

Migratory behaviour and spatial dynamics of large sharks and
their conservation implications

by

James Simon Eaton Lea

A thesis submitted to the University of Plymouth
in partial fulfilment for the degree of

DOCTOR OF PHILOSOPHY

School of Marine Science and Engineering
Faculty of Science

In collaboration with the Marine Biological Association
and the Guy Harvey Research Institute



July 2016

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Abstract

Determining the dynamic nature of animal movement has been an important component in a wider understanding of animal population ecology. Generally, this is because temporal change in the density of a population at a specific geographic location is not only a function of births and deaths but also of movements, including migration. The increased availability of remote telemetry and biologging systems in recent years has enabled many studies tracking marine predators, such as turtles, seabirds and marine mammals, but a general understanding of spatial dynamics in large sharks remains less well developed. This is in part due to few studies having achieved sufficiently long-term, multi-year tracks to detect changes in movement behaviour over time. Determining the timing, repeatability and potential motivations for movements of large sharks is necessary to understand the ecological and evolutionary role of such behaviour more generally in marine predators. Furthermore, given global concerns of declining shark populations, a detailed appreciation of shark movements can reveal the extent

of overlap with area-focused human activities (e.g. fishing), as well as inform assessments of population trends and spatial management options. In order to demonstrate how shark migratory behaviour and spatial dynamics can vary dramatically depending on the species and location, with subsequent contrasting conservation implications, the present work used long-term, remote telemetry to reveal detailed patterns in shark movement behaviour at two very different geographical scales: broad-scale movements of larger species that encompass ocean basins, versus fine-scale movements of reef-associated species at a remote atoll. First, using satellite telemetry, it was revealed for the tiger shark *Galeocerdo cuvier*, that adult males undertake annually repeated, roundtrip migrations of over 7,500 km in the northwest Atlantic. Second, acoustic telemetry was used to determine the fine-scale spatial dynamics of a multi-species shark assemblage at a small, remote atoll in the Seychelles, Indian Ocean, where a number of species displayed perennial residency. While the fine-scale movements of reef sharks in the Seychelles suggest an MPA of moderate size may be an effective management option, the long-distance migrations of the tiger sharks in the Atlantic reveal that conservation efforts targeting them must account for dynamic fisheries interactions over large geographical scales, potentially requiring time-area closures to be effective. Examining the long-term movement behaviour of different shark species over contrasting geographical scales has emphasised the importance of understanding spatial dynamics when informing management decisions, and has contributed to a wider understanding of the population ecology of these species.

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*To Jack:
our next generation,
for whom all this is for*

Author's Declaration

At no time during the registration for the degree of Doctor of Philosophy has the author been registered for any other University award without prior agreement of the Graduate Committee.

Work submitted for this research degree at Plymouth University has not formed part of any other degree either at Plymouth University or at another establishment.

The Founder of the Save Our Seas Foundation provided all funding and facilities for this work, carried out in collaboration with the Marine Biological Association of the United Kingdom (MBA) and the Guy Harvey Research Institute (GHRI).

I declare that the work presented here is my own, including all analyses and interpretation, with additional assistance as follows:

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Relevant scientific seminars and conferences were regularly attended at which work was often presented; external institutions were visited for consultation purposes and several papers prepared for publication.

Publications:

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Lea, J.S.E., Humphries, N.E., Clarke, C.R., Sims, D.W. 2015. To Madagascar and back: Long-distance, return migration across open ocean by a pregnant female bull shark *Carcharhinus leucas*. *Journal of Fish Biology*, **87**, 1313–1321

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Conference Presentations:

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Northwest Atlantic. 20th European Elasmobranch Association (EEA) Conference. Bristol, UK, 28–30 October, 2016

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1 General Introduction

Sharks play important roles both as predators in marine ecosystems and as resources in fishing and tourism industries (Clarke, Milner-Gulland & Bjørndal 2007; Ferretti *et al.* 2010; Vianna *et al.* 2012). Increasingly these roles are jeopardised by overfishing, with many populations experiencing declines that if sustained may threaten them with extinction (Dulvy *et al.* 2008; Ferretti *et al.* 2010; Worm *et al.* 2013). Eliminating the influence of predators, such as sharks, on ecosystems can potentially trigger trophic cascades that may permanently alter community structure and disrupt ecosystem services (Ward & Myers 2005; Heithaus *et al.* 2008). Despite concerns of how declining shark populations may negatively impact marine ecosystems, efforts to manage them sustainably are hindered by a considerable lack of reliable data on their demographics and movement patterns (Sims 2010; Barnett *et al.* 2012; Queiroz *et al.* 2016). Determining the scale of movements and their driving factors, alongside population structure, can prove critical in the development of effective management plans, including marine protected areas, and their strategic enforcement (Griffiths *et al.* 2010; Sims 2010; Block *et al.* 2011; Allen & Singh 2016; Queiroz *et al.* 2016).

1.1 The Value of Sharks

Ecosystem stability is important as human welfare is dependent on the services ecosystems render, many of which are provided by marine ecosystems, including food production, climate regulation and nutrient cycling (Holmlund & Hammer 1999; Díaz *et al.* 2006; McCauley *et al.* 2015). In both terrestrial and marine ecosystems predators can exert strong top-down forces that shape communities over large spatio-temporal scales and promote long term stability (Estes *et al.* 1998; Heithaus *et al.* 2008; Beschta & Ripple 2009; Ferretti *et al.* 2010). Sharks occupy high trophic levels in most coastal, demersal and pelagic food webs (Cortés 1999; Compagno 2001), and are typically well connected trophically as many species display

cosmopolitan diets and wide ranging movements (Cortés 1999; Bascompte, Melián & Sala 2005; Sims 2010). Certain shark species may impose greater influence than other marine predators of equivalent size as the extendable gape and sawing action of many species' jaws allows consumption of comparatively larger prey (Wilga, Motta & Sanford 2007). Consequently many megafauna species (e.g. dolphins, turtles, pinnipeds) have sharks as their primary, or only, predators (Wilga *et al.* 2007; Heithaus *et al.* 2009).

Predators not only influence prey demographics via direct consumption, but can also elicit strong avoidance behaviours in prey through imposition of predation risk (Ripple & Beschta 2007; Heithaus *et al.* 2009). Increasingly prey species have been shown to modify habitat use according to relative predation risk, which can in turn alter their trophic interactions (Ripple *et al.* 2001; Heithaus *et al.* 2009; Ferretti *et al.* 2010; Guttridge *et al.* 2011). For instance, seasonal presence of tiger sharks *Galeocerdo cuvier* in Shark Bay, Western Australia, causes several prey species (e.g. turtles, dugongs, sea snakes) to forgo foraging opportunities to enhance safety, even if only consumed infrequently (Heithaus *et al.* 2007, 2009; Wirsing & Heithaus 2009). Subsequent alteration in prey grazing patterns can then cascade to affect sea grass species composition and nutrient structure (Heithaus *et al.* 2008). Complicating such interactions, prey fitness can influence the degree of avoidance behaviour; green turtles *Chelonia mydas* of poor body condition will favour more productive grazing areas despite the associated higher predation risk (Heithaus *et al.* 2007).

Due to the complex and context dependent nature of these trophic interactions it can be difficult to predict the degree of predator influence within a particular ecosystem (Ferretti *et al.* 2010). Whilst the use of models, such as Ecopath and derivatives thereof, can help gauge the magnitude of cascading predator influence (Pauly, Christensen & Walters 2000), the required parameters are often unavailable due to data deficiency (Stevens *et al.* 2000; Okey *et al.*

al. 2004). In actuality it has been through the removal of predators from various ecosystems that the full extent of their influence has been realised. For instance, poaching of wolves *Canis lupus* from Yellowstone National Park, USA, facilitated elk *Cervus elaphus* proliferation and dramatically reduced vegetation and habitat in riparian areas that elk previously avoided due to risk (Ripple *et al.* 2001). Subsequent reintroduction of wolves has seen riparian vegetation re-established as elk resume risk avoidance behaviours (Ripple & Beschta 2007).

Due to the concealing nature of the marine environment and lack of historical data on commercially unimportant species there are very few well documented marine trophic cascades (Paine 1966; Estes *et al.* 2011), despite widespread reports of predator decline (Baum & Blanchard 2010; Tremblay-Boyer *et al.* 2011; Worm *et al.* 2013). Although the time series was limited, an example from the Aleutian Islands in the Pacific Ocean suggests that the switching of orcas *Orcinus orca* to prey on sea otters *Enhydra lutris* instead of pinnipeds released sea urchins from predation effects and increased grazing pressure on kelp, causing loss of productive kelp forest habitat (Estes *et al.* 1998). In Fiji, surveys have suggested that coral reefs with reduced reef predator densities have dramatically increased starfish densities, with corresponding declines in coral cover and increases in filamentous algae (Dulvy, Freckleton & Polunin 2004). Off Nova Scotia, Canada, declines in cod *Gadus morhua* have been linked to marked increases in small pelagic fish and benthic macroinvertebrates, with subsequent declines in zooplankton recorded, followed by increases in phytoplankton (Frank *et al.* 2005). Moreover, the increased populations of small pelagic fish released from cod predation appear to have also supported increases in the local grey seal *Halichoerus grypus* population (Frank *et al.* 2005).

Although now contested (Grubbs *et al.* 2016), it appeared in North Carolina that declines in coastal shark species since the 1970s correlated with increasing mesopredator abundance and

distribution, particularly for the cownose ray *Rhinoptera bonasus* (Myers *et al.* 2007). This in turn was reported to coincide with significant declines in bay scallop *Agropecten irradians* populations, primary prey of the cownose rays, and subsequent closure of the local scallop fishery (Myers *et al.* 2007). However, the validity of this particular cascade has since been called into question through re-examination of the data, which now suggests that the declines do not coincide well, that there is no significant trophic link between the sharks and rays, and that cownose rays reproduce too slowly to respond to release that quickly (Grubbs *et al.* 2016). In some pelagic systems it is thought that other predators with higher turnover rates (e.g. tuna and billfish) may be able to substitute sharks with minimal influence on trophic dynamics (Kitchell *et al.* 2002). But declines in pelagic predators are rarely limited to sharks, which are typically caught as bycatch, or targeted bycatch, in other fisheries (Dulvy *et al.* 2008; Hutchings *et al.* 2012). For example, 10-fold declines in Pacific Ocean longline catches have been reported for 12 pelagic predators (including tuna, billfish and sharks) from 1950–2000, coinciding with 10–100-fold increases in various mesoconsumers (Ward & Myers 2005).

In addition to promoting ecosystem stability, sharks support global economies through both fisheries and tourism. Sharks are fished for a variety of products, such as squalene for vaccines and cosmetics, but predominantly for their fins, which are primarily sought after as a delicacy in the Far East for shark fin soup (Clarke *et al.* 2007; Lippi, Targher & Franchini 2010). Accelerated development of Asian economies, corresponding availability of disposable income and rapid population growth have seen demand for shark fin soup rise significantly over recent decades (Clarke *et al.* 2007). Consequently there is substantial fishing effort to meet demand, and the value of the trade in shark fins has been estimated at a minimum of USD 400–550 million year⁻¹ (mpy) (Clarke *et al.* 2007). But in direct conflict with the consumptive fin trade, sharks are increasingly valuable to tourism industries in many countries (Gallagher & Hammerschlag 2011). The expanding market for shark watching operations, as tourist values

shift from ‘adventure-seeking hunters’ to ‘nature-appreciating observers’ (Whatmough, Putten & Chin 2011), has prompted studies to evaluate the comparative revenue generated (Table 1). Most recently reef sharks in Palau have been estimated to generate USD 18 mpy as 21% of tourists visit specifically to encounter sharks, accounting for 8% of the gross domestic product (Vianna *et al.* 2012). Moreover this revenue is based on an estimated resident population of 100 sharks at the popular dive sites, worth at most USD 10,800 if harvested for their fins, constituting a mere 0.006% of the revenue these sharks would generate through tourism over their lifespan (Vianna *et al.* 2012). Such discrepancy can provide strong conservation incentive and has been recognised through a ban on all shark fishing in Palau (Vianna *et al.* 2012). Similarly shark fishing was banned in the Maldives after the realisation that shark tourism generated more than double the revenue of shark fisheries (Anderson & Ahmed 1993; Martin & Hakeem 2006).

Table 1: Annual revenue generated through shark tourism operations for several example locations.

Location	Revenue (USD per year)	Reference
Palau	18 million	(Vianna <i>et al.</i> 2012)
Bahamas	78 million	(Cline 2008)
Canary Islands	23 million	(De la Cruz Modino <i>et al.</i> 2010)
Ningaloo Marine Reserve, Australia	5.9 million	(Davis <i>et al.</i> 1997)
French Polynesia	5.4 million	(Clua <i>et al.</i> 2011)
Seychelles	4.9 million	(Rowat & Engelhardt 2007)
Gansbaai, South Africa	4.4 million	(Hara, Maharaj & Pithers 2003)
Aliwal Shoal, South Africa	1.8 million	(Dicken & Hosking 2009)

The considerable value of sharks through tourism has been reported for several other locations (see Table 1 for examples). Despite differing criteria for revenue estimation (e.g. whether or not indirect revenue was considered from hotels, restaurants etc. through tourists visiting specifically to encounter sharks), these studies consistently illustrate the substantial, in principle renewable, value of shark tourism. Yet they represent a small fraction of the numerous shark tourism operations worldwide, most of which remain unevaluated for

revenue contribution (Gallagher & Hammerschlag 2011). If potential can in part be gauged by the estimated global revenue from whale watching (USD 2.1 billion year⁻¹; (O'Connor *et al.* 2009)), it remains conceivable that the global value of sharks through tourism could not only exceed their value to fisheries, but provide an alternative, non-extractive source of exploitation and employment that simultaneously maintains their ecosystem role as predators.

However, exploitation through tourism must be developed with caution to ensure its impacts are sustainable and that the ecosystem functions of sharks are indeed maintained. Many shark tourism operations involve SCUBA diving on coral reefs (Gallagher & Hammerschlag 2011), potentially decreasing reef health through diver damage (Guzner *et al.* 2010; Poonian, Davis & McNaughton 2010), although this can in part be mitigated through more detailed dive briefings (Medio, Ormond & Pearson 1997). Another consideration is the degree of provisioning used; over 40% of operations use food to attract sharks for more reliable encounters (Carwardine & Watterson 2002). Yet there remain concerns that provisioning with a regular food source may alter predator behaviour, condition and community interaction, whilst compromising human safety (Newsome & Rodger 2008; Clua *et al.* 2010; Brena *et al.* 2015). Despite such concerns there are limited empirical studies, which provide varied conclusions: whilst some purport behavioural changes that may impede fitness (e.g. elevated aggression in sicklefin lemon sharks *Negaprion acutidens*, (Clua *et al.* 2010); increased activity and energetic costs in whitetip reef sharks *Triaenodon obesus*; (Fitzpatrick *et al.* 2011; Barnett *et al.* 2016)), others argue impacts may be negligible and outweighed by the economic and protection benefits afforded through tourism over fishing (Laroche *et al.* 2007; Maljković & Côté 2011; Hammerschlag *et al.* 2012). One potential source of disparity between studies is the differing level of food rewards provided to sharks in attendance (e.g. whether or not the sharks are actively fed or simply chummed), which may affect the strength of associative learning and potential for behavioural changes (Guttridge *et al.* 2009).

There has also been little evaluation of how provisioning may affect community interaction and structure. Although studies that have considered this have reported no evidence of changes in ecological impact (Maljković & Côté 2011), it is thought that provisioning influence on tiger shark trophic interactions in the Bahamas may be minimal, assuming their daily ration to be relatively high compared to the quantity and frequency of food obtained during provisioning (Hammerschlag *et al.* 2012). In contrast it has been suggested that the increasing number of bull sharks *Carcharhinus leucas* visiting a provisioning site in Fiji could alter trophic interactions in the region by redistributing predator influence (Brunnschweiler & Baensch 2011). Another concern that seems to have gone broadly unconsidered in present literature and requires further investigation is the sustainability of fisheries that supply the bait for provisioning: extractive use of one species to support the non-extractive use of another could provide unforeseen complications, the sustainability of which must be assessed carefully before shark tourism is actively incorporated into ecosystem management programmes.

1.2 Population Declines

Despite the evident ecological and economic value of sharks, the sustainability of their ecosystem services is threatened globally by factors such as overfishing, pollution, and habitat degradation (Ferretti *et al.* 2010; Juan-Jordá *et al.* 2011; Worm & Branch 2012). Overfishing has been estimated to account for 96.1% of threats to shark populations, followed by habitat destruction (2.9%) and pollution (0.4%; (Ferretti *et al.* 2010)). Global exploitation of large pelagic fish by industrialised fisheries has resulted in dwindling catches of important stocks (Myers & Worm 2005) despite increasing fishing effort (Worm & Branch 2012), emphasising the urgent need for enhanced management and conservation efforts (Ferretti *et al.* 2010). Pelagic sharks are apex or mesopredators that make up over 50% of global longline catches, yet surprisingly fisheries for them remain largely unregulated (Clarke *et al.* 2006; Camhi *et al.*

2009). Management action ideally necessitates evidence of population-wide declines but there is controversy (Burgess *et al.* 2005; Ferretti *et al.* 2010; Pauly, Hilborn & Branch 2013) over whether reported declines in shark catch rates within geographically limited regions reflect decreasing population abundance over entire ranges (Baum *et al.* 2003; Myers *et al.* 2007; Ferretti *et al.* 2008), or are confounded by shifts in shark movements and habitat selection and changes in the areas exploited by fisheries (ICCAT 2009, 2012).

Due to the aforementioned demand for their fins, it has been estimated that 63–273 million sharks are caught annually for the fin trade alone (Worm *et al.* 2013). In general sharks used to be commercially unimportant, typically caught as bycatch and reported with little accuracy: it has been estimated that only 15% of catches reported to the Food and Agriculture Organization (FAO) of the United Nations are to species level (Lack & Sant 2006). Moreover 73% of global shark catch is thought to be illegal and unreported (Clarke *et al.* 2006). Although the true magnitude of declines remain uncertain due to this lack of baseline data and underreporting of catch, and considerable lack of fisheries-independent survey data (Lack & Sant 2006; Ferretti *et al.* 2010), it has been estimated that some populations have been reduced to less than 10% of pre-exploitation levels (Dulvy *et al.* 2008; Ferretti *et al.* 2010), with 52% of pelagic shark species considered threatened with extinction (Field *et al.* 2009; Dulvy *et al.* 2014). Typically, sharks are more susceptible to overfishing than most commercial teleost species due to *k*-selected life history traits that limit recruitment rates (late age of maturity, low fecundity; (Musick 1999; Frisk, Miller & Dulvy 2005; Hutchings *et al.* 2012)). Consequently sharks can only withstand very limited fishing pressure and are prone to more rapid collapse compared to most teleost populations (Frisk *et al.* 2005; Ferretti *et al.* 2010). Accordingly modelling data suggest reductions in mortality of 40–80% would be required in north Atlantic fisheries to ensure the survival of shark populations (Myers & Worm 2005).

Many of the reported declines are from fisheries in the Atlantic, in part due to its longer commercial fishing history and more comprehensive datasets (Baum & Blanchard 2010; Ferretti *et al.* 2010). For instance, silky sharks *Carcharhinus falciformis* and oceanic whitetip sharks *Carcharhinus longimanus* are estimated to have declined by over 90% and 99% respectively in Gulf of Mexico longline fisheries since the 1950s (Baum & Myers 2004). Similarly in the Mediterranean the only shark species with sufficient data to be assessed were found to have apparently declined by between 96% and 99% (Ferretti *et al.* 2008). Ten-fold declines in 12 pelagic predators (both sharks and teleosts) in the Pacific since 1950 have also been reported (Ward & Myers 2005). Consistent with these figures it has been estimated that general predator biomass has declined by over 90% in half of north Atlantic and Pacific coastal areas compared with unexploited levels (Tremblay-Boyer *et al.* 2011). Whilst similar levels of data resolution to the Atlantic and Pacific are not available for the Indian Ocean, several studies from the region indicate shark populations are experiencing declines similar to elsewhere. Fisheries-independent visual surveys of reefs in the Chagos Archipelago, recently designated a Marine Protected Area (MPA), suggest that reef sharks may have declined by over 90% since 1975 (Graham, Spalding & Sheppard 2010; Sheppard *et al.* 2012). Reports prior to the ban of shark fishing in the Maldives indicate declines there may also be severe (Anderson & Ahmed 1993; Martin & Hakeem 2006), with notable declines in large sharks also suggested for the Seychelles (Nevill *et al.* 2007). Although declines in predator biomass in the Indian Ocean may presently be lower than the Atlantic, modelled data suggest they are on a similar trajectory and may simply be lagged due to later industrialisation of commercial fisheries (Tremblay-Boyer *et al.* 2011). The decline of sharks even in remote locations such as Chagos is of particular concern as it highlights the increasing expansion of shark fisheries into the high seas, leaving few, if any, remote sanctuaries.

1.3 Movements and Management

Even though declines in shark populations jeopardise their ecological and economic services, there has been a significant paucity of data on shark demographics and behavioural ecology to reliably inform management decisions on sustainable use. This is primarily due to the concealing nature of the marine environment and logistical difficulties of systematic study, combined with their lack of historical commercial importance (Gruber & Myrberg 1977). In particular simple knowledge on shark spatial dynamics - where they are, when and importantly why - is lacking for many species. Emphasising the value of such information, previous research has shown that management interventions have been less effective when the spatial, or temporal, scales of species movements were not accounted for (Thirgood *et al.* 2004; Moffitt *et al.* 2009). In recent years, however, the application of remote telemetry, using both acoustic and satellite-linked transmitters, has started to provide insights on shark behaviour and habitat use that are of significant management value (Sims, 2010).

Remote telemetry has revealed shark behaviour to be much more varied and complicated than previously thought, including the capacity of several shark species to undertake large scale migrations that span ocean basins, traversing political boundaries and the high seas (Chapman *et al.* 2015). For instance, a white shark was recorded to travel between South Africa and Australia, covering over 10,000 km in 99 days (Bonfil *et al.* 2005). An individual basking shark *Cetorhinus maximus* was recorded moving across a similar distance between the UK and Canada (Gore *et al.* 2008), while basking sharks in the western Atlantic undertake trans-equatorial migrations that extend their known range into tropical waters (Skomal *et al.* 2009). Likewise whale sharks *Rhincodon typus* travel widely throughout the Indian and Pacific Oceans (Eckert & Stewart 2001; Rowat & Gore 2007). In the Pacific a comprehensive, multispecies tracking programme has revealed comparative large scale movements, such as seasonal north/south migrations by the salmon shark *Lamna ditropis* (Block *et al.* 2011). Together these

studies exemplify the need for the management of some species to be framed at an international scale as isolated local efforts may prove ineffective, emphasising the importance of initiatives such as the Convention on Migratory Species.

Tracking shark movements can also help identify areas of temporal significance for reproduction and foraging in wide ranging species (Sims 2010; Block *et al.* 2011). This can then be used to evaluate the effectiveness of management efforts such as time-area closures and gear mitigation to reduce bycatch (Block *et al.* 2011). For instance, discovery of previously unknown seasonal pupping by porbeagle shark *Lamna nasus* in the Sargasso Sea revealed a candidate for time-area closure (Campana, Joyce & Fowler 2010), whilst learning that common thresher sharks *Alopias vulpinus* off California mainly swim near the surface at night suggested that setting nocturnal drift-gillnets for broadbill swordfish *Xiphias gladius* marginally deeper could reduce bycatch (Cartamil *et al.* 2010). In the northeast Atlantic, an overlap of ~76–100% was reported between blue shark *Prionace glauca* nocturnal diving depths and the hook depths of vessels longlining for tuna and swordfish species (Queiroz *et al.* 2012). Such areas of high space-use overlap may also be targets for management efforts such as MPAs or changes in fishing practice to reduce blue shark bycatch (Queiroz *et al.* 2012). More recently, space-use of long-line vessels across the north Atlantic Ocean has been shown to overlap with hotspots of shark movements by 80%, with both associating with steep environmental gradients, such as thermal fronts (Queiroz *et al.* 2016). Such high overlap over an entire ocean basin scale may prohibit spatial management options, with alterations to fishing gear (e.g. monofilament leaders that sharks can bite through) or catch quotas/size limits potentially proving more effective (Queiroz *et al.* 2016).

Conversely some species display highly restricted movements that could exacerbate declines through lack of recruitment from adjacent populations (Robbins *et al.* 2006), especially in

remote locations (Graham *et al.* 2010), but at the same time help target management efforts, such as MPAs, on areas of predictable use. For example, blacktip reef sharks *Carcharhinus melanopterus* tracked at Palmyra Atoll in the Pacific had a mean home range size of only 0.55 km² (Papastamatiou *et al.* 2009). In similarly remote locations grey reef sharks *Carcharhinus amblyrhynchos* also displayed very confined movements (Field *et al.* 2011; Barnett *et al.* 2012), although on less isolated reefs they may range more widely (Heupel, Simpfendorfer & Fitzpatrick 2010; Barnett *et al.* 2012). Other reef sharks, such as the whitetip reef and silvertip *Carcharhinus albimarginatus*, have also been shown to display high fidelity to particular reefs (Barnett *et al.* 2012).

Detailed knowledge of movements and habitat use can inform the efficacy of existing and planned MPAs (Edgar *et al.* 2014; Allen & Singh 2016). Even prior to the aforementioned discovery of basking shark migrations, it had been estimated that basking sharks spent on average only 22% of their time within protected British (territorial) waters, accentuating the need for international collaboration (Southall *et al.* 2006). Tracking of Caribbean reef *Carcharhinus perezei* and nurse sharks *Ginglymostoma cirratum* in the already established MPA of Glover's Atoll, Belize, found that tagged sharks on average spent at least 32% of their time outside of the no-take zone, leaving them vulnerable to fishing and suggesting that the reserve design should be reconsidered (Chapman *et al.* 2005). However, the value of even this partial protection has since been demonstrated using baited camera traps, where Caribbean reef sharks were encountered 3–10 times more frequently in the Glover's Atoll MPA than fished areas of the Mesoamerican Barrier Reef, although it is uncertain whether this is a function of decreased mortality or increased prey availability, or both (Bond *et al.* 2012). The need for informed reserve design is highlighted by the continued decline of reef shark populations on the Great Barrier Reef despite the use of MPAs (Robbins *et al.* 2006). Here, more easily policed no-entry zones contained more sharks than no-take zones, suggesting

continued poaching and emphasising that legislation requires enforcement to be effective, which is often lacking due to limited resources (Robbins *et al.* 2006; Edgar *et al.* 2014).

