MOVEMENTS OF SUB-ADULT SICKLEFIN LEMON SHARKS *NEGAPRION ACUTIDENS* IN A REMOTE INDIAN OCEAN ATOLL

Thesis submitted in fulfillment of the
requirements for the degree of

MASTER OF SCIENCE

of

RHODES UNIVERSITY

By

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December 2011

ABSTRACT

The sicklefin lemon shark *Negaprion acutidens* is a large-bodied (> 3m) coastal shark species, widely distributed in tropical and sub-tropical Indo-Pacific waters. Despite its large size and wide distribution, very little is known about its movement behaviour throughout ontogeny. The primary aim of this thesis was to gain an understanding of the movements of sub-adult *N. acutidens*, in and around the St. Joseph Atoll, Republic of Seychelles, to facilitate the effective conservation of this vulnerable species. A total of 22 sharks (139 – 202 cm TL) were equipped with coded acoustic transmitters and passively monitored using moored acoustic receivers for a period of 20 month from March 2009 to October 2010.

The use of passive acoustic telemetry arrays to study behavioural ecology has increased in popularity in recent years and been successfully applied to study a host of teleost and elasmobranch species in a diversity of habitats, ranging from sheltered estuaries to the offshore pelagic environment. However, the practicalities of designing an effective network of receivers to optimally monitor animal movements can be challenging. In this study the receiver array was optimised through a series of incremental steps to achieve an efficient design that allowed for the specific objectives to be addressed.

The specific objectives of this study were to i) gain an understanding of the long term space use patterns and site fidelity of sub-adult *N. acutidens* within degree of use of the St. Joseph Atoll lagoon and surrounding habitats, and ii) investigate their short term behavioural patterns in response to natural rhythmic cycles.

The important role the atoll plays in the sub-adult stage of this species was demonstrated by the very low numbers of detections outside the atoll compared to the very large numbers of detections inside the atoll. Over the course of a year the tagged sharks showed a high degree of site fidelity to the atoll, with 79 – 100% of the individuals detected during each month and 50% being detected on a near daily basis. This result provides testimony of the nursery role of the atoll and importance of these habitats in the early life history for this species. Individual area use was generally found to be restricted to the eastern part of the atoll incorporating a portion of the central deep lagoon and a nearby adjacent area of the sand flats. The movements of sub-adult *N. acutidens* on and off of the shallow flats surrounding the central lagoon (likely for foraging) were found to be strongly influenced by the tidal height and the diel cycle.

Tagged sharks were found to utilise the flats more regularly when the tidal height was greater than 90 cm and particularly more so during the night and early morning than during daylight times.

The combined results of this study expose the vulnerability of this species to rapid local depletion. Similarly, the effectiveness of spatial management measures, such as no-take marine protected areas is highlighted as an efficient tool for the future conservation of this species. In the St. Joseph Atoll in particular, the use of a multi-levelled protection approach, where the eastern portion on the atoll is completely restricted while the remaining area is utilized for non-consumptive tourism activities, could be highly effective. Future research should investigate changes in area use throughout the ontogeny of this species as well improve the understanding of the breeding site fidelity and population size of reproductive females using the St. Joseph Atoll.

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ACKNOWLEDGEMENTS

A study of this kind is quite obviously not possible without many different kinds of support. As such I would firstly like to thank IRD and SAIAB (in particular Dr. Marc Soria) for providing the scientific equipment.

Secondly this study would never have been possible were it not for the exceptional logistical and technical assistance provided by the D'Arros Research Center. A special mention of thanks must go to Mr. Udo Engelhardt and Mr. Bevil Narty for the many hours of invaluable assistance in the field.

I would like to thank the Eden Island Development Company for kindly sponsoring the use of a kayak.

I would like to thank Manuela Capello for her skills and assistance with the tidal data set.

I would like to thank Monique Simier for her valued statistical and analytical assistance, and in particular for her much needed assistance with R.

I thank Rainer von Brandis, for his photographic skills and valuable local insight.

To my supervisors, Dr. Laurent Dagorn and Dr. Paul Cowley, thank you, firstly for providing me with the amazing opportunity to conduct research in such an incredible location, secondly for your tireless assistance and guidance throughout this adventure and lastly for the many hours of reading and comments that led to the final version of my thesis.

Finally I thank Nancy White. Despite the thousands of kilometers and countless months that separated us, your faith and support remained unwavering.

CHAPTER 1 – INTRODUCTION

The genus *Negaprion* includes two species, namely the lemon shark *N. brevirostris* (Poey 1868) and the sicklefin lemon shark *N. acutidens* (Rüppel 1837) (Fig. 1.1). The lemon shark *N. brevirostris* is arguably one of the most well studied elasmobranch species in the world. Research covering a range of biological, ecological, physiological and ontogenetic parameters as well as aspects of the species behaviour and genetics have been investigated (Gruber et al., 1988; Cortés and Gruber, 1990; Wetherbee and Gruber, 1990; Morrissey and Gruber, 1993a; Morrissey and Gruber, 1993b; Feldheim et al., 2001; Sundstrom et al., 2001; Feldheim et al., 2002, 2004; Wetherbee et al., 2007; Shultz et al., 2008; Chapman et al., 2009). This species has a distribution range focused around the tropical and subtropical regions of North and South America, occurring on both the east and west coast. Isolated populations are also believed to occur along the west coast of central Africa (Shultz et al., 2008). In comparison, the allopatric sister species, *N. acutidens,* has a wider geographic distribution, spanning the tropical and sub-tropical Indo-West Pacific (Shultz et al., 2008), yet it has received very little research attention. The sicklefin lemon shark is a coastal benthic species, typically found in bays, lagoons and estuaries (Randall, 1986). They are generally found in areas with coral reefs (Campagno et al., 1989) and in some remote atolls they can be among the most commonly occurring shark species (Stevens, 1984). Juveniles are known to occupy shallow water in the inter-tidal zone, often occurring over sand flats (Randall, 1986), while adults can be found in depths of at least 30 m (Campagno, 1984).

Figure 1.1. The sicklefin lemon shark *Negaprion acutidens*.

The only knowledge on the biology of this species stems from four peer-reviewed publications (Stevens, 1984; Salini et al., 1992; White et al., 2004; White and Potter,

2004) and a few non peer-reviewed reports and guides (Bass et al., 1975; Campagno, 1984; Randall, 1986; Campagno et al., 1989). Sicklefin lemon sharks attain a maximum length of 3.1 m total length (Campagno, 1984; Randall, 1986; Campagno et al., 1989). Stevens (1984) reported the growth rate for the species from Aldabra Atoll (Seychelles) to be between 12.5 and 15.6 cm yr^{-1}. Randall (1986) and Campagno (1984) reported that males mature at 243 cm TL, while Stevens (1984) reported that both sexes mature at around 220cm at Aldabra. Sicklefin lemon sharks are viviparous and have a gestation period believed to be 10 months (Stevens, 1984), with the time of parturition varying with location. Randall (1986) reported litter sizes ranging from 1 to 13, while Stevens (1984) reported this number to be between 6 and 12 for females at Aldabra. According to Compagno (1984) the size at birth varies between 45 and 80 cm TL, while Stevens (1984) reported a range of between 55 and 60 cm TL at Aldabra. Campagno (1984) suggested that the young are born between October and November in Madagascar while in French Polynesia parturition occurs during December and January. In the Seychelles, Stevens (1984) reported parturition to take place in October, with ovulation and mating occurring during October and November while early pregnancy occurred during December.

A few studies (Stevens, 1984; Salini et al., 1992; White et al., 2004) have examined the dietary habits of sicklefin lemon sharks and all have concluded that they are primarily piscivorous but will opportunistically feed on crustaceans, cephalopods and elasmobranchs. White et al. (2004) suggested that a dietary shift may occur through the species' ontogeny with younger individuals feeding more on teleosts and crustaceans while larger sharks may also feed on batoid species.

Four studies (Stevens, 1984; White and Potter, 2004; Clua et al., 2010; Speed et al., 2011) have addressed aspects of the species movement behaviour, all of which suggested high levels of site fidelity for extended periods. Sicklefin lemon sharks were formerly widespread and abundant throughout their distributional range but population declines in recent years have led to the species being extirpated in India and Thailand, endangered in Southeast Asia and considered vulnerable throughout its range (Pillans, 2003). Despite reduced levels of abundance, this species is still a target of several multi-species shark fisheries throughout its distributional range. In India the species was reportedly taken in both bottom set and surface gillnets and in the line fishery (Pillai and Biju-Parkal, 2000). The flesh was utilized fresh or salted, while the fins are considered particularly valuable for shark fin soup (Pillai and Biju-Parkal, 2000). Evidence of individuals in markets in New Caledonia suggests that the species is also captured for consumption in the Western Pacific. In the Seychelles, the occasional appearance of this species in fresh fish markets suggests it is opportunistically exploited. The flesh is utilized both fresh and salted. Unpublished reports suggest the species may experience high levels of short-term exploitation, primarily for finning, at the more remote southern islands and atolls, using bottom set longline gear. The neonates and juveniles of this species are also captured seasonally by shore-based artisanal fishers in the many shallow bays around the Seychelles' islands of Mahe and Praslin.

The Seychelles government recently drafted a national plan of action for the conservation and management of sharks (Nevill et al., 2007) which calls for the determination of critical habitats, and associated sustainable harvesting. Critical habitats are defined as nursery areas, pupping grounds, aggregation sites and migration corridors (Nevill et al., 2007). The first step to defining such areas is to quantitatively assess the movement behaviour of the species in question. The movements of sharks can be studied using a multitude of techniques ranging from conventional mark-recapture methods to cutting-edge satellite tags. For species with high catch rates the use of conventional tagging may be an appropriate way of obtaining information on movements. However, for species which are less commonly caught and particularly when high resolution data is required, the use of passive acoustic telemetry can provide high quality information on both long-term and short-term movement patterns over finite spatial scales. In the case of sicklefin lemon sharks in the Seychelles, their relatively infrequent capture, higher abundance in remote locations and global population decline are only a few of the properties that make this an ideal candidate for monitoring through the use of automated acoustic telemetry. Similarly the lack of detailed knowledge on the behaviour of this species throughout the world highlights the need for such research.

The St. Joseph Atoll and D'Arros Island complex represent one of the few isolated atoll environments in the Indian Ocean where sicklefin lemon sharks are still abundant. The St. Joseph Atoll, with its extensive sand flats and large lagoon provides an abundance of food resources and shelter for neonate, juvenile and sub-adults of this species. The only record of commercial exploitation of this species at the St Joseph Atoll occurred in 2007. A single vessel using bottom set longlines captured a large number of sharks in the atoll where they were finned and the carcasses dumped in the lagoon (a practice still legal in the Republic of Seychelles) (U. Engelhart, pers. comm.). The impact of this event on the local shark population remains unknown. Subsequent to this event the levels of fishing activity within the atoll have been low (primarily catch and release fly fishing targeting various teleost species for six months of the year). As such the local shark population appears to still be in a healthy state.

The overall aim of this study was to develop an understanding of the movement behaviour of sub-adult *N. acutidens*, thereby aiding in the effective future conservation of this species.

The specific objectives of this study were to:

i) gain an understanding of the degree of use of the interior of the St. Joseph Atoll and surrounding habitats by sub-adult *N. acutidens*;

ii) investigate their longer term (12 months) site fidelity and space use patterns; and

iii) understand their short term movement behaviour within the atoll in response to various rhythmic environmental variables.

The most efficient way to address these objectives was through the use of passive acoustic telemetry methods. This approach provides high resolution spatial and temporal data essential for the understanding of behavioural ecology (Sundstrom et al., 2001; Voegeli et al., 2001).

Thesis outline

This thesis is divided into six chapters

Chapter 2 provides a general description of the study site and methods and materials used.

Chapter 3 describes the development of an effective acoustic receiver array for monitoring the day to day use of the study site by *N. acutidens*.

Chapter 4 deals with the long-term site fidelity and area use patterns of *N. acutidens* in the atoll.

Chapter 5 provides an assessment of *N. acutidens'* day-scale behavioural patterns in relation to cyclic environmental variables. Included within this assessment is the role that different habitat types, within the atoll, play in the ecology of these sharks.

Within Chapter 6 the principle findings are synthesized and contextualized through a general discussion. Here the directions for future research and conservation implications of the results are also addressed.

CHAPTER 2 – MATERIALS AND METHODS

2.1. Study site

2.1.1. Geographic location and climate

D'Arros Island and the St. Joseph Atoll (S 5°24.9'; E 53°17.9') are part of the Republic of Seychelles, in the western Indian Ocean. They form part of a chain of small islands that make up the Amirantes group (Fig. 2.1). The Amirantes group is located on the Amirantes bank, a submerged landmass forming a plateau roughly 180 km long and ranging between 8 and 40 km wide, with a total plateau area of approximately 3220 km^2. Although the bank is relatively shallow with depths generally less than 40 m it is surrounded on all sides by open ocean with depths in excess of 2000 m. D'Arros Island and the St. Joseph Atoll are situated slightly to the north of the center of the group, which includes African Banks to the extreme north and Desnoeuf Island in the south. Deep water separates Desroches Island to the south east of the St. Joseph Atoll and the Alphonse Island group to the south of the main bank (von Brandis, 2011).

The area of the western Indian Ocean, where the D'Arros Island and St. Joseph Atoll are located, experiences two major seasons. Due to their close proximity to the equator the traditional four seasons of the year are not strongly apparent. Rather, the two monsoon periods provide clearer delineations of seasonal change. For approximately eight months of the year (April to November) the area is subject to strong persistent south-easterly winds (15 – 30 $km.h^{-1}$). For the rest of the year, light north-westerly winds (0 – 15 $km.h^{-1}$) predominate. The area experiences the majority of its rainfall during the north-west monsoon, while the south-east monsoon is typically much dryer. Air temperatures tend to be lower during the south-east monsoon season, with an average minimum of 23 °C as opposed to 31 °C during the north-west monsoon season (von Brandis, 2011).

Sea surface temperatures tend to be lower (average minimum 25.5 °C) during the south-east monsoon season than during the calmer north-west monsoon season (average maximum of 29 °C) due to the prevalence of cold water upwelling (Tarbit, 1980; Chang-Seng, 2007) .

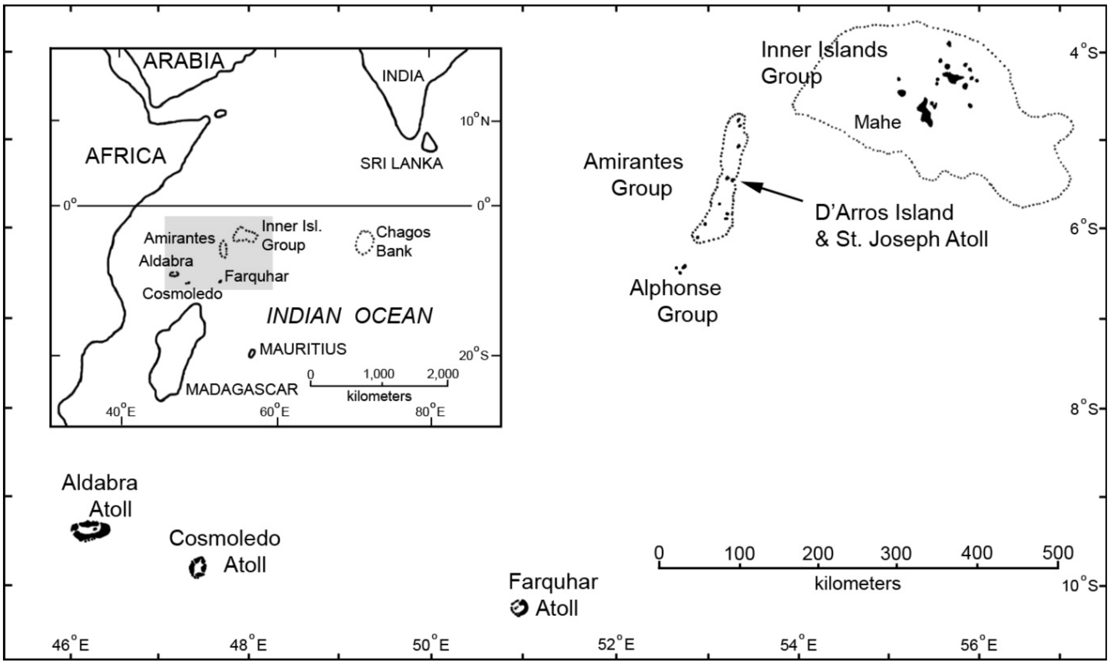


Figure 2.1. Geographic location of the study site in the Republic of Seychelles, in the western Indian Ocean.

2.1.2. Topography and marine habitats

D'Arros Island is an oval shaped sand cay of approximately 1.6 km^2. It is surrounded by waters ranging in depth between 30 and 60 m. The island has roughly 1 km^2 of intertidal reef flats, which are predominantly located on the south-eastern edge. The western edge is characterized by a short reef flat area, which rapidly drops down to 30 m. The St. Joseph Atoll is located to the west of D'Arros Island, and the two are separated by a 1.1 km wide channel with a maximum depth of 72 m. St. Joseph Atoll consists of a ring of 16 small islands (10 named and 6 unnamed) (Skerrett and Skerrett, 2005) located on top of a broad oval shaped reef flat, which surrounds the central lagoon. All 16 islands are entirely unpopulated. Most of the islands are located in the eastern region of the lagoon (Fig. 2.2). These islands constantly undergo topographical changes as sand and coral rubble shifts around the reef flat with tidal currents and seasonal winds (von Brandis, 2009).

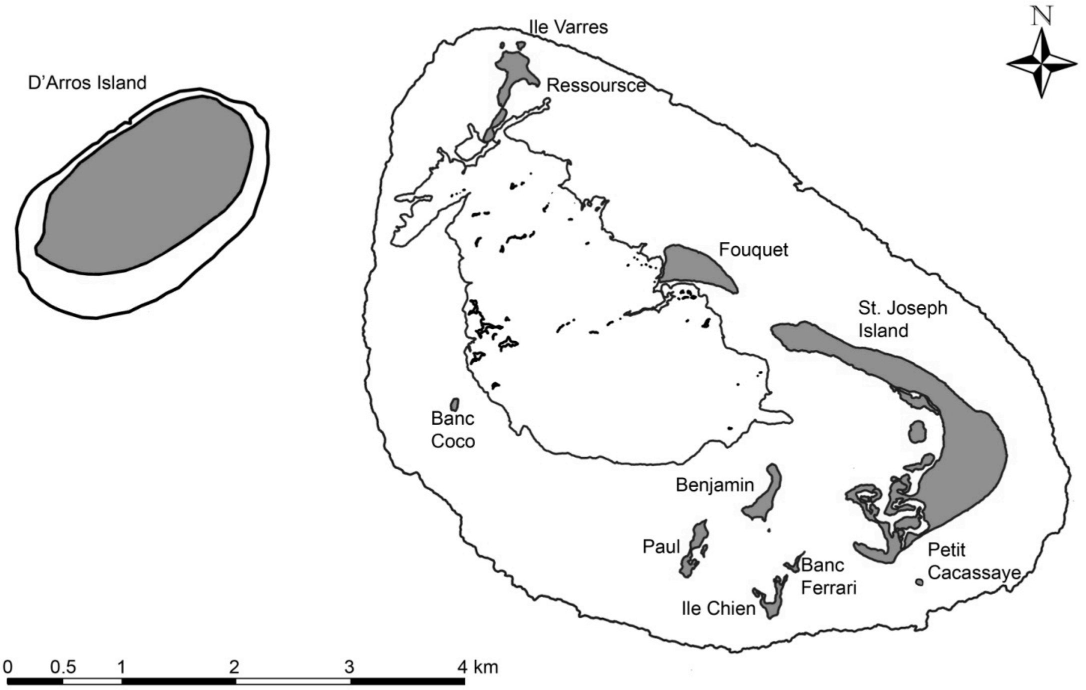


Figure 2.2. Map of D'Arros Island and the St. Joseph Atoll, showing islands (grey shaded areas) and reef flat boundaries with ribbon reef inside the lagoon (black lines).

The atoll's total area measures approximately 21.8 km^2 of which the islands contribute 1.6 km^2 (7%), the lagoon 4.9 km^2 (23%) and the reef flat 15.3 km^2 (70%). The outer edge on the north-eastern side of the atoll is characterized by steep sloping coral reef, 45 – 70° inclination (Selin et al., 1992), and consolidated coral rubble, which rapidly descends to depths in excess of 2000 m within 4 km of the shore. On the southern and eastern edges the slope is more gradual with platform reefs and consolidated coral rubble descending to the Amirantes Bank between 30 and 60 m. The reef flat consists largely of sand flats and areas of unconsolidated coral rubble. Generally the outer edge of the flats comprises more coral rubble, with the substrate becoming sandier further in towards the lagoon. On the western and northern edge of the atoll large areas of the reef flat are covered with sea grass (*Thalassia hemprichii* and *Thalassodendron ciliatum).* The flats in the inner corner of St. Joseph Island are characterized by fine grained muddy sand, due to the deposition of fine silt, which supports sea grasses and sponges. This area also supports an extensive colony of black sea cucumbers (*Holothuria nobilis*). There is no discernable channel leading from the sea into the lagoon and as such, water spills in from all sides during rising tides.

The central lagoon generally consists of soft sediments interspersed with occasional low profile patch reefs, with a maximum depth of 9 m. The lagoon is roughly divided into a series of basins, which are separated by several parallel flat topped reef ridges or ‘ribbon reefs’ (Stoddart et al., 1979). These reefs support thick sea grass beds on their upper surfaces, which are often exposed at low tide. Numerous massive coral outcrops, mostly poriitid and flaviid corals (von Brandis, 2011), are also scattered around the lagoon, rising from the bottom to the surface. In many areas the edges of the lagoon are also fringed by these sea grass covered ribbon reefs. The water in the lagoon is generally turbid with poor visibility. Several sandy channels lead from the lagoon onto the adjacent sand flats at various locations on the northern and eastern areas, although along the south western edge the boundary of the lagoon and sand flats consists primarily of a steep sandy drop-off. Detailed habitat data have been collected for the D’Arros Island and St. Joseph Atoll complex during studies conducted by the Cambridge Coastal Research Unit, Cambridge University. Spencer et al. (2008) used these data to produce a high resolution habitat map of the area using GIS software (Fig. 2.3).

