence that the environmental factors of water depth and temperature had significant influences on movement patterns. This chapter serves as a synthesis of these results and discusses the ecological and conservation ramifications.

6.1 St. Joseph Atoll as a nursery habitat to juvenile porcupine rays

Heupel *et al.* (2007) put forward three criteria that should be considered when attempting to delineate an elasmobranch nursery area. These included that juveniles less than one year should be more abundant within the area investigated, they should display a high degree of residency to the area and the residency should span across years. For these criteria to be met, long term information on juvenile movement patterns is required, and it can be argued that the use of passive acoustic telemetry with strategically placed receivers is one of the best methods to obtain such data. Although this study presents data on a relatively small sample size, the year-long monitoring period means that the behavioural information gathered was robust.

The acoustic monitoring data, as well as other anecdotal evidence, illustrated that the St. Joseph Atoll can be considered a nursery area for juvenile porcupine rays. Juveniles are abundant within the atoll but have rarely been encountered outside this habitat despite numerous annual dives surveying the coral reef cover surrounding

the atoll and the neighbouring D'Arros Island (Von Brandis pers comm.). The juvenile rays displayed high levels of daily residency to the St. Joseph Atoll over the course of a year, particularly to the shallow sand flats. The deeper lagoon was used on relatively few occasions, and can be considered a transient habitat (Chapter 4). Finally the high abundance of juveniles has been noted for a number of years prior to the start of this study (Von Brandis pers comm.) suggesting use of this nursery habitat over multiple years.

It is interesting to note that the juveniles observed within this habitat were relatively large and presumably not young-of-the-year. Even though the size at birth is not known for porcupine rays, other stingray species with similar size ranges are born within the region of 15cm to 25cm DW (Last & Stevens, 2009), yet the smallest porcupine ray seen within the atoll was no smaller than 40cm wide. In addition, no individual caught was seen to have an open umbilical scar. This suggests that either the atoll is not serving as a pupping ground or birthing events are highly seasonal and only occur at a restricted time in the year. Given the isolated nature of the atoll with surrounding deep waters, there are limited nearby habitats safe from predation that young-of-the-year could utilise and where safe birthing may occur, suggesting that this phenomenon should occur in the atoll. Reproductive seasonality has been identified in some batoid species (Marshall *et al.*, 2007; Ebert & Cowley, 2009; Marshall & Bennett, 2010), but not in others (White & Dharmadi, 2007), while some display variable patterns throughout their range (Veras *et al.*, 2014). This makes it difficult to hypothesize whether porcupine rays would display a seasonal birthing pattern at the St. Joseph Atoll. Whichever the reason behind the observed absence of young-of-the-year, it has been suggested that the survival of larger juveniles contributes more to population persistence than survival of young-of-the-year (Kinney & Simpfendorfer, 2009), making the St. Joseph Atoll a critical habitat for this vulnerable species.

Animal behaviours are influenced by their habitat requirements and the benefits that a habitat offers (Filmalter, 2011). Various nursery areas have been identified for juvenile stingrays, from coastal bays to offshore atolls, and the benefits that these nurseries offer has been identified as increased food availability or predator avoid-

ance (Yokota & Lessa, 2006; Dale *et al.*, 2011; Tilley, 2011; Cerutti-Pereyra *et al.*, 2014; Davy *et al.*, 2015). It is unclear whether the movement patterns exhibited by juvenile porcupine rays within the St. Joseph Atoll as a nursery are related to food abundance. Even though most individuals were found to have food in their stomachs (Chapter 3), only individuals that were actively feeding were caught, biasing this result. In addition it was recognised that both the macrohabitat selection of the sand flats (Chapter 4), as well as the microhabitat variation in the usage of the flats (Chapter 5), were unlikely related to an increased foraging potential.