The efficacy of MPAs also depends on temporal variation in MPA use by the target species and the surrounding fisheries (Edgar *et al.* 2014), making it necessary to obtain long-term, multi-year tracks to detect changes in movement behaviour over time (Allen & Singh 2016). For instance, in coastal east Australia, spottail *Carcharhinus sorrah* and juvenile pigeye sharks *Carcharhinus amboinensis* were found to spend on average 32% and 22% of their time, respectively, within two MPAs in Cleveland Bay, but this use varied seasonally, with spottail shark use peaking during winter and pigeye shark use during summer, potentially changing interactions with adjacent fisheries (Knip, Heupel & Simpfendorfer 2012). Sexual disparities in MPA use were also recorded for spottail sharks, highlighting the need for an appreciation of differing space use between sexes when considering management (Knip *et al.* 2012), particularly as spatio-temporal sexual segregation is common in many shark populations (Mucientes *et al.* 2009; Wearmouth & Sims 2010). Similar to Glover's Atoll, despite only partly encompassing shark movements, the Cleveland Bay MPAs may afford the sharks some level of protection, albeit for pigeye sharks this is only for early life stages (Knip *et al.* 2012).

Modelling can be used to clarify what factors might drive shark movements, working towards a framework for better predicting movements in space and time. For example, a variety of shark species have been demonstrated to switch between differing optimal foraging strategies according to the distribution of resources available (Humphries *et al.* 2010; Sims *et al.* 2012). However, recent reviews on tracking studies reveal how remarkably few attempt to relate observed patterns in shark movement to driving factors in this manner (the 'why'), with many simply reporting the 'where' and 'when' (Sims 2010; Hammerschlag, Gallagher & Lazarre 2011). Whilst the latter are most certainly of management use, their power to predict shark

movements is greatly increased if understood in the context of driving environmental factors, and subsequently how shark space-use may change over time (Humphries *et al.* 2010; Sims 2010).

Numerous factors have been proposed to influence shark movement patterns, including their physical condition (Gurshin & Szedlmayer 2004), water temperature (Sims *et al.* 2006), time of day (Shepard *et al.* 2006), currents (Rowat & Gore 2007), light levels (Nelson *et al.* 1997), time of year (Weng *et al.* 2008), geographic location (Stokesbury *et al.* 2005), topographical features (Holland *et al.* 1999), geomagnetic gradients (Klimley 1993), prey availability (Goldman & Anderson 1999) and oxygen levels (Graham, Roberts & Smart 2006). But overall, from studies that have attempted to address the 'why' behind the dynamic nature of observed movements, water temperature has been revealed as a particularly important driver of shark space-use (Weng *et al.* 2008; Abascal *et al.* 2011; Block *et al.* 2011; Queiroz *et al.* 2016), while areas with steep thermal gradients and high primary productivity have been demonstrated to support high shark abundance and diversity (Worm, Lotze & Myers 2003; Sims 2010; Block *et al.* 2011; Queiroz *et al.* 2012). Such an appreciation of shark environmental preferences can then be used to predict population distributions from potentially suitable habitat, as well as how this might change with variation in environmental factors, which in turn allows dynamic evaluation of fisheries interactions in space and time (Sims 2010; Queiroz *et al.* 2016).

Consequently future efforts to explain movement behaviour should endeavour to incorporate factors that might explain the patterns being observed, for instance by also using data-loggers that record acceleration and gastric pH to detect feeding events (Papastamatiou, Meyer & Holland 2007; Wilson, Shepard & Liebsch 2008; Sims 2010; Papastamatiou & Lowe 2012). There has also been a tendency in the literature to focus on charismatic species, despite the general ecological importance of sharks (Simpfendorfer *et al.* 2011). Nonetheless it is evident

that movement data is useful for determining whether management efforts are best focused on MPA development or modification of fishing practices, or indeed a combination of the two.

1.4 Genetics

Although not directly addressed in the present body of work, it is important to mention in brief the emerging role of genetic sequencing in fisheries management. In fisheries catching sharks, either targeted or as bycatch, often only the fins are landed to maximise yield (Clarke *et al.* 2006). But detached shark fins are typically difficult to identify to species level, complicating accurate reporting of catch and hampering enforcement of trade restrictions (Shivji *et al.* 2002). Using species-specific genetic markers, however, identification can be achieved in the field without the need for time consuming processing in the laboratory (Shivji *et al.* 2002; Wong 2009). Consequently it has been possible, for example, to reveal that white shark fins are still traded internationally despite protection under CITES Appendix II (Shivji *et al.* 2005), and to trace scalloped hammerhead shark *Sphyrna lewini* fins in Hong Kong markets back to endangered western Atlantic populations, made possible by geographically specific signatures in their genetic population structure (Chapman, Pinhal & Shivji 2009).

Determining population structure can also help frame the scale at which management is required. For example, use of genetic markers has demonstrated that grey reef shark populations are highly structured throughout the Indo-Pacific, indicative of negligible connectivity between separate populations (Horn 2010), consistent with tracking studies and confirming their management is required at a local scale (Heupel *et al.* 2010; Field *et al.* 2011). In contrast the lack of discernible structure for basking sharks is consistent with their basin-wide movements, reinforcing the need for international co-operation (Hoelzel *et al.* 2006). In particularly extreme cases, however, what was thought to be a single population of one species can actually be separate populations of different species that are almost

indistinguishable morphologically. For instance, a cryptic lineage of the scalloped hammerhead shark has been confirmed in the Northwest Atlantic (Pinhal *et al.* 2012), whilst the already critically endangered common skate *Dipturus batis* in Europe was shown to comprise two separate species that have distributional ranges that only partially overlap in the northeast Atlantic (Griffiths *et al.* 2010; Iglésias, Toulhoat & Sellos 2010). Such situations raise particular concerns as they reduce the known population of the original species whilst presenting a second in need of management.

1.5 Origins of the Present Study

Evident from the preceding sections, there has been growing scientific attention paid to elasmobranchs, in particular sharks, driven largely by observed population declines with the subsequent threat of extinction and their important, interesting ecological roles. In view of this the Save Our Seas Foundation (SOSF), a charitable organisation, has been investing in research on this broad subject area, both in-house and via grants. I was fortunate to join the SOSF Founder's team in 2007 as a research officer, where I assisted shark tracking and population survey projects in several locations across the Red Sea and Indian Ocean (Clarke, Lea & Ormond 2011, 2012, 2013; Clarke *et al.* 2015). The movement behaviour of silky sharks in the Red Sea formed a significant part of my initial thesis proposal in 2010, but by the time I started fieldwork the declines in local silky shark numbers due to commercial fishing were so severe that it became increasingly difficult to find and tag sharks (Clarke *et al.* 2013).

However, through collaboration between SOSF and the Guy Harvey Research Institute (GHRI), in late 2012 Professor Mahmood Shivji made available to me a substantial number of high quality tiger shark satellite tracks to help counter the lack of data for my thesis. The GHRI has been funding and managing the deployment of tags on tiger sharks in the Atlantic with the Bermuda Shark Project, but the various commitments of their partners had prevented detailed

analysis of the data produced, hence their offering of the data for me to analyse. As detailed below, these satellite tracks were used to investigate the migratory behaviour of this species, as well as to determine how movement patterns changed in relation to environmental factors.

Also in late 2012, SOSF acquired D'Arros Island and St Joseph Atoll in the Seychelles and established the SOSF D'Arros Research Centre, with the intention of conserving the islands' ecological value through research and education. I established a comprehensive, long-term shark tracking programme around the islands, using an expansive array of acoustic receivers and tagging species such as blacktip reef sharks, sicklefin lemon sharks *Negaprion brevirostris*, grey reef sharks, tawny nurse sharks *Nebrius ferrugineus*, and silvertip sharks. This multi-species tracking effort should provide unprecedented insight into how these sharks use the available habitats in this remote location over time, whilst allowing interspecific comparison. It is intended that a greater understanding of the sharks' movements will help inform the development of sustainable management plans and protected areas such that ecosystem services may be preserved.

Consequently the present work used long-term, remote telemetry to reveal detailed patterns in shark movement behaviour at two very different geographical scales: broad-scale movements of larger tiger sharks that encompass ocean basins, versus fine-scale movements of reef-associated species at a remote atoll. This made it possible to investigate how shark migratory behaviour and spatial dynamics can vary dramatically depending on the species and location, with subsequent contrasting conservation implications.

1.6 Aims and Objectives

Given the severe population declines reported for many shark species, the overall aim of this thesis is to provide information on the migratory behaviour and spatial dynamics on a

selection of shark species in areas of high exploitation that provides basic ecological information that may contribute to their conservation and sustainable management. As outlined above, attention was focused on tiger sharks in the northwest Atlantic and reef sharks in the Seychelles, to investigate contrasting scales of management. In order to allow informed management decisions, movement studies need to be sufficiently long-term to detect changes in movement behaviour over time, including habitat selection, such that a full appreciation of the dynamic nature of movements can be incorporated (Allen & Singh 2016).

Within this broad framework specific objectives included:

- 1) To determine the broad-scale migration routes, timing of site fidelity, and size/sex differences in behaviour of tiger sharks in the northwest Atlantic.
- 2) To assess how tiger sharks in the northwest Atlantic respond to environmental variation, such as sea surface temperature, primary productivity and thermal fronts, and examine the behavioural dynamics in detail.
- 3) To compare fine-scale habitat use of reef sharks in the outer islands of the Seychelles, including potential partitioning of space use between species and whether there may be any indication that these islands may offer nursery opportunities and promote regional recruitment.
- 4) To reveal how temporal cycles (seasonal, diel, tidal) influence the fine-scale spatial dynamics of reef sharks in Seychelles.

- 5) To use the movement patterns of reef sharks in the outer islands of the Seychelles to estimate the efficacy of potential marine reserve designs.

- 6) To combine the obtained information on migratory behaviour and spatial dynamics of these different species to determine whether there are any consistent patterns both within and between species, which may in turn be of management value.

2 General Methods

This chapter provides an overview of any technology or methods used across multiple chapters in order to avoid repetition across the thesis. Included are: descriptions of the study sites; summaries of the types of transmitter used; details of shark capture and handling; and shared analysis techniques.

2.1 Study Sites

2.1.1 *Challenger Bank, Bermuda*

Fieldwork for Chapters 3 and 4 (studying large shark migrations) was conducted at Challenger Bank (N 32°05', W 065°03') near Bermuda in the northwest Atlantic (Figure 1), in collaboration with the Guy Harvey Research Institute and the Bermuda Shark Project. Challenger Bank is a seamount ~20 km southwest of Bermuda, surrounded by deep water (>1,000 m) and rising to approximately 50 m depth. The area is popular among sports fishers, with catches regularly including yellowfin tuna *Thunnus albacares* and amberjack *Seriola* spp., apparently attracted by large schools of baitfish supported by the local upwelling. The local productivity also attracts various species of large shark, including the tiger shark *Galeocerdo cuvier*, providing opportunities to study their migratory behaviour.

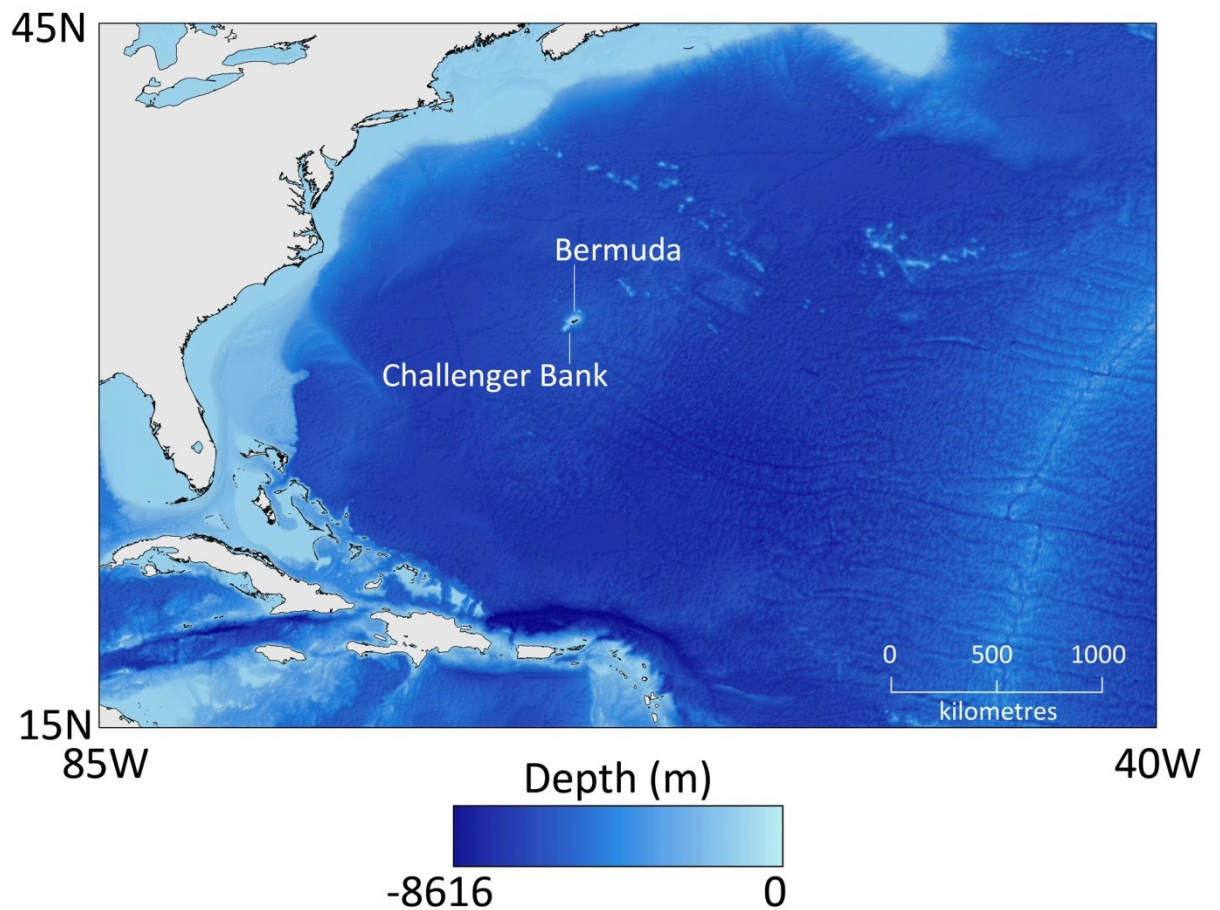


Figure 1: Map shows the location of Challenger Bank relative to Bermuda and the Atlantic Ocean (created in ArcGIS, using GSHHG coastline data and ETOPO2v2 bathymetry data).

2.1.2 *D'Arros and St Joseph, Seychelles*

Fieldwork for Chapters 5–8 was conducted from the D'Arros Research Centre in the Seychelles.

D'Arros Island (S 05°24', E 53°17') is a small sand cay (~1.6 km²) situated on a patch reef (~3.6 km²) in the Amirantes chain of islands of the Republic of Seychelles, western Indian Ocean (Figure 2 and Figure 3). Just over one kilometre east of D'Arros, separated by a channel of 60–70 m depth, is St Joseph Atoll (~22 km²; S 05°25', E 53°20'; Fig. 2.3). St Joseph Atoll has 16 small islands atop an uninterrupted reef flat (~15 km²) that encloses a shallow (3–9 m), access-restricted lagoon of ~5 km² (Fig. 2.3). The flats surrounding St Joseph lagoon are largely exposed at low tide, causing temporary isolation of the lagoon from the outer reef. Up to 2 m of water covers the flats at high tide. The lagoon is predominantly sand bottomed with numerous large coral outcrops that rise to the surface, with patches of seagrass

Thallasodendron sp. along the flats and some mangroves *Rhizophora mucronata* fringing the islands (von Brandis 2011). The reefs surrounding D'Arros and St Joseph have reasonable coral cover and slope steeply from near the surface to 20–25 m depth. These reefs give way to the Amirantes plateau, which varies between 15–60 m depth and stretches 155 km from north to south. The plateau is predominantly covered by patches of seagrass and sandy reef rubble, with occasional patches of high coral cover. The plateau is surrounded by very deep water, with the edges descending from 30–60 m to over 1,000 m deep within a few hundred metres. D'Arros and St Joseph appear to support reasonably healthy populations of various reef sharks, making them an ideal location to study the fine-scale spatial dynamics of multiple shark species.

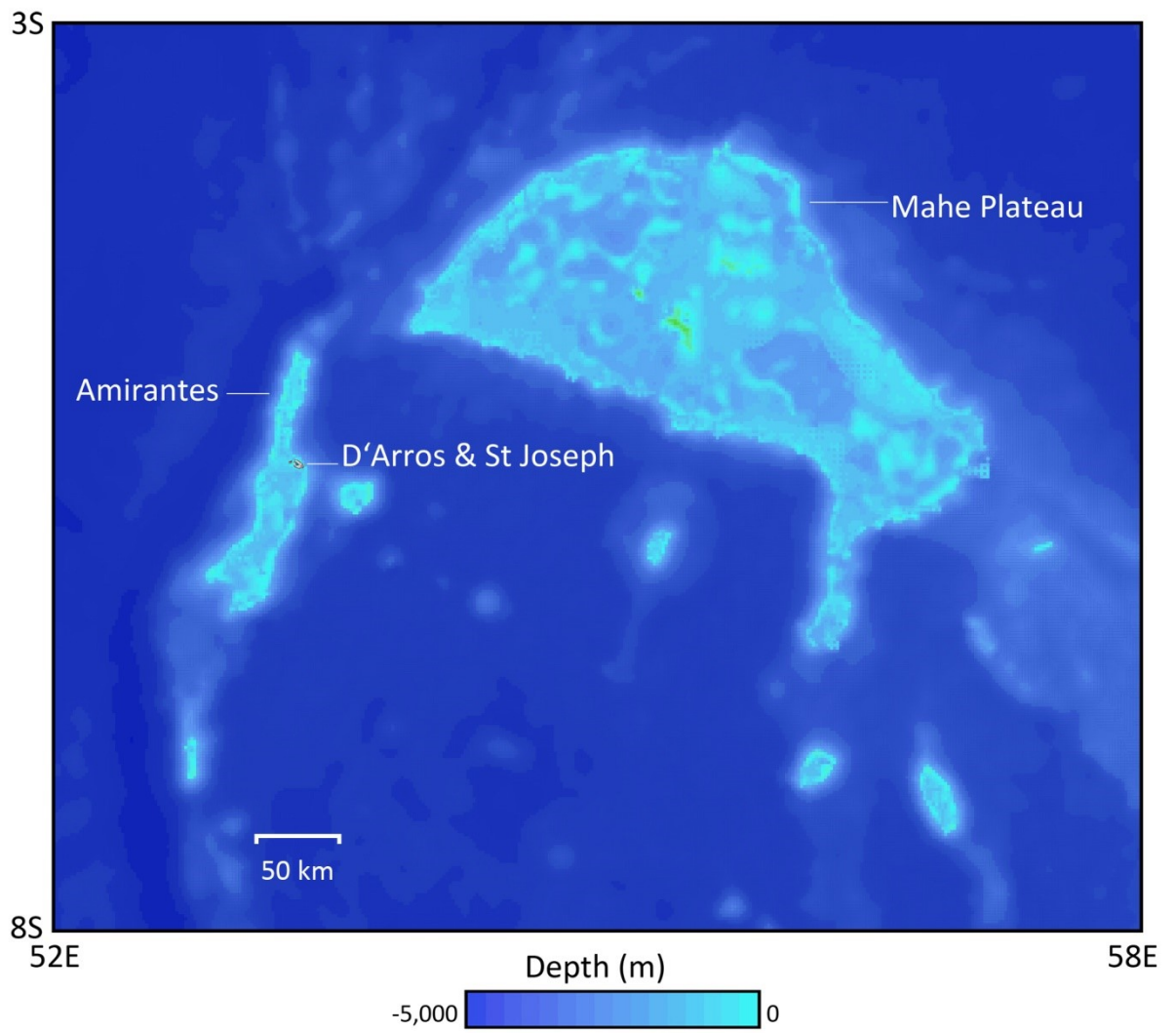


Figure 2: Map shows the location of D'Arros and St Joseph in the Amirantes, Seychelles (created in ArcGIS, using ETOPO2v2 bathymetry data).



Figure 3: Image shows a satellite composite of D'Arros and St Joseph Atoll. Image provided by LAND INFO Worldwide Mapping, LLC, and includes material Copyright © DigitalGlobe (Longmont, Colorado).

2.2 Telemetry Techniques

In order to meet the objectives outlined in Chapter 1, it was necessary to employ remote telemetry techniques to track the movements of the target shark species. Two main types of transmitter, or tag, were used to track sharks across the different chapters: acoustic tags and position-only satellite tags. The former relies on the receipt of sound waves at acoustic receivers, while the latter works via satellite-mediated communication. For reasons that will be outlined in this chapter, satellite telemetry is better suited to larger species of shark that are expected to move away from the study site. As such satellite telemetry was used in Chapters 3 and 4 to investigate the migratory behaviour of large sharks in the Atlantic Ocean. In contrast, acoustic telemetry is better suited to the study of fine-scale movements of animals that can be tracked across an array of acoustic receivers. Consequently, acoustic telemetry was employed

in Chapters 5, 6, 7 and 8, which aimed to characterise reef shark spatial dynamics at a remote atoll in the Indian Ocean.

All field work was approved by, and conducted with the knowledge of, the appropriate authority for each location: the Marine Resources Section of the Bermuda Department of Environmental Protection, and the Ministry of Environment, Energy, and Climate Change, Seychelles. All animal handling and tagging methods were performed in accordance with the approved guidelines of the University of Plymouth, UK.

2.2.1 Satellite Telemetry

In essence satellite positioning tags are relatively simple, consisting of a radio transmitter that continually transmits to Argos satellites while at the surface, and switches off to conserve battery power while submerged by means of saline sensitive conductivity circuits (Eckert & Stewart 2001). Historically this method is most reliably applied to marine mammals that have an obligation to surface and so transmit at regular intervals (Eckert & Stewart 2001). Consequently for elasmobranch research position-only satellite tags are best used on sharks that spend significant amounts of time at or near the surface or can at least be relied on to return to it periodically. Several methods have been developed to try and maximise the likelihood of transmission, including the application of tethers several metres long so the shark only has to be relatively near the surface for the tag to break it (e.g. (Gifford *et al.* 2007)), or by clamping the tag to the apex of the dorsal fin such that a semi-rigid transmission aerial protrudes above it (Weng *et al.* 2005).

Although satellite tags transmit continuously while at the surface, the accuracy of the location estimates obtained, referred to as the location class, is limited by the time spent at the surface and surveillance coverage of the Argos satellite system (Eckert & Stewart 2001). Data

collection relies on surfacing while a satellite is available; there are only two Argos satellites that orbit every 101 minutes, which can detect signals between 6 and 28 times per day depending on the latitude (Eckert & Stewart 2001). The location of the transmitter is calculated via the Doppler shift of successive transmissions during a single orbit, with timing and number of transmissions within that orbit determining the quality of the location class (Eckert & Stewart 2001). The location classes available are 3, 2, 1, A and B, with 3 providing the highest accuracy (to within 250 m of the individual's real position) and B the worst (within ~10 km; (Hays *et al.* 2001; Hazel 2009)). There is another location class, Z, where no position can be calculated, but the general area (within thousands of kilometres) of the tag can be determined by the time at which it was detected and knowing which satellite made the detection (Heithaus *et al.* 2007). Unfortunately in many cases less accurate data have to be used for large fish species as they tend not to surface too often or for long periods, making satellite telemetry better suited for animals likely to move at scales larger than the location class errors - insights can still be obtained from rare uplinks if they occur over large distances (Heithaus *et al.* 2007). Feasibility of displacement estimates is often assessed by comparison with known movement rates, although issues arise from long periods without up-linking as the intervening time may have contained large movements that go undetected (Heithaus *et al.* 2007).

2.2.2 Acoustic Telemetry

As with the aforementioned satellite telemetry, remote sensing is traditionally performed using radio waves for communication between emitter and receiver, however a number of problems make this inappropriate for use in aquatic environments. Electromagnetic energy is rapidly absorbed and scattered as it passes through water, eliminating it as a suitable transmission medium for sub-surface tags on non-surfacing elasmobranchs (Voegeli *et al.* 2001). In addition to being attenuated, radio signals are also reflected from the sea surface (Wilson *et al.* 2006). Consequently acoustic signals in the ultrasonic range of 30–100 kHz tend

to be used for localised telemetry as these are above most animal auditory ranges and transmit with low energy loss through seawater (Nelson 1976). Originally individual sharks were identified according to the frequency of the transmitter or ping interval, but now codes based on the ping interval, such as random repeat infrequent codes (RCODE) are used for more reliable identification (Voegeli *et al.* 2001). RCODE transmitters are exceptionally useful, as the random interval minimises detection collisions on monitors that identify tags based on ping interval, as if two tags collide on one run of their code they won't on the next (Voegeli *et al.* 2001). Depending on the type of transmitter and battery used, useful life of acoustic transmitters can span days to years. The present study used a mixture of V13s with 180 s nominal delay and V16s with 120 s nominal delay, providing batteries lives of four and 10 years, respectively (Vemco Ltd, Bedford, Canada).

Most of recent acoustic telemetry has been automated with the use of secured receivers *in situ* that continuously listen for signals from ultrasonic tags (Hussey *et al.* 2015). In this manner, arrays of permanent listening stations detect the presence/absence of tagged sharks within the detection radius, whereby multiple receivers, located by GPS, can be used to reconstruct movements retrospectively (Voegeli *et al.* 2001). Fully submerged bottom monitors are effective as they are listening at all times and in all weather conditions, but are more difficult to access than surface moored buoys for battery replacement and data retrieval (Voegeli *et al.* 2001). The present study moored VR2W acoustic receivers (Vemco Ltd, Bedford, Canada) to concrete blocks using steel chain and line, attached to a float approximately 5 m above the bottom (Figure 4). The acoustic receiver would be cable tied to the line, sitting 1–2 m off the bottom. Also attached to each receiver mooring was a temperature logger, providing a temperature reading every 10 minutes (HOBO Water Temperature Pro v2 Data Logger, Onset, Bourne, USA). Each receiver had to be retrieved on SCUBA to have its detection record downloaded to a laptop every few months, as well as its battery replaced annually.

Temperature loggers were also downloaded at the same time using an underwater shuttle. To ensure no gaps in the detection records, receivers were swapped out underwater, with the time and date of the swap carefully recorded so that detection data were assigned to the correct location.