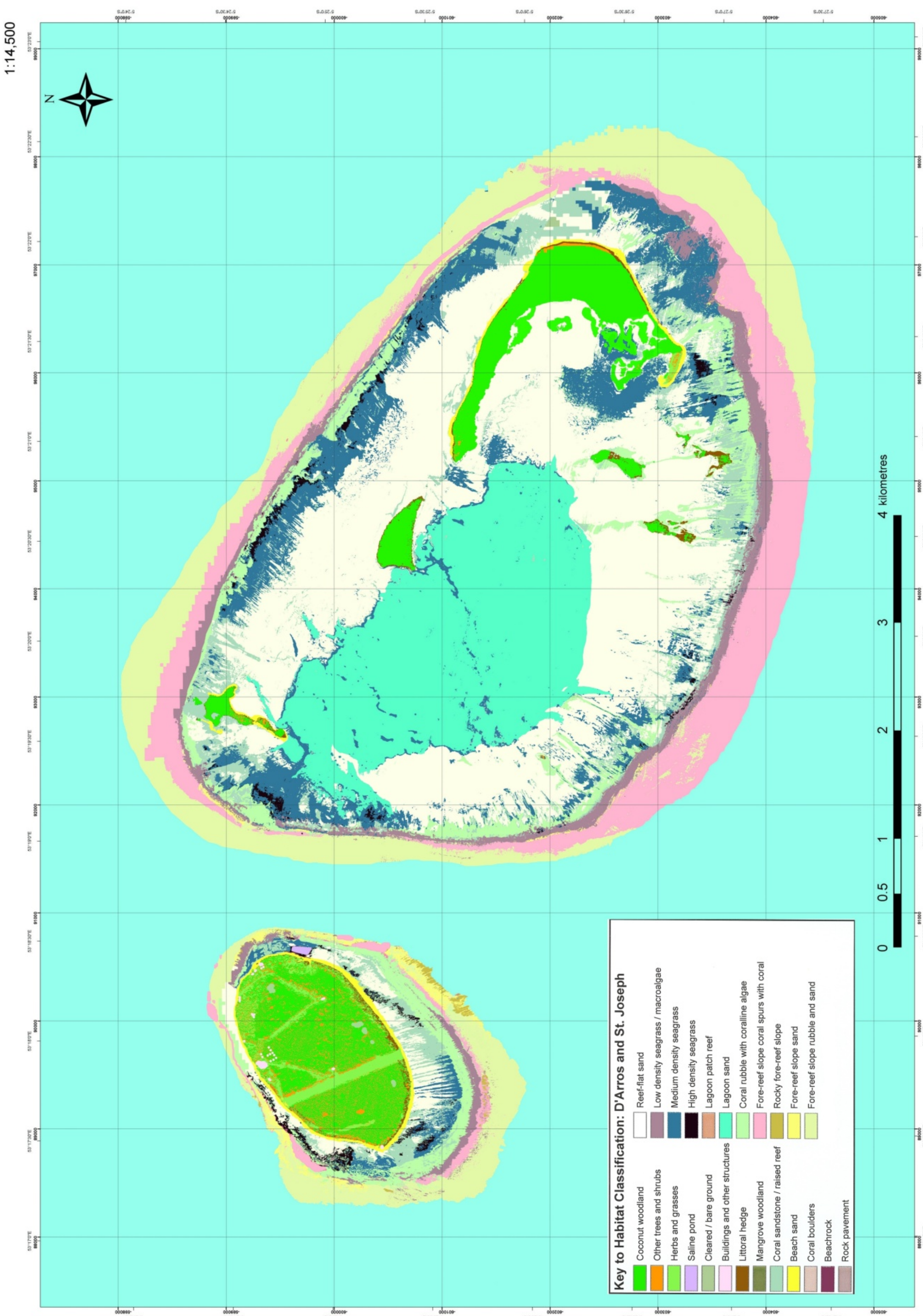


Figure 2.3 Habitat map of D'Arros Island and St. Joseph Atoll. Base map reproduced with the permission of the Living Oceans Foundation and the Cambridge Coastal Research Unit, University of Cambridge (for further information see Spencer et al., 2008).

2.1.3. Tidal regime

The Seychelles area experiences an asymmetric tidal regime of approximately two tidal cycles per day. During neap tides the difference in height between the first and second high or low tides is small, but during spring tides the difference becomes large (Fig 2.4). The maximum tidal range is approximately 2.0 m. As the lunar cycle has a duration of 29.5 days, and a lunar day last 24.8 h (Morgan, 1999), the precise number of tidal cycles in one solar day is actually slightly less than two. Consequently, the time of high and low tide moves later with each successive 24 h cycle. Similarly, this results in the time of the larger of the two tides gradually shifting between morning and afternoon through the calendar month, however, the changing amplitude of the cycle tends to obscure this pattern. Ultimately this pattern results in some months having larger tides occurring more frequently earlier in the day while other months will have larger tides more frequently at later times of the day.

The tidal regime plays an important role in controlling the water depth and currents over the flats of the St. Joseph Atoll. At spring low tide a large portion of the sand flats are either exposed or covered by 10 – 30 cm of water. The flats are also interspersed with occasional depressions, where 1 – 2 m of water may remain during spring low tides. Visibility in these shallow waters is usually very good, but during rising tides turbidity can increase in areas where the substrate consists of soft silts.

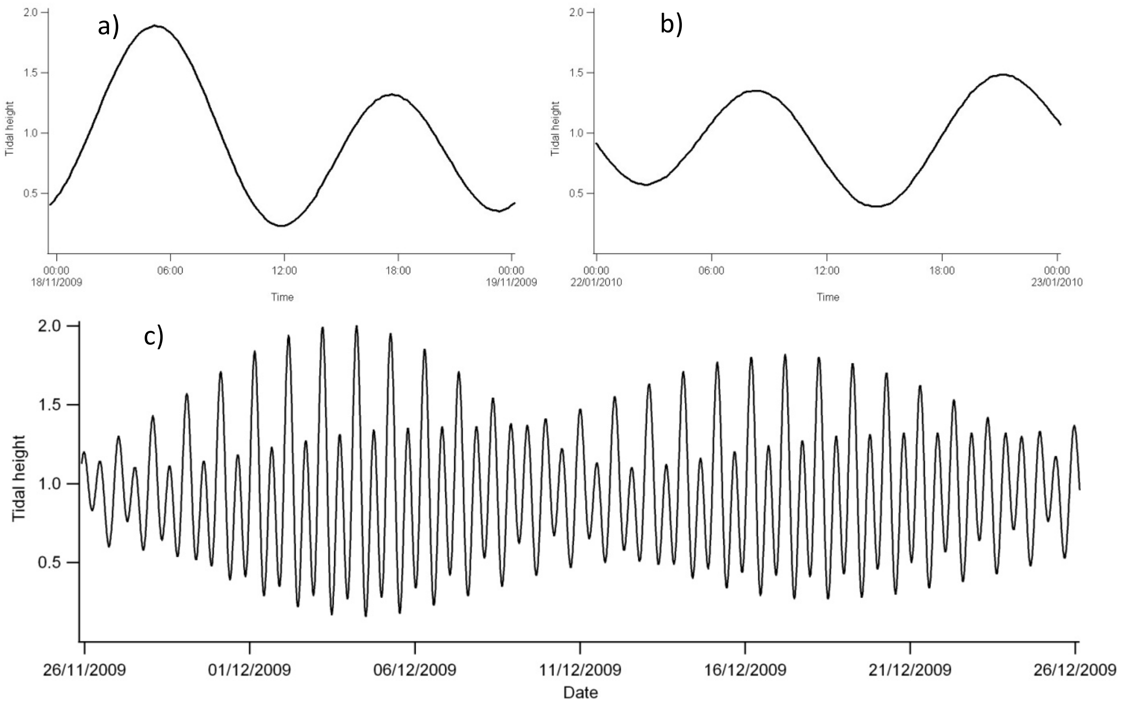


Figure 2.4. Typical tidal regime occurring at D'Arros Island and St. Joseph Atoll complex. a) A 24 hour tidal cycle during a spring tide. b) A 24 hour tidal cycle during a neap tide. c) Tidal fluctuations over a full month, clearly showing differences in the size of the first and second high and low tides occurring each day.

The tidal currents were measured at various location in the atoll following the methods of Childs et al. (2008). The time a neutrally buoyant object took to move 1 m at the water's surface was measured. Using this technique current speeds of up to 0.43 m.s^{-1} were observed on the flats during rising spring tide. These measurements were obtained opportunistically to simply provide some baseline information on current dynamics and not for the correlation with individual movement data.

2.2. Research approach

Acoustic telemetry was used to investigate the short-term movements and longer term space use patterns of sub-adult sicklefin lemon sharks *Negaprion acutidens* in the St. Joseph Atoll over a period of 20 months. All sharks were equipped (hereafter referred to as 'tagged') with coded acoustic transmitter (V13-1L-64K, Vemco® Ltd., Halifax, Canada) transmitting at 69 kHz. The tagged sharks were monitored using an array of omni-directional automated acoustic receivers (VR2 and VR2Ws, Vemco® Ltd., Halifax, Canada) deployed at various locations around the study site as well as with a portable receiver (VR100, Vemco® Ltd., Halifax, Canada). The use of coded transmitters allowed all tagged sharks to be monitored simultaneously, as each tag was recognized by a unique series of closely spaced acoustic ‘signals’ known as a pulse train (Childs et al., 2008; Meyer et al., 2010b).

2.2.1. Receivers and tag specifications

The VR2 and VR2W receivers used in this study are designed to detect transmissions on a single frequency (69 kHz). The receivers use non-volatile flash memory to store data. The battery life of each receiver was estimated at 15 months, but during the course of the study the batteries were changed every six to eight months. The receivers were recovered approximately every three months and the data downloaded onto a portable computer. For the newer model VR2W receivers the data were transmitted via Bluetooth, while for the older VR2s data were transferred using an electromagnetic probe. The specific location of the receivers in the study area was modified as the study developed. Detailed descriptions of the acoustic receiver array designs and resultant detection frequencies are presented and discussed in Chapter 3. The acoustic receivers were deployed in the lagoon for a total of 20 months, with the study starting in April 2009 and ending in November 2010.

The coded acoustic transmitters used in this study were 13 mm in diameter and 36 mm in length. Each tag weighed 11 g in air and 6 g in water. The tags transmitted a pulse train of eight pulses, within which the tags ID was encoded. The entire series of pulses took roughly three seconds to transmit. Transmission output was 147 dB. The tags were programmed to start transmitting each train randomly between 50 and 130 seconds from the end of the previous pulse train. Each tag was estimated to have a battery life of at least 879 days according to the manufacturers’ specifications.

2.2.2. Code collisions

An acoustic receiver records an individual identification by receiving an uninterrupted pulse train from a transmitter. It is possible that a pulse train is interrupted, especially if the individual is at the edge of the receiver’s detection range, as the acoustic energy is absorbed by the water column (Pincock and Voegeli, 2002). Interruptions can also come from sources of ambient noise, or from another tag transmitting simultaneously, resulting in zero tag detections. Alternatively when two tags are within range of a single receiver and the emission of their pulse trains overlap, it is possible that the receiver records a combination of the two pulse trains and generates a tag ID that does not exist in the study, known as a ‘false detection’. In the worst case it is possible that the receiver records a combination of pulse two trains and generates a tag ID that happens to exist in the study but did not belong to either of the emitting tags. The likelihood of such occurrences is increased when tags with short nominal delays are used, and even more so when many individuals are likely to be located around a single receiver (Heupel et al., 2006). To mitigate against this, the tags were programmed to emit their pulse trains at random intervals between pre-defined maximal and minimal times (Pincock and Voegeli, 2002). In the current study, the tags were slow (a long nominal delay, 90 s, compared to the time required to emit a pulse train, 3 s) and as such the likelihood of false detections was very low. Nevertheless, the data were manually screened to remove any false ID’s that were recorded before any analysis was conducted.

2.3. Field methods

2.3.1. Receiver deployment

Four methods were used to anchor the receivers during this study. All receivers deployed around D’Arros Island and the outside of St. Joseph Atoll were attached directly to large (1 m × 1.2 m × 1.2 m) concrete mooring blocks (Fig 2.5). A receiver was secured to a steel peg protruding from the top of each block using a combination of ropes and heavy duty cable ties. Blocks were positioned in such a way that when the receiver was secured on top there were no large structures (coral outcrops) that would obstruct the reception of acoustic transmissions. The mooring blocks were deployed from a floating barge, towed by a small skiff. Blocks were placed on heavy steel pipes atop the barge and secured with ropes. Two 200 L plastic drums were secured to metal eyes on the corners of the block. The barge was carefully positioned above the selected deployment site, the securing ropes removed and the block pushed off the stern, with the pipes acting as rollers. The plastic drums ensured that the block sank upright, so that the steel attachment pegs were always on the upper surface (Fig. 2.5b). Once the block was in position on the sea bed the drums were cut free and recovered at the surface. An acoustic receivers was secured to each of the eight mooring blocks by a diver using SCUBA (Fig. 2.5c).

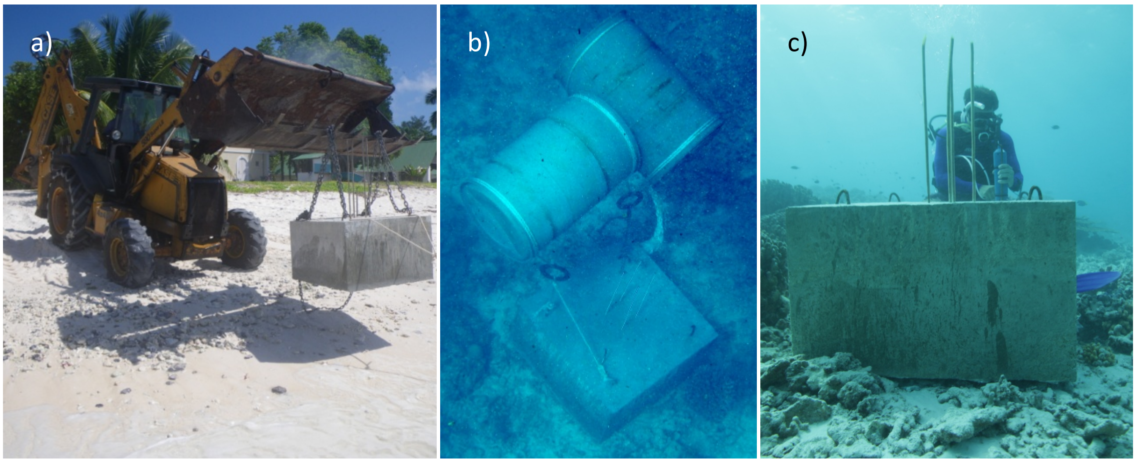


Figure 2.5. Deployment of mooring blocks. a) Mooring block being loaded on to the barge, b) mooring block after deployment with plastic drums attached, c) diver attaching an acoustic receiver to the block.

Receivers deployed inside the lagoon of the St. Joseph Atoll were moored using two different designs with the second design representing an improvement on the first.

The initial design used a small concrete block (50 cm × 50 cm × 50 cm) to which a surface buoy was attached using rope. The VR2W receiver hung from the buoy on a separate rope, 1 m below the surface with the hydrophone pointing down (Fig. 2.6), this design was similar to those used by Ohta and Kakuma (2005) and Clements et al. (2005).

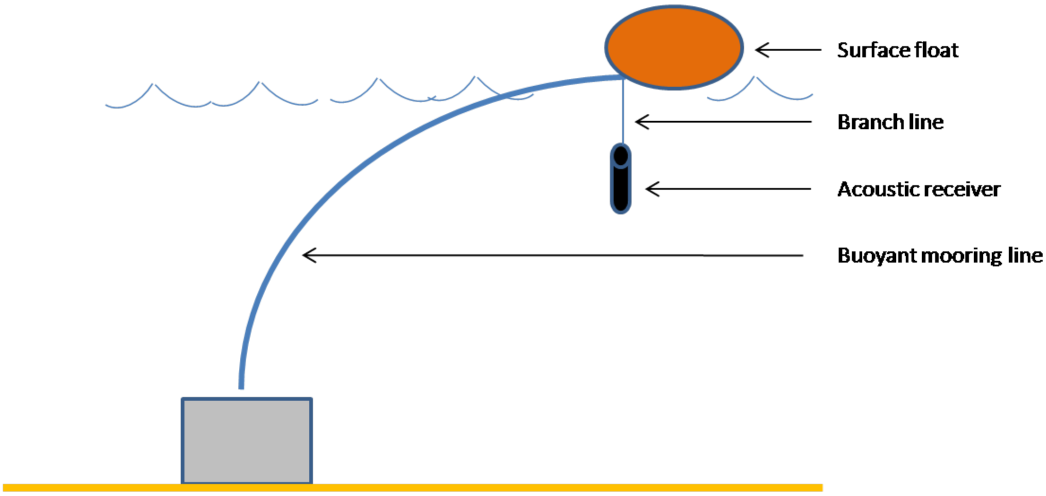


Figure 2.6. Mooring design for acoustic receiver deployed in the lagoon in the St. Joseph Atoll.

The second mooring design was developed after three months (June 2009) as it was felt that the range of detection would be improved if the receiver were further from the wind generated surface noise (Voegeli and Pincock, 1996). A concrete block (50 cm^3) was deployed at each site and a buoyant mooring line was attached to the block, to which a rigid plastic surface buoy was secured. A lighter branch line was secured to the mooring line as close to the surface as possible when the mooring line was pulled tight directly above the block. The receiver was attached to the end of this branch line with a 5 kg weight secured to the base of the receiver. A light rope with a string of three small closed cell foam floats was attached to the top of the receiver, to hold it vertically in the water column. Using this arrangement the receiver was maintained close to the bottom, in an upright position and could be retrieved with ease by simply pulling on the branch line (Fig. 2.7).

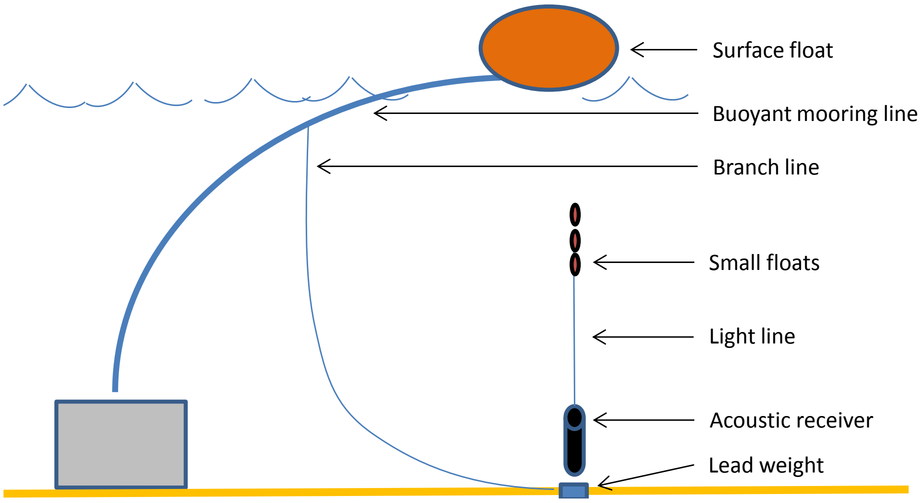


Figure 2.7. Mooring design used for the deployment of nine acoustic receivers in the lagoon of the St. Joseph Atoll.

Receivers deployed on the shallow sand flats in the St. Joseph Atoll were moored in a horizontal orientation to insure that the hydrophone remained submerged as the tide receded (Fig. 2.8a). A narrow strip of high density foam was attached to the upper side of the receiver to ensure that it floated. Receivers were anchored in the sand using a large rigid plastic sheet buried 30 – 40 cm below the surface of the sand. The receivers were attached to the anchor using 0.5 cm braided rope (Fig. 2.8b). The receivers were moored in the same positions on the flat over two separate periods. The first period lasted for 12 days in January 2010 and the second period lasted 55 days during April and May 2010.

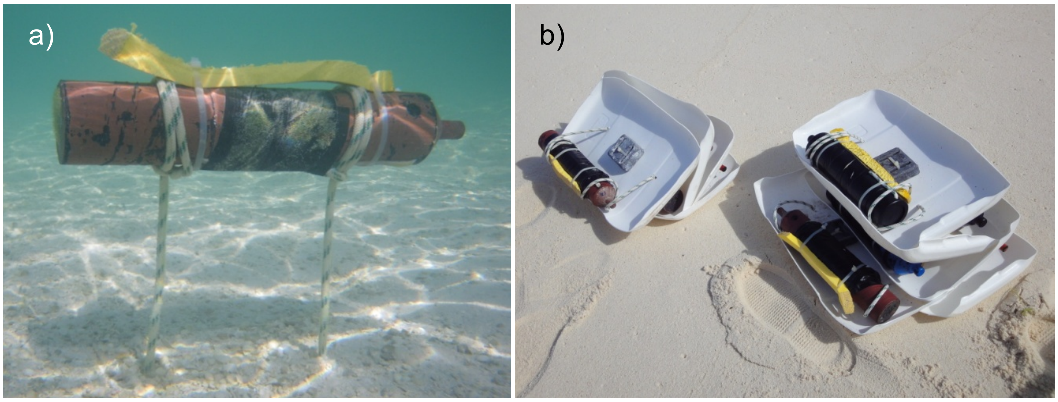


Figure 2.8. a) An acoustic receiver deployed on shallow sand flats with a strip of foam attached to keep it afloat. b) Acoustic receivers ready for deployment on the sand flats showing the plastic sand anchors.

A detailed description of the acoustic array development to effectively monitor the tagged sharks in the St. Joseph Atoll and surrounding areas is provided in Chapter 3.

2.3.2 Capture and tagging of sharks

Three separate tagging trips were conducted during 2009. All sharks were caught using baited handlines configured with a 12/o or 14/o barbless, 0°-offset, circle hook and heavy, multi-strand wire leader. During the first tagging trip (April 2009) sharks were caught from a motorized skiff at four locations within the atoll atoll's lagoon (Fig. 2.10, ID codes 1-8) Once a shark was hooked (Fig. 2.11a) it was brought alongside the skiff as quickly as possible and restrained by placing a rope around its caudal peduncle, this rope was then secured near the stern of the skiff. The hook was left in the shark's mouth and the handline tightly secured towards the skiff's bow. Once both ends of the shark were secure it was turned over so that the ventral side faced up (Fig. 2.11b and 2.11c). Turning the shark over in this way induced a state of catatonic immobility, where, after a few seconds orientated in this way, the shark relaxed and stopped moving completely. During the second and third tagging trips (June and October 2009) sharks were caught at eight locations within the atoll, some of which were in the lagoon and some on the shallow sand flats (Figure 2.10, ID codes 9 -22). When caught in the lagoon, sharks were moved onto the shallow sand flat by slowly motoring the skiff towards the nearest flat while the shark was on the handline. The maneuvering usually took three to five minutes. Once the sand flat was reached the shark was restrained alongside the skiff as before and the tagging team could climb out to perform the tagging operation whilst kneeling in the shallow water. Using this method only one person was required to invert the shark and support its weight during the tag implantation process (Fig. 2.11c). In total 22 sharks (139 – 202 cm TL) were tagged with acoustic transmitters during the three trips. Fourteen of these were males and eight were females (Table 2.1).