Conversely, both Chapters 4 and 5 provided evidence to suggest that the benefit of predator avoidance is an important influence on the nursery habitat usage of porcupine rays. Predators are known to influence the habitat selection of their prey through fear (Brown *et al.*, 1999) and this sub-lethal effect has been used to explain the movements of a variety of animals (Mittelbach, 1986; Wirsing *et al.*, 2008; Tolon *et al.*, 2009; Laundre *et al.*, 2014). The high usage of the shallow sand flats of the atoll, even though this is likely a relatively depauperate habitat, is most likely because it offers a degree of protection from predation. In addition, the deeper sections of the flats were rarely used by porcupine rays at high tide when this microhabitat becomes more accessible to larger predators. Recent studies have begun highlighting the importance that the non-consumptive effect of fear by predators has on the movements of juvenile stingrays (Vaudo & Heithaus, 2009, 2013; Cerutti-Pereyra *et al.*, 2014; Davy *et al.*, 2015) and while there are inevitably other factors affecting the nursery habitat choice by stingrays, future studies should consider the risk of predation as one of the main influences.

Nursery areas are also sometimes considered to offer thermal benefits as warmer inshore waters provide increased metabolic and growth rates for elasmobranchs (Economakis & Lobel, 1998; Vaudo & Heithaus, 2009; Knip *et al.*, 2010). However, it is difficult to determine whether the thermal environment of the St. Joseph Atoll is beneficial to juvenile porcupine rays, or whether it is disadvantageous. The thermally heterogeneous sand flats habitat will have physiological consequences for the porcupine rays and as such they have to respond to the temperature fluctuations. However, they are limited in doing so by their anti-predator behaviours by means

of avoiding the more thermally stable lagoon habitat. The detections of porcupine rays on the flats were found to peak in the late afternoon, when temperatures on the flats were significantly higher than the temperatures within the lagoon. Physiologically, the warmer temperatures on the flats would result in increased metabolic rates (as opposed to if the porcupine rays sought out the cooler lagoon waters) (Di Santo & Bennett, 2011). This would be beneficial if food was abundant as it would lead to increased growth rates. Alternatively, if prey was limiting the cooler temperatures within the lagoon would be beneficial to slow down metabolism and conserve energy resources (Vaudo & Heithaus, 2013). Thus, the availability of food resources would first need to be properly quantified to determine the relative costs and benefits of this nursery habitat choice in terms of physiology. If the thermal environment was indeed advantageous, it could provide a further explanation for the use of the nursery habitat. However, the selection for the deeper sections of the sand flats when water temperatures peaked, regardless of tidal height and potential predation, suggests temperatures may become too high in the shallower safer areas. This indicates that the use of the St. Joseph Atoll as a nursery may not be related to thermal benefits.

6.2 Ecological importance of juvenile porcupine rays within the St. Joseph Atoll

The results from the dietary analysis of porcupine rays (Chapter 3) in combination with their revealed habitat usage (Chapter 4) and the influences on this habitat usage (Chapter 5) enhances the understanding of the ecological effects these rays can have on the St. Joseph Atoll ecosystem. Given the high abundance and reliance of these juvenile porcupine rays to the St. Joseph Atoll, they are likely to be an important structuring force within this ecosystem, particularly on the shallow sand flats where they spent the majority of their time. Rays in general are understood to have three important ecological roles; modifying the physical benthos in soft sediment habitats through bioturbation, exerting top down control over the infaunal invertebrate populations by predation, and providing the link in food webs by oc-

cupying the trophic position of mesopredator (O'Shea, 2012). The magnitude of these roles will vary with different species in different environments, and should be quantified in each ecosystem to gain local understandings of ecosystem functions.

It was recognised that given the opportunistic feeding nature of porcupine rays, they most likely display weak predator-prey interactions and thus potentially have a low influence over prey communities. However, they may play important roles in controlling levels of dominant infaunal prey as they appear to forage on the most abundant prey items available within the substratum (Chapter 3). Porcupine rays do not occur in isolation within the ecosystem and the roles that other animals play must also be considered. Specifically, as porcupine rays occupy the position of mesopredator, their behaviour was seen to be suppressed by top predators. Their macro- and micro-habitat selection appeared to be driven mainly by an attempt to avoid risk of predation. As such sharks within and around the atoll are likely to mediate resource competition within and between the porcupine rays and other mesopredator species present (Tilley, 2011), while also potentially having indirect impacts on the benthic prey resources exploited by juvenile porcupine rays (Ritchie & Johnson, 2009; Vaudo & Heithaus, 2011). However, the wide trophic niche of juvenile porcupine rays increases the stability of the system and potentially limits the effects that top predators can exert on benthic prey (McCann *et al.*, 1998; Post *et al.*, 2000).