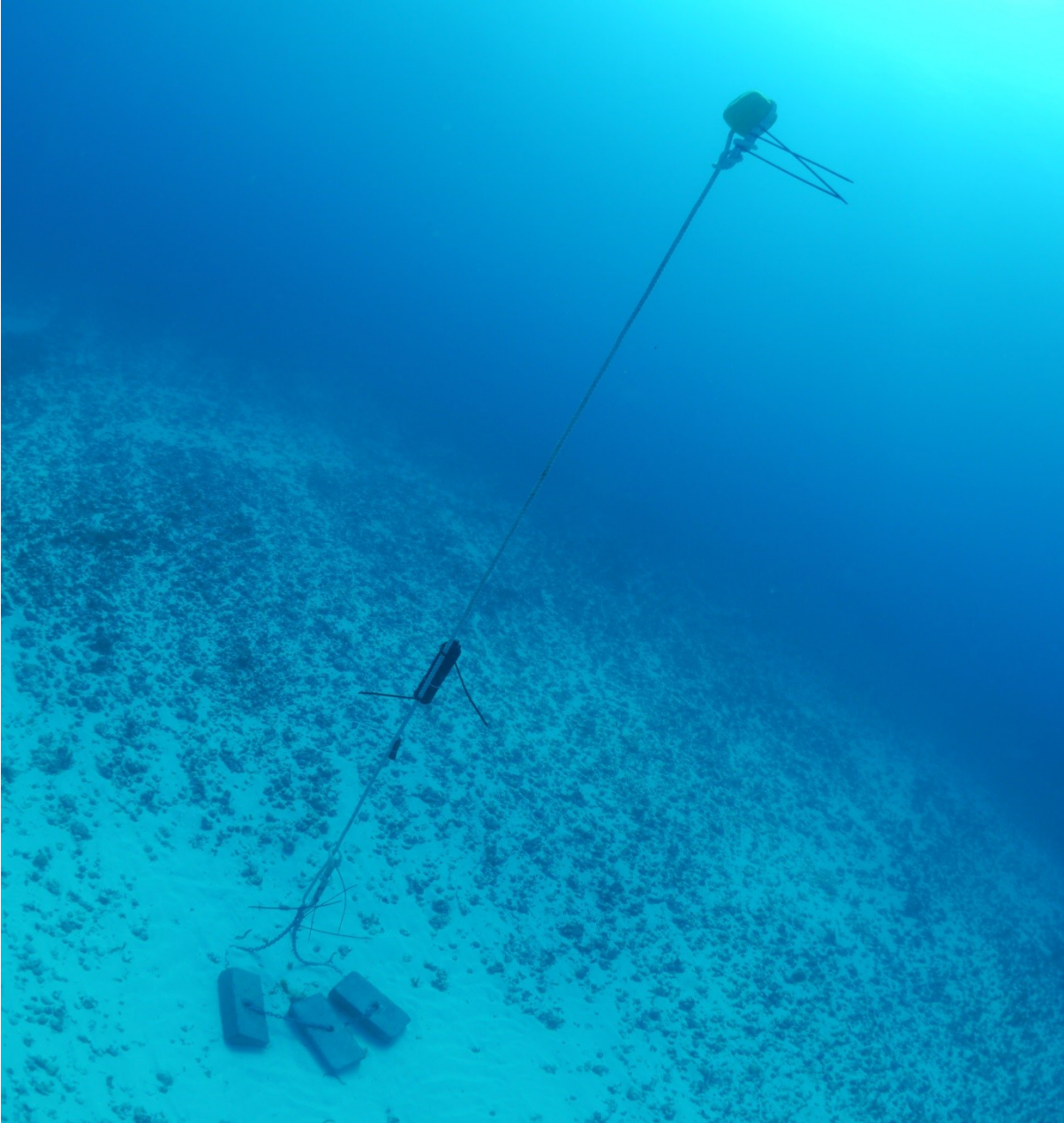


Figure 4: Image of an acoustic receiver mooring with VR2W and temperature logger in situ.

2.3 Shark Capture and handling

Applying a transmitter to a shark first requires its capture. Several different capture techniques were used over the course of the thesis, but shark handling procedures were consistent. Sharks were generally caught using baited hooks, set on scientific longlines, rod-and-reel, drumlines or handlines. Circle hooks, as opposed to traditional J-hooks, were used to minimise the incidence of animals being hooked in the gut – circle hooks are designed to hook fish in the corner of the mouth (Cooke & Suski 2004). This should improve post-release survival as it is much easier to remove a hook from the mouth than the gut. All hooks were also de-barbed to facilitate their removal.

Scientific longlines were predominantly used in shallow habitats (<6 m), where a 100 m line was anchored to the substrate at both ends, with 10 hooks set along it at regular intervals (Figure 5). Floats were placed along the line to keep it off the bottom. Each hook was on a 2 m 'gangion': this is where the hook is attached to some metal trace to mitigate bites, the trace is then attached via a swivel to some monofilament to make the line harder to see for the fish, the monofilament is then attached (again via a swivel) to a short piece of line, making the gangion easy to handle. Each gangion is attached to the main longline using a tuna clip, allowing it to be separated from the main line when a shark is caught. To avoid any captured sharks waiting on the line, small floats were attached to each gangion, which were pulled under whenever a shark took the bait. Once a longline was set, it would be left to soak for one hour, with the research vessel waiting nearby to watch the floats and deal with any caught sharks. In the event of capture (signalled by a submersed float), the research vessel would approach the line and an extension line (with a tuna clip) would be clipped onto the gangion. The gangion could then be removed from the longline, allowing the boat to drift away with the shark, without interfering with the longline. The boat would then be anchored when clear of the line and the shark drawn in to be worked up.



Figure 5: Image shows a longline set in the lagoon of St Joseph Atoll, Seychelles.

Alternative capture methods included rod-and-reel, drumlines or handlines. Traditional rod-and-reel from the research vessel was used to capture some sharks, using metal trace attached to the end of the monofilament to prevent the line being bitten through. When a shark was caught it would be gradually reeled in to the boat, allowing the workup to commence. Handlining was performed in a similar fashion: a baited hook with metal trace was attached to the end of a line and lowered into the water from the research vessel. When a shark took the bait, it could simply be pulled in by hand to allow for the workup. Drumlining was used for larger sharks, and involved suspending the baited hook and line from a large float or drum – any shark caught would then initially tire fighting the large float, allowing the research vessel to then pick up the drumline and pull the shark in to be worked up.

Where possible, another capture method was used that did not involve hooking the sharks: manually lassoing them by the tail whilst SCUBA diving. Ground bait was used to chum the

water and bring the sharks close enough to capture: a premade noose carried by a diver would be placed over the caudal fin of the shark and tightened (Figure 6). This noose was also attached to the research vessel, allowing the shark to be drawn up to the boat and worked up.



Figure 6: Image shows a tawny nurse shark being captured on SCUBA using a lasso. Photograph by Kyle Gordon.

The workup and shark handling techniques were universal for all capture methods and species. Once the captured shark had been brought up alongside the research vessel, it would be restrained by tying a rope around the base of its caudal fin (or pectoral fin, if caught on SCUBA). This provided control over both the head and tail of the shark, allowing it to be positioned appropriately alongside the research vessel for the workup. The head would always be orientated towards the bow of the boat so that the current maintained water flow over the gills. If the boat was not anchored (e.g. water too deep), a salt water pump was placed into the shark's mouth to maintain water flow over the gills. Once in position, the lines would be tied off and the shark rolled over such that its ventral surface faced up. In this position the shark

goes into a state called tonic immobility, where it relaxes and stops responding to most stimuli (Watsky & Gruber 1990; Brooks *et al.* 2011), making the subsequent workup significantly easier, quicker, and less stressful.

If the shark were to receive an acoustic transmitter, this was usually done first while the shark was upside down and in tonic immobility. Acoustic transmitters (either V13 180 s nominal delay or V16 120 s nominal delay, Vemco Ltd, Bedford, Canada) were surgically implanted into the shark's abdominal cavity, via a small incision (~2.5 cm) made through the abdominal wall (Figure 7). The small incision was closed with three sutures (Ethibond Excel 4 x 75 cm non-absorbable coated, Ethicon Inc., Somerville, USA). A small tissue sample (~1 cm) would then be taken from the tip of the shark's anal fin for genetic analysis by collaborators. This also served as an indicator of previous surgery if a tagged shark was recaptured, as the incisions healed so well – a shark recaptured nine days after tagging was almost fully healed. While upside down the shark's sex was noted, as well as notable features that may indicate sexual maturity (e.g. calcified claspers for males, mating scars/abdominal movement for females).



Figure 7: Image showing implantation of an acoustic tag into a shark's abdominal cavity. Photograph by Rainer von Brandis.

The shark would then be rolled over so its dorsal fin faced upwards again. This allowed several length measurements to be taken, all to the nearest centimetre and starting from the tip of the nose. The first was the precaudal length, measured to the precaudal peduncle at the base of the tail. This provides a universal measure of body length, independent of any damage there may be to the caudal fin (e.g. bites). The second is the fork length, measured to where the tail forks, with the third being total length, measured to the tip of the upper caudal. If the shark were to receive a satellite tag, it would be performed at this point due to the easy access to

the dorsal fin. Satellite tags (SPOT5, Wildlife computers, Redmond, Washington, USA) were attached near the tip of the first dorsal fin - using the nylon bolts, steel washers and steel nuts provided by the manufacturer - to maximise chance of signal transmission to overpassing satellites when the animal was near the surface (Figure 8). A drill and template was used to create the holes in the appropriate places (shark fins are predominantly cartilage with very little innervation (Compagno 2001)). The shark would then also be tagged with a small Floy Tag (T-bar anchor, Floy Tag, Seattle, Washington, USA), which was anchored with a small barb under the skin and contained contact details in the event of recapture by someone else.



Figure 8: Image shows a SPOT5 bolted to the first dorsal fin of a tiger shark. Photograph by Daniel Beecham.

With the workup complete, the shark would then be released. First, while the shark was held by the dorsal fin, the hook would be removed using a pair of pliers or bolt-cutters. Then the tail rope would be removed, but the dorsal still held to make sure the shark was swimming before being released. Once swimming, the dorsal would be released, allowing the shark to swim away and be tracked by the corresponding method.

2.4 Track Analysis

The raw data from both types of tag need to be processed before they can be reconstructed into the animal tracks used for subsequent data analysis. The satellite data in particular needs to undergo a geolocation process to ensure the tracks are comparable between individuals, while the acoustic data need to be collated across the receivers into track files that can be exported for analysis. Network analysis, described below, was the primary track analysis technique used for the acoustic data.

2.4.1 *Satellite Tag Geolocation*

As the Argos positions produced by the satellite tags vary in frequency and quality it was necessary to process the data to obtain normalised positions that were comparable between individuals and over time. The raw Argos positions were processed in three steps, each adopted to address a specific issue. Firstly, it was necessary to avoid inclusion of steps between positions that were deemed too large to be biologically plausible. To do this raw positions were analysed point-to-point with a 3 m s^{-1} swim speed filter and 20 km distance filter: any position separated from both adjacent positions by either too great a distance or speed were shifted to a linearly interpolated position between the two (i.e. the most parsimonious location). Positions where either the distance or speed to only one of the adjacent positions was too great were ignored. Secondly, because each raw position has a different error field according to its Argos location class, it was necessary to decide the most

probable location for each point within its error field. This was achieved by using a Bayesian state-space model (SSM) that adjusted the filtered tracks by producing regular positions based on the Argos location class, mean turning angle, and autocorrelation in speed and direction, producing the most probable track through the error fields (Jonsen, Flemming & Myers 2005; Jonsen, Myers & James 2007). The SSMs were applied to the tracks of each individual tiger shark using the R software package (R Foundation for Statistical Computing, Vienna, Austria), primarily using packages 'bsam', supported by 'winBugs', 'snow', 'dclone' and 'rjags' (Jonsen *et al.* 2005, 2007). Given that 80.1% of gaps between positions in the present tracks were under 12 hours (Figure 9), a time step of 12 hours was used in the SSM to produce two positions per day for each shark's track. However, the SSM produces regular positions for the entire track, even on days where there were no raw positions. Consequently all positions for days on which there were no real Argos transmissions were deleted. This step resulted in the normalised track positions and formed the dataset used for the plotting of positions on maps by season and plotting latitude over time to display how the distribution of animals changes over time.

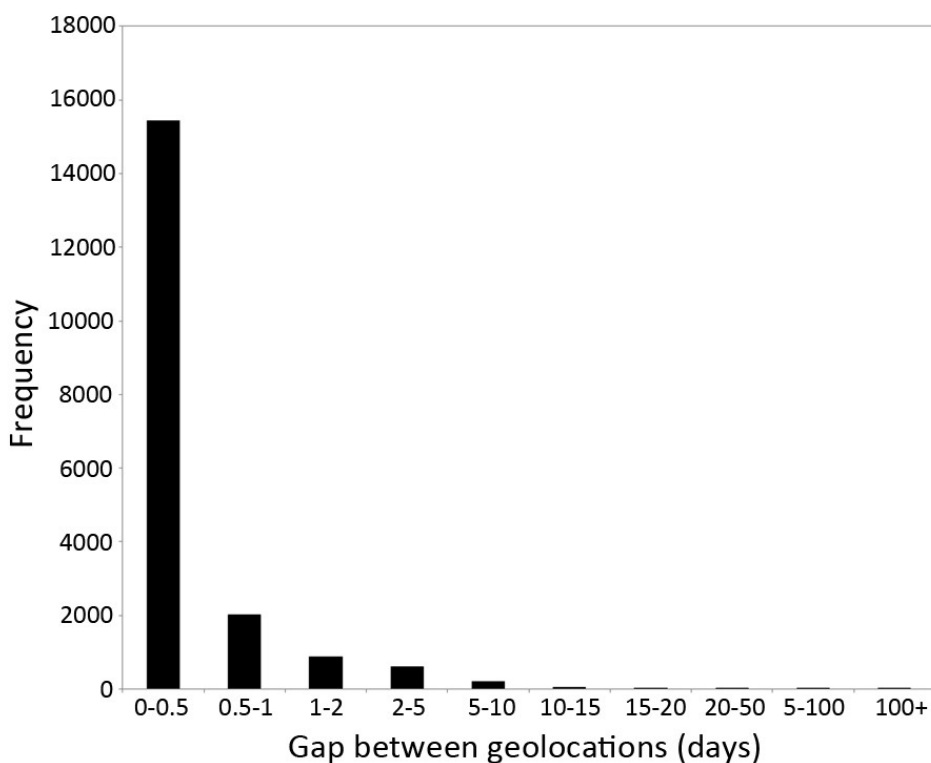


Figure 9: Frequency distribution of time between subsequent geolocations for all sharks.

Argos tracks only have locations for when the sharks were at the surface; consequently there is high variability in the number of locations in a given area, as a result of the shark's varied surfacing behaviour rather than because of its actual location. This would introduce a bias into the analysis of time spent in different areas. To correct this bias, linear interpolation was used to normalise the transmission frequency by generating points at 12 hour intervals along track gaps of <20 days. Where gaps >20 days were encountered the track was split into sections to avoid spurious interpolation. Moreover, in order for space-use analyses to be as conservative as possible, all were conducted at a grid resolution of 0.5°×0.5°, greater than the reported errors of the worst location class (B, ~10 km; (Hays *et al.* 2001; Hazel 2009)). Examples of how track positions varied between each processing step can be found in Figure 10.

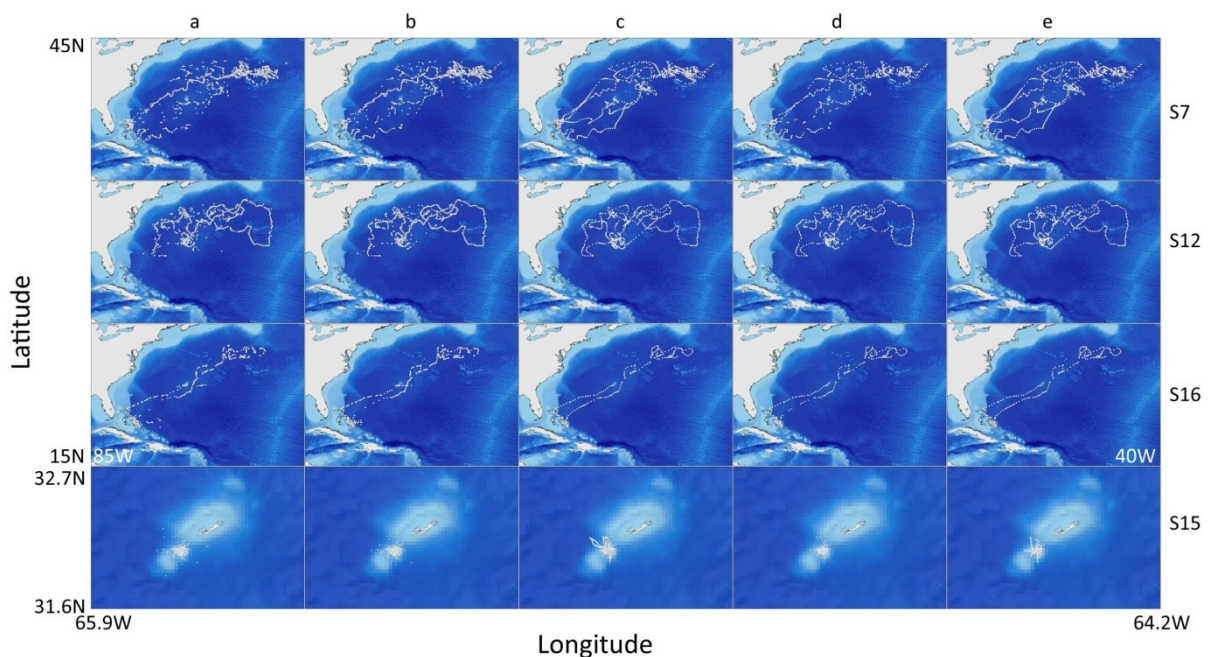


Figure 10: Maps to show how the positions varied between each stage of track processing for four different sharks (S7, large male; S12 small female; S15 small male; S16 large female): a = raw Argos positions, b = speed filtered positions, c = SSM positions, d = SSM positions with interpolation on data-less days, e = SSM positions with linear interpolation across gaps <20 days. Maps created in ArcGIS, using GSHHG coastline data and ETOPO2v2 bathymetry data.

To determine track sections with higher turning frequency from those with more directed movement, the 'straightness' of individual trajectories was calculated for successive 12 day portions of each SSM processed, linearly interpolated track, where:

Straightness = displacement over 12 days / distance travelled over 12 days

Values closer to 1 indicate periods of straighter movement, and values closer to 0 indicate periods of higher turning frequency, providing a proxy for station-keeping or area-restricted searching (foraging) behaviour (Sims 2010). Straightness was calculated over 12 day periods as this was, on average, the time taken for the sharks to traverse a distance greater than the error of the worst location class (B, ~10 km; (Hays *et al.* 2001; Hazel 2009)).

2.4.2 Acoustic Network Analysis

Acoustic arrays have the potential to provide vast quantities of data, however in turn this requires extensive database management (Lowe, Wetherbee & Meyer 2006). All downloaded detections were imported into a Microsoft Access (Microsoft Corporation, Redmond, USA) database, which assigned transmitter detections (pings) to the appropriate sharks and receiver locations, and filtered out any pings that did not match an active tag or receiver (i.e. false positives). Receiver clock-drift time corrections were also made during the import process, being calculated from the difference between the receiver and PC clock at the time of download, assuming linear drift. Tags were detected within ~150 m of the receiver, as determined by range testing: mean range 165 m \pm 33 (S.D.). This database could then be queried to extract track data under any selection criteria, e.g. by species, size, sex etc.

Network analysis was used to determine both where sharks spent more time and how they moved through the array (Jacoby *et al.* 2012). Each receiver location was treated as a node within the network, with node strength weighted according to the number of detections at that location. Any pair of subsequent pings that occurred between different nodes was treated as a connection between those nodes, with connection strength weighted by the number of

times that specific pairing occurred. In this way matrices were constructed that detailed the connections between receivers and the detections at each receiver, allowing networks to be constructed and graphed to visualise shark movements and occupancy throughout the array for each species.

Due to the different ping frequencies of the V13 and V16 tags (180 s vs. 120 s nominal delays), the node and connection strengths of V13 networks were increased by 50% to account for the decreased probability of detection compared to the V16 networks. All network maps were produced using ArcGIS (ESRI Inc., CA, USA), with bathymetry data obtained from the U.S. Department of Commerce, National Oceanic and Atmospheric Administration (NOAA): 2-minute Gridded Global Relief Data (ETOPO2v2).

Several network metrics were used to describe each network: occupancy (or node strength) was computed from the number of detections occurring at each node and provided a measure of how much time individuals spent at each receiver location. Connectivity (or node centrality) is calculated from the total number of connections made to that node, i.e. the proportion of other nodes to which there is a connection. Transit (or node betweenness) represents the total number of paths to pass through that node and is computed by counting pings occurring at a receiver where the prior and subsequent pings for that individual occur at a different receiver. Transit therefore measures the extent to which a node is part of a corridor of movement as opposed to an area of occupancy. Node density is the proportion of total available nodes actually used in the network, measuring the extent of the array occupied, and edge density is the proportion of total available connections actually formed within the network, providing a measure of mobility within the network, both ranging 0–1.

3 Migratory behaviour and philopatry of tiger sharks *Galeocerdo cuvier* in the Atlantic Ocean

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3.1 Introduction

The increased availability of remote telemetry and biologging systems in recent years has enabled many studies tracking marine predators, such as turtles, seabirds and marine mammals, many of which reveal long-distance movements consistent with population-level migration (González-Solís *et al.* 2007; Block *et al.* 2011; Hays & Scott 2013). By comparison, a general understanding of migratory behaviour in large sharks is less well developed, including whether sharks fit the more classical migratory behaviour exemplified by many turtles, bony fish, birds and mammals. One reason for this knowledge gap is that few studies have achieved sufficiently long-term, multi-year tracks to detect repeated seasonal patterns (Weng *et al.* 2008; Jorgensen *et al.* 2009; Block *et al.* 2011; Domeier & Nasby-Lucas 2013; Papastamatiou *et al.* 2013), with only one in the Atlantic Ocean (Hammerschlag *et al.* 2012; Howey-Jordan *et al.* 2013; Vandeperre *et al.* 2014). Determining the timing, repeatability and potential motivations for annual movements of large sharks is necessary to understand the ecological and evolutionary role of such behaviour more generally in marine predators.

More reliable interpretation of population size trends from shark fishery catch data will benefit from identifying the migratory ranges, routes and residency patterns of exploited species, particularly in the Atlantic where an increasing appreciation of the spatial dynamics between sharks and fishing fleets shows their overlap to be exceptionally high (Queiroz *et al.* 2016). With few exceptions (e.g. white shark *Carcharodon carcharias* (Jorgensen *et al.* 2009; Domeier & Nasby-Lucas 2013); salmon shark *Lamna ditropis* (Weng *et al.* 2008)), detailed movement information remains unknown for most large shark species, making it very difficult to assess the potential efficacy of oceanic Marine Protected Areas (MPAs) for these highly mobile species (Game *et al.* 2009).

The tiger shark *Galeocerdo cuvier* (Péron & Lesueur, 1822) is an interesting and suitable species to investigate migratory patterns because it is one of the largest predatory sharks, reaching up to ~5.5 m in length and ~600 kg in mass, and is found circumglobally in tropical and warm temperate coastal/pelagic waters (Compagno 2001). It is taken by coastal and offshore fisheries, and is listed as *Near Threatened* in the Red List of the International Union for Conservation of Nature (IUCN) (Simpfendorfer 2009). Surprisingly however, there is a deficit of detailed, long-term information on its spatial behaviour, particularly in the Atlantic Ocean (Hammerschlag *et al.* 2012; Vaudo *et al.* 2014). The tiger shark typically occupies the highest trophic level available where it occurs, often being the sole predator on a wide range of other large, highly mobile marine vertebrates (e.g. marine mammals, turtles, other elasmobranchs) (Lowe *et al.* 1996; Simpfendorfer, Goodreid & McAuley 2001; Matich, Heithaus & Layman 2011; Heithaus *et al.* 2013). Moreover, tiger sharks have a very cosmopolitan diet and, consequently, are highly connected in marine food webs, displaying a wide niche breadth that is mostly attributable to high individual variation in prey consumed and depth utilisation (Matich *et al.* 2011; Vaudo *et al.* 2014). A wide niche breadth of a predator could indicate an adaptation allowing it to remain within relatively localised areas,

thus foregoing the necessity for seasonal migration to specific foraging grounds to feed on seasonally abundant prey. A few long-distance movements have been documented for individual tiger sharks (Kohler, Casey & Turner 1998; Heithaus *et al.* 2007; Hammerschlag *et al.* 2012; Papastamatiou *et al.* 2013; Werry *et al.* 2014; Vaudo *et al.* 2014), but detailed spatial behaviour recorded over multiple years consistent with more classical migratory patterns between discrete focal habitats across seasons has not been described.

This chapter uses long-term satellite tracking of tiger sharks to determine movement patterns across multiple years, including examination of whether a large, marine predator with high intraspecific variability in diet and vertical habitat use shows any predictable migratory behaviour.

3.2 Methods

The study site for this chapter was Challenger Bank near Bermuda, as described in the General Methods (Chapter 2). Between August 2009 and July 2012, 24 tiger sharks were tagged with Argos satellite platform terminal transmitters, or PTTs (SPOT5, Wildlife Computers, Redmond, Washington, USA), as described in the General Methods (Chapter 2).

As Argos positions vary in frequency and quality it was necessary to process the data to obtain normalised positions that were comparable between individuals and over time. This was achieved following the satellite telemetry geolocation techniques outlines in Chapter 2. The mean distance travelled per month was also calculated for each individual, and correlated with individual total length using a Spearman's rank correlation (SigmaPlot, Systat Software, San Jose, CA).

To perform analyses on space-use and movement behaviour, the state-space model (SSM) normalised, linear interpolated tracks were plotted on a $0.5^{\circ} \times 0.5^{\circ}$ grid cell in ArcGIS (ESRI Inc., CA, USA). Coastline and bathymetry data were obtained from the U.S. Department of Commerce, National Oceanic and Atmospheric Administration (NOAA): coastlines from the Global Self-consistent, Hierarchical, High-resolution Geography Database (GSHHG) and bathymetry from the 2-minute Gridded Global Relief Data (ETOPO2v2). Sea surface temperature (SST) data were obtained from the Operational Sea Surface Temperature and Sea Ice Analysis (OSTIA) system via the U.K. National Centre for Ocean Forecasting. All maps were created using the Plate Carrée projection.

The total time spent within each cell (occupancy) was calculated by summing the number of 12-hourly points located within cells. The mean straightness for each $0.5^{\circ} \times 0.5^{\circ}$ cell was calculated by averaging the straightness values associated with points located within them.

This was performed for all sharks combined as well as individuals, and for both complete tracks and tracks separated by season to address any seasonality in distribution. The seasons were defined as follows: Winter, Dec–Feb; Spring, Mar–May; Summer, Jun–Aug; Autumn, Sep–Nov. When occupancy was calculated for all sharks combined, the results were corrected for tagging location by dividing the occupancy value for each 0.5°×0.5° cell by the number of tags active in that cell. In addition, the speed of travel between successive locations was calculated for each track, and then averaged across all sharks within each 0.5°×0.5° grid cell to produce a map of mean rate of movement across the study area. The overall geographical range of tracked sharks was calculated in ArcGIS using the 95% isopleth of the kernel density estimate for all locations.

For qualitative comparison of seasonal distribution of locations with sea surface temperature (SST), track locations were overlaid in ArcGIS on seasonal SST means throughout the northwest Atlantic. In addition, the mean monthly SST for 5°×2° areas at the northern and southern extents of the tracked sharks' range were calculated to examine the SSTs likely experienced by sharks at the surface when in those areas compared to the typical annual variation in SST. The bounding for the northern extent was 37–39 °N by 62–57 °W, and for the southern extent was 24–26 °N by 76–71 °W.