Figure 2.9. Tagging localities of 22 sicklefin lemon sharks *Negaprion acutidens* equipped with acoustic transmitters in the St. Joseph Atoll.

Surgical implantation of the transmitter began only once the shark was completely immobilised. Each shark was measured, to the nearest centimeter, from the tip of its nose to the fork of its caudal fin (fork length, FL), as well as to the tip of the upper lobe of its caudal fin (total length, TL). Measurements were made using a plastic tape measure. Two people were required to hold the shark up, and lift its abdomen clear of the water surface. Following this, a small incision, roughly 2 cm in length, was made along the ventral midline using a sharp scalpel blade. Once the lining of the peritoneal cavity was slightly pierced, the incision was widened by inserting a gloved finger, to prevent damage to any of the internal organs. The tag, which had been sterilized with ethanol, was then inserted into the peritoneal cavity through the incision. Two independent absorbable sutures were used to close the point of incision. The shark was then turned over into an upright position and a uniquely coded plastic dart tag, with a stainless steel anchor, was inserted into the base of the first dorsal. After the tagging procedure was complete, a small piece of one anal fin was removed using sharp scissors and stored in a vial containing 100% ethanol, for later genetic analysis. The sex of each shark was recorded before the hook was removed. Hooks were removed using a pair of pliers. Once all measurements were taken sharks tagged on the flats were gently guided by hand back to the edge of the lagoon and released. The time taken to perform the entire tagging operation from hooking to release was approximately 15 minutes.

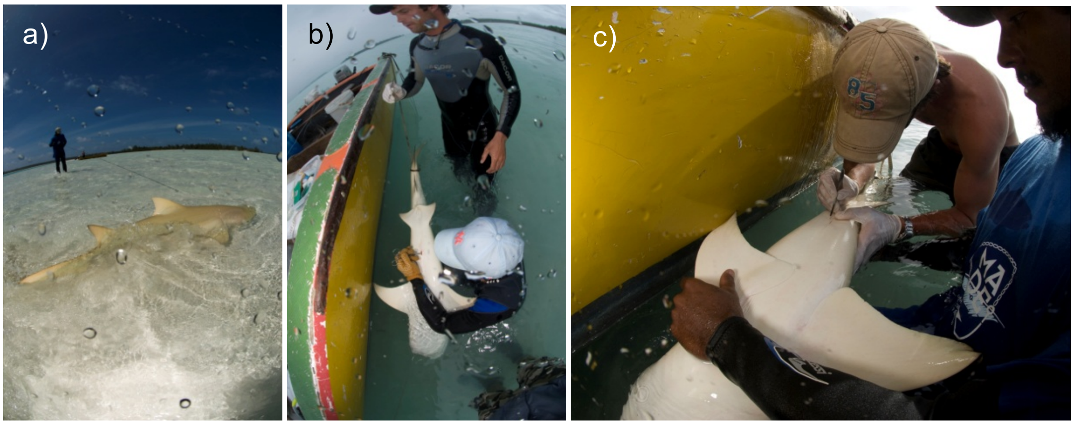


Figure 2.10. a) Capturing a sicklefin lemon sharks on the sand flats, b) once restrained alongside the skiff, c) acoustic transmitters were surgically implanted.

Table 2.1. Summary information for all sicklefin lemon sharks *Negaprion acutidens* equipped with acoustic tags in the St. Joseph Atoll, Seychelles

Shark ID Code	Tagging Date	FL (cm)	TL (cm)	Sex
1	05/04/2009	129	159	M
2	05/04/2009	155	189	F
3	05/04/2009	146	172	M
4	05/04/2009	155	193	F
5	05/04/2009	147	176	F
6	06/04/2009	136	170	F
7	08/04/2009	145	173	F
8	08/04/2009	136	161	M
9	29/06/2009	151	174	M
10	29/06/2009	124	148	M
11	29/06/2009	135	160	M
12	30/06/2009	163	202	F
13	30/06/2009	138	163	M
14	01/07/2009	134	164	M
15	04/07/2009	115	141	M
16	05/07/2009	115	139	M
17	05/07/2009	129	152	M
18	05/07/2009	120	144	F
19	05/07/2009	132	158	M
20	06/07/2009	124	148	F
21	12/10/2009	119	144	M
22	15/10/2009	121	146	M

2.3.3 Reception range testing

A range test was conducted inside the atoll, once the receivers were deployed in their final configuration (See Chapter 3). The range over which acoustic tags can be detected can vary significantly due to the influence of a multitude of environmental factors. Childs et al. (2008) working in a turbid tidal estuary suggested that tidal phase, current strength, physical obstruction and water physico-chemical conditions all affected reception range in their estuarine study site. Heupel et al (2006) suggested that transmitter type (output strength) as well as local site conditions will strongly influence reception range. More specifically, environmental factors such as biological noise (Heupel et al., 2006), wave action (Voegeli and Pincock, 1996; Klimley et al., 1998), haloclines and thermoclines (Voegeli and Pincock, 1996) and sediment type (Heupel et al., 2006) can also affect signal detection.

The range test in the atoll was performed by hanging an acoustic transmitter from a kayak. The tag was secured to lengths of light monofilament fishing nylon using insulation tape as described by Clements et al. (2005). Care was taken to ensure no air was trapped within the tape or between the tag and fishing line. The tag was suspended 40 cm off the bottom, using a lead weight below the tag and a small float 120 cm above the tag. The kayak was anchored at various distances from a moored receiver, starting directly above it and moving away in increments of between 10 - 20 m up to approximately 150 m. Beyond this distance larger increments (± 50 m) were made. Distances from the receiver were measured using a hand held GPS accurate to 10 m. At each distance the transmitter was lowered over the side of the kayak until the tag emitted five pulse train signals. A Vemco VR100 acoustic receiver was used to quantify the emission of these signals. By comparing the number of detections emitted at each distance and the number recorded on the receiver it was possible to calculate various indices to describe the functional reception range. These include the distance at which 95% and 50% of the emissions were recorded as well as the approximate minimum and maximum range of detection.

The maximum distance that a signal was detected was 220 m. Using a linear regression (Fig. 2.12) it was observed that ninety-five percent of the emitted pulse trains were detected at a distance of 29 m while 50% of emissions were recorded when the tag was 144 m from the receiver.

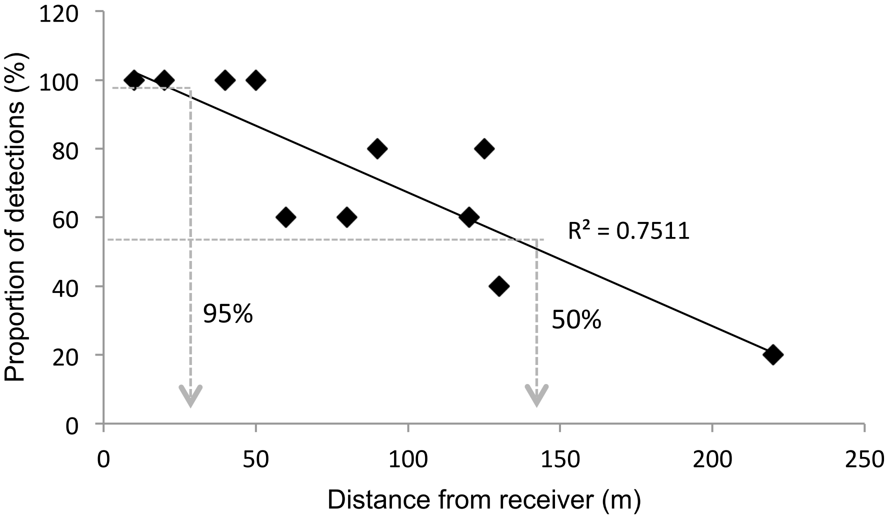


Figure 2.11. The distance and proportion of detections recorded by an acoustic receiver in the lagoon of the St. Joseph Atoll

Other researchers working in coral reef environments have observed detection ranges of 20 - 50 m (Lowe et al., 2006). These relatively short distances were attributed to background noise generated by the reef and physical obstructions scattered throughout the lagoon in the St. Joseph Atoll. Similarly the wall-like ribbon reefs that divide the lagoon are likely to impede the transmission of acoustic signals. Maximum reception ranges of up to 800 m and 1100 m have been reported in estuarine (Heupel et al., 2006) and the open ocean (Dagorn et al., 2007) environments respectively. However it appears that low reception ranges (50 – 200 m) are common in coastal coral reef environments (Lowe et al., 2006; Chateau and Wantiez, 2007).

CHAPTER 3 – DEVELOPMENT OF AN ACOUSTIC ARRAY TO EFFECTIVELY MONITOR *N. ACUTIDENS*.

SUMMARY

Question: Developing an array of acoustic receiver that is both effective and efficient is a complicated process. When does one have enough receivers to address the study objectives?

Objectives: Determine the ‘minimum’ array to 1) understand how regularly tagged sharks use the study area on a day to day basis and 2) provide enough data to assess the finer scale behavioural patterns.

Methods: Data were sampled from four study periods of varying lengths, each with their own array design, and used to produce two indices allowing the comparison of the frequency of shark detections in the lagoon as well as the amount of data collected during each study period.

Conclusion: The third study period with 17 receivers, 9 of which were inside the atoll, proved sufficient to understand the frequency with which tagged sharks used the area. For the analysis of detailed behavioural patterns the fourth study period, with 29 receivers, 12 of which covered portions of the sand flats, provided sufficient amounts data to produce robust behavioural results.

3.1 Introduction

The methodological approach of stationary data logging acoustic telemetry can be used to investigate a variety of ecological and behavioural questions (Heupel et al., 2006). The information provided in the previous chapter explains the technical mechanisms of this method. However, as this approach employs static equipment to infer behavioural information on mobile animals the design of the array of receivers will have a strong impact on the results (Heupel et al., 2006). Ideally a large number of receivers can be used to clog up a confined study site and allow for the continuous monitoring of all individuals in the study area. Heupel et al. (2004) were able to effectively clog a small Florida embayment to the extent that they could successfully use the data collected via passive monitoring to estimate the home range of tagged juvenile blacktip sharks *Carcharhinus limbatus*. However, an important aspect that often has to be considered in the array design stage is the limited resources available to many researches. This is particularly significant in studies conducted by students or in developing countries where funding is often limited. As such obtaining a design that is both economically efficient and effective in terms of data collection can be a critical component of some passive telemetry studies. For this and other reasons (spatial scales or environmental constraints) many passive telemetry studies place a limited number of receivers in strategic locations to optimise the collection of data to address their specific objectives (Meyer et al., 2007a; Kerwath et al., 2009; Papastamatiou et al., 2009; Meyer et al., 2010b; Papastamatiou et al., 2010; Simpfendorfer et al., 2010; Field et al., 2011; Murchie et al., 2011; Speed et al., 2011). Irrespective of the approach adopted all passive acoustic telemetry studies tend to adhere to a typical protocol involving seven steps (Fig. 3.1) to address specific questions about their study species.

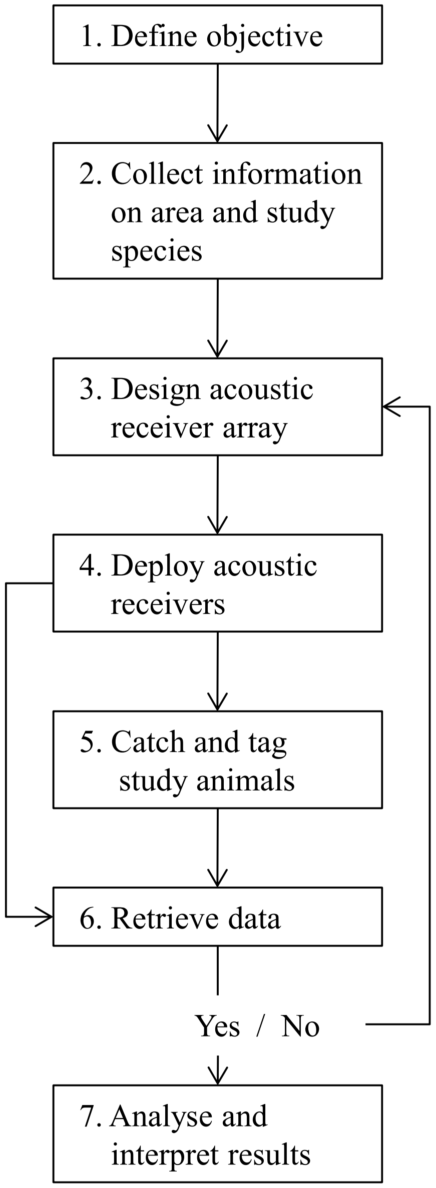


Figure 3.1. Flow diagram portraying the typical seven step protocol involved in a passive acoustic telemetry study.

Between steps 6 and 7 a rapid assessment of the data obtained can be conducted to determine whether sufficient data has been, or is likely to be, collected to address the objectives of the study as defined in step 1. If the data is insufficient then the process loops back to step 3 and the array is re-designed. This in turn leads to a secondary loop between steps 4 and 6 (new animals may not need to be tagged), however, depending on the transmitter specifications and the time taken to retrieve the data for the first time, this loop may not be followed. Following this general outline, the overall objective of this study was to develop an understanding of the movement behaviour of *N. acutidens* to assist in its future conservation as explained in Chapter 1.

Owing to the lack of previous work on this species in the study area, knowledge on the distribution and abundance of *N. acutidens* primarily consisted of anecdotal reports which suggested that they occur inside the St. Joseph Atoll as well as around its outer edges and also around the perimeter of D’Arros Island.

In this chapter the re-development loop between steps 3 and 6 of the protocol described above are discussed in light of obtaining sufficient data to address the objectives of the study and as such, move from step 6 to step 7. This approach led to four discrete study periods, each of which had their own receiver array design. By developing indices that reflected the efficiency of each design, comparisons could be made between these four study periods. The specific objectives of this chapter were to determine the ‘minimum’ array configuration that would 1) provide an understanding of the frequency with which the tagged sharks utilized the study area on a day to day basis and 2) provide sufficient data to produce robust results on their fine scale area use and behavioural patterns.

3.2 Materials and Methods

3.2.1 Acoustic array development

i) Study period 1

During April 2009 eight receivers were deployed around the perimeter of the St. Joseph Atoll and D’Arros Island, and one receiver in the centre of the Atoll (Fig. 3.2). The water depth where the outer receivers were located ranged from 5 m to 12 m, while the receiver inside the lagoon was in 6 m of water. The acoustic receivers were left in this configuration for 80 days.

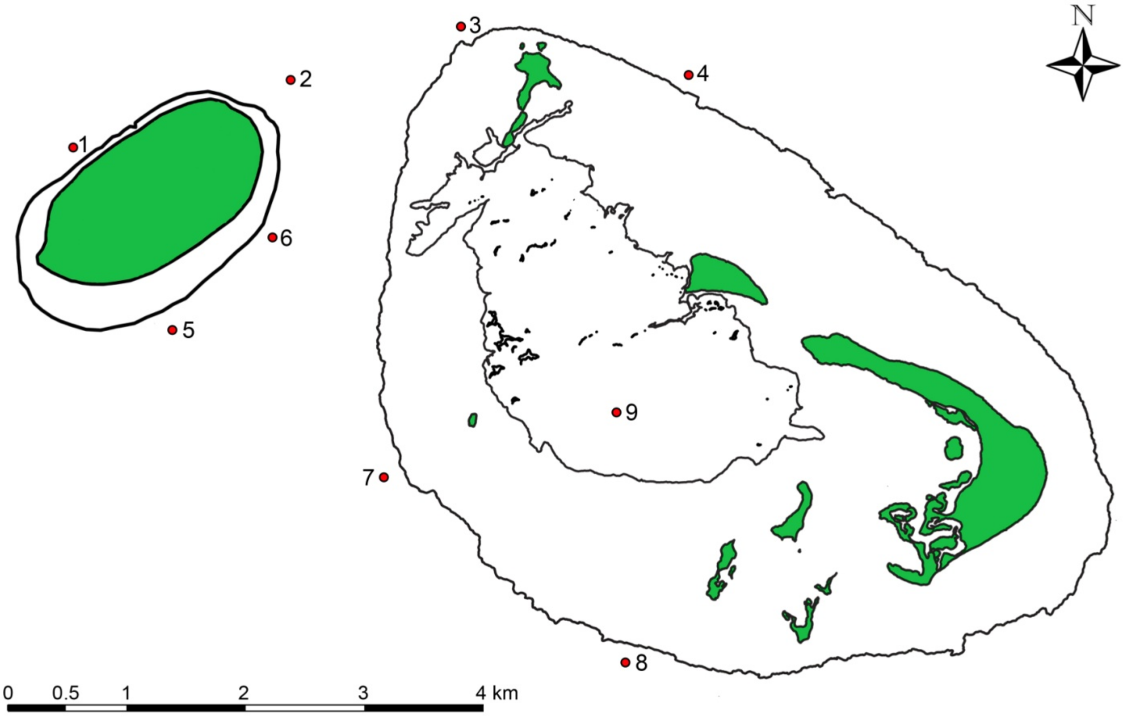


Figure 3.2. Locations of the nine VR2W acoustic receivers around the D'Arros Island and St. Joseph Atoll complex during the first study period.

ii) Study period 2

During June 2009 two more VR2W receivers were added to the array within the atoll. The original receiver within the atoll (Station 9) was moved, so that a triangle could be created with the two additional receivers (Fig. 3.3). Each receiver was positioned in an area free of large coral structures to maximize the reception potential. The outer array, fringing the edges of the atoll and D'Arros Island remained unchanged. This configuration was maintained for 100 days, however, Station 9 broke off its mooring after roughly 85 days, and as such only data from the 85 day period was considered.

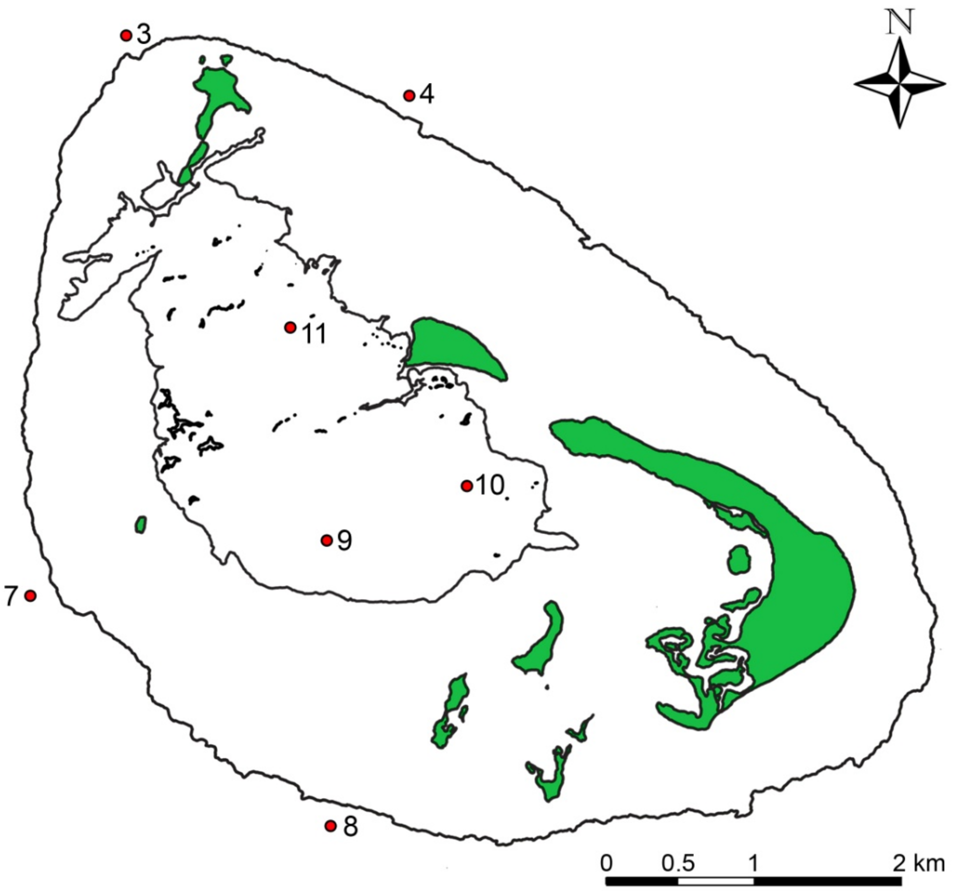


Figure 3.3. Location of three additional acoustic receivers (9-11) placed in the St. Joseph Atoll during the second study period.

iii)Study period 3

During October 2009 a further six VR2 acoustic receivers were added to the array inside the St. Joseph atoll. The three existing receivers were once again repositioned to maximise the area covered by the array inside the lagoon. Attempts were made to arrange the network of nine receivers in such a way that the distance between adjacent receivers was similar, while simultaneously ensuring that each receiver was positioned in an area devoid of coral heads (Fig. 3.4). Receivers were deployed in water between 4 m and 6 m deep. This configuration remained in place for 373 days, however receiver 12 shifted during the study period (study months 2 and 3), resulting in the removal of all data collected during these two months, as such the array was effectively maintained for 313 days (see Chapter 4 for details).

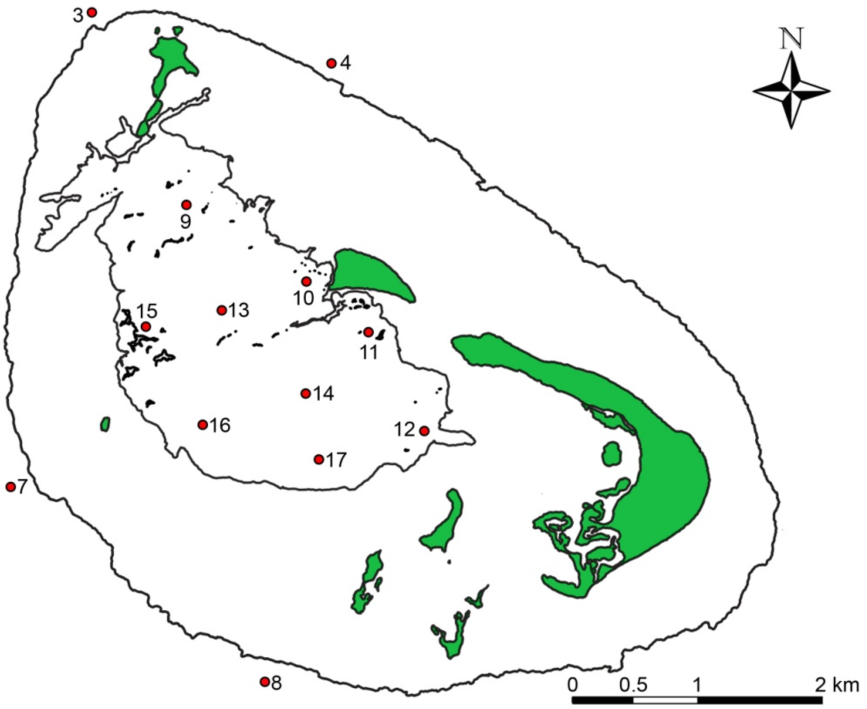


Figure 3.4. Locations of nine acoustic receivers (9 - 17) place inside the lagoon of the St. Joseph Atoll during the third study period.

iv) Study period 4

In order to study the effect of environmental variable such as tide and time of day on the movements of sharks between the lagoon and surrounding shallow sand flats, it was necessary to deploy an additional array of receivers on the sand flats. As the number of receivers was limited it was important to place them in strategic locations on the flats where sharks were likely to be detected. This required some understanding of possible spatial patterns in abundance of sharks on the flats. This information was obtained using a visual census approach, where the number of sharks observed in fixed areas of equivalent sizes at various locations on the flats was compared.