The effects of bioturbation by porcupine rays could be accentuated in comparison to other stingrays as visual observations in this study and others revealed that they strongly plough up the benthos, more so than other species, leaving a trail of suspended sediments (Last & Stevens, 2009; Theiss *et al.*, 2010). This active ploughing is further evidenced by the dominance of deep burrowing infaunal organisms in their stomach contents (Chapter 3). However, while other rays have been seen to feed in seagrass beds and have been noted to disrupt the rhizomes of sea grasses (Valentine *et al.*, 1994; Nelson & Brown, 2009), porcupine rays were not observed feeding on seagrass beds and were rarely seen adjacent to seagrass beds. This suggests that their bioturbative effects are restricted to the sand flats and do not encompass the sea grass microhabitat. This process of bioturbation is vital to the resuspension of

organic nutrients into the water column (Yahel *et al.*, 2008) and in providing habitat for early colonist species of amphipods that are absent in more structured sediments (Hines *et al.*, 1997).

One final facet to consider about the ecological roles of porcupine rays is that of resource partitioning. It was recognised in Chapter 3 that resource partitioning between the three abundant stingray species (porcupine rays, *Himantura granulata* and *Pastinachus sephen*) within the St. Joseph Atoll was likely necessary to reduce competitive effects inter-specifically and that the foraging behaviour of porcupine rays may facilitate this. However, intraspecific resource partitioning is also common in elasmobranchs. This is most often facilitated through ontogenetic shifts in diet and habitat use (Ebert & Cowley, 2003; Wetherbee & Cortés, 2004; White *et al.*, 2004). This is presumably the case at the St. Joseph Atoll given the general absence of adults, however, the high abundance of juveniles on the sand flats means that resource partitioning among this single life history stage is also likely necessary. There is some evidence for this phenomenon given that there was not one area on the flats where the porcupine rays congregated. Rather, each individual had a restricted high use area at various locations on the flats related to their tagging location. Individuals were also observed and caught feeding throughout all locations on the flats of the atoll. This suggests that even though the porcupine rays had overlapping activity spaces, they may be partitioning the flats on a small scale to reduce competition amongst each other.

6.3 Conservation and threats

When considering the threats faced by elasmobranchs, the increased levels of marine resource exploitation, combined with the high economic value of sharks (Clarke *et al.*, 2007), means that fishing pressures placed on their populations have led to declines even in remote places, such as offshore atolls (Graham *et al.*, 2010). Conversely, the relatively low economic value of stingrays means they are generally not specifically targeted by larger fisheries (Dulvy *et al.*, 2008), protecting these remote populations from declines. Therefore places like the St. Joseph Atoll can be considered as

relatively pristine ecosystems in terms of stingray abundance. Research done here can provide important information on ecological baselines with which to compare impacted systems and the results can be separated from anthropogenic pressures, increasing its implementation in applied ecology (Tilley, 2011).

While porcupine rays are not the targets of fishing pressure at the St. Joseph Atoll, they are occasionally taken as by-catch at other locations in the Seychelles (Seychelles, 2012). There are a number of isolated ecosystems within the Republic of Seychelles (Tilley, 2011), and given the high degrees of residency of these rays and the large distances between the ecosystems, spill-over of individuals between these environments is unlikely. This highlights the need for localised management of these environments, and it is indeed beneficial that the St. Joseph Atoll has been declared an MPA.

At a global scale, porcupine rays are caught as by-catch in fisheries around the world and are commonly targeted by small fisheries in South East Asia (Compagno, 2005; Theiss *et al.*, 2010). In the Bay of Bengal particularly, stocks have declined due to high levels of by-catch, which is one of the reasons for their Vulnerable listing by the IUCN (Compagno, 2005). It is therefore important to identify whether this species utilises nursery areas and where these nursery areas are located. Juveniles display high degrees of residency to nursery areas, making them appropriate areas for spatial management tools, and protecting juveniles is considered important for population persistence (Kinney & Simpfendorfer, 2009). Given the evidence that juvenile porcupine rays utilise nurseries in a variety of habitats (at a remote offshore atoll (Chapter 2) and a shallow coastal bay (Cerutti-Pereyra *et al.*, 2014)) identifying potential nursery areas where these rays are most exploited could greatly aid conservation efforts.