A number of sharks displayed focused space-use in both winter and summer, so potential philopatry was tested for in individuals with sufficiently long tracks to cover repeat seasons ($n = 9$ sharks). First, central locations were calculated for individuals for each winter and summer period, defined as the central point, or centroid, of the 5% isopleth of the kernel density estimate for that season, and calculated using Geospatial Modelling Environment (Beyer 2011). Season-to-season centroid displacement was then plotted against intervening centroid

displacement for both successive winters and summers to test the spatial resolution at which sharks returned to a particular location given the intervening long-distance migration.

Through collaboration with Instituto de Investigaciones Marinas, Spain, it was possible to opportunistically retain the stomachs of the five tiger sharks caught by a Spanish commercial long-lining vessel operating in the northwest Atlantic in 2012 for contents analysis. The stomachs appeared to predominantly contain juvenile loggerhead turtles *Caretta caretta*, and so maps of spatial and temporal variation in the straightness index were compared to the locations of juvenile loggerhead turtles as determined by satellite tracks reported in McClellan and Read (2007) and Mansfield *et al.* (2009). The loggerhead tracks were digitised using ArcGIS, where they were projected to the correct spatial reference and had their features recreated manually. To quantify any spatial overlap, the percentage of 0.5°×0.5° grid cells in which both tiger sharks and loggerhead turtles were tracked was calculated in ArcGIS.

3.3 Results

A total of 24 tiger sharks, 20 of which were male, varying in total length from 1.73 to 3.96 m were tagged (mean 3.03 m; Table 2). Overall, tiger shark movements were tracked for a total of 411 months (mean 17.1 months), providing over 150,197 tracking days and covering an estimated distance of 356,085 km (mean 14,836 km), averaging 865.3 km month⁻¹. Tracking periods for individual sharks ranged from 41 to 1101 days (mean 514 d), generating between 19 and 2404 geolocations (mean 821) of varied Argos location class. Four individuals experienced intermediate transmission absences of 100 days or more.

Table 2: Summary data for 24 tiger sharks tagged with SPOT5 transmitters at Challenger Bank, Bermuda.

ID	Sex	TL (cm)	Date tagged	Overall Detection Period (months)	Total Locations	Minimum distance (km)	Minimum distance/month (km)
1	m	343	31-08-09	36.7	1163	42996	1172
2	m	334	19-07-09	32.6	83	9413	289
3	m	313	02-08-09	26.9	401	10540	392
4	m	361	29-07-10	25.8	1985	41158	1597
5	m	244	28-07-10	25.6	94	2431	95
6	m	295	03-08-09	24.9	1433	27723	1113
7	m	384	11-09-10	24.9	2404	31677	1274
8	m	371	07-09-10	24.8	809	26265	1058
9	m	333	28-07-10	24.6	1871	25066	1018
10	m	274	27-07-10	20.2	1628	19914	986
11	m	330	25-07-10	18.6	928	25012	1342
12	f	259	24-10-10	17.3	2352	19517	1128
13	m	259	14-10-10	14.0	335	7725	553
14	m	396	27-07-10	13.7	563	13081	953
15	m	216	18-08-10	13.4	285	622	46
16	f	354	16-08-09	13.1	1263	12197	933
17	m	346	05-08-09	13.0	312	15623	1199
18	m	292	25-07-09	12.2	279	5200	426
19	m	351	24-07-10	10.2	523	13083	1287
20	f	173	21-11-11	7.2	452	1292	179
21	m	305	28-07-10	5.9	19	1624	275
22	f	233	10-07-12	2.8	446	2224	804
23	m	348	28-07-10	1.9	38	1417	759
24	m	323	05-09-10	1.4	49	284	208

Tiger sharks tagged at Bermuda displayed extensive space-use throughout the northwest Atlantic, ranging between latitudes of 17–40° N and longitudes of 48–79° W (Figure 11), covering 6.7 million km², as determined by the 95% isopleth of a kernel density plot for all sharks. This varied seasonally, however, revealing long-distance north-south migrations (Figure 11). Locations occupied during winter were primarily associated with coral reef-bound islands in the Bahamas, Turks and Caicos Islands, and Anguilla/Saint Martin. None of the tiger sharks was recorded entering the Caribbean Sea, nor crossing the mid-Atlantic Ridge. In contrast, during summer the majority of sharks adopted an oceanic habit, with most occupying open water north or northeast of Bermuda. There was a more dispersed distribution of locations in both spring (sharks generally moving north) and autumn (generally moving south), representing migratory transitions between the winter insular and summer oceanic phases.

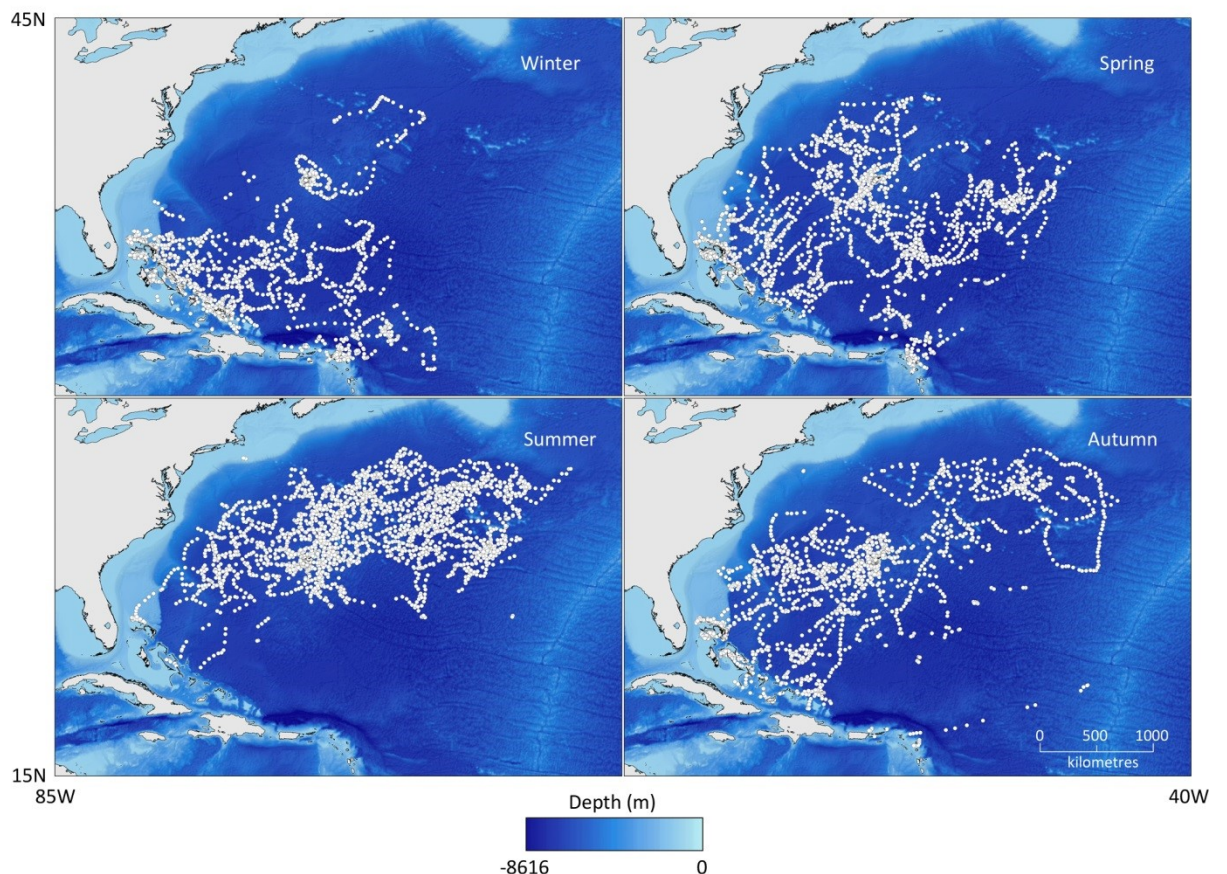


Figure 11: SSM adjusted geolocations for all tiger sharks separated by season and overlaid on bathymetry.

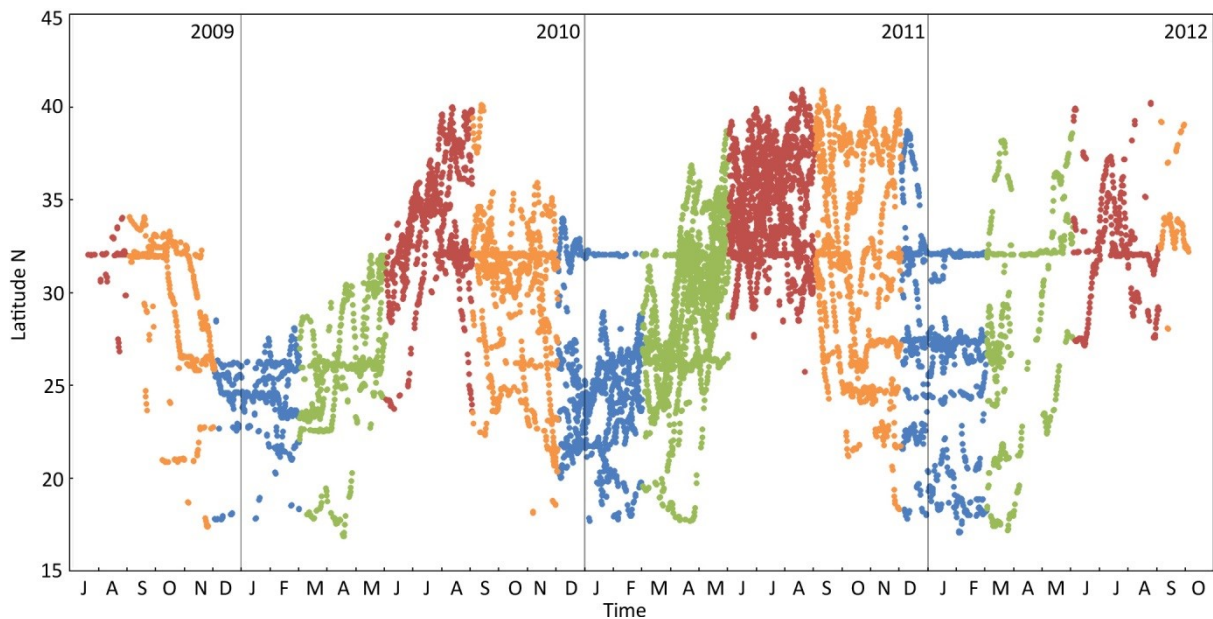


Figure 12: Latitude of all tiger shark locations over time (2009–2012), colour coded by season (blue = winter; green = spring; red = summer; orange = autumn).

The majority of individuals (16, ranging 273–396 cm TL) displayed a seasonal pattern of considerable latitudinal displacement (up to 2,500 km), between southern islands in winter and northern oceanic areas in summer (Figure 12). The precise timing and duration of these phases varied both between years and individuals. Five individuals did not conform to this general seasonal pattern, staying in the vicinity of Bermuda over winter (Figure 12 and Figure 13). Notably, these were five of the smallest sharks tagged (two females and three males: sharks 5, 12, 13, 15, and 20; 173–259 cm TL; Table 2). The two largest winter residents (12 and 13, both 259 cm TL at tagging) did eventually undertake longer distance movements, but not until eight and eleven months after tagging, respectively, and neither migrated in the first winter season of their tracks. Recorded speeds ranged 0–4 m s⁻¹, but on average individuals travelled at 0.29 m s⁻¹ ±0.18 S.D. In addition, larger individuals tended to travel at increased rates (Spearman’s rank correlation between mean number of kilometres travelled per month and shark total length: $\rho = 0.58$, $p < 0.01$). Both patterns – seasonal migrations and Bermuda winter residence – were displayed by both sexes.

During winter, migratory individuals occupied the warmer, southern waters of the northwest Atlantic, and the expansion in range north during the summer coincides with warmer waters (>25 °C) extending up to the Gulf Stream (Figure 13). The mean SST of the southern insular regions exceeds that of the northern oceanic area throughout the year; however only during late summer and early autumn (July, August, September) does the mean SST in the north exceed the mean winter SST in the southern extent (Figure 14). Consequently, the individuals that undertook the annual north-south migrations occupied waters with surface temperatures of approximately 24–26 °C in both winter and summer, although some experienced lower surface temperatures (18–20 °C), such as those remaining near Bermuda over winter.

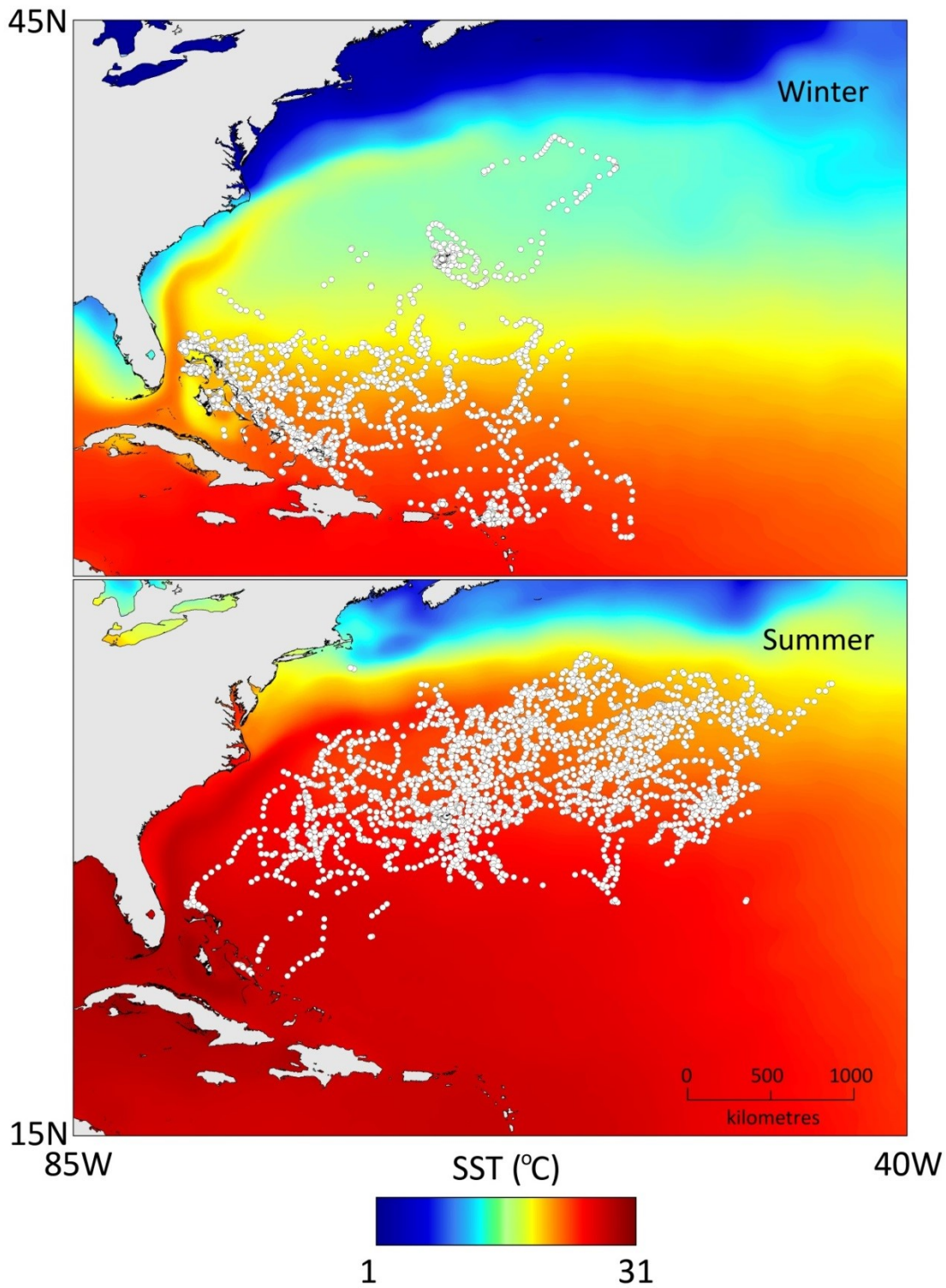


Figure 13: SSM corrected geolocations for all tiger sharks in winter and summer, overlaid on mean seasonal sea surface temperature (SST). Maps created in ArcGIS, using GSHHG coastline data and OSTIA SST data.

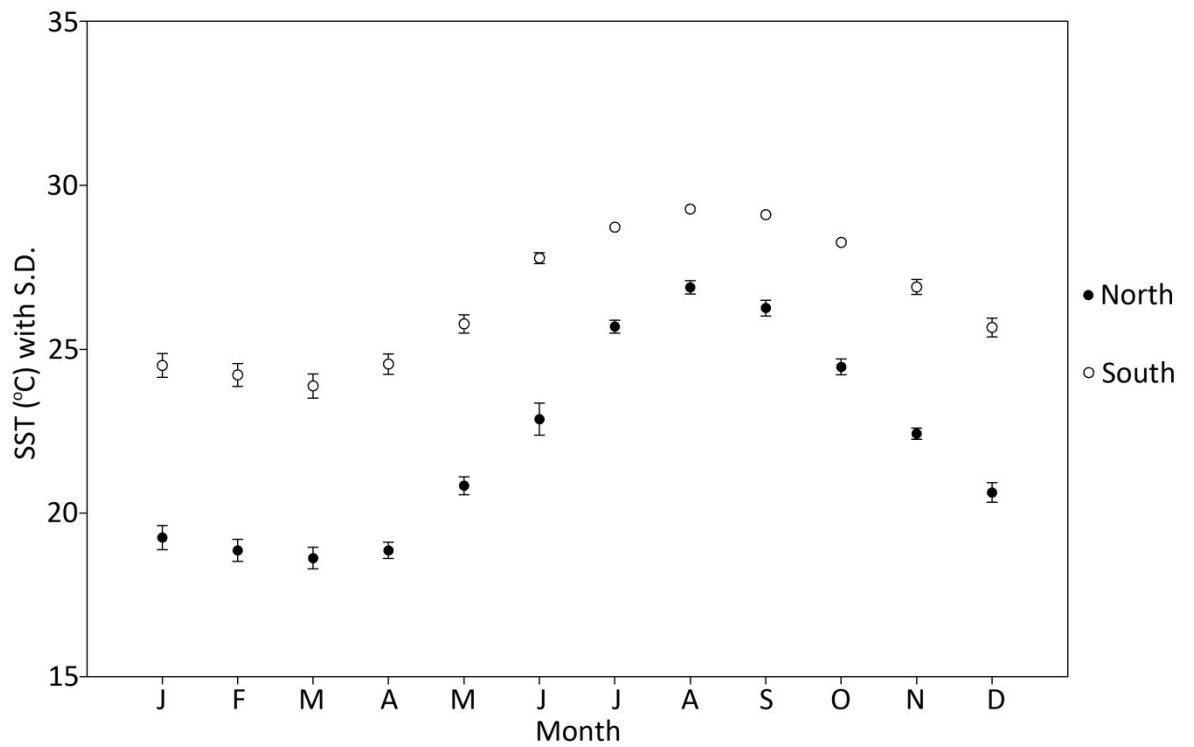


Figure 14: Mean monthly sea surface temperature (SST) for the northern and southern extents of the tracked sharks' range. Error bars represent standard deviation. Figure created using OSTIA SST data.

Despite the very broad overall range of movements by most tiger sharks, occupancy was spatially restricted while in insular southern areas: up to 6–12 weeks within a given 0.5°×0.5° cell (Figure 15). In contrast, occupancy in oceanic areas was considerably more transient. Little time was spent in any given oceanic cell, although there was elevated space-use around Bermuda, especially Challenger Bank, in the northeast of their tracked range.

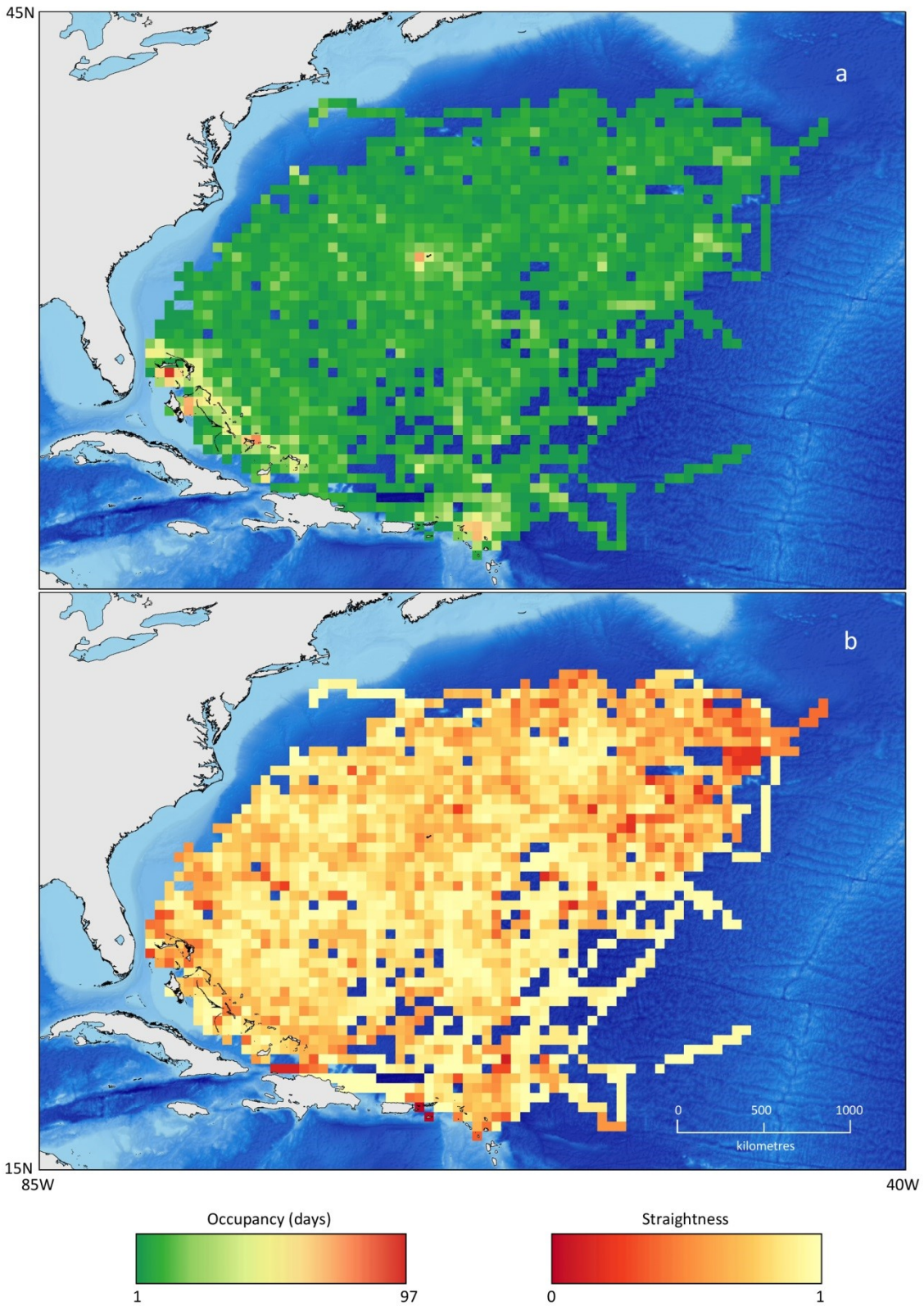


Figure 15: Maps of the overall occupancy (a) and mean straightness of movement (b) for all tiger sharks, overlaid on bathymetry. Maps created in ArcGIS, using GSHHG coastline data and ETOPO2v2 bathymetry data.

Although speed and straightness are not necessarily correlated – high speed and high turning can produce low straightness, while directed slow movements produce high straightness – the tracked sharks typically travelled at slower speeds in areas of high occupancy and low straightness: the lowest speeds were observed around insular reefs in the Caribbean, Bahamas and Bermuda, with higher speeds being recorded in open ocean (Figure 16), where movements were considerably more direct (Figure 15). However, despite low straightness in the northeast of the tracked range, sharks also displayed high speed, possibly due to proximity to the Gulf Stream, where displacement rates may be increased by stronger currents (Carey, Scharold & Kalmijn 1990).

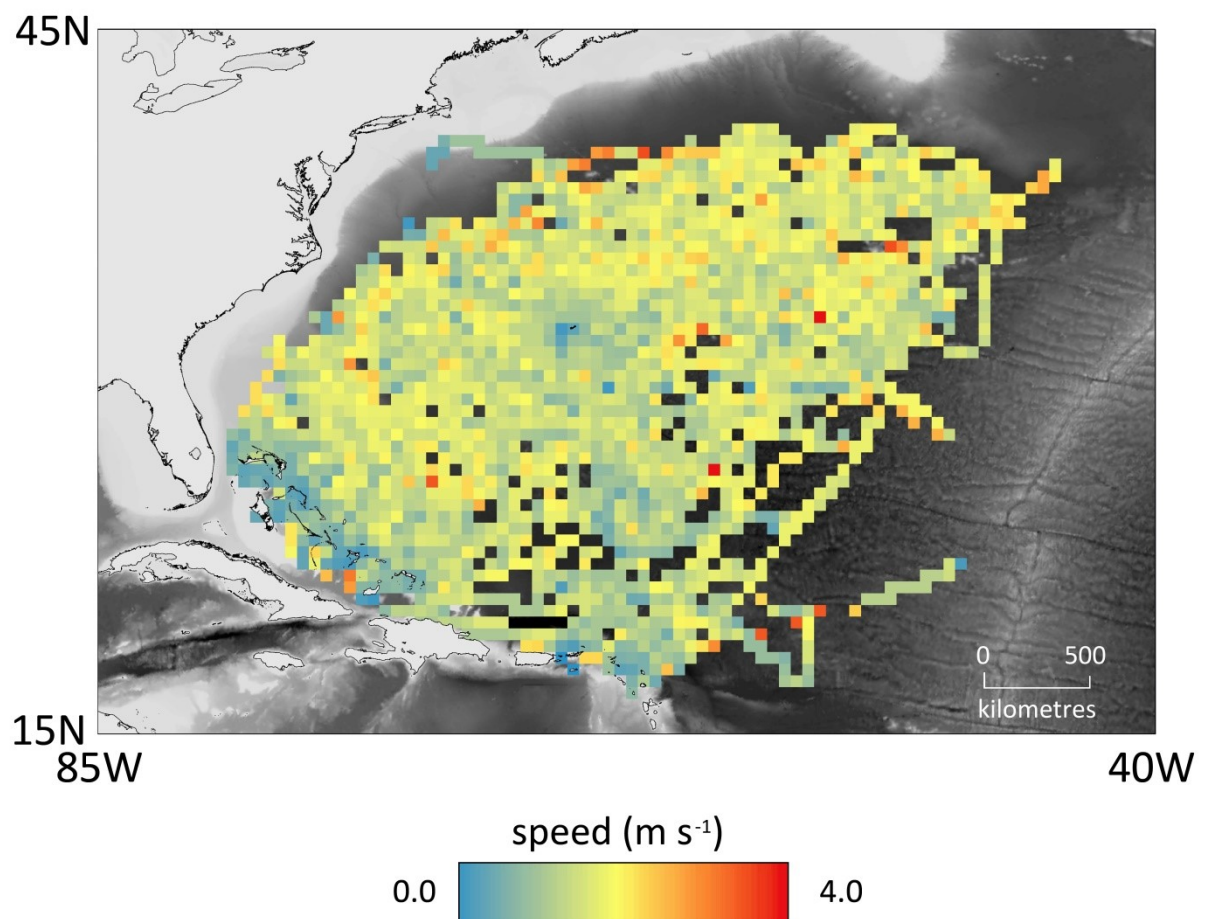


Figure 16: Map of the overall speed for all tiger sharks, overlaid on bathymetry. Maps created in ArcGIS, using GSHHG coastline data and ETOPO2v2 bathymetry data.