Visual and acoustic census

Rectangular survey areas, 600 m long by 400 m wide, were sampled during the visual census with the protocol for each census involving three longitudinal transects 100 m apart traversing the rectangular area (see Fig. 3.5).

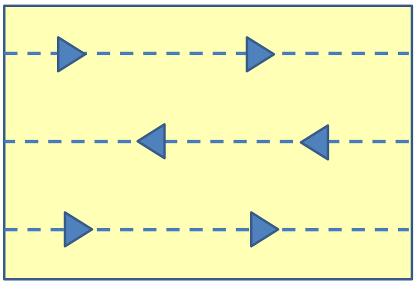


Figure 3.5. Layout of the survey path followed in the field during visual surveys conducted on the shallow sand flats in the St. Joseph Atoll.

The survey path (track) was generated on a computer, uploaded onto a GPS and traversed in the field. Six rectangular areas were sampled at fixed locations on the sand flats. See Fig. 3.6 for details on the location of the census areas. Censuses were replicated six times for each survey area and were carried out at a variety of tidal heights and at varying times of the day. Censuses were conducted either on foot or in a kayak, depending on the height of the tide.

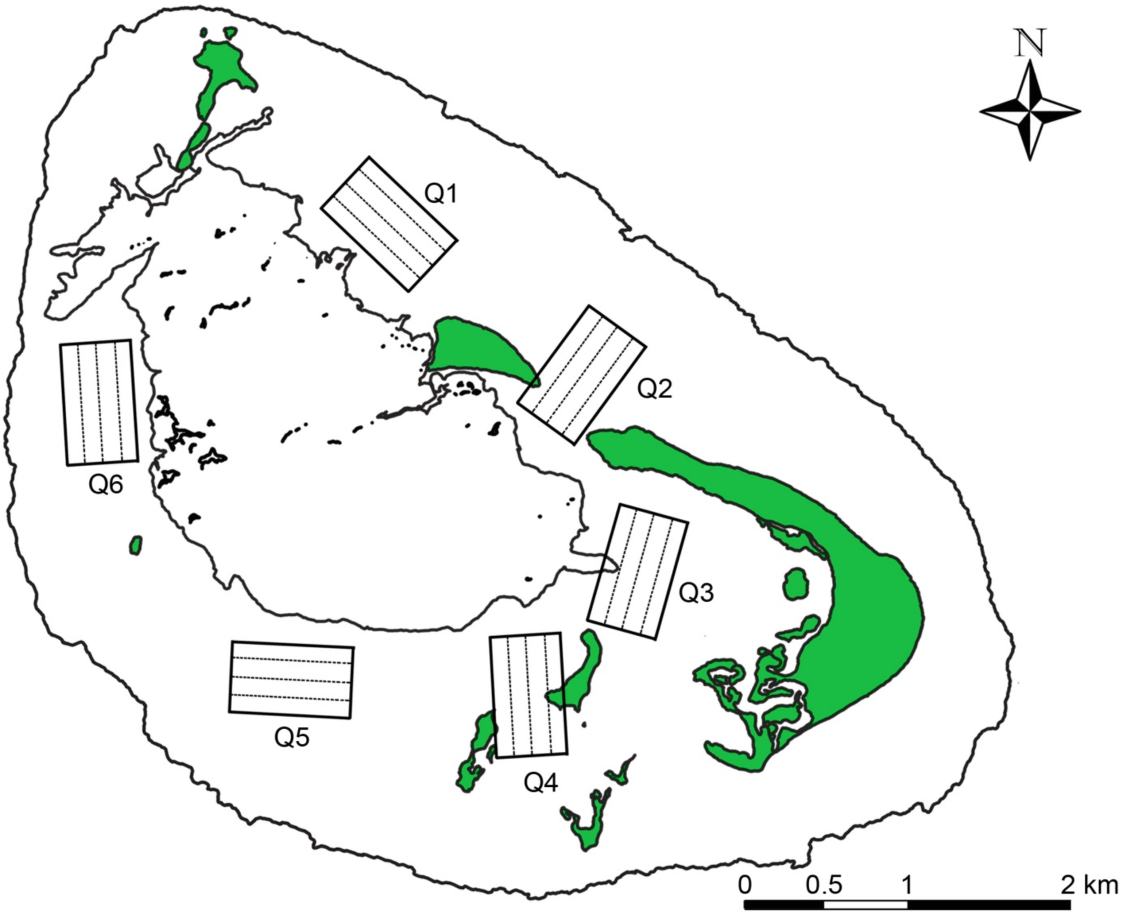


Figure 3.6. Location of six quadrants for the visual and acoustic census of *N. acutidens* on the reef flat of the St. Jopseph Atoll. Stippled lines represent the transects covered during each census.

A portable Vemco VR100 acoustic receiver with an omni-directional hydrophone was also used during each census to identify the presence of tagged sharks. When on foot the receiver was carried in a water proof back pack with the hydrophone trailing behind, similarly when in the kayak the hydrophone was allowed to trail behind the kayak with the VR100 secured to the front of the kayak. When walking, the kayak was anchored roughly 100 m from the survey area. When a shark was observed, the observer stopped for 1 – 2 min to reduce noise and allow time for transmitter identification (if tagged). During this time the shark's position and size class were noted along with the time of observation. Four size classes were used; pups (< 80 cm), small juveniles (80 – 140 cm), sub-adults (140 – 200 cm) and adults (> 200 cm). Observations were limited to the area within 50 m either side of the transect line during each of the three longitudinal transects. Polarized sun glasses were worn by the observer to minimize glare and improve visibility.

As each of the censuses differed slightly in duration, depending on whether they were conducted on foot or from the kayak, shark abundance was represented as the number of individuals observed or detected per unit time (hour). Tagged sharks that were only detected on the VR100 acoustic receiver and not observed visually were also added to the final total. Abundance was compared using an ANOVA. *N. acutidens* were observed in all six census quadrants but tagged individuals were only detected in quadrants 3 and 4 (Annex 1). The results indicate that *N. acutidens* were more abundant on the flats to the north-eastern and eastern sides of the atoll with significant differences observed between the number of sharks observed per hour in each quadrant (ANOVA, $p = 0.002$, d.f. = 5).

Receiver location

In light of these observations, the array of receivers deployed on the sand flats was concentrated on the eastern side of the atoll (Fig. 3.7). Twelve additional receivers were deployed on the flats, bringing the total number of receivers deployed inside the atoll during this period to 21. For the comparisons dealt with in this chapter, data for the periods 11/01/10 – 23/01/10 and 04/04/10 – 29/05/10 (67 days in total) collected from all 21 receivers were considered.

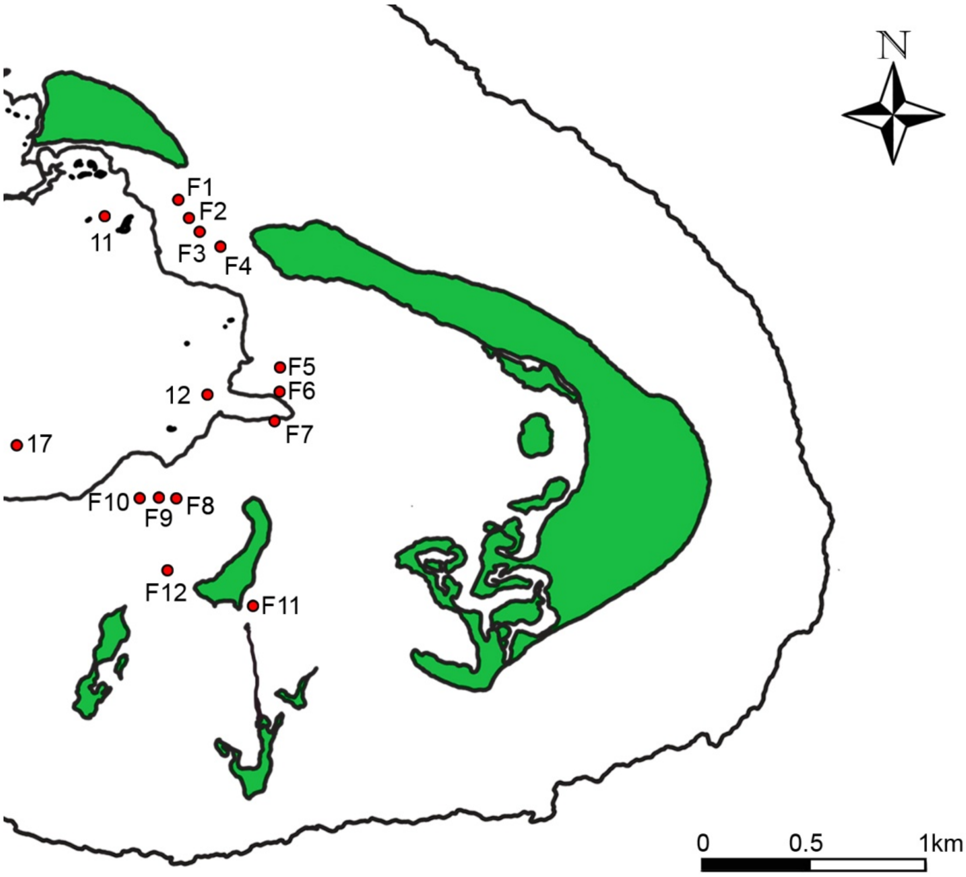


Figure 3.7. Locations of the 12 acoustic receivers placed on the shallow sand flats in the St. Joseph Atoll.

3.2.2 Data analysis

To compare the efficiency of the array utilized during each study period a standardized approach was used. This was necessary as the number of sharks tagged and receivers used differed between each study period. This standardization was obtained by only using data from six sharks that were considered to be present for the entire duration of the overall study. Two indices were used to address the two objectives of this study.

The first index represented the percentage of days that all tagged shark (n = 6) were detected inside the lagoon during each study period. This assessment followed the methods of Heupel et al. (2010) and Simpfendorfer et al. (2010) who considered an individual to be present in their array if at least two detections were recorded on any receiver during a given day. Similarly, the frequency with which the tagged individuals utilized the atoll (i.e. general behaviour) was assumed to be constant over the entire duration of the study (20 months). As the duration of each study period differed comparisons were based on a sample of 30 days, consisting of three replicates (i.e. 10-

day sub-samples) that were drawn at random, without replacement, from each period. Randomisation was achieved using a random number generator in Microsoft Excel and assigning each day of the study period a number. For the third study period only data from before the time the first shark permanently left the atoll (ID code 7, see Chapter 4) was considered for this analysis. The presence or absence of a shark was determined for each of the 30 days. The average percentage of days present could then be compared between the study periods, each with a unique array configuration. Comparisons were made using an ANOVA.

The second index used represented the amount of data (number of detections) that was obtained for each individual during each of the four study periods. Again the same six individuals were assessed using the same randomly drawn 30 day samples as before. The average number of detections recoded during each period was calculated per individual and for the group as a whole. Comparisons were then made between the four study periods using an ANOVA

3.3 Results

The largest increase in days observed occurred between study periods 2 and 3, where the mean number of days observed for all individuals jumped from 20% to 89%, with the addition of 6 receivers (Fig. 3.8). The addition of 12 more receivers on the flats only increased the mean percentage of days observed slightly (from 89% to 95%) (Fig. 3.8). Results of the ANOVA show that there was a significant difference between the number of days the sharks were detected during each study period (ANOVA, $p < 0.001$, d.f. =3).

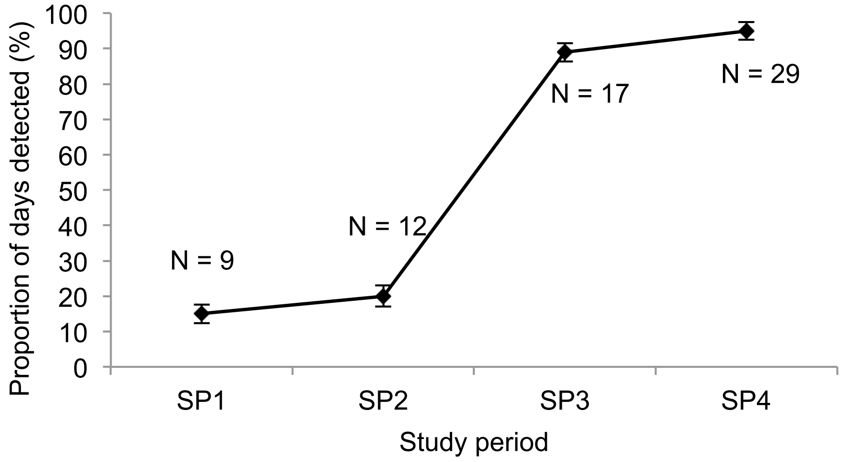


Figure 3.8. The mean proportion of days all tagged *N. acutidens* were detected in 10 day samples drawn from each study period. N represents the number of receivers in the array. Error bars indicate standard errors.

On average the number of detections recorded per individual showed very little increase between the first two study periods while a steady increase was observed from the second to the third and from the third to the fourth periods (Fig. 3.9). Results from the ANOVA showed a significant difference in the number of detections per individual recorded during each study period (ANOVA, p = 0.017, d.f. = 3).

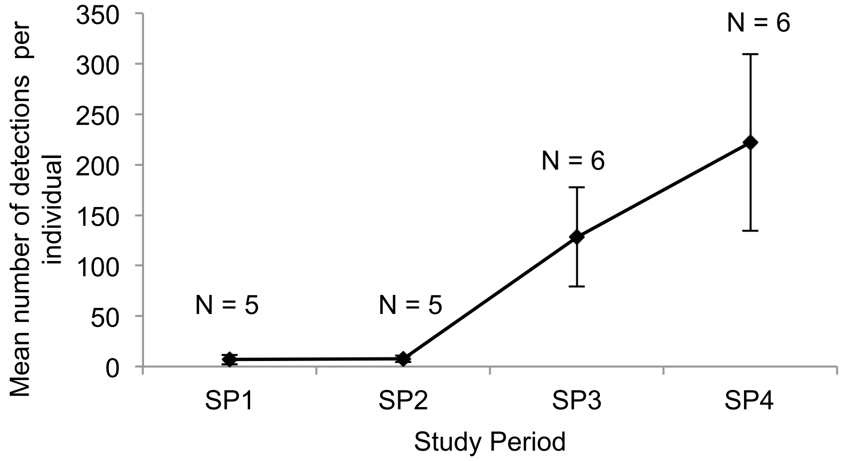


Figure 3.9. Average number of detections recorded per individual *N. acutidens* during the four study periods. N represents the number of individuals recorded during the 10 day samples from each study period. Error bars represent standard errors.

3.4 Discussion

3.4.1 Visual census

The results of the visual census clearly demonstrate a strong spatial relationship in shark abundance, while the observed increase in detections recorded by the receivers on the flats suggest their locations were appropriate. Speed et al. (2011) also used a visual census approach to assess the temporal abundance of *N. acutidens* among other species, in a coastal embayment in Western Australia. The details of their method differed in that the observer was located on top of a high dune, but their observational data also showed that visual census techniques can be a powerful tool when working with large marine organisms in shallow tropical environments. The findings of this study also highlight the benefits of using a light silent vessel when working in such environments where avoiding the disturbance of the study species is a priority. Meyer and Holland (2001) demonstrated the effective use of such a vessel for actively tracking *Naso unicornis* over very shallow reef environments. Here, despite the limitations of being low to the water in terms of visual range, this method was clearly both useful and effective.

3.4.2 Comparison of array efficacy

i) Days detected

The array configurations during the first and second study periods did not yield much information on the sharks' presence in the atoll. Data from these two study periods were insufficient to address the study objectives and provided no insight on how dependant the sharks' are on the atoll environment. However, once the nine receivers had been installed, during the third study period, the coverage of the array was sufficient to address this question. A threefold increase in listening potential (i.e. the number of receivers) yielded slightly more than a fourfold increase in the number of days in which the sharks were recorded in the atoll. This modification to the array configuration significantly ($p < 0.001$) increased the ability to monitor the tagged sharks' day to day use of the atoll. Interestingly the efficiency of the acoustic array did not increase much further with the addition of the 12 receivers on the flats. This 133% increase in listening potential inside the atoll only resulted in an average increase of 7% of days detected.

Consequently, if a shark was present in the atoll, the lagoon array alone provided sufficient coverage to record its presence.

ii) Amount of data obtained

The total number of detections recorded were extremely low during the first and second study periods but increased greatly between the second and third study periods and again between the third and fourth study periods. Although the greater number of detections recorded during study period four may not be necessary to better understand the day to day use of the atoll, they are vital for the investigation of finer scale area use and behavioural patterns. Such analyses were the focus of much of the research described throughout the rest of this thesis. Heupel et al. (2006) suggested that the design of an acoustic array will be dictated by the nature of the research question. However, the current assessment clearly demonstrates that *a priori* knowledge on the movements of the study species is also a vital component to the design of an acoustic receiver array. The step-by-step approach adopted here is not necessarily the optimal strategy as it is both time consuming and there is a risk that the behaviour of the study animals may change over time (i.e. ontogenetic shifts), however this can be directly tested from the data recorded during the long-term deployment of the final array. This staggered approach has also been employed to some degree in other studies (see Heupel and Hueter, 2002). Another approach that could be utilized involves active manual tracking techniques to gain empirical knowledge of the short term space use of the studied species. For example Atwood et al. (2007) tracked four white stumpnose *Rhabdosargus globiceps* to establish whether this species utilized shallow flats on the Langebaan lagoon MPA (South Africa). The information gleaned from this study was then adopted by Kerwath et al. (2009) to deploy a comprehensive static array of receivers to monitor the long-term movements and space use patterns of white stumpnose in the same lagoon system. Clearly, the assimilation and use of information on the area (study site) and study species within this area is beneficial when designing an array. This information can include local ecological knowledge (Valbo-Jorgensen and Poulsen, 2001; Grant and Berkes, 2007) as well as any other scientific studies or surveys that may provide some insight on the species ecology or behaviour or the study site. In this study, the only information available before the first deployment was a good description of the study sight (Spencer et al., 2008; von Brandis, 2009), while anecdotal information on *N. acutidens* provided little value to the initial array design. Based on the findings of this analysis only the data collected during the third and fourth study periods were used in the analyses in the forthcoming chapters.

CHAPTER 4 – AREA USE PATTERNS AND SITE FIDELITY

SUMMARY

Question: *N. acutidens* are known to occur in the St. Joseph Atoll as well as around its perimeter and that of D'Arros Island. How much of this area do these sharks use and how long do they stay there for?

Objectives: **1)** Determine the area use patterns of sub-adult *N. acutidens*.

2) Investigate the degree of site fidelity shown by *N. acutidens* over the year-long study period.

Methods: Data were collected on the movement patterns and site fidelity of 19 tagged sharks using 17 passive acoustic receivers in and around the St. Joseph Atoll and D'Arros Island.

Conclusions: Tagged sharks showed a high degree of site fidelity, with almost all detections recorded inside the atoll's lagoon and most sharks using the area for the entire study period. Area use was typically restricted to a small part of the lagoon, with most sharks using only the eastern portion.

4.1 Introduction

The identification of key habitats is critical to the formation of sound spatial management approaches for any species. In the case of elasmobranchs, such habitats will include areas of importance for reproduction and parturition (Springer, 1967), juvenile nurseries (Simpfendorfer and Milward, 1993; Heupel and Hueter, 2002; Garla et al., 2006; Heupel et al., 2007; Knip et al., 2010) and aggregation sites (Klimley et al., 1988; Economakis and Lobel, 1998; Speed et al., 2011). To understand the relative importance of such habitats basic knowledge on the species long-term area use and site fidelity to each key habitat is essential. Furthermore, detailed assessment of space use within a particular key habitat (eg. Gruber et al., 1988; Papastamatiou et al., 2009; Papastamatiou et al., 2010) can provide additional information which could facilitate finer scale management approaches such as the adoption of varying degrees of protection across a range of areas within an identified site.

In 2009 the D’Arros Research Centre produced the D’Arros Island and St. Joseph Atoll Conservation Management Plan (2009) with the principle objective of maintaining and enhancing the marine and terrestrial biodiversity of D’Arros Island and the St. Joseph Atoll. An additional objective of this plan was to promote the protection of the surrounding marine environments through the potential future implementation of a marine protected area (von Brandis, 2009). This broad plan covers all species found in the area and calls for dedicated research to facilitate the effective management of key species. *N. acutidens* was identified as one such species (von Brandis, 2009), with early juveniles and sub-adults known to commonly occur in the area. However, critical information regarding the temporal scales over which individuals remain associated to the area is lacking. Similarly the extent to which these individuals make use of the total available habitat is also not known.

Passive acoustic telemetry is an ideal technique for obtaining the spatial and temporal data required to address these knowledge gaps. In many instances acoustic telemetry has been used to make post hoc assessments of the effectiveness of previously established marine protected areas (Lindholm and Auster, 2003; Lowe et al., 2003; Egli and Babcock, 2004; Meyer and Holland, 2005; Starr et al., 2005; Meyer et al., 2007a; Meyer et al., 2007b; Afonso et al., 2008; Kerwath et al., 2009). In comparison, few studies (Bruce et al., 2005) have adopted this approach to delineate areas for effective protection based on the observed movement and residency patterns of the species concerned. Although data on the *N. acutidens* population that inhabits the St. Joseph Atoll is lacking, other studies on this species across its distribution range (Stevens, 1984; Clua et al., 2010; Speed et al., 2011) have suggested that it may be highly resident, utilizing the same area for multiple years.