This study also highlights the potential effects that climate change can have on juvenile porcupine rays. Chapters 4 and 5 provided evidence to suggest that porcupine rays displayed behavioural thermoregulation through the avoidance of the shallowest and warmest micro-habitats when temperatures peaked and through the usage of the cooler lagoon and surrounding fringe reef environments in the warmer, less windy north-west monsoon season. The St. Joseph Atoll is located in near proximity

to the equator and as such the most extreme temperatures may be approaching the lethal maxima limit for porcupine rays. In fact, the need to avoid these temperature extremes was strong enough to over-ride the need to avoid potential predators which may suggest that the avoidance of these temperature extremes is not merely linked to physiological disadvantages, but to survival itself.

As climate change continues, increasing water temperatures may increase the frequency of high temperature extremes within microhabitats and may even reduce the benefit of shallow waters to a point where they are no longer a viable refuge. This would potentially lead to greater time spent in deeper waters where the frequency of predation events might increase (Vaudo & Heithaus, 2013). In addition the shift in habitat usage may affect the population dynamics of the benthic prey resources exploited by porcupine rays. Conversely if the rays remain in shallow waters, the higher temperatures may lead to unsustainably high metabolic rates and increased starvation within the population (decreasing growth rates with increasing temperatures have been observed in marine fishes (Hofmann & Fischer, 2003; Saoud *et al.*, 2008)).

6.4 Future work

Porcupine rays are a study species that are easily handled given their lack of a tail spine, they are abundant in the St. Joseph Atoll, and as they occupy a mid-trophic position they can shed light on their predators, which are apex predators within atoll environments. Given this, and the under-studied nature of porcupine rays, future research efforts can focus on a variety of questions.

Firstly, understanding basic biological parameters forms the basis for research for any species. These biological parameters are missing for many stingray species, including the porcupine ray. As they are highly abundant and easy to catch within the St. Joseph Atoll, it provides an ideal system in which to investigate these parameters.

Further influences on short-term movement and habitat usage also need to be in-

vestigated. While this study highlighted that predation risk has a large effect on movement patterns, other factors might also contribute to habitat choice. Food availability needs to be quantified to determine whether an abundance of prey is potentially driving the use of this habitat. In addition, given the high abundance of two other stingray species within the atoll, inter-specific competition might also be affecting movement patterns. Finally experimental work could determine the threshold of thermal stress for this species and provide further insights into the effects of temperature.

While this study focused on juvenile porcupine rays, the other life history stages also need to be considered. An investigation into the habitat usage of the young-of-the-year would increase the understanding of the role of the atoll to this species. In addition, as adults are rare within the atoll it is assumed that they disperse from this safe habitat. Using genetics to determine the levels of connectivity between the juveniles within the atoll and the adults occurring on the reefs surrounding the atoll and D'Arros Island would highlight whether the St. Joseph Atoll is the source of these adults, or whether they potentially come from other populations. The acoustic tracking of adults could also provide answers to some of these questions, and would highlight whether these individuals are reliant on one reef system only or if they migrate over long distances to other reefs. Finally BRUV surveys within the lagoon could provide light into whether adults occur in this habitat and it could further quantify the presence of large sharks.

Further dietary investigations and stable isotope analyses could provide deeper insights into the ecology of atoll environments. There are two other stingray species that are abundant within the atoll, and identifying their dietary components would highlight degrees of dietary overlap and levels of competition. In addition, stable isotope analyses could provide information on long-term dietary shifts for the porcupine rays. Even though they were not found to feed in the seagrass beds, carbon isotope values will determine if their trophic pathway is reliant on carbon sources from seagrass. Stable isotope analyses would also provide a more comprehensive understanding of their trophic roles within the atoll ecosystem. Lastly given the high abundance of porcupine rays within the St. Joseph Atoll and their reliance

on this ecosystem, quantifying their ecological impact is important. Experimental procedures could provide more definitive information on their impacts on prey populations and insights into the effects of bioturbation.

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