There were nine individuals with enough data to investigate seasonal philopatry across years, six of which displayed distinct repeatability in the locality of their space-use. Winter philopatry was high, whilst summer philopatry appeared low (Figure 17). The mean winter-to-winter centroid displacement was 191.4 km (ranging 12.4–1036.2 km, \pm 331.6 S.D.), whereas the mean summer-to-summer centroid was displacement 756.1 km (ranging 51.0–1308.2 km, \pm 386.2 S.D.). The repeated, philopatric migration pattern is exemplified by shark 7, which displayed spatially restricted use of a particular insular region and offshore oceanic regions over 3,500 km away, punctuated by relatively direct dispersals (Figure 18). In both years of its two year track, shark 7 occupied the same area in the Bahamas during winter, displaying a winter-to-winter centroid displacement of only 65.7 km, although its centroid displacement between summers was 819.2 km. Over a three year track, shark 1 displayed similar insular winter philopatry (centroid displacements of 24.3 and 56.2 km), but also some degree of philopatry to offshore areas over 2,500 km away across consecutive summers, with summer-to-summer centroid displacements of 51.0 km and 545.3 km. In contrast, use of insular areas by shark 4 was comparatively dispersed, spending no more than 13 days within any given cell and providing multiple centroids for each season (Figure 19).

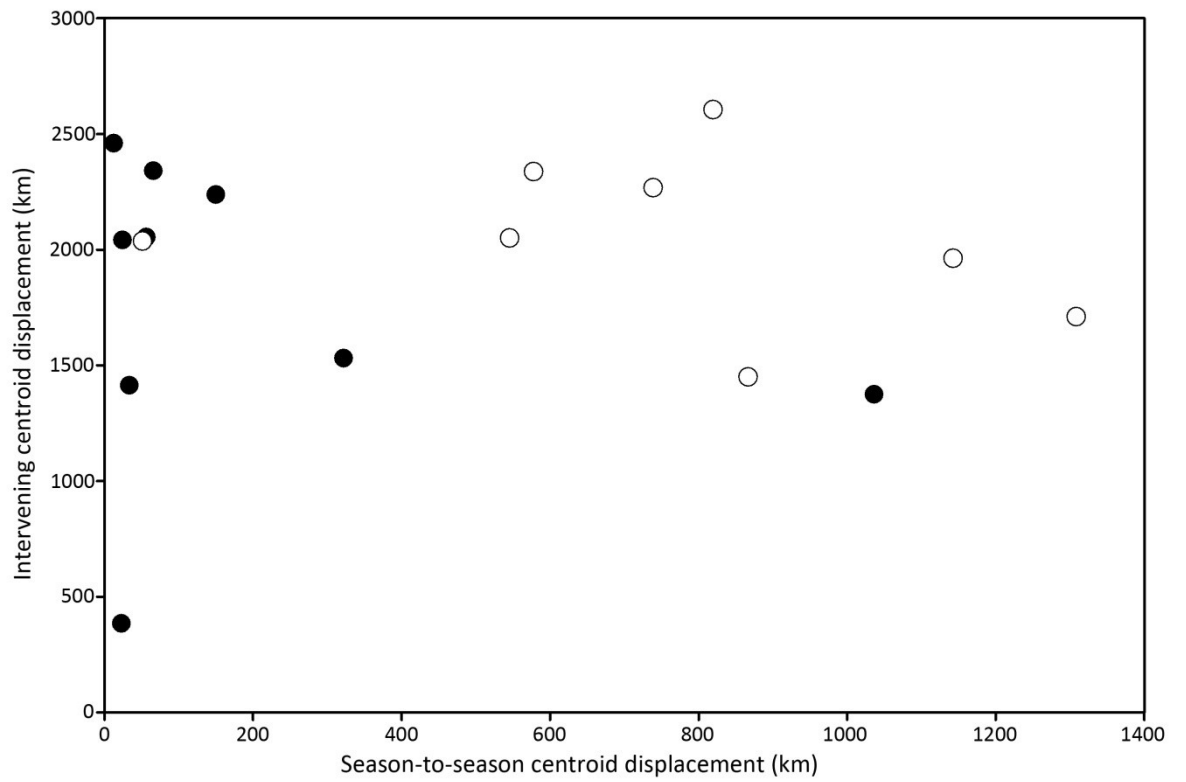


Figure 17: The relation between season-to-season centroid displacement ('●' = winter; '○' summer) and the intervening centroid displacement for both successive winters and summers, from sharks with tracks of two years or more.

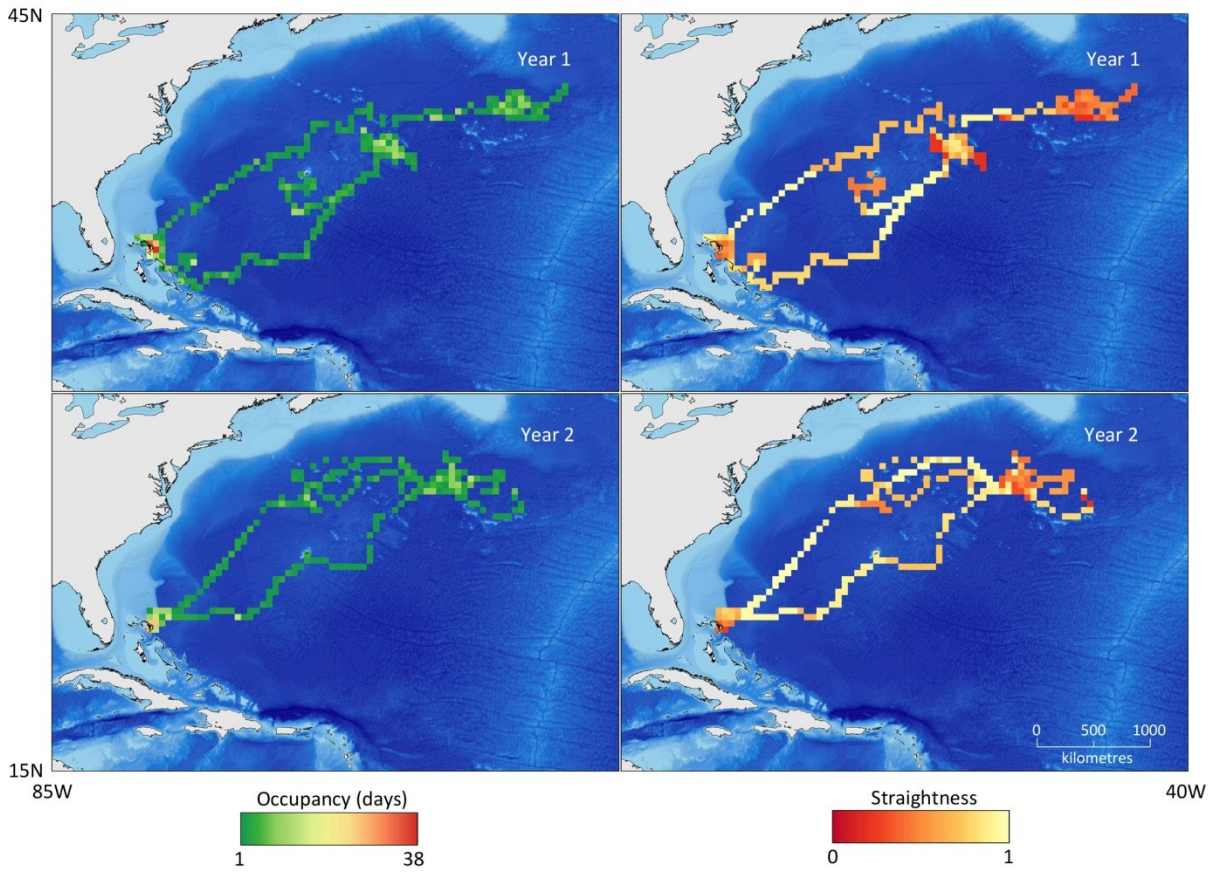


Figure 18: The occupancy and mean straightness of movement for shark 7 (384 cm male) for the first and second year of its track (measured from tagging date).

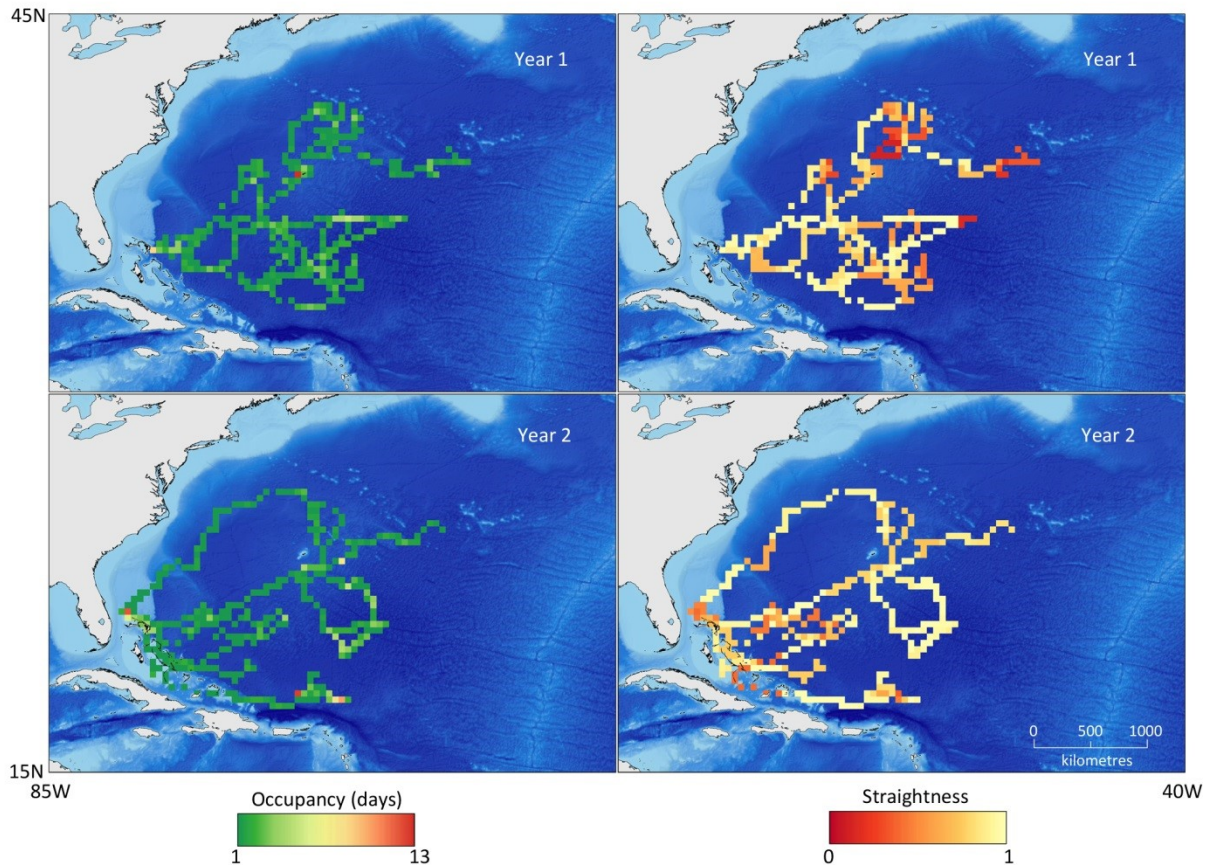


Figure 19: The occupancy and mean straightness of movement for shark 4 (361 cm male) for the first and second year of its track (measured from tagging date). Maps created in ArcGIS, using GSHHG coastline data and ETOPO2v2 bathymetry data.

Movements were generally more directed in the oceanic environment, but were less straight around islands and on the northern edge of the recorded range, adjacent to the Gulf Stream (Figure 15). Despite low occupancy compared to insular regions, the north-eastern area of the tracked sharks' range (south of the Flemish Cap and in the general proximity of the Corner Rise Seamounts) appears to be an area of particularly high turning frequency. Considering only summer straightness of movement emphasises this high turning frequency further (Figure 20). Overlaid with the juvenile loggerhead turtle tracks of McClelland and Read (2007) and Mansfield *et al.* (2009), this area of high turning overlaps with the pelagic distribution of loggerhead turtles both in summer and year round (Figure 20). These turtle tracks overlapped with 37.6% of the $0.5^{\circ} \times 0.5^{\circ}$ cells in which the tiger sharks were recorded during summer. Moreover, the stomachs of four out of five tiger sharks opportunistically sampled from a

commercial long-lining vessel contained loggerhead turtle, including small juveniles consumed whole (Table 3; Figure 20; Figure 21). Loggerhead turtles were also recorded by McClellan and Read (2007) and Mansfield *et al.* (2009) to pass close to Bermuda.

Table 3: Summary data of stomach contents from tiger sharks caught in the West Atlantic by a commercial long liner.

Shark	TL	Sex	Date	Lat	Long	Content (g)	<i>Caretta</i> %	Hydrobatidae %	<i>Balistes</i> %
T1	-	-	-	40	-49	140.8	100.0	-	-
T2	246	f	03-11-12	40.17	-49.11	0.0	-	-	-
T3	234	m	01-11-12	41.09	-48.14	200.8	66.1	0.5	33.9
T4	223	f	03-11-12	39.03	-49.37	92.0	98.9	1.1	-
T5	-	-	-	40	-49	156.8	100.0	-	-

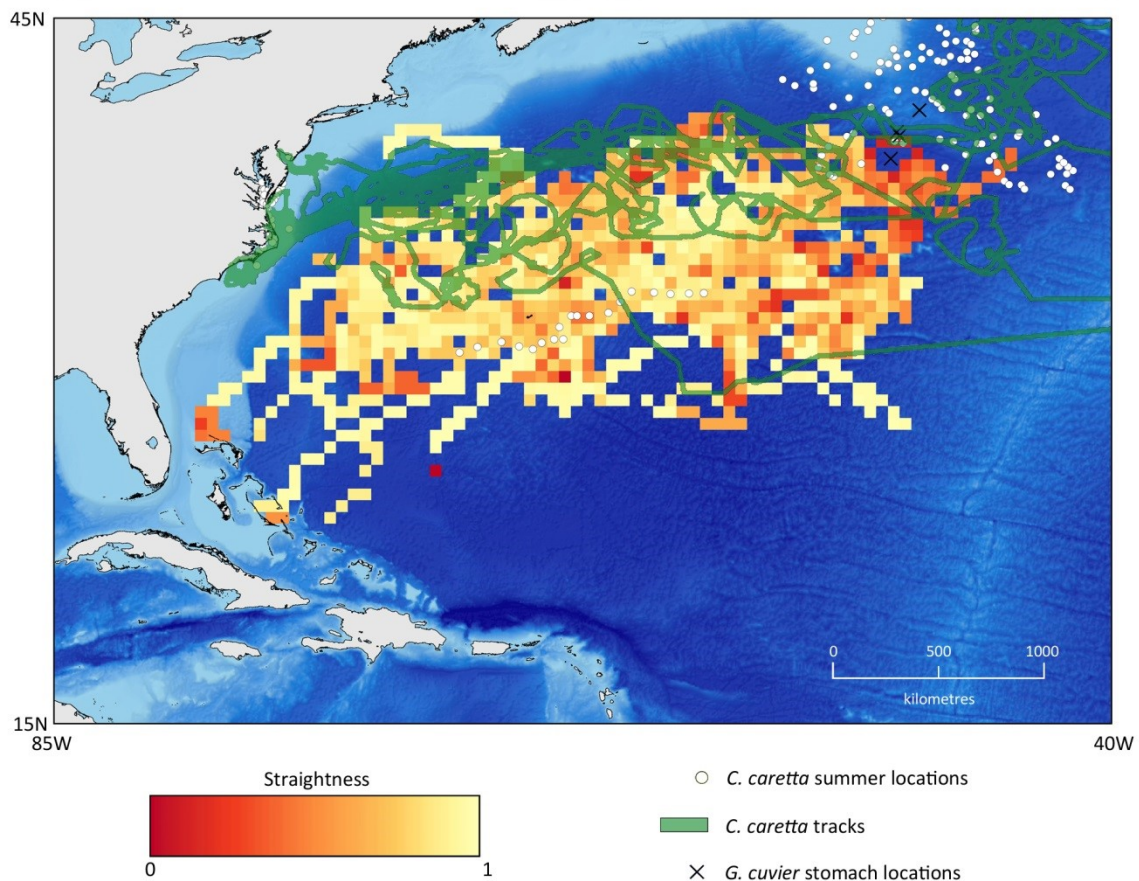


Figure 20: Overall mean straightness of movement in summer, overlaid with juvenile loggerhead turtle summer locations from Mansfield *et al.* (2009) and tracks from McClellan and Read (2007), as well as catch locations of tiger sharks from which stomach contents were obtained.



Figure 21: Image shows a whole juvenile loggerhead turtle found in the stomach of a tiger shark from the northwest Atlantic.

3.4 Discussion

This chapter has revealed remarkable plasticity in habitat use by an apex marine predator, the tiger shark, accomplished by extensive, seasonal migrations between insular, coral reef ecosystems in winter and temperate oceanic, foraging areas in summer. These round-trip migrations span over 7,500 km annually, with individuals displaying marked philopatry to overwintering areas. These migrations are also partial in nature: the five sharks that remained close to Bermuda over winter were all juveniles (including both sexes), whilst all migrants were large males, with the exception of the single mature female tracked. This study also represents the longest (1101 days) reported satellite tracks of tiger shark movements to date (previously 517 days, (Ferreira *et al.* 2015)), and is the first report of annually repeated, distinct seasonal migrations for tiger sharks in the Atlantic, as revealed by tracks spanning multiple years.

3.4.1 Repeated long-distance migration

This study is unusual in obtaining multi-year, high resolution tracks of individual fish migrations (Weng *et al.* 2008; Jorgensen *et al.* 2009; Block *et al.* 2011; Papastamatiou *et al.* 2013; Vandeperre *et al.* 2014). Use of disparate, contrasting habitats is common among diadromous fish, but the repeated switching between such markedly different ecosystems (in terms of thermal regime, bathymetry, structural complexity and insular coral reef to oceanic ecosystems) as shown here for the tiger shark is not commonly reported for marine fish species. Consequently it is particularly notable that the tracked sharks invested in dual strategies, switching between highly focused use of coastal reef systems and dynamic use of open ocean, in addition to exhibiting strong, repeated philopatry to overwintering sites. Philopatry may improve foraging success and be less costly than searching for other suitable habitat elsewhere, potentially enhancing individual fitness (Stamps 1995; Schofield *et al.* 2010).

Few marine fish have been shown to adopt such marked behavioural plasticity, especially when repeated within individuals across years. The closest parallel reported among elasmobranchs is for warm-bodied sharks in contrast to the ectothermic tiger shark (Emery 1986). For example, the white shark in the Pacific and Indian Oceans switches between high fidelity to particular coastal areas and long-distance migrations to oceanic areas (Jorgensen *et al.* 2009; Sims *et al.* 2012; Domeier & Nasby-Lucas 2013). The related salmon shark also makes long-distance migrations offshore in the Pacific Ocean, before returning to specific regions of the Alaskan coast (Weng *et al.* 2008). For ectothermic sharks, philopatry to tropical insular regions has been shown for the sympatric oceanic whitetip shark *Carcharhinus longimanus*, which returns to particular areas of the Bahamas after long-distance movements into the Atlantic (Howey-Jordan *et al.* 2013), however this has not been demonstrated across multiple years. Among teleosts, some large, temperate, demersal species such as Atlantic cod *Gadus morhua* are known to return to within a few kilometres of the previous year's spawning sites, despite long-distance migrations in between to foraging grounds (Robichaud & Rose 2001). However, the behaviours displayed by the tiger sharks migrating between tropical islands and higher latitude oceanic zones are seemingly more similar to some turtle, bird and mammal movements than to other fish. For instance, loggerhead turtles display a marked dichotomy of ranging behaviours, switching between coastal and oceanic habits, often returning to within a few kilometres of previous foraging sites (Schofield *et al.* 2010; Hawkes *et al.* 2011). Among birds, Cory's shearwaters *Calonectris diomedea* in the Atlantic undertake long-distance, trans-equatorial, round-trip migrations between particular nesting sites and foraging areas (González-Solís *et al.* 2007), as do sooty shearwaters *Puffinus griseus* in the Pacific (Shaffer *et al.* 2006). Baleen whales, such as the humpback whale, *Megaptera novaeangliae*, exemplify similarly substantial repeat migrations in mammals, which move thousands of kilometres seasonally between near-polar feeding grounds and tropical breeding grounds (Lockyer & Brown 1981; Stone, Florez-Gonzalez & Katona 1990).

Understanding the motivations behind such migrations will better enable prediction of how movements might respond to environmental changes (see Chapter 4). However, despite a number of tracking studies correlating animal movements with environmental variables (Hays *et al.* 2006; Bestley *et al.* 2010; Queiroz *et al.* 2010; Block *et al.* 2011; Papastamatiou *et al.* 2013), the motivation for migration often remains unknown (Jorgensen *et al.* 2009; Papastamatiou *et al.* 2013; Werry *et al.* 2014). The tiger sharks migrating north in the summer may be motivated by foraging opportunities in the area, possibly on juvenile turtles. The very high turning frequencies in the north and north-eastern extent of their range in summer may reflect potential searching or foraging activity (Sims 2010). This area of high turning overlaps spatially and temporally with the distribution of juvenile loggerhead turtles that migrate from the western Atlantic (McClellan & Read 2007; Mansfield *et al.* 2009, 2014). Moreover, tiger shark predation on turtles was confirmed in this region, which is consistent with dietary studies on tiger sharks from other regions that have revealed turtle species to be preferred prey items of larger individuals (Lowe *et al.* 1996; Simpfendorfer *et al.* 2001). Fitzpatrick *et al.* (2012) found that tiger sharks at Raine Island, Australia, targeted turtles seasonally when adults aggregate along nesting beaches. More recently, Werry *et al.* (2014) reported that, in contrast to this study, some mature male tiger sharks appear resident within the Chesterfield Islands, Coral Sea, but suggested that this may be related to a perennial abundance of suitable prey species, including green turtles *Chelonia mydas*. Hence, it appears that the tiger sharks tracked in the present study may make these long-distance migrations annually to target an abundance of preferred prey in the summer, and in so doing connect the trophic ecologies of disparate coral reef and oceanic ecosystems.

As the majority of sharks tagged in this study were mature males, a possible reason for them to return from foraging to their overwintering areas is to find mates. Mature females are

present in the Bahamas during winter, often remaining relatively close to the Bahamas and Florida (Hammerschlag *et al.* 2012), where there is an apparent peak in pupping during early summer (Natanson *et al.* 1999). Given that tiger sharks in the northwest Atlantic have a 13–16 month gestation period (Branstetter, Musick & Colvocoresses 1987), mating should have peaked in later winter/early spring, when adults of both sexes are known to be in tropical insular regions. This is consistent with the recent finding that incidence of mating scars on female tiger sharks in the Bahamas also peak during winter (Sulikowski *et al.* 2016). Although other factors may be involved, including foraging and thermal preferences (see Chapter 4), given the available information it is reasonable to hypothesise that a driver of winter philopatry is returning for mating opportunities.

3.4.2 *Partial migration*

Complex population structure and extensive movements by a segment of the population can result in regional fishing activity having disproportionate effects on different population components (Mucientes *et al.* 2009). Thus, understanding potential demographic segregation and partial migration patterns – who goes where, when and why – is crucial for the sustainable management of any population. Partial migration is widespread across taxa, although the driving processes often remain unclear, with animal size, sex, condition and personality (e.g. boldness) all reported as factors contributing towards the propensity to migrate or not (Brodersen *et al.* 2008; Jahn *et al.* 2010; Chapman *et al.* 2012). Partial migration has been reported for female tiger sharks in Hawaii based on presence/absence data from acoustic telemetry, where seasonal presence appears to be associated with reproductive state and individual foraging targets (Papastamatiou *et al.* 2013). From work on other species it has been suggested that swim speed and migration propensity may be linked to size-related dispersal ability (Weihs 1977; Chapman *et al.* 2011). This is consistent with the observation in the present study that distance travelled per month increased with tiger shark length and,

furthermore, all individuals observed overwintering around Bermuda were comparatively small and immature (Branstetter *et al.* 1987). Similarly in Hawaii larger tiger sharks were also more likely to undertake long range movements (Papastamatiou *et al.* 2013), and year-round residency has been reported for sub-adult tiger sharks at the Chesterfield Islands in the Coral Sea (Werry *et al.* 2014). Work on salmonids *Coregonus* spp. suggests that smaller individuals within a species may incur a greater metabolic cost in warmer waters, potentially reducing the benefits of migration (Mehner & Kasprzak 2011). If such a size-dependent metabolic cost were applicable to tiger sharks, it would be consistent with our observation of fewer smaller individuals migrating seasonally to exploit prey elsewhere.

Individual condition may therefore be a strong driver of migration propensity in tiger sharks: adults may be of sufficient condition to absorb the costs of migration to exploit disparate, but profitable, food sources, whilst juveniles may have to invest more in somatic growth.

3.4.3 Conservation implications

Such segregated use of large oceanic areas by size, as shown here, combined with high fidelity to particular coastal regions, can result in differential exploitation by spatially-focused fisheries and contribute towards rapid population declines (Ford 1921; Mucientes *et al.* 2009). With the observed size-related migration differences in tiger sharks, such differential exploitation by long-line fisheries in summer (where tiger sharks are known to be caught (Domingo *et al.* 2016)) could disrupt the age structure of the population, exacerbating any impact of fisheries-induced mortalities. Some overwintering sites are covered by the Bahamian Exclusive Economic Zone (Graham *et al.* 2016), where long-lining and commercial trade of shark is prohibited, whereas sharks migrating to oceanic areas may be at greater risk of fishing mortality, where large shark and fishing vessel movements have been shown to overlap by up to 80% (Queiroz *et al.* 2016). This highlights the need for informed, spatially dynamic,

management and conservation measures, such as the designation of MPAs or time/area closures of fisheries in summer foraging areas, or for greater spatial protection of philopatric overwintering sites.

This chapter has revealed unexpected predictability in tiger shark movements in the northwest Atlantic. They seasonally and repeatedly switch between coastal coral reef and temperate oceanic habitats, displacing thousands of kilometres in the process, yet also showing marked philopatry to overwintering sites. However, the expansive movements of tiger sharks throughout the northwest Atlantic leaves them exposed to international fisheries for extended periods of time. Understanding these migration patterns, particularly when partial in nature and size segregated, is crucial for future conservation efforts. Identifying where tiger sharks may focus their movements and use migration corridors will inform assessments of where, when and how high space-use areas overlap with commercial fisheries in the North Atlantic.