To ensure the efficient management of this species in the St. Joseph Atoll, information regarding the movements and fidelity of individuals is essential. In light of this requirement this chapter uses data collected through passive acoustic telemetry, in and around the St. Joseph Atoll, to address the following objectives:

1) To determine the area use patterns of sub-adult *N. acutidens*, and

2) To investigate the degree of site fidelity over the one-year study period.

4.2 Materials and methods

4.2.1 Field methods

Area use patterns and site fidelity of the acoustically tagged *N. acutidens* were assessed using an array of acoustic receivers. Data were collected for a period spanning 373 days which represented the third study period, as described in the previous chapter (also see Fig. 4.1). Details regarding the capture and tagging of the sharks are provided in Chapter 2.

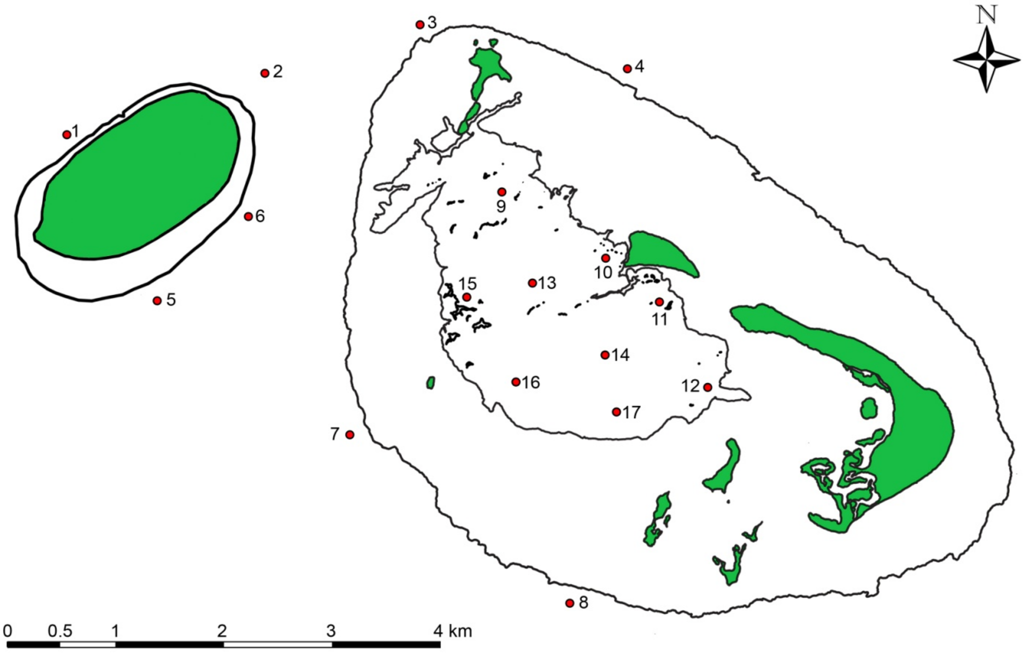


Figure 4.1. Location of 17 acoustic receivers around D'Arros Island and the St. Joseph Atoll

4.2.2 Data analysis

Monitoring was initiated one day after the last shark was tagged (16/10/09) and ended on the 25/10/10 when the receivers were finally removed. Unfortunately, not all data collected during this period could be used as two of the 17 receivers experienced technical problems. On approximately 23/11/09, station 12 came adrift from its original deployment location and moved nearly 1 km across the lagoon. It was located and re-deployed at its original location on the 14/01/2010. The receiver at this location contributed a major portion of the total data set (52% of all detections), hence the data collected by all receivers during this period had to be removed from the analysis. To accommodate the removal of this data and maintain monthly comparisons over the 12-month study period, the starting date for each month was taken as the 16th day, rather than the 1st day of each calendar month. In this way the data collected during the 52 days mentioned above could be removed with a buffer of seven days before the station was believed to have moved. As such all data from study months 2 and 3 was removed. Similarly, all data collected after the 15/10/10, the end of study month 12, was removed from the analyses. Consequently, the effective monitoring period spanned a total of 313 days over a 12 month period.

The second acoustic receiver that experienced technical problems was on station 9, where the battery was depleted three months prior to the end of the study. This station contributed < 1% of all the detections recorded during the study and as such had negligible influence on the outcomes of the various analyses. Hence all analyses included data from other receivers while the receiver at station 9 was inactive.

Data from 19 tagged individuals considered to be present at the start of the monitoring period was assessed.

i) Area use

To assess whether the tagged sharks used certain areas of the atoll more regularly than other the proportion of detections recorded on each receiver was compared using a Kruskal-Wallis test following the method of Papastamatiou et al. (2009). To visually assess the long-term space use of the tagged population, month barycentres (or centres of mass) were calculated. The barycentre provides a single mean weighted positional estimate over a defined period. Here barycenters were calculated using the predefined study months. Before calculating the barycenters the data were filtered such that individuals with < 60 detections per study month and less than six such months of data were removed from the analysis. The threshold of 60 detections was developed from the requirement that a shark was detected at least twice in a day to be considered present in the area. Furthermore it was felt that fewer detections would not provide a robust estimate of area use patterns at the scale of a month.

This positional estimate was calculated using the location of each receiver and the proportion of detections recorded by each during the period in question, as follows:

$$\text{Barycenter } (a, b) = \left(\textstyle\sum_{i=1}^{n}(p_i x_i), \sum_{i=1}^{n}(p_i y_i)\right)$$

Where a = barycentre latitude

b = barycentre longitude

p_i = proportion of detections on receiver *i*:

$$p_i = \frac{n_i}{N}$$

n_i = number of detections on receiver *i*

N = total number of detections on all receivers

x_i = latitude of receiver *i*

y_i= longitude of receiver *i*

To provide a metric for comparisons between individuals, the distance (D) between the two most extreme barycenters was calculated for each individual.

These monthly barycentres were then used to identify high use areas by dividing the lagoon into a grid of 400 m × 400 m squares and calculating the density of monthly barycentres from all individuals within each square.

ii) Site fidelity

Fidelity to the D'Arros Island and St. Joseph Atoll study site was assessed at a variety of temporal scales. The criteria for determining the presence of a tagged shark was set at a minimum of two detections per day, recorded on one or more receivers. Single detections were excluded to reduce the possible inclusion of false detections in the various analyses. Similar assumptions have been used previously to monitor long-term presence of acoustically tagged bull sharks in estuaries (Heupel et al., 2010) and sawfish in coastal embayments (Simpfendorfer et al., 2010). To assess monthly dependence the number of individuals recorded during at least one day in each study month, was calculated for each study month.

4.3 Results

4.3.1 Area Use

The number of detections recorded on each receiver during the 10 months of observation was extremely skewed. Only seven detections were recorded on receivers outside of the St. Joseph Atoll, while none were recorded on receivers around D'Arros Island (Fig. 4.2a). A total of 37 813 detections were recorded by the nine receiver inside the lagoon of the atoll. A Kruskal-Wallis test revealed significant differences ($H = 75.54$, d.f. = 8, $P < 0.001$) between the number of detections recorded on each of these nine receivers (Fig. 4.2b). Receiver number 12, in the south-eastern corner, was clearly the primary receiver within the lagoon and recorded 56.4% of all detections made. Following this, the two receivers nearest to number 12 (11 and 17) recorded the next highest with 15.8% and 8%, respectively. Receiver number 9 in the north-western corner of the lagoon recorded the fewest detections with less than 0.5% of all detections made.

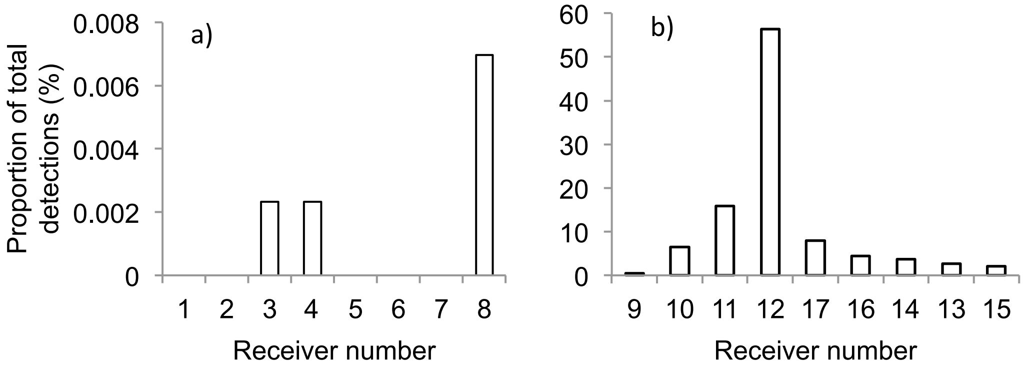
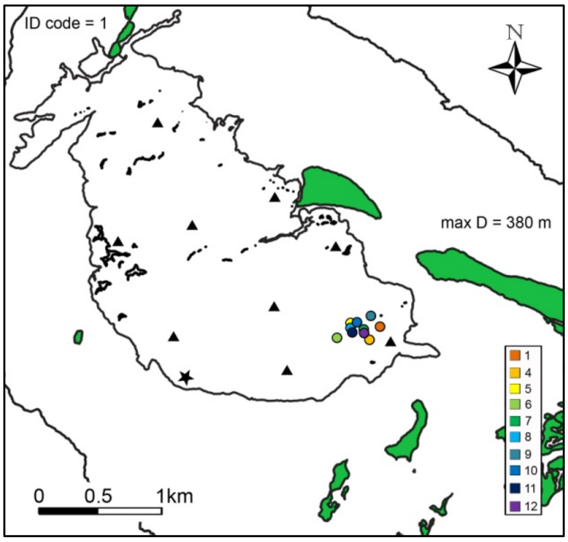


Figure 4.2. Proportion of total detections recorded on acoustic receivers: a) located around D'Arros Island and the outside of the St. Joseph Atoll and b) located inside the central lagoon of the St. Joseph Atoll.

A total of 12 tagged sharks met the minimum criteria for the calculation of monthly barycenters, although not all individuals had enough data to support this calculation for every study month. No marked temporal shift in the location of each shark's barycenter was apparent from one study month to the next. At the individual level barycenters were typically clustered together across all months. The maximum distance between barycenters (D) from each individual ranged from 160 – 840 m (median = 515 m, SD = 220 m) (Fig 4.3). For several individuals (n = 9) the cluster of monthly barycenters was located close to their tagging site, however, for three tagged sharks (ID codes 1, 2 and 11) there was a clear difference between the group of barycenters and their tagging location.

When looked at on a monthly basis, across all individuals (i.e. the location of all dots with the same colour for each shark in Fig. 4.3), no clustering was apparent.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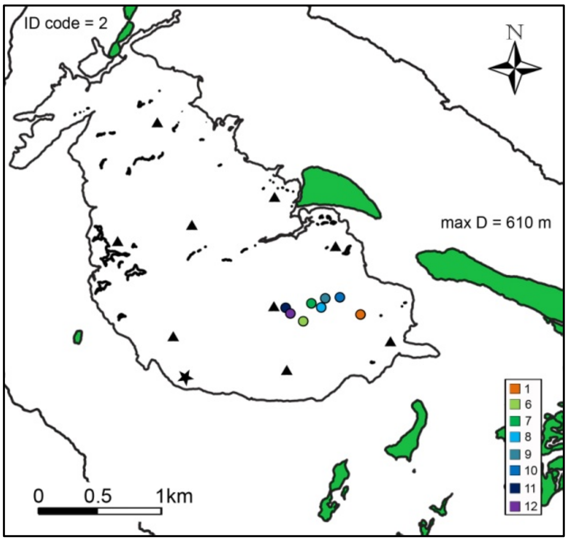
4
5
6
7
8
9
10
11
12
0
0.5
1km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6
7
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9
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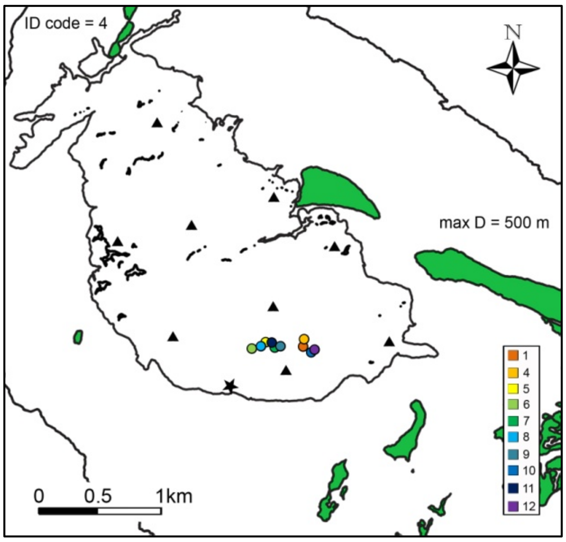
12
0
0.5
1km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5
6
7
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9
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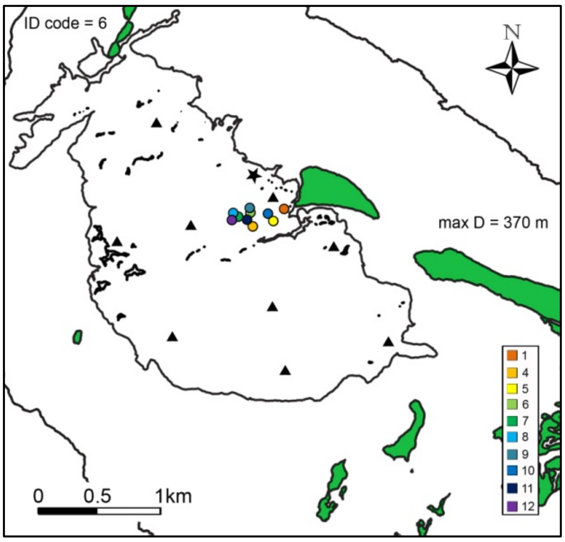
1km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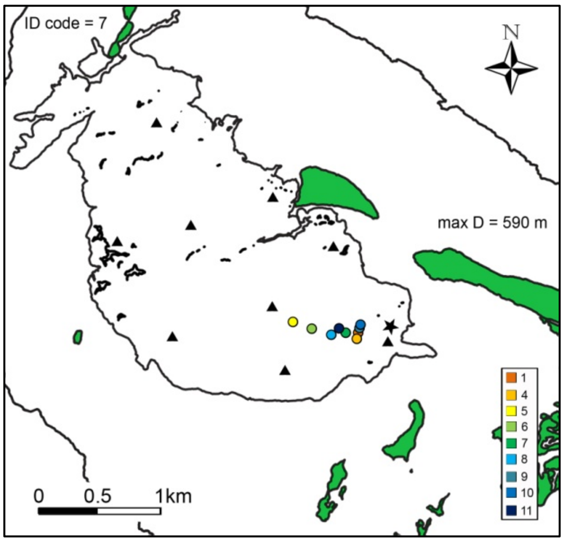
1km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max D = 590 m
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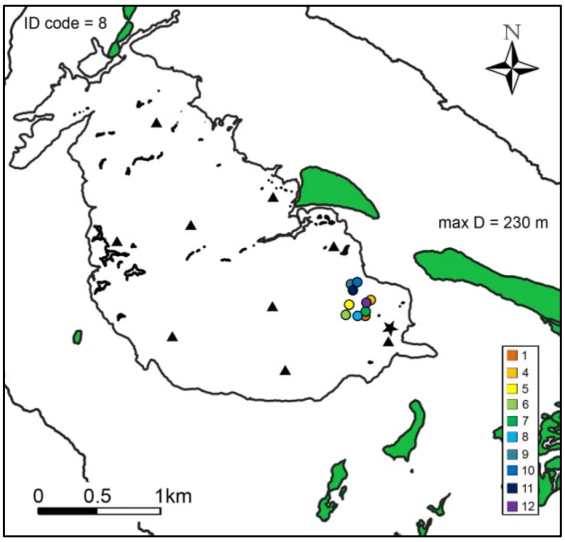
1km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max D = 230 m
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12
0
0.5
1km

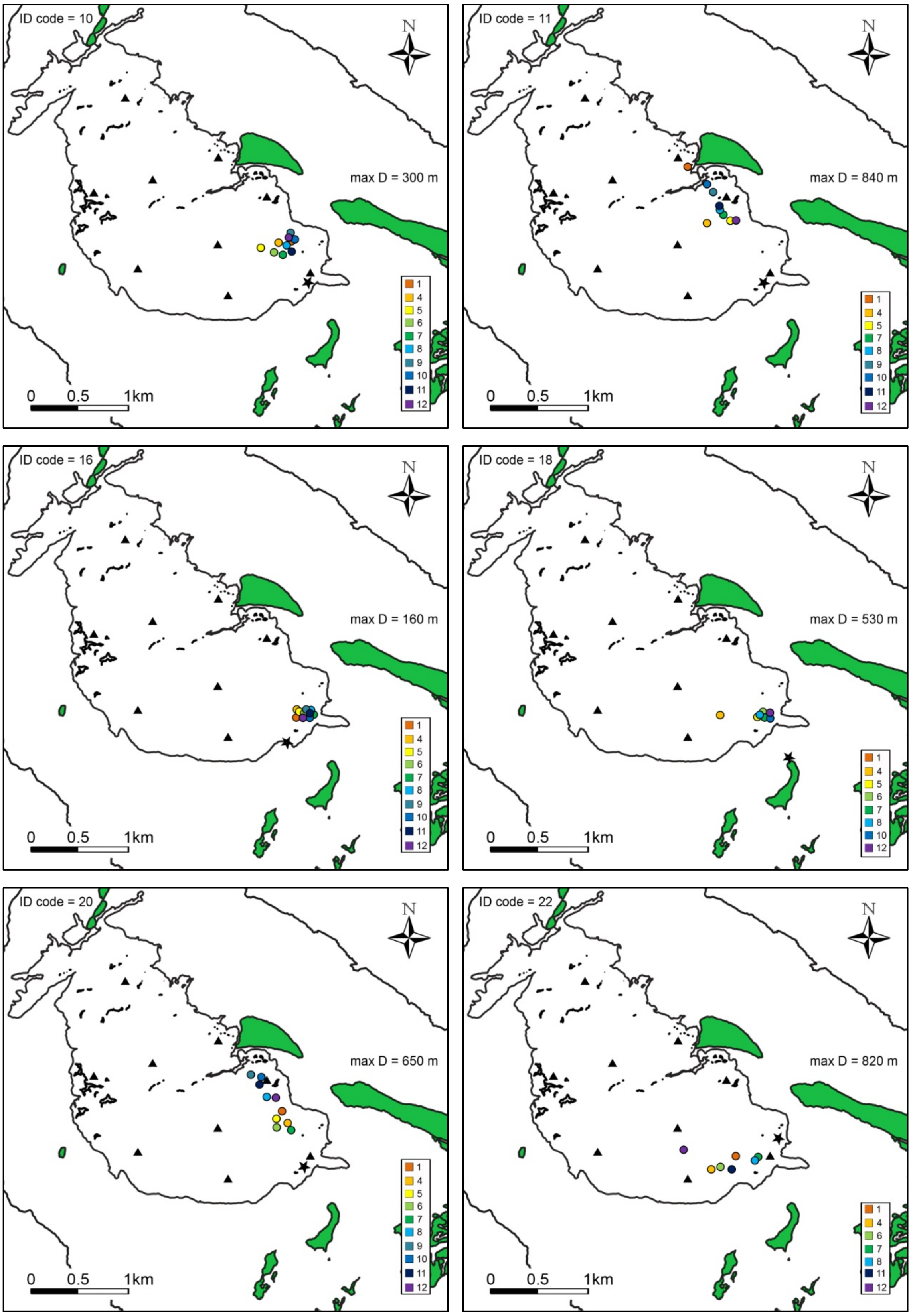

Figure 4.3. Barycentre locations for each study month for 12 acoustically tagged *N. acutidens* inside the lagoon of the St. Joseph Atoll. Colour-coded numerical key identifies each month. Black stars represent tagging locations and black triangles indicate receiver locations.

The density of all barycenters (n = 110) was highest in the south-eastern corner of the atoll lagoon (Fig. 4.4), near the location of receiver number 12.

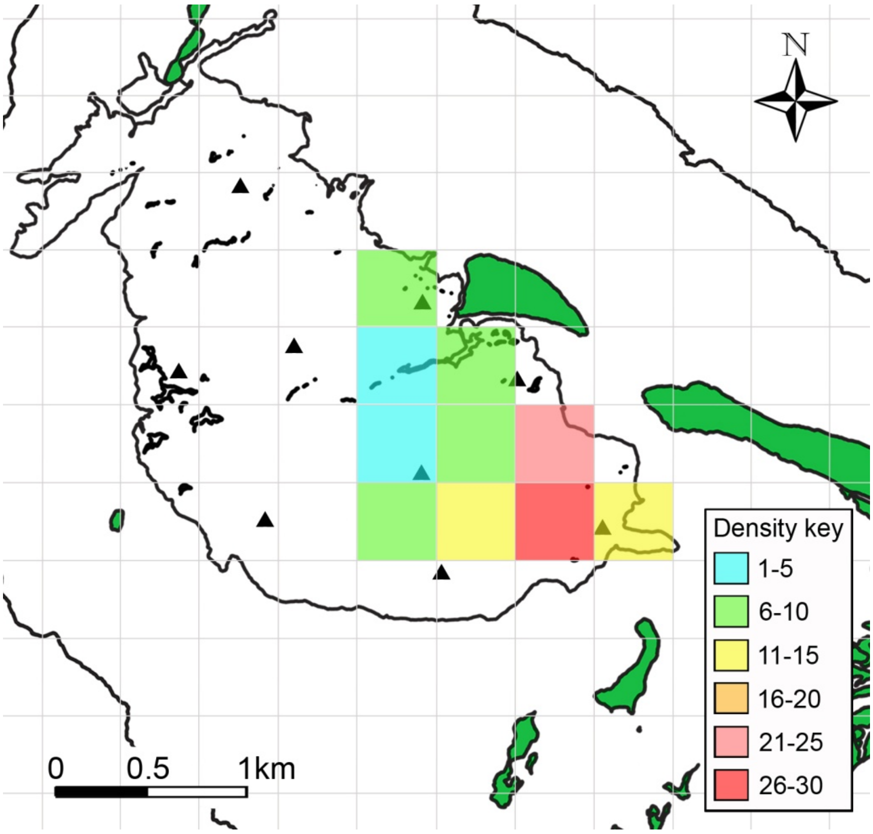

Figure 4.4. Density plot of monthly barycenters (n = 110) calculated for 12 acoustically tagged individual *N. acutidens* in the lagoon of the St. Joseph Atoll.

4.3.2 Site Fidelity

Of the 19 tagged sharks that were present at the outset of the study in October 2009, 15 individuals (79%) were still present at the end of the 12th study month in October 2010. Of the four tagged sharks that were no longer present, one was recaptured (ID code 13) and a second shed its tag (ID code 14). The recapture occurred near Marie-Louise Island at the southern tip of the Amirantes bank, approximately 80 km south of the tagging location inside the St. Joseph's Atoll. This shark, a male, was last detected within the array on 21/02/10 and was reported recaptured during March. It was not released after being caught. ID codes 12 and 7 left the study area on 08/03/2010 and 04/09/2010 respectively and were subsequently never recorded again.

Besides the four sharks mentioned above (7, 12, 13 & 14), all other tagged sharks displayed long-term fidelity to the atoll. They were recorded every month during the one-year study period, with the exception of one individual (ID code 9) that was not recorded during study month 4.

At the day scale more variation was apparent. Ten individuals (ID codes 1, 2, 4, 6, 7, 8, 10, 14, 16, 20) displayed near daily use of the study site while seven others (ID codes 9, 11, 17, 18, 19, 21, 22) displayed less regular patterns with longer undetected periods (Fig. 4.5). Only two of the tagged sharks (ID codes 11 and 18) appeared to change their behaviour during the study, displaying periods of both regular detection and more infrequent detection. These periods appeared to be temporally independent (Fig. 3) with one shark being detected more frequently during the first 200 days and the second more frequently during the last 100 days.

All of the three sharks that appeared to have left the study site before the monitoring period was concluded displayed high degrees of residency up until they departed. Shark number 7 went undetected for only 2 days before departing after 331 days, while ID codes 12 and 13 were undetected for 18 days and 8 days respectively (Fig. 4.5).

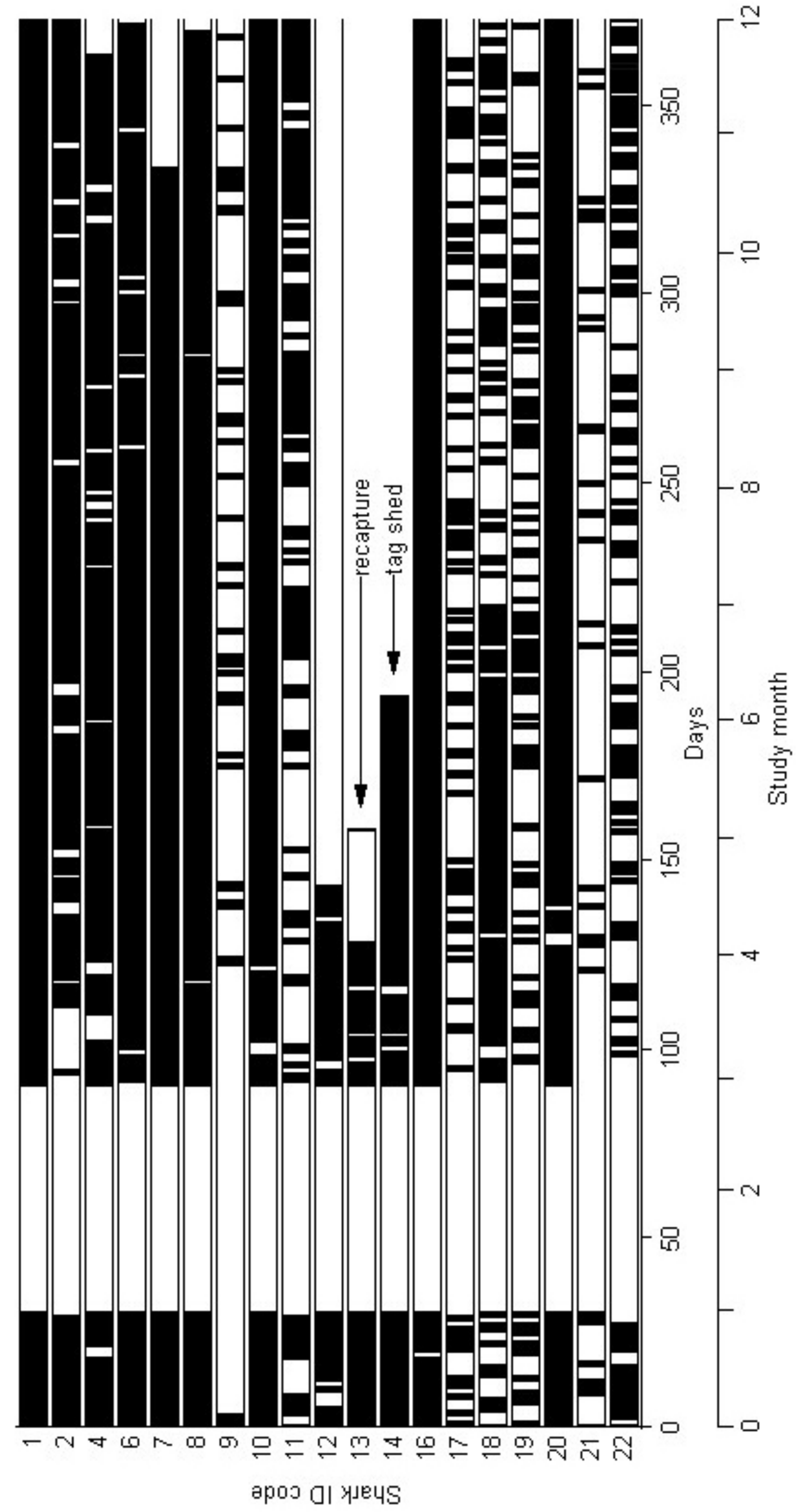

Figure 4.5. Daily presence of acoustically tagged *N. acutidens*, in the St. Josephs Atoll. Black bars represent days when detections occurred while white bars represent no detections.

4.4 Discussion

The findings of this study strongly suggest that the lagoon habitat of the St. Joseph Atoll plays a major role in life history of sub-adult *N. acutidens*. Most tagged sharks were recorded in the atoll lagoon throughout the year. The lack of any seasonality suggests that environmental conditions and the availability of food resources within the atoll are favourable year round. Speed et al. (2011) found that slightly smaller *N. acutidens* were generally more resident during the summer months in a coastal embayment in western Australia. However, they also observed that two individuals utilized the site on a near-daily basis throughout the year. The observed differences between that study and the current results are possibly a reflection of the Australian study site experiencing a more seasonal climate due to its lower latitude. For management purposes it is not necessarily the day scale use that is of critical importance, rather the longer term dependence. Nonetheless, even at this fine scale, the current study also found that the majority of tagged individuals utilized the atoll environment on a near-daily basis throughout the 10 month study. Theoretical ecological models predict that animal turnover rates will decrease with increasing habitat quality (Griffen and Drake, 2008). As such the high degree of site attachment exhibited by many of the individuals in this study suggests the St. Joseph Atoll environment offers prime habitat conditions for the sub-adults of this species.

Only sub-adult sharks were tagged in an attempt to avoid potential behavioural changes due to maturation (Gruber et al., 1988) and mating (Clua et al., 2010) for larger individuals and predator avoidance by smaller juveniles (Wetherbee et al., 2007). Nonetheless it is noteworthy that the largest individual in the study was the first one that appeared to have left the study area. This individual, a female, (ID code 12) was 202 cm TL at the time it was tagged, and would have been approximately 210 cm TL, using the average growth rate reported by Stevens (1984) of 104 mm.month^{-1}, when it left the atoll. Stevens (1984) also reported that both sexes mature at approximately 220 cm TL at Aldabra Atoll, but noted that this figure might be an overestimation as a result of the small sample size in his study. It is therefore possible that this individual attained sexual maturity and moved away from the atoll for mating purposes. Investigations on the allopatric *N. brevirostris* (Gruber et al., 1988) have suggested that as these sharks grow they expand their home range from an initial settlement site within a nursery, until they eventually move out and inhabit deeper reefs with the onset of sexual maturity. If the ontogenetic expansion in space use by *N. acutidens* is similar to that of *N. brevirostris*, the sharks monitored in the current study should represent those approaching the last few years of their residency period in the atoll. Similarly, the entire time that these individuals are dependent on the atoll environment should span from birth until the early stages of maturation. According to the growth rates reported by Stevens (1984) this would equate to between 10 and 12 years, using the size at departure of the largest tagged individual (ID code 12) as the upper size limit. These results further demonstrate the importance of the St. Joseph Atoll in the life history of these sharks.

To date no work has been conducted on female natal homing for either of the *Negaprion* species but investigations into parental genotypes in *N. brevirostris* have revealed that females often utilize the same nursery habitat for parturition in consecutive breeding years (Feldheim et al., 2004). Feldheim et al. (2004) showed that over six years of sampling the number of females utilizing a single island lagoon (Bimini, Bahamas) was limited to 58 individuals, most of which used the lagoon for parturition every two years. Although the reproductive cycle in *N. acutidens* is not well documented, Stevens (1984) reported that about half of the mature females at Aldabra Atoll give birth each year, suggesting that their reproductive cycle may mirror that of *N. brevirostris*. Consequently, it is possible that a small number of females support the *N. acutidens* population at the St. Joseph Atoll.

The minute proportion of detections recorded around the outside the St. Joseph Atoll strongly suggests that the tagged sharks inside the atoll seldom ventured over the reef crest to utilize the outer reef slope. Furthermore the lack of detections around D’Arros Island also provides evidence that immature individuals (i.e. the size class in the current study) do not cross the 70 m deep channel that separates D’Arros Island from the St. Joseph Atoll. Conversely, as more than 99.9% of the detections were recorded on a similar number of receivers inside the atoll’s lagoon, the critical importance of this protected environment is emphasised. Stevens (1984) reported recapturing many conventionally tagged *N. acutidens* from Aldabra Atoll, most of which were recaptured during the same year, however, two long-term recaptures were also made, which occurred 1426 days later. It is important to note that Aldabra Atoll is isolated, surrounded by water thousands of meters deep. Coastal sharks are generally recognised to be limited in their movements by the 200 m isobath on the edge of continental shelves (Shultz et al., 2008), which would suggests that *N. acutidens* inhabiting an atoll such as Aldabra are unlikely to ever leave. Conversely, the St. Joseph Atoll is located on the Amirantes bank, which offers 3220 km^2 of demersal habitat less than 40 m deep. Despite this, the individuals in this study preferred the shallow atoll environment over this vast expanse of potential habitat. The recapture of shark ID code 14 at the southern end of the Amirantes bank indicates that these sharks are capable of undertaking large movement and do make use of deeper habitats at times.

Within the lagoon the observed significant differences in detection proportions among the various receivers clearly indicated an area of increased occurrence of tagged sharks. Furthermore, results from the detailed area-based analysis also demonstrated that the tagged sharks typically utilize restricted areas of the lagoon, when they are within this habitat. Individuals appeared to be highly attached to relatively limited areas throughout the many months of observation. This result is highlighted by the small maximum distances between extreme barycenters (D), which were between 4 - 24% of the length of the entire lagoon. Stevens (1984) found that 54% of recaptures made on conventionally tagged *N. acutidens* from Aldabra Atoll occurred at the tagging site while 91% occurred within 2 km of the tagging site, also suggesting highly restricted movements.

Little evidence was found to suggest temporal grouping of individuals within the atoll at any given time. Rather the distribution of monthly barycenters appeared to reflect individual area selection, which showed little variation of time. Although each individual displayed unique spatial patterns the combination of all individual barycenters across all months revealed a strong preference towards the south-eastern portion of the lagoon, corroborating the finding from the detection distribution analysis. The combination of these results indicates a favoured high-use area in this region of the lagoon. It could be argued that this pattern is purely a reflection of the tagging location of the studied individuals, however, it is important to note that one quarter of the analysed sharks were tagged far (a factor of 0.7 – 3.4 times D) from their respective nearest barycenter, which reflects a certain degree of spatial preference. Papastamatiou et al. (2010) reported significantly higher proportions of detections of acoustically tagged blacktip reef sharks, *Carcharhinus melanopterus*, in the Palmyra Atoll, on receivers in close proximity to coral ledges, where prey abundance was recognized to be higher. It is possible that a similar situation occurs in the current study, where the distribution of sharks reflects the availability of prey. Similarly this may also be an indirect reflection of prey distribution, where *N. acutidens* utilize the deeper lagoon as a resting area following feeding forays onto the adjacent sand flats. As no quantification of prey abundance or activity patterns was conducted during this study it is only possible to hypothesis the existence of such relationships, and suggest further investigations in this direction in future.

As barycenters are average positions based on detections recorded by stationary receivers it is important to remember that these do not directly represent the movements of the tagged individuals. However, since the probability of detection was assumed to be equal for each receiver and the receivers were spread homogeneously around the lagoon, these average positions are likely to closely represent broad scale area use. It is still possible and probable that some individuals ranged wider within the lagoon than their cluster of barycenters suggest however, if the regularity of such excursions was high they would be expected to be visible in the distribution of barycenters.

Seven individuals were not included in the assessment of area use due to data deficiency. Three of these were ruled out as they were not present within the study site for long enough, while the other four were recorded too few times during each month. There are two possible explanations for this result. Firstly these individuals may have had large home ranges of which the lagoon formed only a minor part, or they too utilized small areas, as with the other analysed individuals, which just happened to fall outside of the receiver array. Based on the results presented here, the second hypothesis seems more likely, although some degree of individual variation is to be expected.

Finally, the findings of this study suggest that the protection of the entire atoll environment would provide an effective conservation measure for the *N acutidens* population of St. Joseph Atoll. However, the identification of a single high use area in the south-east portion of the lagoon suggests that partial closure may also be an adequate solution. Currently the St. Joseph Atoll is most often frequented by recreational fly-fishermen, targeting various teleost species in a voluntary catch-and-release fishery. The proposition of a no-access zone in the south-eastern region of the atoll could potentially provide *N. acutidens* with an undisturbed sanctuary while simultaneously reducing the interactions between such fly-fishermen and the sharks. Nonetheless, irrespective of detail of the approach adopted, the high degree of dependence on the atoll environment that the studied individuals displayed unquestionably illustrates the need for some area protection.

CHAPTER 5 - MOVEMENT PATTERNS LINKED TO NATURAL RHYTHMIC CYCLES

SUMMARY

Questions: Sicklefin lemons sharks are known to occur in the atoll's lagoon and are also regularly observed on the surrounding shallow flats. Do these sharks have core areas on the flats similar to those observed in the lagoon (Chapter 4)? Do they use both habitats on a daily basis and is this linked to natural rhythmic cycles?

Hypotheses:

i) *N. acutidens* display diel behavioural patterns between the use of the flats and the lagoon.

ii) *N. acutidens* use of the flats and the lagoon is linked to tidal fluctuations.

iii) Individual core areas on the flats and in the lagoon are in close proximity.

Methods: Two acoustic receiver arrays (one on the flats and one in the lagoon) were used to monitor the movements of 19 tagged sharks between these two habitats for 67 days. The spatial distribution of detections was assessed in relation to time and tidal height as well as to the interaction between these two non-synchronous cyclic variables.

Conclusions: Sub-adult *N. acutidens* used the flats most often during high tides at night or in the early morning and the lagoon mostly during low tides at any time of the day. Individuals showed a strong propensity to use areas on the flats that were close to the areas they typically used in the lagoon.

5.1 Introduction

Apex predators such as sharks are known to regulate community structures and effect community dynamics both directly, through top-down predation effects (Bascompte et al., 2005), and indirectly, through non-lethal interactions (Heithaus et al., 2007). The relative influence of both these factors depends directly on the movement patterns, area usage and habitat selection of the sharks (Speed et al., 2010). Developing a detailed understanding of the short-term movement behaviour and habitat selection as well as the factors that influence these patterns is thus fundamental to the understanding of how sharks shape and influence local ecosystems. Similarly, by understanding these factors and patterns, management decisions regarding essential habitats can be correctly informed. This is of particular significance for tropical reef associated shark species as both overfishing and climate change increasingly threaten the few remaining healthy populations (Graham et al., 2010).

A large number of studies have investigated the day-scale movement patterns of elasmobranch species to assess how they utilise their environments. Typically, sharks display diel behaviour. This has been witnessed in the form of range expansions (Ortega et al., 2009), increased movement rates (McKibben and Nelson, 1986; Ackerman et al., 2000; Ortega et al., 2009) or movements between habitat types (Tricas et al., 1981; Holland et al., 1993; Ackerman et al., 2000; Sundstrom et al., 2001; Heupel et al., 2010; Speed et al., 2011). Generally increases in nocturnal activity have been attributed to foraging behaviour (McKibben and Nelson, 1986; Holland et al., 1993; Ackerman et al., 2000; Sundstrom et al., 2001; Barnett et al., 2010).

In shallow coastal environments such as estuaries, bays, lagoons and atolls, tidal currents have also been recognized to have significant influence on the movement of elasmobranchs (Huish and Benedict, 1977; Medved and Marshall, 1983; Economakis and Lobel, 1998; Ackerman et al., 2000; Rechisky and Wetherbee, 2003; Wetherbee et al., 2007; Papastamatiou et al., 2009). Generally where environments included habitats such as shallow sand or mud flats, sharks have been found to move onto the flats during high tides (Economakis and Lobel, 1998; Ackerman et al., 2000; Wetherbee et al., 2007; Papastamatiou et al., 2009). These movements have also often been attributed to foraging behaviour (Nelson and Johnson, 1980; Wetherbee et al., 2007) but also as a means of predator avoidance (Morrissey and Gruber, 1993b; Wetherbee et al., 2007;

Papastamatiou et al., 2011) or for thermoregulation (Economakis and Lobel, 1998; Hight and Lowe, 2007). In light of these findings it is surprising that the behavioural responses of coastal elasmobranchs to the interactions between tidal fluctuations and the diel cycle have not yet been investigated.

The sicklefin lemon shark, *N. acutidens*, is one of the two shark species that dominate the St. Joseph Atoll in the Seychelles (von Brandis, 2009). This species is an excellent candidate for developing an understanding of the interactions between these two variables. *N. acutidens* is known to inhabit atolls similar to St. Joseph for several years from the time of birth (Stevens, 1984) and within the St. Joseph Atoll are often seen on the shallow sand flats surrounding the central lagoon (J. Filmalter, pers. obs.). Visual observations suggest that the shallow flats may represent an important feeding habitat for the sharks in this study. As such the overall objective of this chapter was to investigate the day-scale spatial dynamics of *N. acutidens* within the St. Joseph Atoll, in relation to natural cycles. More specifically the principle objectives of this study were to:

- Assess whether *N. acutidens* exhibited diel movements between the flats and the lagoon to test the hypothesis that this species displays diel behavioural patterns similar to those observed in other elasmobranch species.
- Assess the influence of tidal fluctuations on the movement of *N. acutidens* between the flats and the lagoon in order to test the hypothesis that tidal height influences the sharks' use of these two habitat types.
- Identify individual core areas on the flats and in the lagoon in order to test the hypothesis that these areas are in close proximity to each other.

In this chapter, data from 19 of the 22 *N. acutidens* equipped with acoustic transmitters (see Chapter 2) collected during study period 4 (see Chapter 3) were used to address these objectives. This study period lasted 67 days and incorporated two acoustic arrays (on the sand flats and in the lagoon).

5.2 Materials and Methods

5.2.1 The acoustic arrays

A detailed description of both the deployment methods and the location of the lagoon and flats acoustic receiver arrays are provided in Chapters 2 and 3 however the locations of the receivers on the flats are indicated in Fig. 5.1 for reference.

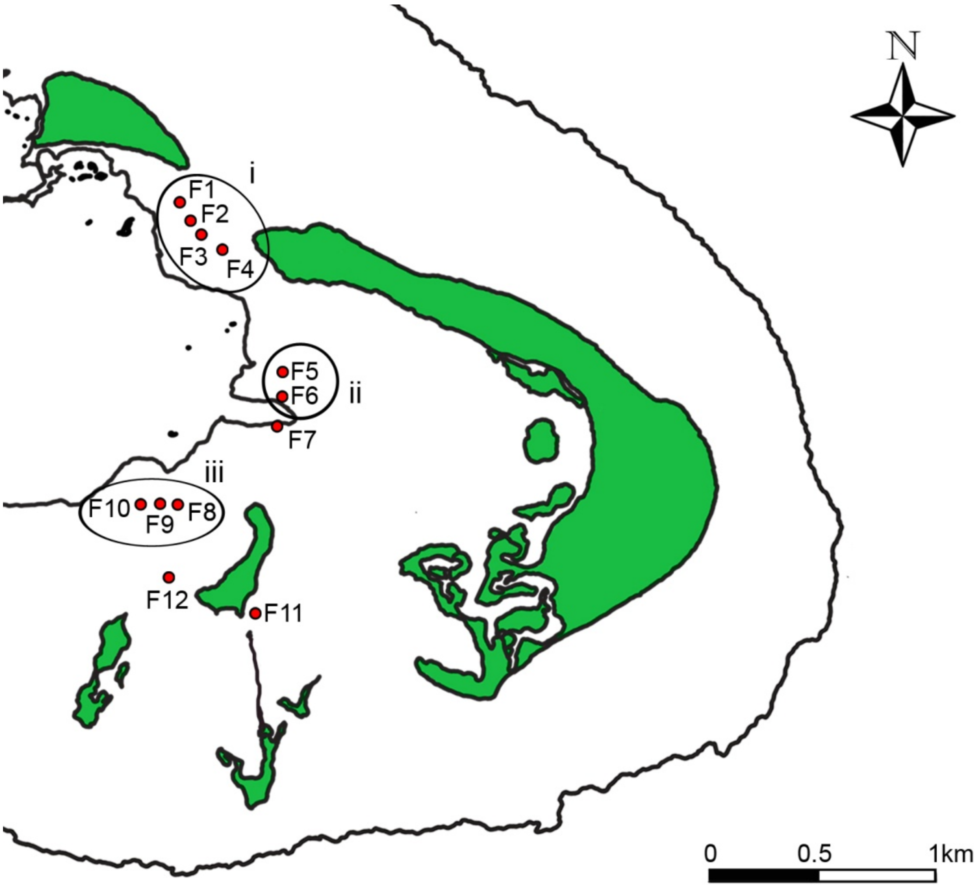

Figure 5.1. Location of the 12 acoustic receivers deployed on the eastern flats of the St. Joseph Atoll. Circled receivers indicate groups i, ii and iii used in habitat use analysis, see text for details.

5.2.2 Data Analysis

After a preliminary review of the detections recorded by each receiver located on the flats it was apparent that only receiver F7 recorded detections at all times of the day. F7 was located on the edge of a long channel that funnelled off the flats, and as both the data and later visual observation suggested, sharks were able to access this channel even during the lowest tides. Consequently it was impossible to determine whether the detections were recorded from tagged sharks in the channel, in the lagoon (at the mouth of the channel) or on the sand flat itself. As a precautionary measure the data from this receiver were excluded from all analyses.