4 Ontogeny of environmental influences on tiger shark *Galeocerdo cuvier* distribution and movement behaviour

4.1 Introduction

Given the partial nature and apparent isotherm preference reported for tiger shark *Galeocerdo cuvier* migrations in the previous chapter (3), a more detailed analysis was conducted into how variation in environmental variables might influence tiger shark spatial dynamics, including distribution and behaviour. The observed movements will have been the product of the sharks responding to a combination of factors including intrinsic state (e.g. size, sex), physiological constraints (e.g. energetic budgets, thermal tolerances) and environmental variation (e.g. temperature, resource distribution) (Gurarie, Andrews & Laidre 2009). A detailed appreciation of the factors driving movement decisions significantly improves the power to predict predator movements and distribution, and subsequently how they may interact with human activities such as fishing (Humphries *et al.* 2010; Sims 2010).

The observation in Chapter 3 that larger sharks displayed greater migration propensity than smaller sharks suggests that intrinsic factors, perhaps related to dispersal ability and maturation stage, may play an important role in the movement patterns adopted and the distribution of tiger sharks in the northwest Atlantic. Intrinsic factors can be important drivers of migratory patterns in a variety of other species (Chapman *et al.* 2012), and is investigated further in this chapter.

In combination with shark size, this chapter also aims to evaluate how variation in a number of environmental factors may influence tiger shark distribution and movement behaviour. Given

the apparent relationship with isotherms described in Chapter 3, the effect of sea surface temperature (SST) on tiger shark movement was of particular interest. Adopting a thermal niche by tracking isotherms may help manage energetic budgets in ectothermic species (McMahon & Hays 2006); water temperature has been revealed as an important driver of movements for several shark species (Weng *et al.* 2008; Abascal *et al.* 2011; Block *et al.* 2011; Queiroz *et al.* 2016), as well as other marine predators such as bluefin tuna *Thunnus thynnus* and loggerhead turtles *Caretta caretta* (Lutcavage *et al.* 1999; Mansfield *et al.* 2009).

Thermal fronts – oceanographic features distinguished by marked temperature gradients – are typically associated with upwelling of nutrients and display increased productivity through accumulation of plankton (Bakun 2006), which can aggregate a variety of fish species that in turn support high abundance and diversity of large predators (Worm, Lotze & Myers 2003; Sims 2010; Block *et al.* 2011; Queiroz *et al.* 2012; Scales *et al.* 2014). Consequently thermal fronts were included in evaluation of tiger shark space use as a potentially important feature of predator habitat use, with fronts incorporated into analysis here by testing the influence of SST gradients on movement behaviour.

Chlorophyll- α concentration can be used as a proxy for photosynthetic activity and indicator of primary productivity and phytoplankton abundance, which in turn may support further biomass and improved foraging opportunities for higher trophic levels (Hays *et al.* 2006). As such chlorophyll- α concentration, as a correlate of high biomass and potential prey, may also be used to predict the distribution and migratory behaviour of tiger sharks, as it does for other marine predators like loggerhead turtles, albacore tuna *Thunnus alalunga* and whale sharks *Rhincodon typus*, amongst others (Polovina *et al.* 2001; Hays *et al.* 2006; Block *et al.* 2011; McKinney *et al.* 2012).

In addition, high predator abundance and diversity can be associated with topographic features such as insular reefs and seamounts (Worm *et al.* 2003), as described for tiger shark occupancy in Chapter 3. These features are typically characterised by increased water turbulence and mixing, enhancing local production by transporting nutrients into the euphotic zone (Wolanski & Hamner 1988; Oschlies & Garçon 1998). As such, association with topographical features should be included in assessment of environmental influence on tiger shark movements.

Consequently, the present chapter evaluates the relative influence of SST, thermal fronts, productivity and topographic features on tiger shark distribution and movement behaviour in the northwest Atlantic, and how this may differ depending on shark size. Such an appreciation of environmental influence on shark movements can help predict dynamic population distributions from variation in environmental factors across potentially suitable habitat, subsequently allowing assessment of how shark space-use and fisheries interactions may change over time (Sims 2010; Queiroz *et al.* 2016).

4.2 Methods

The study site for this chapter was Challenger Bank near Bermuda, as used in the previous chapter and described in the General Methods (Chapter 2). Tiger shark movements were tracked using satellite telemetry (SPOT5, Wildlife Computers, Redmond, Washington, USA), using the same capture, tagging and geolocation methods as described in the General Methods (Chapter 2). This chapter uses the same tags, track data and study period as described in the previous chapter (3). Given the multivariate nature of the analysis, a variety of techniques were adopted, including Spearman's rank correlation and the application of generalised additive mixed models.

4.2.1 Spearman's Rank Correlation

As a preliminary assessment of the data, Spearman's rank correlation was used to determine how tiger shark movements varied with certain environmental variables. As described in Chapter 3, the occupancy and straightness of movement were calculated for the duration of each shark's track. For this chapter, however, additive inverse straightness was used as an approximation of tortuosity ($1 - \text{straightness}$), to make subsequent correlations and model responses easier to interpret (i.e. positive correlations represent more tortuous movements).

The environmental variables correlated against shark occupancy and tortuosity were sea surface temperature (SST), SST-slope (an approximation of thermal fronts), chlorophyll- α concentration (a proxy for primary productivity) and bathymetry. As in the previous chapter, SST data ($^{\circ}\text{C}$) were obtained from the Operational Sea Surface Temperature and Sea Ice Analysis (OSTIA) system via the U.K. National Centre for Ocean Forecasting (25 km resolution), and bathymetry data (m) were obtained from the 2-minute Gridded Global Relief Data (ETOPO2v2). SST slope ($^{\circ}\text{C}$) was calculated as the maximum difference from the surrounding SST grid cells when compared to the central occupied cell. Chlorophyll- α concentration (mg m^{-3})

³) was obtained from Moderate Resolution Imaging Spectrometer (MODIS), GlobColour level-3 Product 0.25° Weekly.

Each shark occupancy and tortuosity value along a track was assigned a corresponding bathymetry, SST, SST slope and chlorophyll- α value that matched the time and location. Spearman's rank correlations were then calculated for each response (occupancy and tortuosity) against each environmental variable to test for any covariation between shark behaviour and the environment (SigmaPlot, Systat Software, San Jose, CA). This was performed for the overall study period, as well as for tracks split by season, in order to reveal any seasonal variation in response. The correlation coefficients (ρ) for each response variable were then plotted to visualise the impact of each environmental variable.

4.2.2 *Generalised Additive Mixed Models*

To test how well deviance in the environmental variables described above might predict tiger shark presence/absence across the study area, along with their occupancy and tortuosity, a series of generalised additive mixed models (GAMMs) were constructed. GAMMs relate a univariate response variable (in this case presence/absence, occupancy or tortuosity) to a series of predictor variables (in this case SST, SST slope, bathymetry and chlorophyll- α), with an exponential distribution specified for the response (e.g. Poisson) and a link function (e.g. logarithm) relating the response to the predictor variables (Wood 2006). The functional response of each predictor variable may be specified using either parametric or non-parametric forms, with the latter applied with smoothing functions (e.g. a locally weighted mean; (Wood 2006)).

Three different GAMMs were applied to address specific questions: the first used tiger shark presence/absence as the response variable to test how environmental variables may be used

to predict tiger shark space use in the northwest Atlantic; the second used tiger shark occupancy as the response, testing how the environmental variables predicted where tiger sharks spent more time along their observed tracks; and the third had tortuosity as the response, testing how the environmental variables predicted where tiger sharks performed more tortuous movements within the observed tracks. Given the observed partial migration pattern in tiger shark movements in the northwest Atlantic (Chapter 3), it is reasonable to assume that tiger sharks may display different responses to environmental variation depending on their size. Consequently each GAMM produced separate environmental variable smooth functions for small and large sharks, with size split by tiger sharks smaller ($n = 5$) and larger ($n = 19$) than 270 cm (the partial migration cut-off identified in Chapter 3).

For the binomial presence/absence model the data were split so that 75% was used for model training, while the remaining 25% was used to test the performance of the model with a receiver operating curve (ROC) (Zuur *et al.* 2009). Each of the environmental variables was measured on a different scale (e.g. °C versus mg m^{-3}), so they needed to be standardised to allow their contributions to the model to be comparable. This was achieved by subtracting the mean and dividing by the standard deviation for each environmental variable, prior to being incorporated into the models (Zuur *et al.* 2009). The performance of each final model output was assessed using the c index, which is equivalent to the ROC with values closer to 1 indicating better performance, and the corresponding Somers' Dxy rank correlation, which is a measure of ordinal association between the response and predictor variables. This was performed using the `rcorr.cens` function in the 'Hmisc' package in R (R Foundation for Statistical Computing, Vienna, Austria), while the models were run using the 'mgcv' package (Wood 2006). In order to prevent potential overfitting of smooth functions to the data, the maximum number of degrees of freedom for each smooth function was restricted to five in 'mgcv'.

For the presence/absence model, it was necessary to compute pseudo absences within the study area to enable assessment of environmental variables where the tracked tiger sharks were not recorded but could have gone. This was achieved by creating simulated random ('null') tracks based on the movement parameters of the original sharks. The real frequency distributions of both turning angles and step lengths were used to construct a total of 50 null tracks, the initial position of which was set at the original tagging location (Challenger Bank). The value of 50 simulated tracks was chosen based on the number of simulated tracks required for the mean and standard deviation of the standardised variables to stabilise (Figure 22). The initial turning angle was derived from a uniform distribution, with subsequent steps and turning angles sampled from the real step length and turning angle distributions, with the former limited by the actual number of individual steps. Any steps that were placed on land were replaced with a new angle and step, and all simulated tracks were constrained to the minimum convex polygon formed by the full complement of tracked sharks. No simulated tracks were used in the occupancy and tortuosity models, as these were testing where sharks spent more time/performed tighter movements within their own tracks with respect to environmental variation.

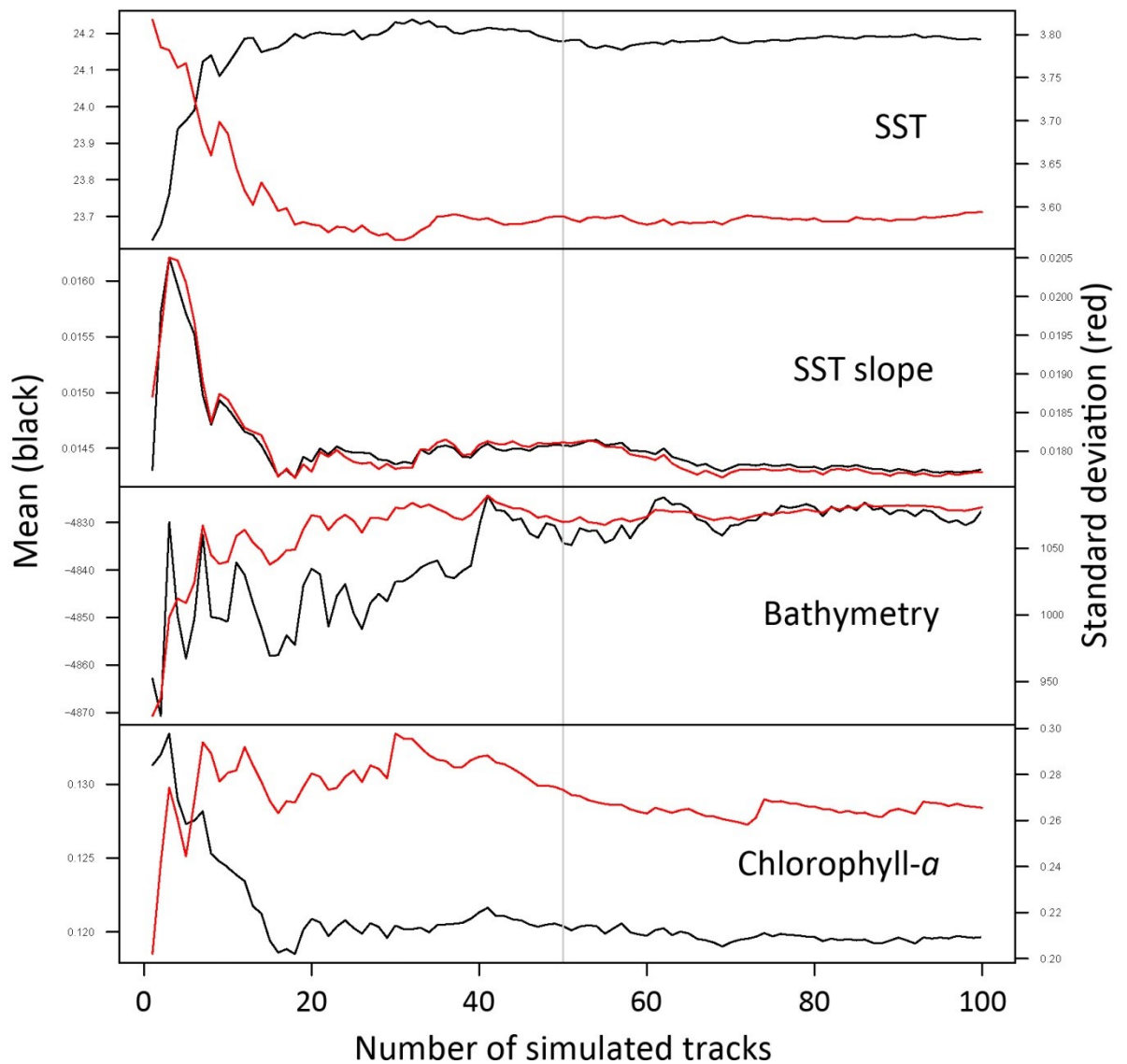


Figure 22: Mean and standard deviation of environmental variables plotted against number of simulated tracks. Vertical grey line marks 50 simulations.

In order to avoid pseudo-replication and reduce potential autocorrelation between locations, as well as account for the different scales at which the environmental variables were remotely sensed, only positions separated by at least 0.25° along a track were used to run each model (Queiroz *et al.* 2016; Sousa *et al.* 2016). This resolution was chosen to match the lowest resolution of environmental variables used in the models (MODIS chlorophyll- α); environmental variables sensed at a finer scale (e.g. SST, bathymetry) had mean values calculated per 0.25° cell such that the model considered all variables at the same conservative scale. The predictor variables were subsequently tested for collinearity using a Spearman's

rank correlation matrix (Zuur *et al.* 2009): none of the variables exceeded the 0.75 correlation coefficient, allowing each to be included in the models. Due to the observed distribution of values of each response variable, a binomial distribution was used for the presence/absence, and a Poisson distribution for both the occupancy and tortuosity models. In addition, to account for variation specific to the individual, shark ID was incorporated into the model as a random effect by making use of the `s(...,bs="re")` term in the 'mgcv' package (Wood 2006). Some of the best fit models required transformation (e.g. logarithm) of the predictor variables to ensure they conformed to a normal distribution. Potential violation of GAMM assumptions was investigated using 'gam.check' in R (R Foundation for Statistical Computing, Vienna, Austria). As well as providing the statistical outputs of each model in tables, the smoothed response of each model was plotted against each environmental variable.

4.3 Results

As with Chapter 3, over 150,197 tracking days were obtained from the 24 tiger sharks tracked between August 2009 and July 2012 – the same tracks were used for analysis here (Table 2).

Examination of the residuals for each GAMM revealed them to be appropriately distributed given the use of binomial and Poisson distributions in the different models (Figure 23). For instance, a Poisson regression is expected to be heteroskedastic as the variance is equal to the mean, while the residual plots for a binomial regression are not expected to be normally distributed (Wood 2006).

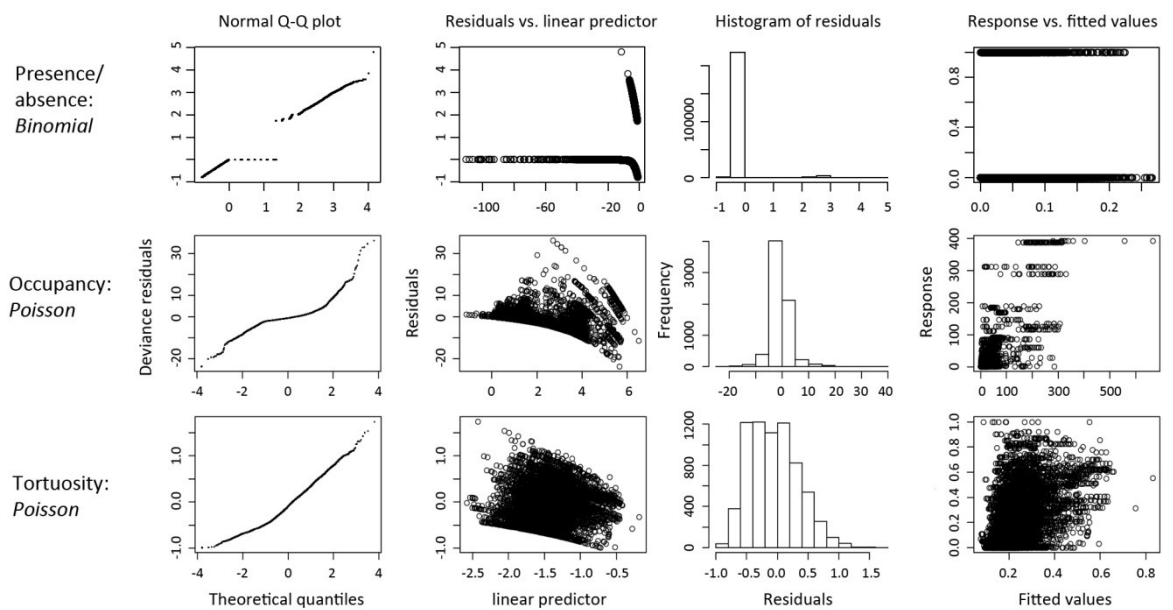


Figure 23: Plots showing the distribution of residuals for the three different GAMMs: presence/absence, occupancy and tortuosity.

4.3.1 Spearman's Rank Correlations

All Spearman's rank correlations performed proved significantly different from 0, apart from between overall occupancy and SST (although all seasons were significant), and between SST slope and occupancy in spring (see Table 4 for all test results).

For the occupancy correlations, tiger sharks spent more time in shallower waters across all seasons, as indicated by the strong negative correlations (Figure 24), although the correlation was weaker during summer. Overall occupancy correlated little with SST, but there were significant correlations by season (Table 4; Figure 24). During winter shark occupancy increased slightly at lower temperatures, whereas occupancy increased with SST across all other seasons. Regarding SST slope, occupancy was higher at steeper slopes during winter and autumn, with the correlation appearing slightly weaker during summer (no effect observed for spring; Figure 24). After bathymetry, the strongest correlations were between occupancy and chlorophyll- α concentration, with sharks spending significantly more time in higher chlorophyll- α concentrations, particularly during winter and spring. In contrast, occupancy was higher in slightly lower chlorophyll- α concentrations during summer.

In many respects the correlations between tortuosity and the environmental variables were similar to those for occupancy (higher tortuosity usually equates to greater occupancy of that spatial unit), but were slightly more consistent across the seasons (Figure 25). Shark movements were more tortuous over shallower water for all seasons, although the correlation was much less pronounced during summer. Apart from spring, tortuosity correlated negatively with SST across all seasons, with turning occurring more frequently in cooler waters. Tortuosity correlated positively with SST slope across all seasons, with higher turning frequency recorded in areas of steeper slope. Tortuosity also correlated positively with chlorophyll- α concentration across all seasons.

Table 4: Spearman’s rank correlation coefficients between shark occupancy, speed, tortuosity and environmental variables, by season. This shows that both occupancy and tortuosity showed significant correlations with all environmental variables in all seasons, apart from between occupancy and SST-slope in spring.

	Occupancy			Tortuosity		
	ρ	n	p	ρ	n	p
Bathymetry						
All	-0.62	15132	<0.001	-0.38	15132	<0.001
Winter	-0.67	3676	<0.001	-0.41	3676	<0.001
Spring	-0.62	3651	<0.001	-0.35	3651	<0.001
Summer	-0.42	3740	<0.001	-0.14	3740	<0.001
Autumn	-0.65	4065	<0.001	-0.53	4065	<0.001
SST						
All	0.01	15132	0.203	-0.07	15132	<0.001
Winter	-0.12	3676	<0.001	-0.05	3676	<0.001
Spring	0.13	3651	<0.001	0.05	3651	<0.001
Summer	0.21	3740	<0.001	-0.14	3740	<0.001
Autumn	0.09	4065	<0.001	-0.17	4065	<0.001
SST-slope						
All	0.13	15132	<0.001	0.13	15132	<0.001
Winter	0.22	3676	<0.001	0.13	3676	<0.001
Spring	0.02	3651	0.309	0.1	3651	<0.001
Summer	-0.03	3740	0.0395	0.07	3740	<0.001
Autumn	0.13	4065	<0.001	0.18	4065	<0.001
Chl-α						
All	0.32	15132	<0.001	0.29	15132	<0.001
Winter	0.57	3676	<0.001	0.26	3676	<0.001
Spring	0.41	3651	<0.001	0.27	3651	<0.001
Summer	-0.15	3740	<0.001	0.2	3740	<0.001
Autumn	0.23	4065	<0.001	0.38	4065	<0.001

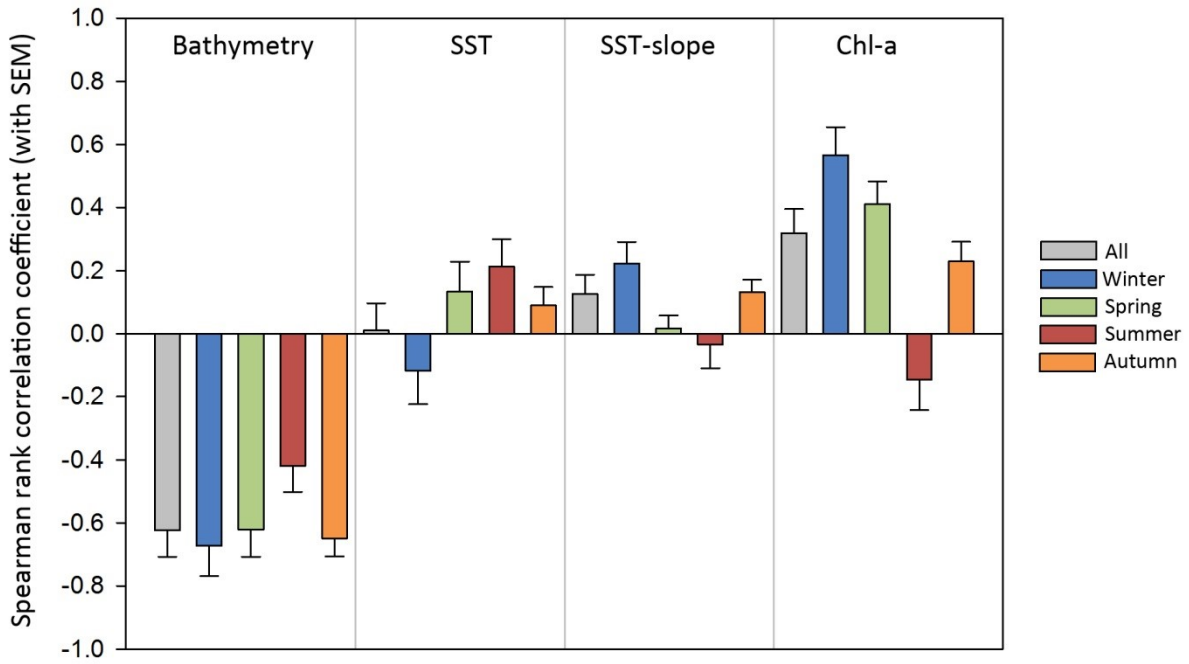


Figure 24: Spearman's rank correlation coefficients for shark occupancy versus environmental variables. Error bars represent the standard error of the mean.

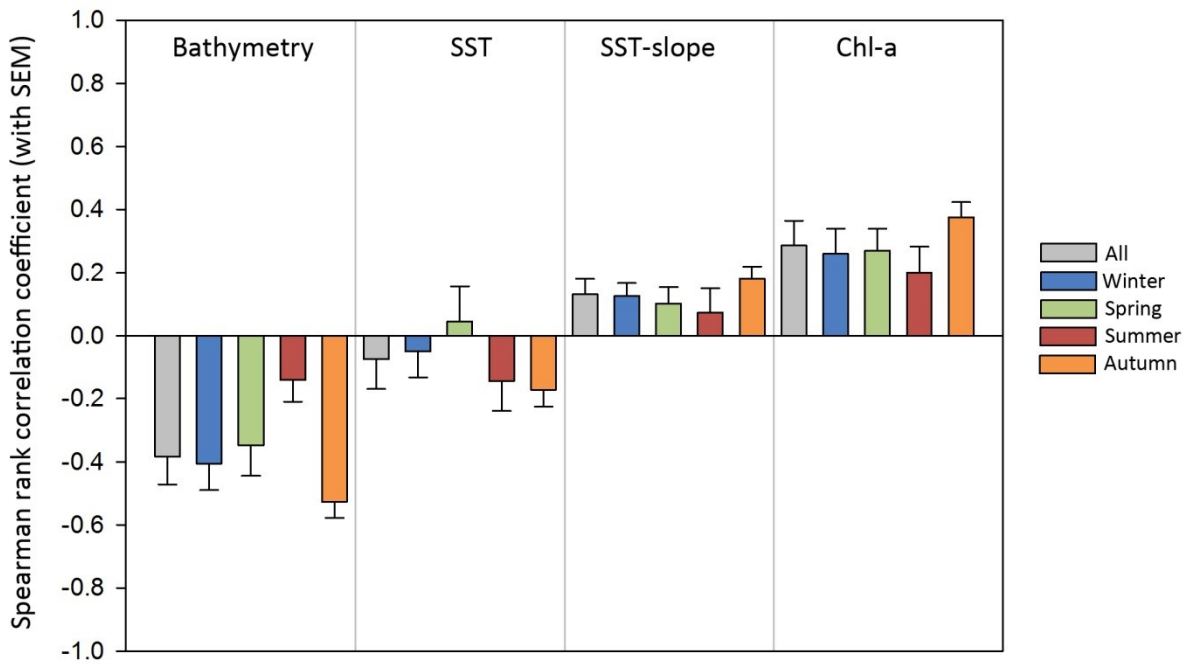


Figure 25: Spearman's rank correlation coefficients for shark tortuosity versus environmental variables. Error bars represent the standard error of the mean.

4.3.2 Presence/absence GAMM

Plotting of the ROC revealed a reasonable area under curve value of 0.747 – values closer to 1 denote good classification results, with those approaching 0.5/linear suggesting the model performed no better than random. The GAMM predicted shark presence with moderate success, with 9% of observed variation in presence/absence explained overall (Table 5). The final model used was:

$$Presence = size + s(SST) + s(\log_{10}(Chl-\alpha)) + s(\log_{10}(SST-slope)) + s(Bathymetry) + s(ID)$$

Table 5: GAMM validation results.

Model	C index	Dxy	S.D.	n	Variance explained
Presence/absence	0.74	0.48	0.01	229808	8.6%
Occupancy	0.52	0.04	0.01	6957	76.4%
Tortuosity	0.53	0.06	0.01	6957	17.4%

Table 6: GAMM coefficient estimates for both small and large sharks.

Small						Large				
Model	Variable	edf	Ref.df	F	p-value	Variable	edf	Ref.df	F	p-value
Presence/absence	SST	2.16	2.16	6.27	<0.01	SST	3.26	3.26	229.75	<0.001
	Chla_log ₁₀	3.83	3.83	23.55	<0.001	Chla_log ₁₀	3.97	3.97	61.57	<0.001
	SST-slope_log ₁₀	2.83	2.83	9.03	<0.001	SST-slope_log ₁₀	3.76	3.76	23.14	<0.001
	Bathymetry	1.00	1.00	27.58	<0.001	Bathymetry	3.94	3.94	71.35	<0.001
	ID	20.12	22.00	15.75	<0.001	ID	20.12	22.00	15.75	<0.001
Occupancy	SST	3.80	3.80	9.09	<0.001	SST	3.03	3.03	14.16	<0.001
	Chla_log ₁₀	2.36	2.36	5.87	0.018	Chla_log ₁₀	3.42	3.42	21.94	<0.001
	SST-slope_log ₁₀	2.55	2.55	6.36	<0.001	SST-slope_log ₁₀	1.81	1.81	6.31	0.018
	Bathymetry	3.89	3.89	194.11	<0.001	Bathymetry	3.93	3.93	654.66	<0.001
	ID	19.84	22.00	83.10	<0.001	ID	19.84	22.00	83.10	<0.001
Tortuosity	SST	2.07	2.07	1.69	0.2647	SST	3.76	3.76	25.46	<0.001
	Chla_log ₁₀	2.97	2.97	5.42	<0.01	Chla_log ₁₀	3.77	3.77	36.34	<0.001
	SST-slope_log ₁₀	1.00	1.00	1.35	0.246	SST-slope_log ₁₀	1.00	1.00	0.32	0.574
	Bathymetry	2.61	2.61	22.41	<0.001	Bathymetry	3.46	3.46	82.06	<0.001
	ID	17.46	22.00	10.49	<0.001	ID	17.46	22.00	10.49	<0.001

Overall for smaller sharks, most of the variation was attributable to bathymetry, followed by chlorophyll- α concentration, SST slope and SST, as indicated by the F-values in the model output (Table 6). Probability of presence was typically increased in shallower habitats (<2,000 m) of low chlorophyll- α concentration, with smaller SST slopes also favoured, as indicated by where the standardised residuals and their confidence intervals exceed 0 in the plotted response curves (Figure 27).

For larger sharks, observable variation in presence was largely attributable to variation in SST, followed by bathymetry, chlorophyll- α concentration, and SST slope, with all factors proving significant predictors (Table 6; Figure 27). Overall, the probability of larger sharks being present increased with higher SST (>21 °C), both high and low chlorophyll- α concentration (bimodal peak), shallower waters (<2,000 m) and steeper SST slopes (>0.4 °C; Table 6; Figure 27). The random effect of shark ID also had a significant effect on presence/absence (Table 6), revealing intraspecific variation in spatial distribution.

The latitude of all tiger shark locations was also overlaid on monthly averages of SST at a resolution of 0.25° for the duration of the study (Figure 26). Visual inspection highlights the contrasting interaction with SST between small and large tiger sharks: smaller individuals remaining near Bermuda (~32 °N) experienced a range of temperatures across the seasons (20.6 °C \pm 1.1 S.D. in winter versus 26.4 °C \pm 1.6 S.D. in summer), whereas larger, migratory individuals seemingly track along temperatures ranging 24–26 °C (24.8 °C \pm 1.5 S.D. in winter versus 26.3 °C \pm 1.9 S.D. in summer), with very few locations out of this range.

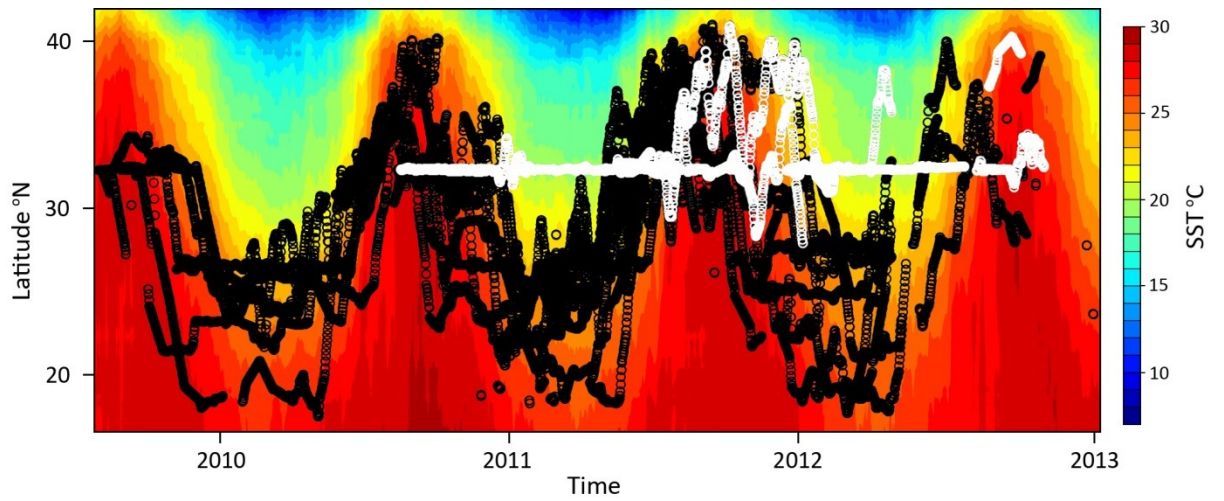


Figure 26: Tiger shark latitude overlaid on monthly averages of SST at a resolution of 0.25°. White circles = sharks <270 cm, black circles = sharks >270 cm.

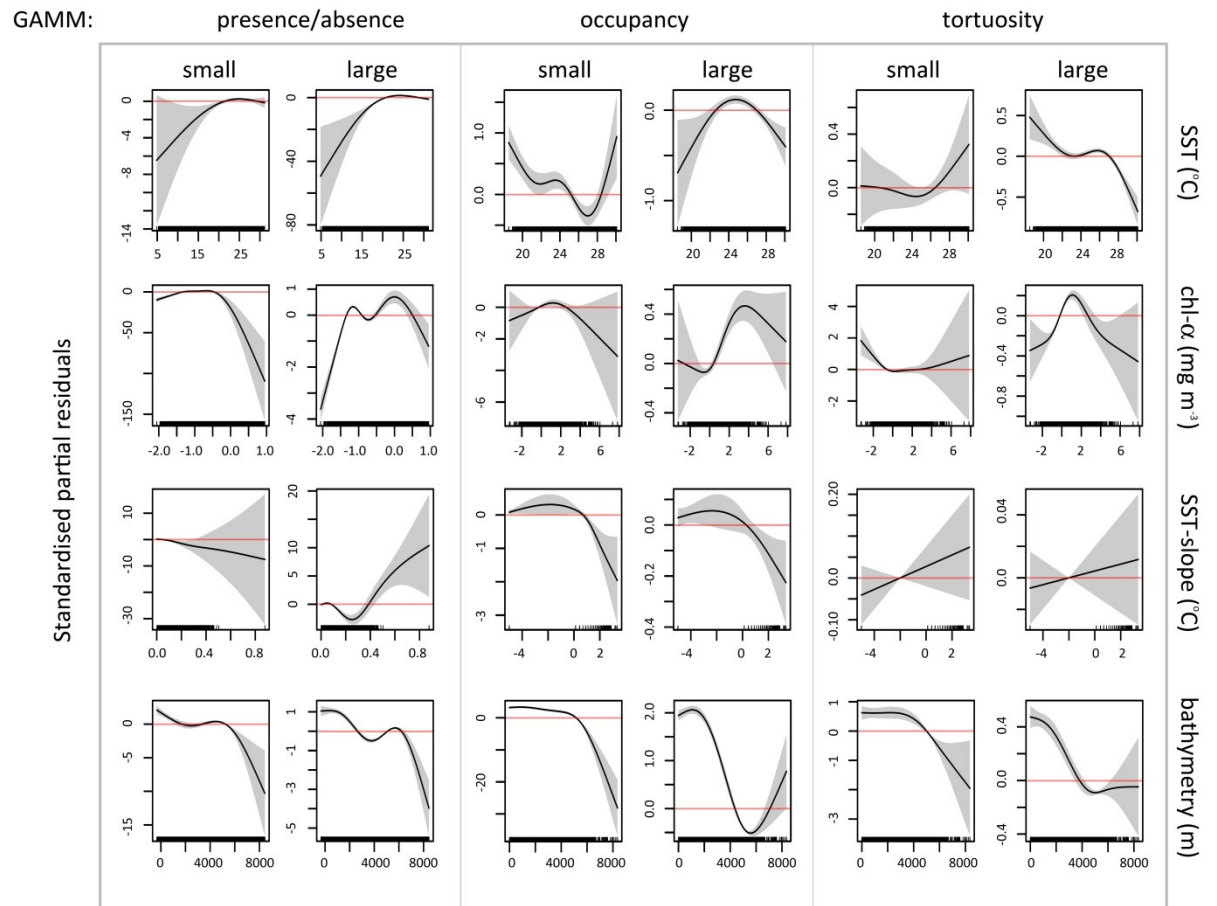


Figure 27: Overall influence of predictor variables on presence/absence for small and large sharks. Note the different scales on the y-axes. Black tick marks above x-axis represent the distribution of empirical data. $Y = 0$ is marked with a red line, above which the predictor positively affects the response.

4.3.3 Occupancy GAMM

In contrast to the presence/absence GAMM, the occupancy GAMM achieved much higher predictive power, with 76% of the variance being explained (Table 5). The final model produced was:

$$\text{Occupancy} = \text{size} + s(\text{SST}) + s(\log_{10}(\text{Chl-}\alpha)) + s(\log_{10}(\text{SST-slope})) + s(\text{Bathymetry}) + s(\text{ID})$$

Overall, for smaller sharks, more time was spent in shallow waters, but there was a bimodal response for SST, whereby occupancy increased at temperatures below 21 °C and above 29 °C (Table 6; Figure 27). This varied relationship with SST is also apparent from the tracks overlaid on SST (Figure 26). Smaller sharks also spent more time in areas with shallower thermal gradients and in regions with chlorophyll- α concentrations greater than 0 (Table 6; Figure 27).

Larger shark occupancy was considerably higher in shallower waters, and increased with higher chlorophyll- α concentration, particularly exceeding $\sim 1 \text{ mg m}^{-3}$ (Figure 27). Typically large sharks spent more time in waters 23–27 °C and with relatively shallow SST slopes (Figure 27), consistent with the SST-overlaid tracks (Figure 26). The random effect of shark ID was highly significant for the occupancy GAMM (Table 6; Figure 27), demonstrating strong intraspecific variation in where individuals spent more time.

4.3.4 Tortuosity GAMM

While less powerful than the occupancy GAMM, the tortuosity model still accounted for a considerable portion of the variation in tortuosity of both smaller and larger sharks (17%; Table 5). SST-slope was kept in the tortuosity GAMM despite being non-significant for both size classes because its removal from did not improve model performance (as determined by

comparing the Akaike weights of models both with and without SST-slope). The final model produced for the tortuosity GAMMs was:

$$\text{Tortuosity} = \text{size} + s(\text{SST}) + s(\log_{10}(\text{Chl-}\alpha)) + s(\log_{10}(\text{SST-slope})) + s(\text{Bathymetry}) + s(\text{ID})$$

Overall for smaller sharks, movements were more tortuous over shallower water with low chlorophyll- α concentrations, while the effects of SST and SST-slope were insignificant (Table 6; Figure 27).

Bathymetry and chlorophyll- α concentration were the most influential factors for larger sharks, with higher tortuosity occurring in shallower waters and in chlorophyll- α concentrations 1–2 mg m⁻³ (Table 6; Figure 27). High tortuosity was also associated with water temperatures cooler than 22 °C, but the effect of SST slope was insignificant (Table 6; Figure 27). Shark ID also proved significant in the tortuosity GAMM (Table 6), illustrating intraspecific variation in where individuals performed higher turning frequency.

4.4 Discussion

The results presented here reveal that the partial migration pattern evident in Chapter 3, seemingly attributable to a size disparity in migration propensity, extends to an ontogenetic shift in tiger shark response to environmental variation in the northwest Atlantic. While all sharks associated more frequently with shallower topographical features, smaller sharks were typically found in cooler, but less productive regions, whereas adult distribution was more strongly predicted by warmer temperatures and higher chlorophyll- α concentration. The presence model also had a second peak at low chlorophyll- α concentration for large sharks – this is presumably attributable to high occupancy of coral reef systems in winter (Chapter 3), which are typically characterised by clear water with low free-living phytoplankton concentrations (Tada *et al.* 2003). SST slope, the approximation of thermal fronts, had little influence on the presence of smaller tiger sharks, whereas larger sharks were present more frequently in moderate SST slopes. Combined, these results demonstrate a marked response by tiger sharks to environmental features (e.g. SST), governed by intrinsic state (e.g. size).

While lacking the complexity of the GAMMs and possessing caveats such as increased autocorrelation issues, the Spearman's rank correlations echoed the final model outputs reasonably well, making them a worthwhile preliminary exploration of the data. Modelling only accounted for a relatively small proportion of the observed variation in shark distribution, suggesting that other factors not accounted for here also influence shark distribution.

However, extending beyond the presence/absence model to where the sharks spent more time (occupancy), the models acquired significantly greater predictive power while the contrast between smaller and large sharks is maintained. Smaller sharks displayed higher occupancy at a range of temperatures (particularly below ~ 21 °C), while larger sharks adopted a relatively narrow thermal niche of ~ 23 – 27 °C, consistent with the apparent isotherm tracking

observed in Chapter 3 and Figure 26. This could be attributable to the intrinsic contrast in migration propensity: smaller sharks remained near Bermuda during winter, thereby tolerating a range of temperatures across the seasons, whereas the larger sharks remain within a thermal niche whilst migrating. In Australia, tiger sharks are reported to leave Shark Bay when temperatures drop below 19 °C (Wirsing, Heithaus & Dill 2006), yet the smaller sharks remaining at Bermuda rarely experienced temperatures <20 °C, suggesting Bermuda remains sufficiently warm to be tolerated by the smaller sharks all year. The smaller sharks may also favour cooler temperatures due to the physiological constraints of their smaller size: being ectothermic and with a higher surface area to volume ratio, the smaller sharks will have reduced thermal inertia and when in warmer water will gain heat faster than larger sharks, increasing their metabolic rate and affecting their maintenance budget, which may be detrimental if it cannot be offset by increased foraging success (Sims *et al.* 2006a; Mehner & Kasprzak 2011; Chapman *et al.* 2012). The only two smaller sharks that performed any kind of seasonal movement away from Bermuda (as seen in Figure 26) did so during the second winter of their tracks, having previously overwintered at Bermuda (see Chapter 3). Around the time of their broader movements these two sharks were estimated to have been ~280 cm TL, based on published growth parameters for the region (Branstetter, Musick & Colvocoresses 1987), suggesting they may have been observed over the cusp of the ontogenetic shift in migratory behaviour.

The larger tiger sharks also had a much stronger association with areas of higher primary productivity than smaller sharks. Large sharks spent more time in higher chlorophyll- α concentrations, indicative of a greater ability to target areas of high primary productivity, given that chlorophyll- α concentration may be a reasonable predictor of biomass and foraging opportunities (Hays *et al.* 2006; Block *et al.* 2011). Such increased impact of productivity on occupancy, as has been reported for a variety of marine predators (Sims & Quayle 1998; Sims

et al. 2003; Block *et al.* 2011), suggests migratory patterns adopted by larger sharks may in part be driven to increase prey encounter rate. This is further supported by the larger sharks displaying increased tortuosity at higher chlorophyll- α concentrations, which may reflect increased foraging activity (Sims 2010). It is notable that the presence of juvenile loggerhead turtles in the northwest Atlantic, reported to overlap with tiger shark movements in Chapter 3, peaked in chlorophyll- α concentrations of $\sim 0.18 \text{ mg m}^{-3}$ (Mansfield *et al.* 2009), principally because the present study revealed that occupancy and tortuosity of tiger sharks increased significantly at higher chlorophyll- α concentrations. Dietary studies have also revealed an ontogenetic shift in tiger shark foraging behaviour, with turtle species constituting an increasingly greater proportion of diet in larger individuals, presumably due to the increased ability of larger sharks to penetrate the defensive shell (Simpfendorfer, Goodreid & McAuley 2001). It may be that larger shark environmental preferences serve to increase encounter rates with preferred prey species such as loggerhead turtles.

Despite spending more time in areas with steeper temperature gradients, from the tortuosity model there was no evidence to suggest that either size class of tiger shark displayed any association between turning frequency and SST slopes. This suggests that thermal fronts may not have influenced the foraging activity of the tracked tiger sharks, which is in contrast to the behaviour observed for various other marine predators (Sims 2010; Block *et al.* 2011; Queiroz *et al.* 2012; Worm *et al.* 2013). The strong association of all response variables with shallower topographical features predominantly reflects the large amounts of time spent around Caribbean islands in winter and Bermuda in summer (and winter, for the smaller sharks). This may also imply an affinity for seamounts whilst offshore, such as the Corner Rise Seamounts near the Flemish Cap, which rise to within 800 m of the surface, and may be areas of high productivity due to associated upwellings that concentrate food supply and have been shown

to provide potential foraging opportunities for a variety of pelagic species (Wolanski & Hamner 1988; Oschlies & Garçon 1998).

These findings are highly concordant with a comprehensive analysis of environmental influence on tiger shark space use in Hawaii (Papastamatiou *et al.* 2013). There it was found that tiger sharks typically displayed higher occupancy in temperatures ranging 23–26 °C and chlorophyll- α concentrations greater than 0.11 mg m⁻³, with the models accounting for up to 62.5% of the observed variation (Papastamatiou *et al.* 2013). Similarly in the present study, the occupancy model explained 76.4% of the observed overall variation, and preferences for 23–27 °C and chlorophyll- α concentrations \sim 1 mg m⁻³ were recorded in larger sharks. Moreover, maturity stage was a significant predictor of occupancy in the Hawaiian tiger shark model (Papastamatiou *et al.* 2013), consistent with the interpretation here that there may be an ontogenetic shift in how tiger sharks respond to variation in environmental features. More recent work comparing the movements of tiger sharks tagged in the Bahamas to environmental variables found that higher SST and stronger thermal fronts were significant predictors of tiger shark presence, whilst chlorophyll- α concentrations had a positive but insignificant effect (Queiroz *et al.* 2016). However, the tracks from the Bahamas were on average only \sim 100 days long, limiting their capacity to predict patterns of tiger shark space use to the season they were tracked in (predominantly winter).

What this apparent ontogenetic change in environmental preferences emphasises, along with the partial nature of the migrations observed in Chapter 3, is that intrinsic factors such as size, sex, condition and reproductive stage may have a significant impact on the spatial dynamics of tiger sharks, in addition to extrinsic environmental factors (e.g. temperature, resource distribution, topography). The relatively low ability of the presence/absence GAMMs to predict tiger shark distribution could be attributable to the strong influence of various intrinsic factors,

as also indicating by the strong significance of the random effect of shark ID in all models. For instance the increased migration propensity in larger sharks, whether it be to mate, exploit foraging targets or maintain a thermal niche, reveals that intrinsic factors may play a significant role in where the sharks go and when. Although the repeated patterns within individuals are similar, which is reflected by the high performance of the occupancy and tortuosity models, the high intra-specific variability of summer foraging targets and philopatric overwintering sites, as revealed in Chapter 3, reduces the power of the models to predict presence and absence. The very broad use of the northwest Atlantic during the summer, where environmental conditions can be very similar over a considerable area of ocean (see Chapter 3), likely also decreases the efficacy of the model. The distribution of smaller sharks may also be more predictable due to their lack of migration propensity and foraging experience, with distribution dictated more by environmental preferences.

The long distance migrations of the larger sharks appear highly directional, as revealed by the high straightness while migrating (e.g. Figure 18) and supported by the strong philopatry observed in Chapter 3. Given the migration targets are typically well beyond the sensory range of the tiger sharks, these observations suggest that tiger shark movement may in part be based on individual experience. The directionality of the movements require an ability to navigate or orientate effectively, potentially cued by factors other than those recorded here e.g. memory, olfaction gradients, magnetic fields (Papastamatiou *et al.* 2011). Indeed, the ontogeny of migration targets for various turtle species appears to be informed by individual experience, with adults migrating to regions they personally encountered as drifting hatchlings (Scott, Marsh & Hays 2014). Larger sharks may also increase their encounter rates with more productive areas based on previous experience, as suggested for other marine predators like the basking shark *Cetorhinus maximus* and narwhal *Monodon Monoceros* (Laidre *et al.* 2004; Sims *et al.* 2006b), which may explain the increased association with higher chlorophyll- α

concentrations compared to smaller sharks. If larger sharks target known patches – perhaps cued by environmental gradients, but not merely by following them – this may also contribute to the reduced performance of the presence model. Experience has also been suggested as an important driver of tiger shark movements in Hawaii, where their movement decisions are thought to be informed by both their sensory ranges (governing the response to variables such as SST) and memory and knowledge of the surrounding environment (Holland *et al.* 1999; Papastamatiou *et al.* 2011, 2013). The latter will increase with age, as supported by the ontogenetic shift in environmental response and presence predictability in the present study. It may be that movement drivers vary across different scales, with longer distance (e.g. migratory) movements cued or directed more by intrinsic factors (e.g. experience), with more local movements (e.g. foraging) reflecting environmental preferences, constrained by intrinsic needs (e.g. food, mates) and physiological constraints (e.g. energetic costs, thermal tolerances).

While variation in environmental features such as SST and chlorophyll- α concentration may have relatively limited power for predicting the migratory patterns of tiger sharks in the northwest Atlantic, especially in larger individuals, they appear to be very good at predicting where more time was spent, or movements had higher turning frequency, within a known distribution. Similar to tiger sharks in Hawaii, it appears reasonable to suggest that these partial migrations represent a conditional strategy based on intrinsic factors (e.g. age, experience) as well as flexible extrinsic states (e.g. temperature, resource abundance), which combined drive an ontogenetic shift in response to environmental variation.

5 Fine-scale spatial dynamics and habitat selection of reef sharks in the Amirantes, Seychelles

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5.1 Introduction

To contrast the broad-scale, oceanic migrations of tiger sharks *Galeocerdo cuvier* described in the preceding chapters, the following chapters take a more focused case study of fine-scale shark spatial dynamics at a remote atoll in the Indian Ocean: D'Arros and St Joseph, in the Amirantes chain of islands, Seychelles. Existing data suggest that the habitats provided by D'Arros and St Joseph, as described in the General Methods (Chapter 2), may provide rare, critical nursery habitat for a variety of species, as well as being an important nesting and foraging ground for the regions' recovering turtle populations (von Brandis, Mortimer & Reilly 2010; Mortimer, Camille & Boniface 2011; Filmalter, Dagorn & Cowley 2013).

Shallow, coastal habitats like the mangroves, seagrass beds and intertidal flats of St Joseph are known to offer important foraging grounds and nursery areas for a wide range of elasmobranch species (Vaudo & Heithaus 2009; Knip, Heupel & Simpfendorfer 2010; Guttridge *et al.* 2011). Nurseries are often crucial habitat for promoting recruitment, owing to increased growth and survival of juveniles, and their characterisation is particularly important for understanding population structure and identifying potential management targets (Heupel,

Carlson & Simpfendorfer 2007; Nagelkerken 2009). Coastal foraging and nursery habitats may also be linked to offshore ecosystems through migration and ontogenetic shifts in movements (Jones *et al.* 2010), as illustrated by the tiger shark movements described in Chapters 3 and 4, whereby degradation of coastal habitats may have adverse impacts on fish diversity and abundance (Taylor *et al.* 2007).

Consequently, it is necessary to identify how coastal areas like D'Arros and St Joseph may provide important habitat and nursery grounds for the region's elasmobranch species. But presently there is a significant lack of data concerning both the behavioural ecology and demographics of sharks in the Seychelles (Nevill *et al.* 2007; Filmlalter *et al.* 2013), such as is necessary to inform management decisions relating to their conservation or sustainable use: simple information such as the spatial and temporal patterns of shark habitat use in the Seychelles remain largely unknown.

The following chapters start to address this deficit. A preliminary survey of elasmobranch abundance and diversity at D'Arros and St Joseph revealed the islands to harbour a diverse, multi-species assemblage of elasmobranchs, including blacktip reef *Carcharhinus melanopterus*, sicklefin lemon *Negaprion acutidens*, grey reef *Carcharhinus amblyrhynchos*, tawny nurse *Nebrius ferrugineus*, silvertip *Carcharhinus albimarginatus* and whitetip reef sharks *Triaenodon obesus* (J. Lea, unpubl. data). Understanding sicklefin lemon shark spatial dynamics is particularly important as they are considered *Vulnerable* on the IUCN Red List, and in several areas have been exploited to the point of extirpation, including India, Thailand and Southeast Asia (Pillans 2003).

As such this chapter evaluated the relative importance of the habitats provided by D'Arros and St Joseph for the shark assemblage, including whether there may be any indication that these islands may offer nursery opportunities and promote regional recruitment.

5.2 Methods

The study site for this chapter was D'Arros and St Joseph Atoll, as described in the General Methods (Chapter 2).

5.2.1 *Animal telemetry*

Between August 2012 and March 2015 a total of 116 sharks of five different species (blacktip reef, sicklefin lemon, grey reef, tawny nurse, silvertip shark) was tagged with acoustic transmitters (either V13 180 s nominal delay or V16 120 s nominal delay, Vemco Ltd, Bedford, Canada). Although present on preliminary surveys, no whitetip reef sharks were caught. Shark capture and tagging was performed as described in the General Methods (Chapter 2).

Shark movements were tracked using an array of 88 acoustic receivers (VR2W, Vemco Ltd, Bedford, Canada) (Figure 28). The array was installed in stages for logistical reasons. Initially 50 receivers were installed around D'Arros and St Joseph between August and November 2012, 25 in the immediate vicinity of the islands covering lagoon and coastal reef habitats, and another 25 spread across the surrounding plateau up to 15 km away, covering plateau and drop-off habitats. In October 2013 a further 10 receivers were added so there was at least one at each of the other islands across the whole Amirantes plateau. In November 2013, 10 more receivers were installed along the reef flats of D'Arros and St Joseph to monitor their use during the high tide and in August 2014 a further 18 receivers. Given the staggered deployment of the array over time, only a subset of the detection records were used for analysis in the present study to avoid biases caused by the developing array design. Firstly, only receivers that had been deployed for over two years were included in this study, reducing the working array for analysis to all receivers installed up until November 2013 ($n = 70$ in total; 35 coastal to D'Arros and St Joseph and 35 across the plateau). Three of these receivers experienced failure causing gaps in their detections records and were omitted from

subsequent analysis. Secondly, track data before November 2013 were discarded so that only track data when all 67 receivers were active were considered, also reducing the effective sample size to 86 sharks.