5.2.3 Circadian effects

To investigate diel behaviour data from the receivers on the flats and those in the lagoon were analysed independently and were treated as follows:

> Firstly the percentage of detections recorded during each hour of the day for each individual from all receivers on a) the flats and b) the lagoon were calculated.
>
> Secondly the average hourly percentage of detection for all individuals (n = 19) was calculated across all individuals separately for the two receiver arrays.

This allowed for a comparison of the temporal trends in detections between the flats and lagoon arrays.

5.2.4 Effect of tide

Tidal movements between the sand flats and the lagoon were assessed by comparing the corresponding tidal height at the time that each detection was recorded on every receiver for both the flats and lagoon arrays. Tidal data were obtained from the Service Hydrographique et Océanographique de la Marine (SHOM), France. The data provided information on tidal height at the study site at 10 minute intervals for the duration of the study period. Tidal height data were arranged into 19 bins of 10 cm. The average daily detection percentage was calculated for each bin for the flats and lagoon arrays independently. Individual averages were combined to obtain sample means and standard deviations for each bin.

5.2.5 Interactions between circadian and tidal effects

After analysing the effects of time and tide independently it was apparent that further investigation was required to understand how these two non-synchronous rhythmic variables interact and concurrently influence the sharks’ movements. The first step in this investigation was to understand the relationship between time and tidal height. Such information was necessary to understand the times of occurrence and frequencies of different tidal heights during the study period. Although the study period covered more than one complete lunar cycle, knowing the time of day at which the largest tides occurred was imperative for the understanding of when the sharks could access the flats. To assess the distribution of tidal data both temporally and in magnitude it was necessary to assign the data into hourly bins for the temporal component and 10 cm bins for the height component. These data were then used to generate a cross-table, where the frequency of tidal heights that occurred during the 67 day study period was calculated for each corresponding pair of time and height bins using the ’ftable’ function in the R software package. This resultant frequency is from here on referred to as the time and tidal height frequency (TTHF). This cross-table was then represented graphically using a density plot generated with the ‘table.value’ function available in the *ade4* package in R.

After assessing the distribution of the TTHF the same analysis was carried out on the tidal data that had been assigned to each detection, here on referred to as the detection tidal height frequency (DTHF). The information gained from the assessment of the TTHF showed that it was necessary to standardise the observed DTHF by the TTHF as the TTHF was not homogenously distributed. Essentially this standardisation was analogous to the catch per unit effort (CPUE) index commonly used in fisheries management. Here the ‘catch’ is represented by the number of detections per hourly bin while the ‘effort’ is represented by the frequency of the various tidal heights across the hourly bins. Following this logic the standardisation was carried out by dividing the cross table of DTHF (for all detections) by the cross table of TTHF. This produced a standardized matrix consisting of the frequency of detections per frequency of different tidal heights. This matrix initially appears to have complex units as it represents one frequency divided by another (numbers of detections per tidal height bin per hour divided by the number of tidal heights per height bin per hour), which is equivalent to the number of detections weighted by each tidal height occurrence. Following this standardization the resultant standardized matrix was separated into its two principle components, (i) the frequency from detections on the flats and (ii) the frequency from detections in the lagoon.

After standardisation the frequency tables for the lagoon and flats data were statistically assessed. The data sets were assessed along both the tidal height and temporal axes using two sample t-tests. The tidal height axis was divided around the median tidal height observed during the study period. This allowed for comparison of the number of detections recorded in the lagoon and on the flats at higher and lower tides. The temporal axis was divided at 9h00 and 21h00 as this allowed for the separation and comparison of the number of detections recorded during the observed morning and evening peaks in tidal height.

5.2.4 Lagoon vs. sand flats habitat use

Short term spatial distribution between the two adjacent habitat types (lagoon and sand flats) was assessed by comparing the distances between each tagged individual's mean barycenter in the lagoon and the central point of each group of flats receivers. Barycenters were calculated using data from the nine receivers in the lagoon as described in Chapter 4, however, only data recorded during study period 4 (see Chapter 3) were considered for this calculation. Similarly, for the flats array, only data from receivers near the edge of the flats were used for this analysis. This was necessary as the two receivers (F 11 and F 12) located further back on the flats did not allow for fair comparison between each of the three major areas of sand flats. The receivers were arranged in three groups; i) F1, F2, F3, F4; ii) F5, F6 and iii) F8, F9, F10, corresponding to the three areas where they were moored on the sand flats (Fig. 5.1). For each shark the number of detections per receiver group was calculated and then standardized by the number of receivers in the group resulting in an average number of detections per receiver for each of the three groups. The distance between the barycenter in the lagoon and each group of flats receivers was then compared to the percentage of detections for each receiver group. Only sharks that had more than 50 detections recorded on the flats during the study period were considered. A shark was considered to show site fidelity if the shortest distance between the barycenter and the group of receivers corresponded to the group with the highest standardized detection percentage. Site fidelity was also only considered valid if one group of receiver recorded at least 50% of the standardized detections. Using this criterion a primary group of flats receivers was allocated to each individual.

5.3 Results

Large numbers of detections were recorded by the receivers deployed on the sand flats (Table 5.1). In total 20 of the 22 sharks tagged were detected by the flats array. The remaining two sharks (ID codes 3 and 5) had left the lagoon prior to the first deployment of the flats array. One of the 20 sharks (ID code 15) was only detected twice by the lagoon array during the entire study period and could therefore not be included in the comparative analyses.

Table 5.1. Summary of detections from *N. acutidens* (n = 19) recorded on the various acoustic receivers located on the flats of the St. Joseph atoll during the 56 day study period.

Receiver number	**F1**	**F2**	**F3**	**F4**	**F5**	**F6**	**F8**	**F9**	**F10**	**F11**	**F12**
Total number of detections	876	466	867	264	520	1008	1043	333	747	450	2644
Total number of sharks	16	14	15	12	18	18	14	14	15	11	15

5.3.1 Diel patterns

There were distinct differences between the time at which the sharks were detected on the flats and in the lagoon. Detections recorded on the flats showed a strong bimodal distribution with peaks occurring around 04h00 and 18h00 – 19h00. A distinct drop in detections occurred between 09:00 h and 14:00 h. Detections recorded in the lagoon also showed a bimodal distribution, however it was more asymmetrical than that of the flats. A strong peak in lagoon detections occurred around 11h00 with a weaker peak occurring around 22h00 (see Fig. 5.2).

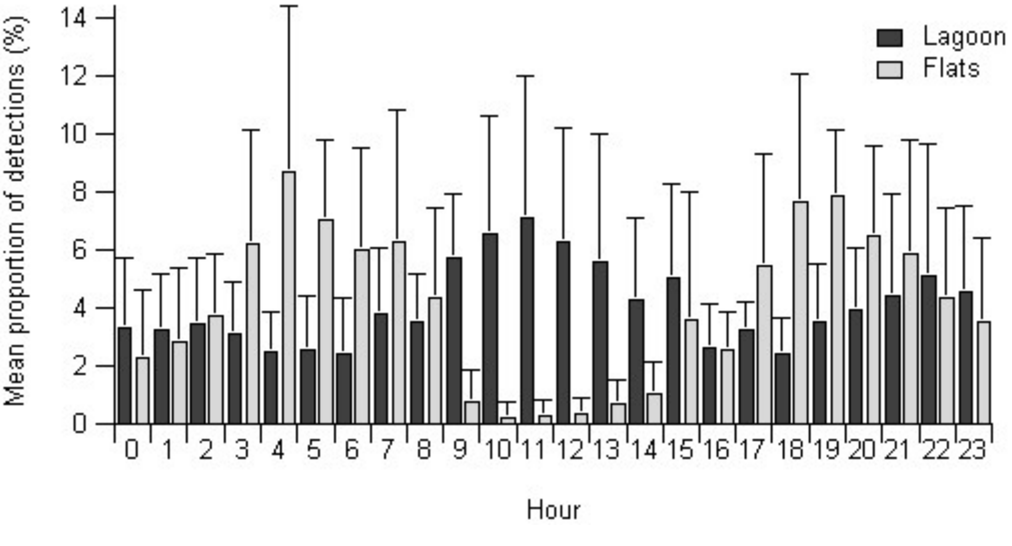

Figure 5.2. Distribution of the mean hourly proportion of detections of all tagged *N. acutidens* recorded by the lagoon and flats acoutic receiver arrays. Error bars show standard deviations.

Using the approximate times of the ephemeral periods as 06h00 and 18h00 an assessment of the total number of detections recorded during daylight and dark hours for the two habitat types showed that significantly more detections were recorded on the flats at night than during the day (t-test, $p < 0.001$, d.f. = 5) while significantly more detection were recorded in the lagoon during the day than at night (t-test, $p = 0.008$, d.f. = 5) (Fig. 5.3).

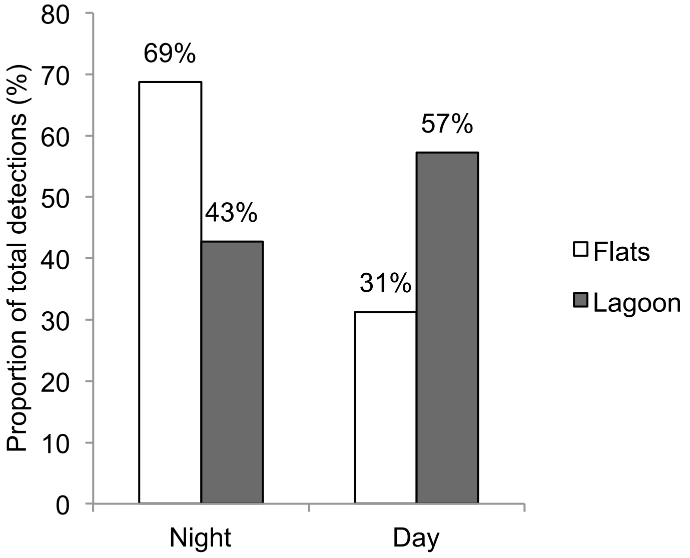

Figure 5.3. Diel changes in mean detection percentages recorded by receivers on the sand flats and in the lagoon for sicklefin lemon sharks *N. acutidens* in the St. Joseph Atoll.

5.3.2 Tidal patterns

The proportion of detections relative to tidal height showed clear differences between the two arrays. Detections recorded in the lagoon were typically associated with lower tidal heights (mean = 77 cm, SD = 32 cm) whilst those recorded on the flats tended to occur at higher tides (mean = 120 cm, SD = 39 cm). This trend was observed for all individuals however some variation was observed (Fig. 5.4).

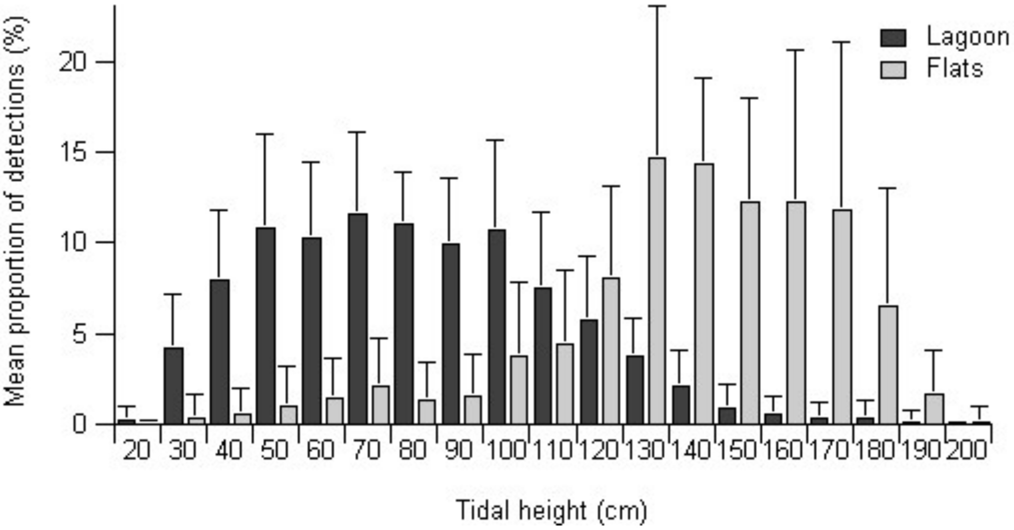

Figure 5.4. Distribution of the mean proportion (%) of detections of all tagged sharks recorded on acoustic receivers arrays inside the lagoon and on the sand flats relative to tidal height. Error bars represent standard deviations.

5.3.3 Tidal vs. diel patterns

i) Tidal data

Bi-factoral assessment of the temporal distribution of tidal heights that occurred over the 67-day study period (TTHF) revealed that the tides with the highest amplitudes (> 180 cm) commonly occurred between 04h00 – 06h00 and 16h00 – 18h00, while tides with the lowest amplitude (< 30 cm) typically occurred between 10h00 – 14h00 and 22h00 – 01h00 (Fig. 5.5). Higher tides were also found to occur more frequently in the evening than in the morning (Fig 5.5).

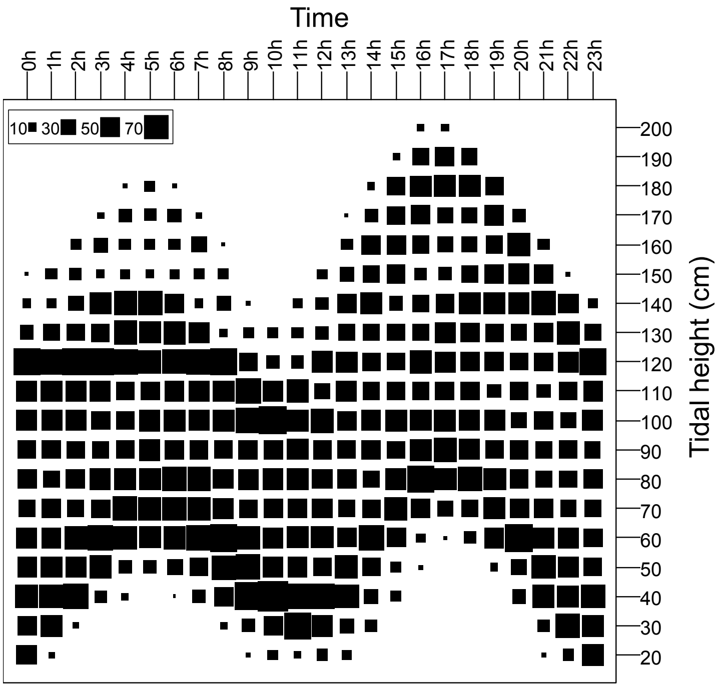

Figure 5.5. Bi-factoral density distribution of time and tidal height frequency (TTHF), from actual tidal heights observed over the 67 day study period. Scale indicates the number of tidal observation per block size.

ii) Shark detections

The distribution of detections from the flats and the lagoon were found to be very different. Tagged sharks were found to utilise the flats with higher tides (> 120 cm) (Fig. 5.6a). A Welch two sample t-test revealed a significant difference ($p = 0.031$, d.f. = 7.63) in the number of detections above and below the median tidal value of 90 cm. Along with this tidal response, a strong temporal relationship was also visible from the density plot in Fig. 5.6a. As both peaks in tidal heights occurred over the dawn and dusk periods the most appropriate temporal division of the two tidal cycles was 09h00 and 21h00. This allowed for the comparison of the two cycles each containing high tide peaks. Using this division tagged sharks were found to use the flats significantly more during morning high tides (two sample t-test, $p = 0.003$, d.f. = 19.34) compared to evening high tides.

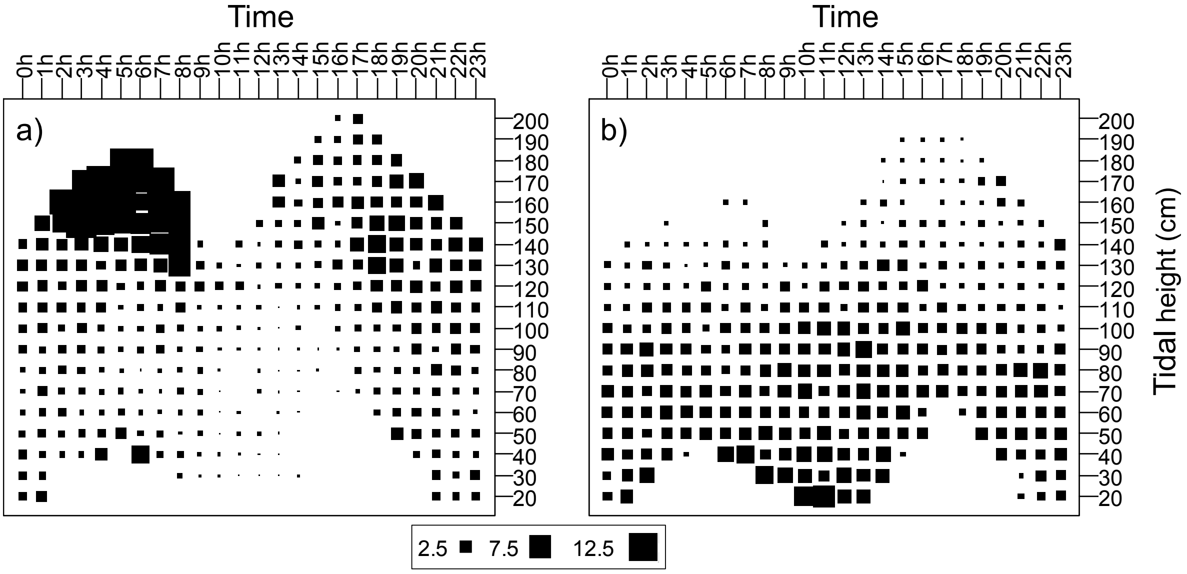

Figure 5.6. Bi-factoral density plots of tidal and detection data (DTHF) from sicklefin lemon sharks *N. acutidens* tagged with acoustic transmitters, a) shows the distribution for detections weighted by the occurrence of tidal heights recorded on the flats receiver array while b) shows the distribution for detections weighted by the occurrence of tidal height recorded on the lagoon array.

The presence of tagged sharks in the lagoon was also found to be strongly linked to tidal height, see Fig. 5.6b. Significantly more detections were recorded during tides lower than the median value of 90 cm (two sample t-test, $p < 0.001$, d.f. =16.56). Tagged sharks showed no apparent response to the time of day from lagoon detections. Moreover, no significant difference was found (two sample t-test, $p = 0.256$, d.f. = 14.76) when the distribution was divided at 09h00 and 21h00 as applied to the flats data.

5.3.4 Spatial correlation between habitats

A total of 16 sharks had more than 50 detections recorded on the flats and were thus included in the spatial correlation analysis. Of these, 10 individuals (62.5%) were found to have lagoon barycenters closest to their primary area utilised on the flats (i.e. where more than 50% of their standardized detections were recorded). Only four individuals (Sharks 1, 7, 12 and 18) had their lagoon barycenters closer to a group of flats receivers other than their primary group. However, the difference in the distance between the primary receiver group and the nearest receiver group was typically small (range: 14 – 22% further).

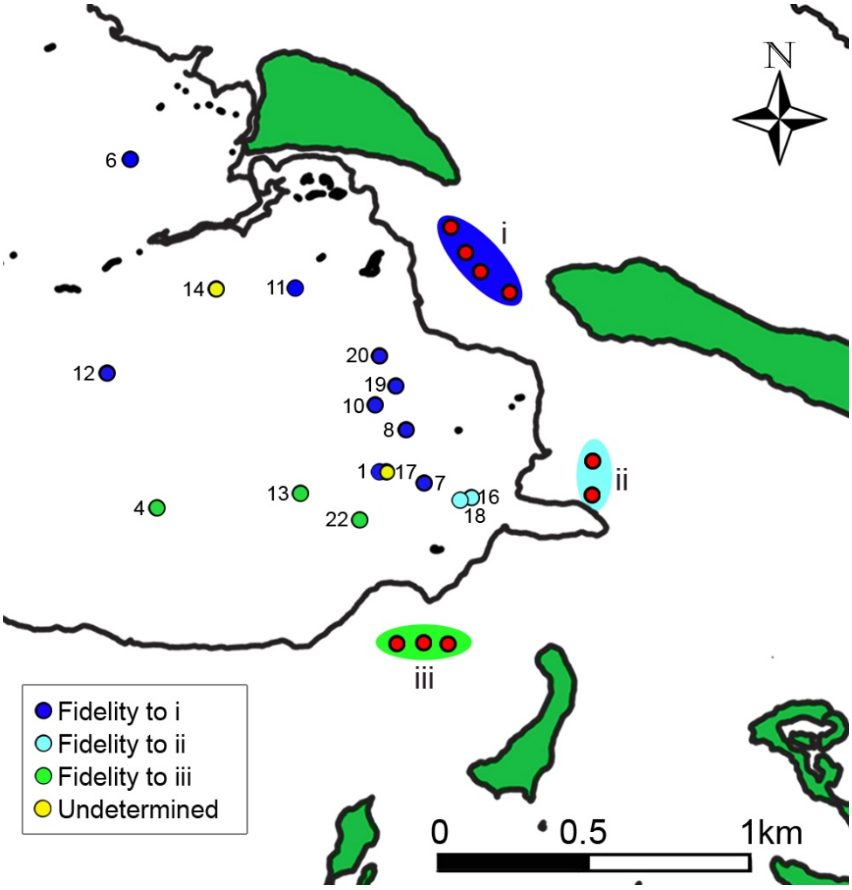

Figure 5.7. The south eastern portion of the St Joseph Atoll showing receiver groups (i, ii and iii) (red circles encircled in different colours) on the sand flats. Individual lagoon barycenters are indicated by coloured circles, for 16 tagged *Negaprion acutidens*. Fidelity is indicated through colour coding between barycenter and flats receiver group.

Most sharks (87.5%, n = 14) utilised a specific area (linked to a group of receivers) on the sand flats (Fig. 5.7). Of these 14 sharks, 10 individuals had more than 75% of their detections recorded on a single group of flats receivers (Table 5.2), suggestive of restricted movements and strong site attachments between areas on the sand flats and adjacent lagoon.

Table 5.2 Standardized detection percentages and distances between lagoon barycenters and the three groups of flats receivers (i, ii and iii) for tagged *N. acutidens*, in the St. Joseph Atoll. *No preference shown.

Shark ID code	**Standardized percentage of detections**			**Distance between barycenter and flats groups (m)**		
	i	**ii**	**iii**	**i**	**ii**	**iii**
1	13.8	**86.2**	0.0	722	**661**	543
4	0.0	11.4	**88.6**	1279	1370	**919**
6	**73.0**	27.0	0.0	**1125**	1764	1765
7	12.2	**84.9**	2.9	720	**627**	530
8	**75.0**	24.0	1.0	**568**	586	664
10	**56.0**	39.5	4.5	**544**	703	748
11	**81.7**	18.3	0.0	**556**	1102	1174
12	7.6	**69.7**	22.7	1203	**1558**	1290
13	0.0	34.3	**65.7**	901	900	**584**
14*	32.1	29.8	38.1	808	1320	1276
16	1.1	**64.1**	34.8	750	**358**	485
17*	10.8	40.5	48.6	714	506	493
18	0.0	9.4	**90.6**	760	395	**460**
19	**71.8**	28.2	0.0	**456**	664	802
20	**76.4**	22.8	0.8	**410**	754	898
22	0.0	1.3	**98.7**	888	727	**409**

5.4 Discussion

The importance of the sand flats as a habitat type for *N. acutidens* in the St. Joseph Atoll was confirmed by the fact that all of the tagged sharks, considered to be present in the atoll at the time the receivers were deployed, were detected.

5.4.1 Diel patterns

There was a strong relationship between the time of day and when the tagged sharks utilised the adjacent lagoon and sand flats habitats. The general trend suggests that sharks primarily utilised the flats during the early morning and late afternoon/evening and moved into the deeper lagoon during midday. A secondary peak in lagoon use occurred prior to midnight. Sharks were also detected more consistently throughout the diel cycle in the lagoon than on the sand flats, suggesting that individuals do not always leave the lagoon. The principle hypothesis for explaining the sharks' use of the flats is that they utilise this area for feeding. Not only is the density of prey items likely to be higher on the flats but also the shallow water essentially removes a dimension, potentially making the process of prey capture far simpler. White et al. (2004) found that the diet of *N. acutidens* from Shark Bay, Western Australia, consisted primarily of teleost species, however they noted that the three largest individuals in their sample (> 120 cm TL) had also ingested batoid species. Campagno (1984) also reported dasyatid and teleost species in the diet of *N. acutidens*. Several species of teleost and batoids are known to be abundant on the sand flats of St. Joseph including Mugilid species as well as large numbers of *Albula vulpes*, *Pastinachus sephen* and *Urogymnus asperrimus* (von Brandis, 2009). Targeting such species at night is likely to present the sharks with several advantages. Increased nocturnal activity related to feeding has been suggested for many shark species in the past (McKibben and Nelson, 1986; Holland et al., 1993; Ackerman et al., 2000; Sundstrom et al., 2001). The principle benefit of nocturnal or crepuscular feeding is that the sharks are less conspicuous to prey and are likely to have a further advantage through the detection of prey using their electroreceptive abilities (see Tricas and Sisneros, 2004). Furthermore, several coastal shark species have been shown to have improved visual acuity under scotopic conditions (McComb et al., 2010).

The only other detailed study on the movement of *N. acutidens* using acoustic telemetry, conducted by Speed et al. (2011) in Western Australia also found a strong diel pattern in the movements of this species into a shallow coastal embayment. In contrast to the current study, Speed et al. (2011) observed a peak in *N. acutidens*' use of a shallow embayment around 10h00, while the sharks were most often absent between 18h00 and 22h00. These authors suggested that larger individuals may move out of the bay at night to forage in the adjacent lagoon. Although the habitat types differ between the two studies (a coastal bay and an isolated atoll) this result suggests that local conditions play an important role in the patterns of habitat utilisation for this species.

5.4.2 Tidal patterns

The tidal patterns influenced the distribution of tagged sharks in the atoll with individuals using the sand flats more regularly at greater tidal heights and the lagoon more often during lower tides. Interestingly most sharks were observed on the flats in the middle of the high tide range and in the lagoon in the middle of the low tide range (Fig. 5.5). The primary explanation for such mid-range peaks, as opposed to high and low tide peaks, is the lower frequency at which the extreme high and low tides occurred during the study period. Ackerman et al. (2000) also observed such tide related movements when examining the behaviour of leopard sharks, *Triakis semifasciata*, in a coastal embayment with extensive mud flats. These sharks typically used the mud flats at higher tides and the deeper central bay during lower tides. In the current study these findings suggested that, not only were the movements of the sharks closely tied to the diel cycle as described above, but were also driven by the height of the tide. To understand how these non-synchronous cyclic variables simultaneously influenced the sharks' movements it was essential to understand if and how the factors themselves, were related.

5.4.3 Interactions of time and tide on movements

The tidal regime at the St. Joseph Atoll was found to show a high degree of regularity during the study period. The time of day at which monthly tidal maxima and minima occurred was fairly constant. During the study period the largest tides always occurred in the morning and evening and never over the midday period. Notably the occurrence of large tides in the morning was far less frequent than in the evening. With this information, the results from the independent analyses of time and tidal height are easily explained. Sharks appear to be utilizing the flats at higher tides, which only occur during the morning and evening. During midday and midnight the lower tides appear to force the sharks off the flats and into the lagoon. However, separate analysis of the lagoon and flats detections relative to both time and tidal height revealed further details that would otherwise have gone unnoticed. From the lagoon detections it was clear that tidal height was the primary factor driving the sharks into the lagoon. This bi-factoral approach also revealed that there was, in fact, very little temporal influence on the use of the lagoon, a result not clearly revealed by the independent diel analysis. Following the same approach, the movements of sharks onto the flats appeared to be more complex. Not only was there a clear tidal component influencing movements, but a temporal aspect was also apparent. The higher proportion of detections recorded during the morning high tide suggests that a third factor is likely to influence the sharks' movements. The magnitude of this difference is further enhanced when the lower frequency of morning high tides is considered. Not only does this suggest a diel rhythm in the occurrence of the additional factor, but also illustrates that, whatever the reason for the sharks using the flats, conditions for doing so are far more favourable in the early morning. A notable result of this analytical approach is that the correlation of only two variables cannot always be used to correctly infer causality, or dismiss the influence of co-occurring factors. Heupel et al (2010) suggested that, due to a consistently observed diel shift in activity space, juvenile bull sharks, *C. leucas*, in a Florida estuary, were not responding to tidal fluctuations. The same result could have been concluded in the current study were it not for the bi-factoral analysis, which in fact lead to the exposure of at least one additional undetermined variable.

Although the nocturnal foraging hypothesis explains the clear diel pattern of detections on the flats it still does not clearly explain the observed discrepancy in the distribution of detections weighted by tidal occurrence between the two peaks in higher tides. Both peaks occurred close to the crepuscular periods, suggesting that in both cases there would have been some point at which the sharks would have been able to utilise the flats during the hours of darkness, be that pre-dawn or post-dusk. Rogers et al. (1984) suggested that peaks in the activity of predators should correlate well with the period when biological and environmental factors are optimal for prey capture. Although more detections does not necessarily imply greater feeding activity *per se*, the frequency of occurrence of individuals on the flats was certainly likely to be higher. Following this logic and the hypothesis that sharks utilise the flats for foraging, it would appear that the additional factor dictates the degree of optimality for prey exploitation. One potential factor that may explain this discrepancy and that could have a direct impact on the foraging behaviour of the sharks is the temperature of the water on the sand flats. Throughout the day the water temperature on the sand flats increases due to the intense solar radiation common in the tropics. By the late afternoon this water can be several degrees warmer than the water in the adjacent lagoon (up to 36 °C, which may be 8 °C warmer than the lagoon waters at times, unpublished data). Papastamatiou et al. (2007) investigated the effects of temperature on digestion in captive blacktip reef sharks *Carcharhinus melanopterus*. They hypothesised that sharks may prefer to feed when temperatures are lower as the natural delay in gastric motility following feeding events would relate to the optimization of digestion rates as temperatures increase later in the day. Considering the rise in water temperature that occurs on the flats during the day it makes sense that higher tides occurring at the end of the night will coincide with lower water temperatures than those occurring at the end of the day. This may well explain why the sharks show such a strong preference for morning high tides. However, if the sharks primarily occupy the deeper lagoon during the day, as the results suggest, they may not be exposed to such large increases in temperature. Di Santo and Bennett (2011) suggested that elasmobranchs that are intermittent feeders would derive greater benefits from adopting the ‘hunt warm - rest cool’ strategy. This strategy would effectively slow the absorption process but improve the efficiency of food uptake. Further investigation into the temperature preferences and feeding periodicity of this species in the St. Joseph Atoll is clearly required to successfully understand the mechanism behind the observed behavioural patterns.

5.4.4 Spatial correlation between habitats

Generally sharks showed a strong fidelity to a particular area of the sand flats with only two individuals displaying a wider ranging behaviour with no apparent spatial preference. Sharks also displayed a tendency to predominantly utilise areas in the lagoon that were directly adjacent to their most used flats area. This suggests that, at the individual level, space use over both the flats and the lagoon may be extremely restricted and that individuals likely move between a small area encompassing both lagoon and sand flat habitats. Several studies have described movements of elasmobranchs between habitat types (McKibben and Nelson, 1986; Domeier and Nasby-Lucas, 2008; Johnson et al., 2009; Papastamatiou et al., 2009; Meyer et al., 2010b), however, few have estimated the distance between preferred areas at the day scale. Ackerman et al. (2000) found that *T. semifasciata* moved just far enough off the mud flats (mean = 1.2 km) to avoid stranding as the tide receded. In both this and the current study the observed behaviour could be explained as a means of minimising movements, and as such, energy expenditure.

5.5 Conclusion

The sub-adult sicklefin lemon sharks in the St. Joseph Atoll were found to utilise the flats extensively on a daily basis, in addition to the regular use of the lagoon described in Chapter 4. The combined results of this investigation align well with the optimal foraging theory (Stephens and Krebs, 1986). To maximise energy intake whilst minimizing energy outputs sharks potentially utilise refuge areas close to feeding areas. Both lemon sharks, *N. brevirostris*, and blacktip reef sharks, *C. melanoptris*, have been found to settle in shallow sand flat areas soon after birth and gradually increase their home range or modify their habitat selection with increasing size (Morrissey and Gruber, 1993a; Papastamatiou et al., 2009). As *N. acutidens* is likely to follow a similar ontogenetic strategy, it is possible to hypothesise that these sharks may utilise the same area on the sand flats from early on their life, and modify their habitat types to include sections of the lagoon closest to their natal flats area as they grow. Following the nocturnal feeding hypothesis, the sharks potentially maximise the efficiency of prey capture on the flats, whilst simultaneously maximising digestive uptake following the thermoregulatory strategy proposed by DI Santo and Bennett (2011).

CHAPTER 6 – GENERAL DISCUSSION

6.1 Synthesis

Understanding the movements of exploited species is of critical importance if spatial management tools are to be employed to enhance their protection (Chapman et al., 2009; Knip et al., 2010). This is particularly relevant when little information exists on the species in question. Recent reports on population declines (Shultz et al., 2008) and its recognized vulnerability to rapid local depletion (Pillans, 2003) coupled with the dearth of peer-reviewed literature regarding its behaviour or ecology highlight the requirement for such investigations on *N. acutidens*.

Through the use of passive acoustic telemetry this study addressed aspects of these knowledge gaps and has provided information pertinent to a spatio-temporal management approach. As with many telemetry studies, the sample size in this study represents a small portion of the local population. However, the extended observation period in this study has provided sufficiently robust behavioural information that can be extrapolated beyond the studied individuals.

Following several deployment iterations, it was possible to establish an array of acoustic receivers that effectively monitored the tagged sharks and allowed for the quantitative assessment of their long-term site fidelity and space use. Heupel et al. (2006) indicated that the design of an array of acoustic receivers will be influenced by the objectives of the study. Here, the array of 17 receivers inside and outside the St. Joseph lagoon was clearly effective in addressing the broader hypotheses concerning site fidelity and space use patterns. For finer scaled analysis of daily behavioural responses to environmental variables covering multiple habitat types, another design with the deployment of additional receivers on the sand flats was necessary. The deployment of these receivers proved to be vital for the discovery of the complex relationship between the movements of sharks, tidal height and the time of the day.

Several studies on coastal reef sharks have shown high degrees of site fidelity. These include young Caribbean reef sharks *C. Perezi* in Fernando de Noronha Archipelago, Brazil (Garla et al., 2006), juvenile and adult blacktip reef sharks *C. Melanopterus* in Palmyra Atoll (Papastamatiou et al., 2010), juvenile and adult lemon sharks *N. brevirostris* at Bimini Island (Gruber et al., 1988; Edrén and Gruber, 2005; Chapman et al., 2009), juvenile blacktip and lemon sharks in the Virgin Islands (DeAngelis et al., 2008), juvenile and adult grey reef sharks *C. amblyrhincos* at the Rowley Shoals, Australia (Field et al., 2011) and Enewetak Atoll (McKibben and Nelson, 1986) and juvenile and adult sicklefin lemon sharks *N. acutidens* at Aldabra Atoll (Stevens, 1984), in Skeleton Bay, Western Australia (Speed et al., 2011) and at Moorea Island, French Polynesia (Clua et al., 2010). This common pattern suggests that specific habitat requirements influence behaviour as they are likely to offer particular or multiple benefits to the various life stages for the different species. For example, site fidelity and the dependence on nearshore nursery habitats is well documented for juvenile sharks (Morrissey and Gruber, 1993b; Heupel et al., 2007; Wetherbee et al., 2007; Knip et al., 2010), and is probably in response to food availability or predator avoidance (Chapman et al., 2009). Site fidelity in adults, on the other hand, is likely for reproduction (Pratt and Carrier, 2001; Feldheim et al., 2004) or as a result of prey abundance (Lowe et al., 2006).

Chapman et al. (2009) showed that lemon sharks *N. brevirostris* disperse at a very slow rate from their natal site, often remaining closely associated with their place of birth for several years, even after leaving the confines of the nursery. In the current study a similar situation is likely to occur, where the observed high degree of site fidelity reflects the attachment of individuals to their natal area. This hypothesis can be expanded to explain the patterns of area use within the lagoon.

The results of spatial analyses suggested that, within the lagoon, individual sharks used a restricted portion of the total available habitat. There was also considerable overlap of the specific area used, which incorporated both a portion of the lagoon and a portion of the adjacent sand flats. The identification of this common high-use area suggests that *N. acutidens* display little territoriality. As these areas incorporate portions of the sand flats and early juveniles are likely to settle close to shore in these shallow environments soon after birth (Morrissey and Gruber, 1993a), the observed area use displayed by each individual may reflect an outward expansion of the primary settlement area, gradually incorporating a portion of the lagoon.

The strong relationship between the shark's use of the lagoon at low tidal heights and during the middle of the day suggests that individuals may use this area as a refuge site between forays, under more favourable conditions, onto the flats. Here the term refuge is used in accordance with the definition of McKibben and Nelson (1986) to reflect low levels of activity during part of the diel cycle and does not imply any form of predator avoidance. It is possible that individuals that were infrequently detected inside the lagoon throughout the study utilized other areas, possibly on the outer edge of the flats, as refuge sites during low tides. The use of the flats was strongly linked with larger tidal heights and was greatly intensified when these occurred during the night and early morning. These finding indicate a strong influence of environmental factors and suggest these sharks prefer to utilize the flats when temperatures are lower, the water is deeper and visibility is minimal. The combined effect of these three factors suggests that the motivation for regular visits to the flats was linked to the capture of prey.

The movement behaviour of *N. acutidens* in the St. Joseph Atoll can be summarised as follows. The sharks utilize the confines of the atoll on a near daily basis, move on and off the flats with the rise and fall of the tide, and remain in the deeper lagoon when the water recedes or becomes too warm. Individuals use relatively small portions of the atoll, which possibly represent expansions of their natal home range. However, with the onset of sexual maturity they are likely to leave the atoll lagoon and have the ability to migrate long distances (as witnessed by the one recapture). It is further hypothesized that the adults return to their natal nursery habitats to give birth.

6.2 Conservation implications

Recent declines in shark populations have been widely reported (Myers et al., 2007; Ferretti et al., 2008; Ferretti et al., 2010). Particular emphasis has been placed on declines in coastal sharks species, as these populations are typically the first to experience the pressure of human exploitation and habitat modifications (Knip et al., 2010; Ward-Paige et al., 2010). Due to the constant expansion of the human population and concomitant increase in exploitation of marine resources, the pressure placed on shark populations has even led to significant declines in some of the world's most remote atolls (Graham et al., 2010). Consequently, the conservation of relatively pristine environments with healthy populations of threatened species, such as the one in this study, should be a major priority.

The findings presented in this thesis have shed light on the conservation needs of *N. acutidens*. The observed high degree of site fidelity suggests that localized spatial management approaches such as marine protected areas could significantly contribute to the protection of *N. acutidens*. This approach is likely to be relevant for all remaining population of this species in similar isolated atoll environments. Within the Republic of Seychelles, several environments of this kind exist but are mostly isolated from one another by large distances. The spillover from one atoll to another is highly unlikely and hence the need for localised (atoll-scale) management of *N. acutidens* is required. Such measures have also been proposed for the management of *N. brevirostris* in the Bahamas (Chapman et al., 2009).

In the case of the St. Joseph Atoll, the distribution of sharks within the different atoll-associated habitats provides the potential for a multiple zoning protection approach. Here, through the exclusion of all human activity from the south-eastern region of the atoll, while allowing some non-consumptive activities in other areas (such as catch-and-release fishing) the effective local protection of *N. acutidens* will be achieved whilst simultaneously and sustainably contributing to the local economy. An added benefit of such an approach is that it is far more likely to be accepted by local stakeholders than one of complete area closure.

The restricted area use displayed by *N. acutidens* suggests that it is not only vulnerable to rapid local depletion but will also be strongly affected by habitat degradation. Tourism is a major contributor to the economy of the Republic of Seychelles, and although not yet developed, in time, many of the remote outer islands will likely become tourist destinations. The development of hotels and resorts poses a potential threat to the identified critical-habitat utilised by these sharks. If the behaviour of *N. acutidens* in the St. Joseph Atoll is used as a model, then it is clear that obtaining an understanding of high use areas within each atoll before any development begins, would provide the best chance for the long-term health of local populations of these sharks.

6.3 Directions for future research

This study has revealed new information on the movements of this poorly studied species and allowed for the development of several new hypotheses. Consequently, this thesis would be incomplete without providing some thoughts on future research needs. These will be addressed by answering the following questions:

1. Why do the sharks move between the flats and the lagoon?

There are several approaches that can be used that would shed light on the motivation behind this behaviour. Firstly an *in-situ* assessment of the fluctuation in water temperature throughout the diel cycle is essential to test the hypothesis that the sharks use the flats less as water temperatures rise. Additionally an assessment of the detailed activity patterns of *N. acutidens* within each habitat type can be conducted. This could be done using the traditional method of active tracking, but would have high manpower costs and, as night time tracking in such environments is seldom possible, may only provide data during daylight hours. Similarly the number of individuals tracked would be low. An alternative approach would be the use of tags which incorporate tri-axis accelerometers to provide information on specific physical activities such as resting, sustained swimming and rapid swimming bursts (Whitney et al., 2007; Murchie et al., 2011). These accelerometers can be incorporated into data storage tags (Whitney et al., 2007) which can provide long-term, high resolution data. However such tags require that the study animal is recaptured for data retrieval, which may not necessarily be practical or possible. Alternatively accelerometers can be utilized within acoustic transmitters (O'Toole et al., 2010; Murchie et al., 2011) allowing the data to be telemetered to an array of acoustic receivers. Such information would provide critical insight into the activities of *N. acutidens* in the various habitats and as such further improve our understanding of their natural behaviour.

2. Is the observed behaviour linked to prey availability?

The apparent heterogeneous distribution of *N. acutidens* within the atoll is also a result that could be further explained with the investigation of additional variables. The distribution of predators is believed to often reflect the distribution of prey (Chapman and Mackay, 1984; Heithaus et al., 2002; Meyer et al., 2010b; Papastamatiou et al., 2010). Therefore, a quantitative assessment of the spatio-temporal distribution of prey (Heithaus et al., 2002; Heupel and Hueter, 2002) both on the flats and in the lagoon would provide information to improve the understanding of this relationship for *N. acutidens* in the St. Joseph Atoll. As such it would first be necessary to understand the dietary habits of *N. acutidens* in the St. Joseph Atoll. This information could be obtained through non-lethal methods such as gastric lavage. The distribution of potential prey items could then be assessed through either a visual survey approach (Heithaus et al., 2002) or through extensive seine-net sampling or the use of fish traps (Heupel and Hueter, 2002).

3. Do *N. acutidens* display long-term (multiple year) fidelity and residency to their natal nursery habitats?

Based on the high degree of site fidelity displayed by the sharks in this study and the findings of Chapman et al. (2009) for the allopatric *N. brevirostris* it is hypothesized that juvenile *N. acutidens* settle in the shallow nursery areas with the atoll and gradually expand their home range as they grow. As such individuals are likely to remain associated with the atoll for many years from the time they are born until they reach maturity. A future study on the changes in space use throughout these individuals ontogeny from birth would provide much needed insight into the validity of this hypothesis, and further assist in the species' management. Such a study could either incorporate an assessment of space use of each cohort (either through active or passive telemetry methods) including a number of individuals from each size class, or through the use of long-life transmitters placed in early juveniles and the deployment of a large number of acoustic receivers throughout the atoll environment.

4. Do the atoll-associated populations of *N. acutidens* exist in isolation or are they well-mixed?

Research on the *N. brevirostris* has shown that discrete populations tend to be maintained by relatively few mature females (Feldheim et al., 2004), and there is even evidence to suggest that female may return to their natal site for parturition (Edrén and Gruber, 2005). Owing to the general similarity in behaviour and ecology of the two *Negaprion* species, it is hypothesized that *N. acutidens* will show similar patterns of natal site fidelity with low numbers of females regularly utilizing the atoll for parturition. This hypothesis can be tested following the methods of Feldheim et al. (2004). This would involve the collection of genetic samples from as many young of the year as possible during several consecutive years. Through the comparison of highly polymorphic microsatellite loci the breeding biology can then be examined. Similarly the use of long life acoustic transmitters place in large female *N. acutidens* captured within the atoll could provide insight into the frequency with which such females utilize the atoll. Knowledge on such population processes is a high priority as it will aid in understanding the species vulnerability to rapid local over-exploitation (Pillans, 2003). Furthermore, through a detailed genetic assessment of the populations occurring in each atoll throughout the Republic of Seychelles, the degree of isolation and/or mixing of the greater stock can be assessed. Such information is of critical importance for the effective management of this species.

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APPENDIX 1

Table 1. Visual and acoustic census results for *N. acutidens* counts from six locations on the reef flats of the St. Joseph Atoll.

Quadrant	**Relative position**	**Total individuals observed**	**Total individuals detected**	**Number of surveys conducted**	**Total survey time (hours)**	**Individuals observed hour $^{-1}$**
Q1	N	5		6	4.08	1.22
Q2	NE	28		6	3.95	7.85
Q3	E	15	3	6	3.08	7.46
Q4	SE	7	4	6	4.28	4.44
Q5	S	1		6	3.25	0.31
Q6	SW	2		6	3.82	0.52