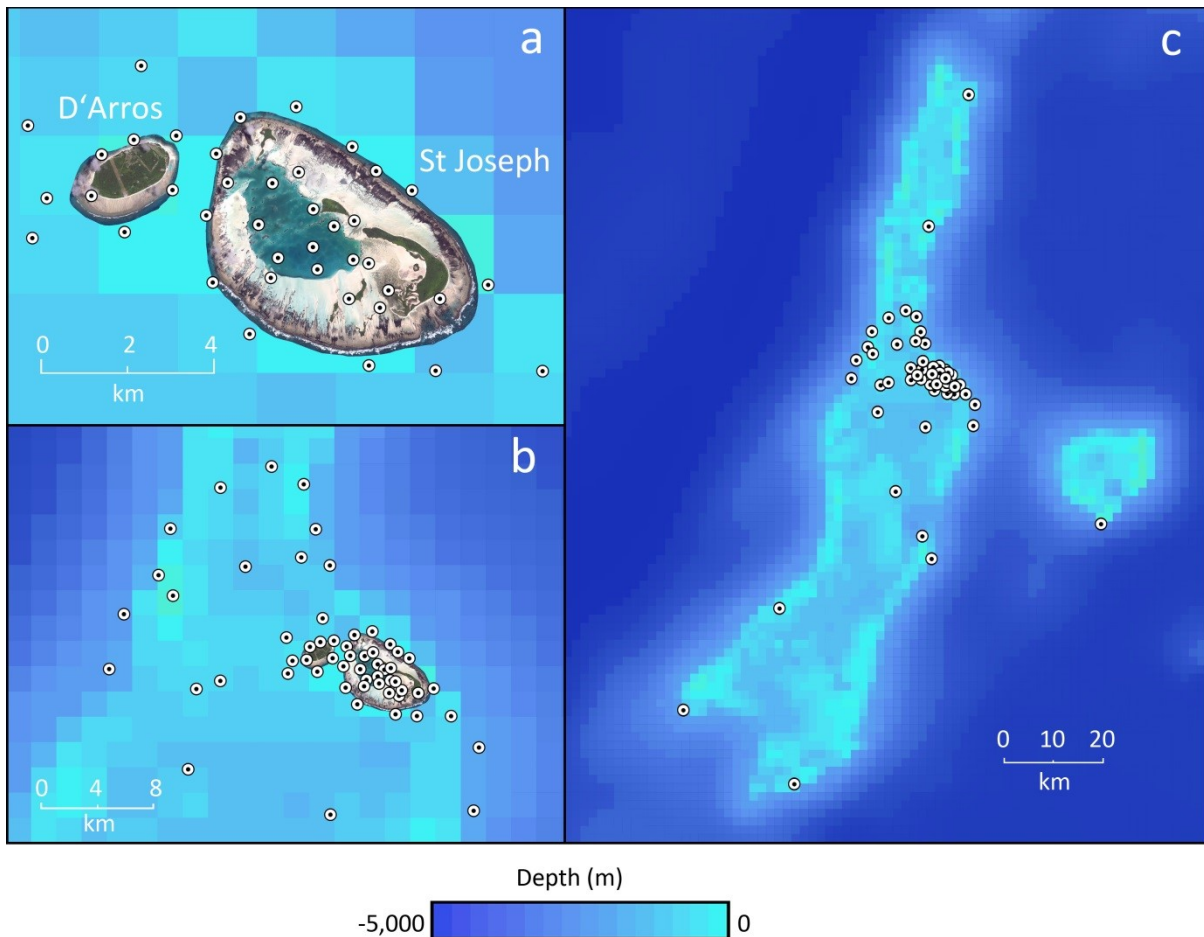


Figure 28: Distribution of acoustic receivers ($n = 67$) around D'Arros and St Joseph (a), the surrounding plateau (b) and across the Amirantes (c). Receiver locations marked with \odot . Maps created in ArcGIS, using satellite imagery from LAND INFO Worldwide Mapping and ETOPO2v2 bathymetry data.

5.2.2 Network analysis

Network analysis was used to determine both where sharks spent more time and how they moved through the array (see General Methods). To test whether the observed movement networks were different from random, random networks were generated and their node metrics were tested against those of the real tracks using Wilcoxon matched-pairs signed rank tests (SigmaPlot, Systat Software, San Jose, CA). For node and edge density, the values produced by the random networks were tested against the real network values as the

population mean in one-sample signed rank tests. Random networks were constructed as follows: for a given set of detections (i.e. for a single animal), the node and connection matrix was first constructed as normal to provide the observed data. For each randomisation, the first ping at the first receiver was kept, and then a swim distance was calculated based on the time between detections and a 1 m s^{-1} swim speed. Receivers were then selected at random until two were found within range of the swim distance. The closer of the two was then selected as the next receiver in the random track. If no receiver was found in range after 100 random selections then no move was deemed to occur and the current receiver was assigned (i.e. the animal was deemed not to have moved). This was repeated for the duration of the track, producing a random walk through the array with steps constrained by the observed detection intervals. This was repeated 100 times for each track, to provide mean random network metrics to test against the observed real track metrics.

Each receiver location was designated a habitat type: lagoon (habitat within St Joseph Atoll, including the flats), coastal reef (sloped reefs bordering islands), plateau (flat bottomed areas of patchy reef rubble and seagrass beds) or drop-off (the edge of the plateau, before it drops to hundreds of metres). To reveal differences in space use between habitats for each species, node metrics were grouped according to habitat type and had their values compared to those of the same habitat type in the random networks. This was achieved by calculating a randomisation index:

$$Rnd_i = \frac{O_m - R_m}{R_m} \times 100$$

Where O_m is the observed and R_m the random metric. Mean values were then plotted for each node metric in each habitat type, according to species. For each individual a residency index

was calculated, representing the percentage of days during its track that it was detected within the array:

$$Res_i = \frac{D_d}{D_{al}} \times 100$$

Where D_d is days detected and D_{al} is days at liberty.

5.3 Results

Over the course of the study (August 2012 to November 2015) 116 acoustic transmitters were deployed on five different shark species: blacktip reef shark ($n = 34$), grey reef shark ($n = 30$), sicklefin lemon shark ($n = 27$), tawny nurse shark ($n = 6$), and silvertip shark ($n = 19$), providing a total of 65,843 tracking days. Due to the staggered deployment of acoustic receivers (see Methods for details), the study period was reduced to November 2013 to November 2015, the array to 67 receivers and the effective tag sample to 86 individuals: blacktip reef ($n = 25$), grey reef ($n = 22$), sicklefin lemon ($n = 20$), tawny nurse ($n = 6$), and silvertip sharks ($n = 13$), providing over 41,655 tracking days (Table 7). All further analysis only refers to these individuals. A range of juveniles and adults was tagged for each species, apart from silvertip sharks, all of which were juvenile. Mean track duration across all sharks was 484.4 days \pm 265.2 S.D. ($n = 86$), with 64.0% of tracks lasting more than a year. All shark species showed a bias towards females amongst tagged individuals, with grey reef sharks displaying the largest disparity of six females for every male tagged.

Table 7: Summary data for the 86 tags used for data analysis. RI = residency index.

Species	n	TL range (cm)	Mean TL (cm)	Sex ratio (M:F)	Liberty Range (days)	Mean Liberty (days)	Mean RI
Blacktip	25	77 - 130	107.6	1.0 : 2.6	34 - 753	563.8	54.2
Grey	22	84 - 158	127.5	1.0 : 6.3	49 - 746	473.2	20.1
Lemon	20	109 - 213	168.1	1.0 : 2.3	3 - 755	589.6	64.0
Nurse	6	155 - 274	210.3	1.0 : 2.0	79 - 749	559.3	50.1
Silvertip	13	79 - 120	95.7	1.0 : 3.3	11 - 349	154.1	22.1

Blacktip reef sharks displayed very restricted movements, with 99.8% of all detections occurring within the confines of St Joseph Atoll (Figure 29), residency that is reflected by their moderate node density (0.522). Blacktip reef sharks displayed very high occupancy of lagoon habitats compared to random networks (Figure 34). Even within the atoll, blacktip movements were largely focused on the eastern end of the lagoon, consistent with their very low edge density, 0.086. There was very limited movement between D'Arros and St Joseph across the

deep channel, with little time spent on the coastal reefs. When around D'Arros, blacktip reef sharks appeared to spend the majority of their time on the more expansive reef flat to the west. Some blacktip reef sharks were only detected infrequently by the subset of receivers used for analysis, reducing the mean residency index. However, evidence from newer receivers not included in the present analysis suggests that these individuals spent the majority of their time in pools along the atoll flats. These individuals were therefore within lagoon habitat but often outside the range of this study's acoustic monitoring array.

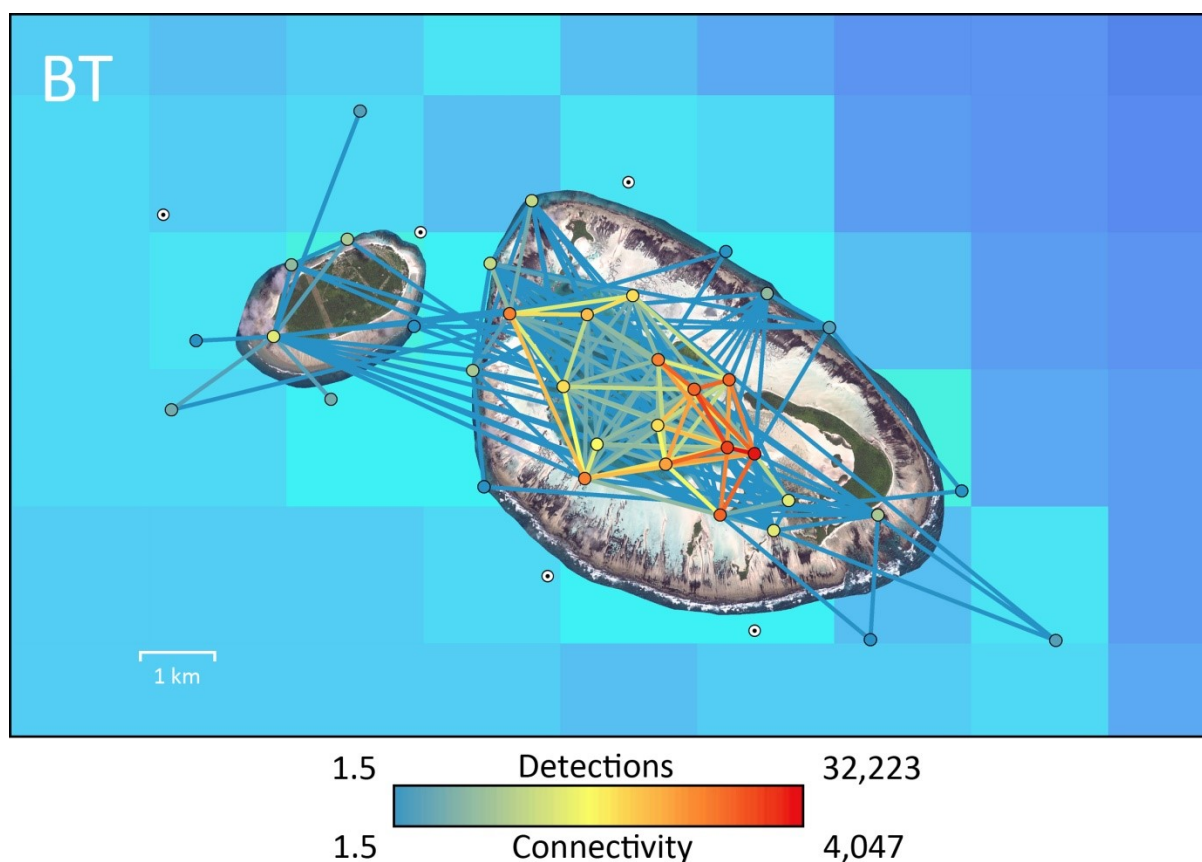


Figure 29: Network displaying blacktip reef shark detection frequency at each receiver (node colour) and how often each receiver was connected by subsequent detections (edge colour). Receivers with no detections marked with \emptyset . Maps created in ArcGIS, using satellite imagery from LAND INFO Worldwide Mapping and ETOPO2v2 bathymetry data.

Broadly, the sicklefin lemon sharks showed a similar pattern to the blacktip reef sharks, with 98.8% of all detections occurring within the atoll (Figure 30). Moreover, comparison of node metrics by habitat type revealed elevated occupancy of atoll habitats in real networks

compared to random ones, with other habitats being used less frequently (Figure 34). However, the sicklefin lemon shark network shows greater movement throughout the atoll, particularly around the deep lagoon perimeter where it borders the flats. Lemon shark movements also connect more frequently to the coastal reefs outside the atoll and, most notably, several individuals were recorded making wider movements across the Amirantes plateau, including to Desnoeufs Island 94 km south of D'Arros. This is reflected in their higher node density of 0.836, along with a higher edge density of 0.150, revealing much greater use of the array. One tagged lemon shark was also caught by fishermen at Marie-Louise 80 km south of D'Arros, while another was caught at Bird Island, 300 km away across deep water (>1000 m). Two lemon sharks were also recorded by a receiver at Marie-Louise, but this location was one of the three receivers excluded from the present analysis due to incomplete temporal coverage. All lemon sharks recorded moving away from the islands and across the plateau ($n = 9$) were ≥ 177 cm total length, whereas those smaller remained exclusively within the confines of the atoll and its coastal reefs. Similar to the blacktip reef sharks, evidence from newer receivers not included in the present analysis suggests that some individuals spent the majority of their time in pools along the atoll flats.

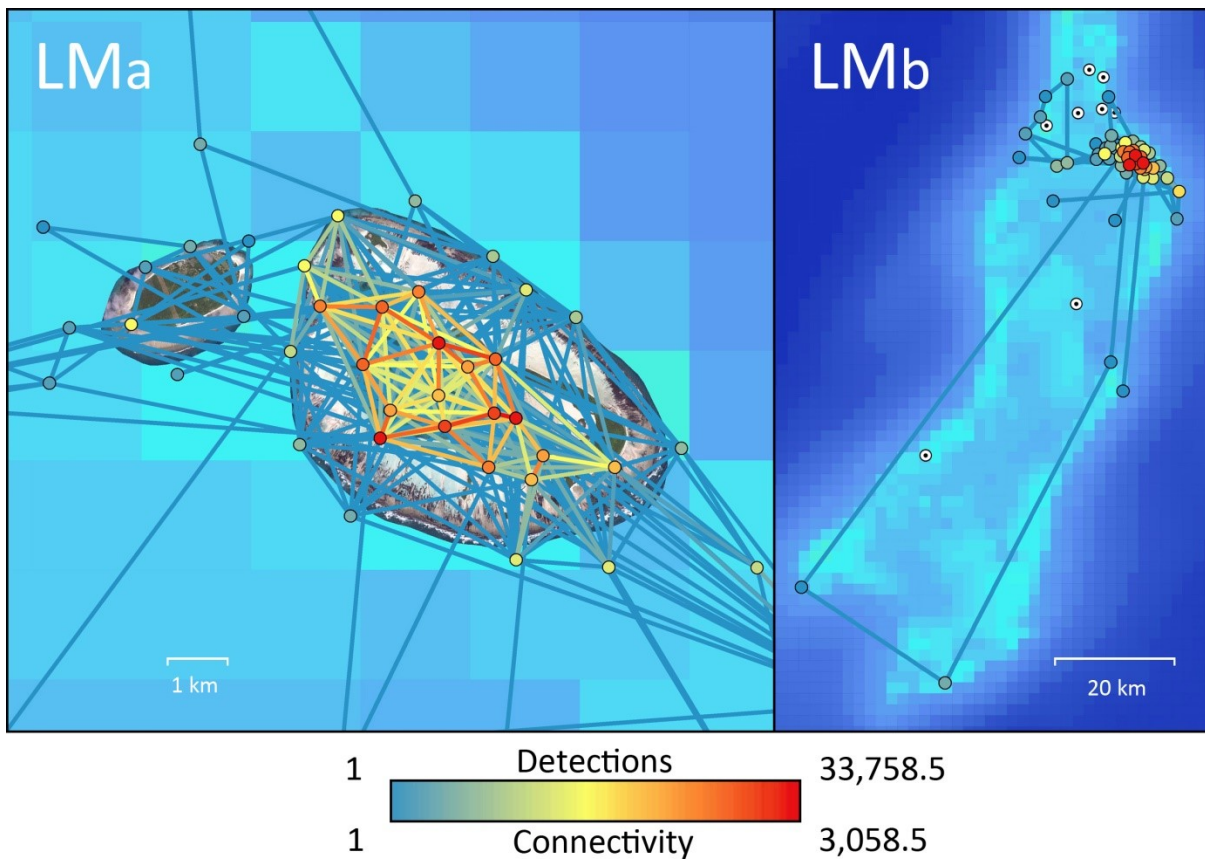


Figure 30: Networks displaying lemon shark detection frequency at each receiver (node colour) and how often each receiver was connected by subsequent detections (edge colour) at fine (a) and broad (b) scales. Receivers with no detections marked with \emptyset . Maps created in ArcGIS, using satellite imagery from LAND INFO Worldwide Mapping and ETOPO2v2 bathymetry data.

Despite similar node and edge densities to blacktip reef sharks (0.448 and 0.038 respectively), grey reef shark movements differed significantly to blacktip reef and sicklefin lemon sharks in that no detections occurred within the atoll (Figure 31). Instead, grey reef sharks were largely recorded along the coastal reefs (62.1% of detections), with 30.4% of detections also occurring along the drop-off. This is emphasised by the comparison of node metrics by habitat type between real and random networks, which show elevated occupancy of drop-off and coastal reef habitats in real sharks versus random ones (Figure 34). Coastal reef areas involved more patrolling movements, indicated by high transit values for those receivers, whereas drop-off use was more focused and had low transit values. Grey reef movements also produced fragmented networks, with some tagged nearer the drop-off not being recorded on the coastal reefs of

D'Arros and *vice versa*. One tagged grey reef shark is known to have been caught by fishermen on the reefs of D'Arros.

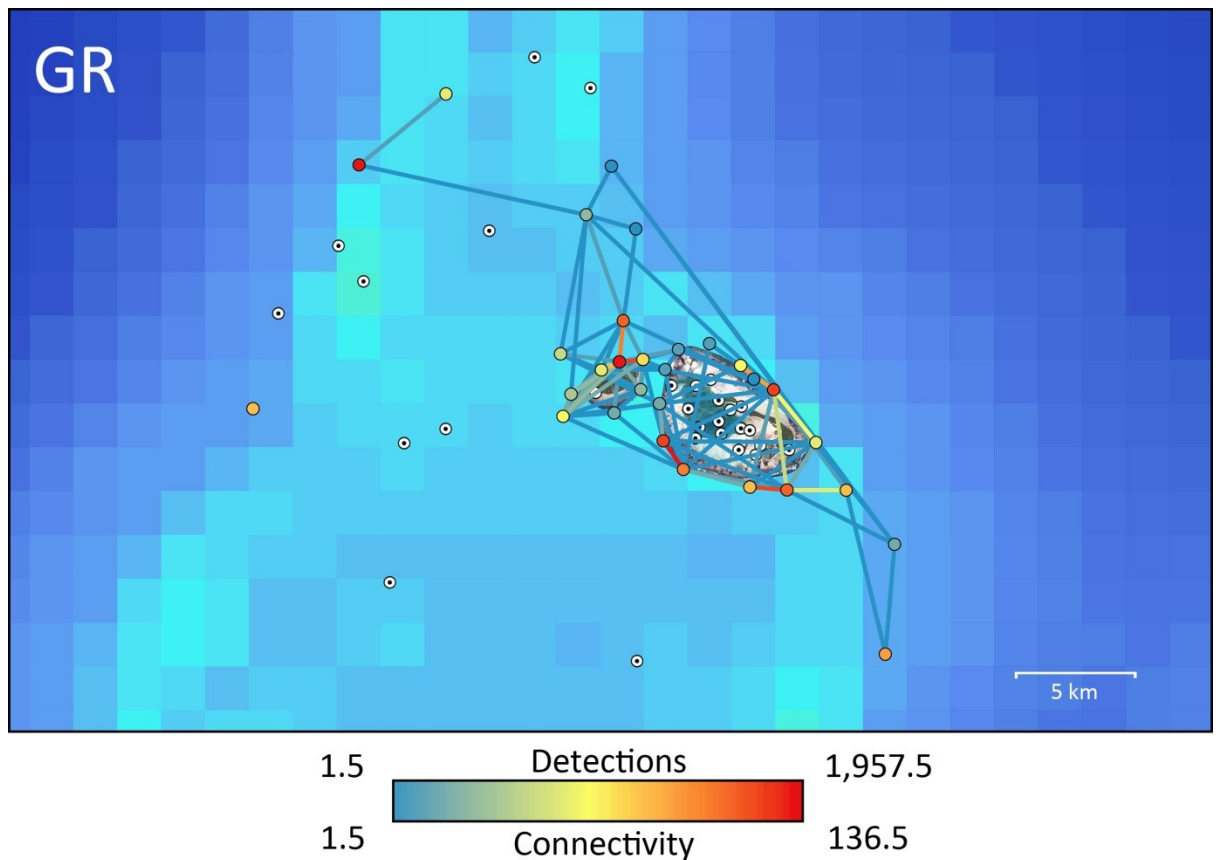


Figure 31: Network displaying grey reef shark detection frequency at each receiver (node colour) and how often each receiver was connected by subsequent detections (edge colour). Receivers with no detections marked with \emptyset . Maps created in ArcGIS, using satellite imagery from LAND INFO Worldwide Mapping and ETOPO2v2 bathymetry data.

Although fewer individuals were tracked, the tawny nurse sharks displayed a range of movements similar to the lemon sharks (Figure 32), reflected by similar node and edge densities (0.761 and 0.120 respectively). The majority of nurse shark detections (70.0%) occurred within the atoll, with regular movement throughout. Almost all (98.1%) of nurse shark detections within the lagoon were from individuals <200 cm ($n = 3$), whereas 84.0% of all nurse shark detections outside the lagoon were from individuals >200 cm ($n = 3$). These larger nurse sharks frequently circumnavigated D'Arros and travelled more widely across the plateau, particularly spending time at a sandy patch several kilometres south of the islands. Chance

encounters during underwater visual surveys have also revealed large aggregations (50+ individuals) of adult nurse sharks of both sexes along both the eastern and western drop-offs of the Amirantes. The high use of the atoll is apparent in the comparison between real and random habitat use, where tawny nurse sharks occupied the lagoon more often than random sharks, but also the disparity for other habitats was smaller compared to other species (Figure 34).

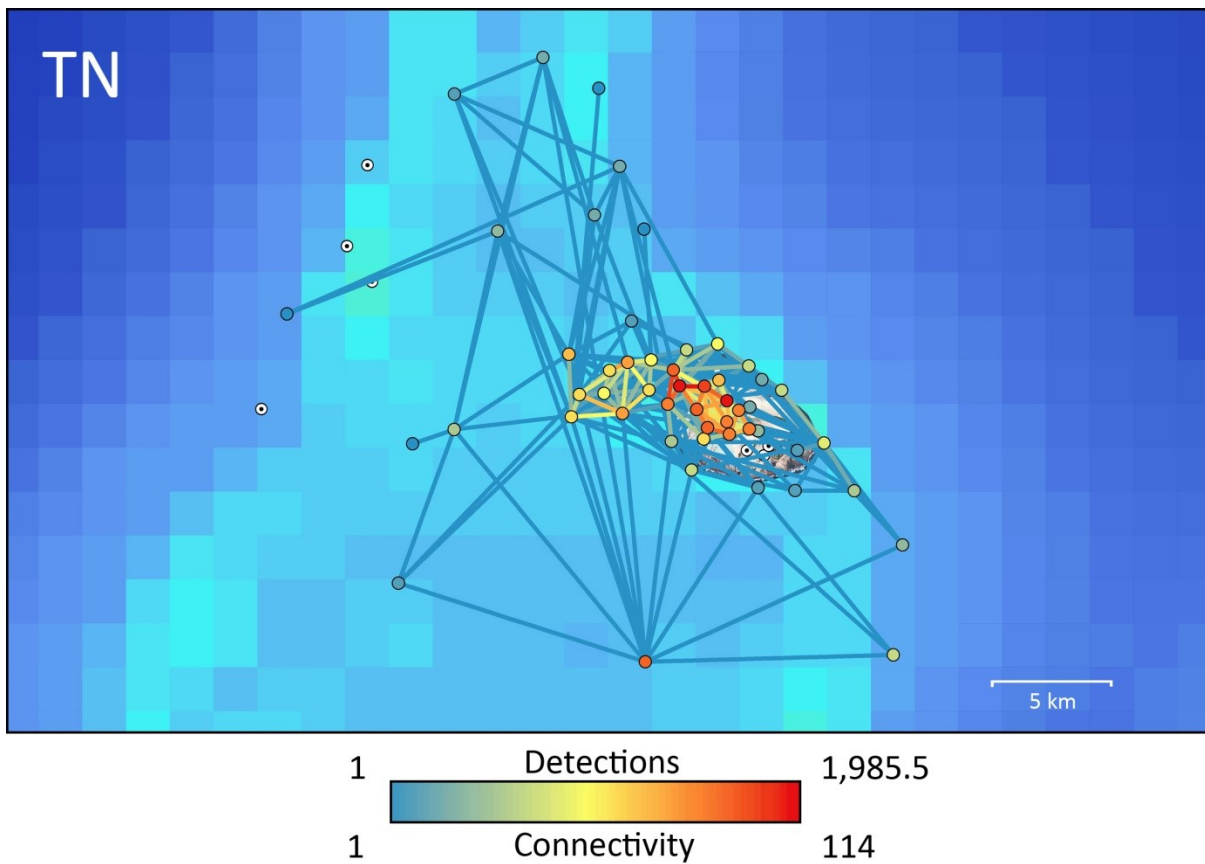


Figure 32: Network displaying tawny nurse shark detection frequency at each receiver (node colour) and how often each receiver was connected by subsequent detections (edge colour). Receivers with no detections marked with 0. Maps created in ArcGIS, using satellite imagery from LAND INFO Worldwide Mapping and ETOPO2v2 bathymetry data.

Silvertip sharks showed the most restricted movements (node density 0.134, edge density 0.005), producing fragmented networks that almost exclusively associate with the drop-off (96.5% of all silvertip detections were along the drop-offs; Figure 33). This is again reflected in the real vs. random network comparison, which showed that real silvertips occupied drop-off

habitats much more than random ones, even transiting along the drop-offs more than random sharks did (Figure 34), revealing significant patrolling behaviour. All tagged silvertip sharks were small juveniles, one of which still had a healing umbilical scar (this shark was 78 cm total length). Four of the 19 tagged silvertip sharks are known to have been caught by fishermen at their original tagging location, which is reflected by their low mean time at liberty (Table 7).

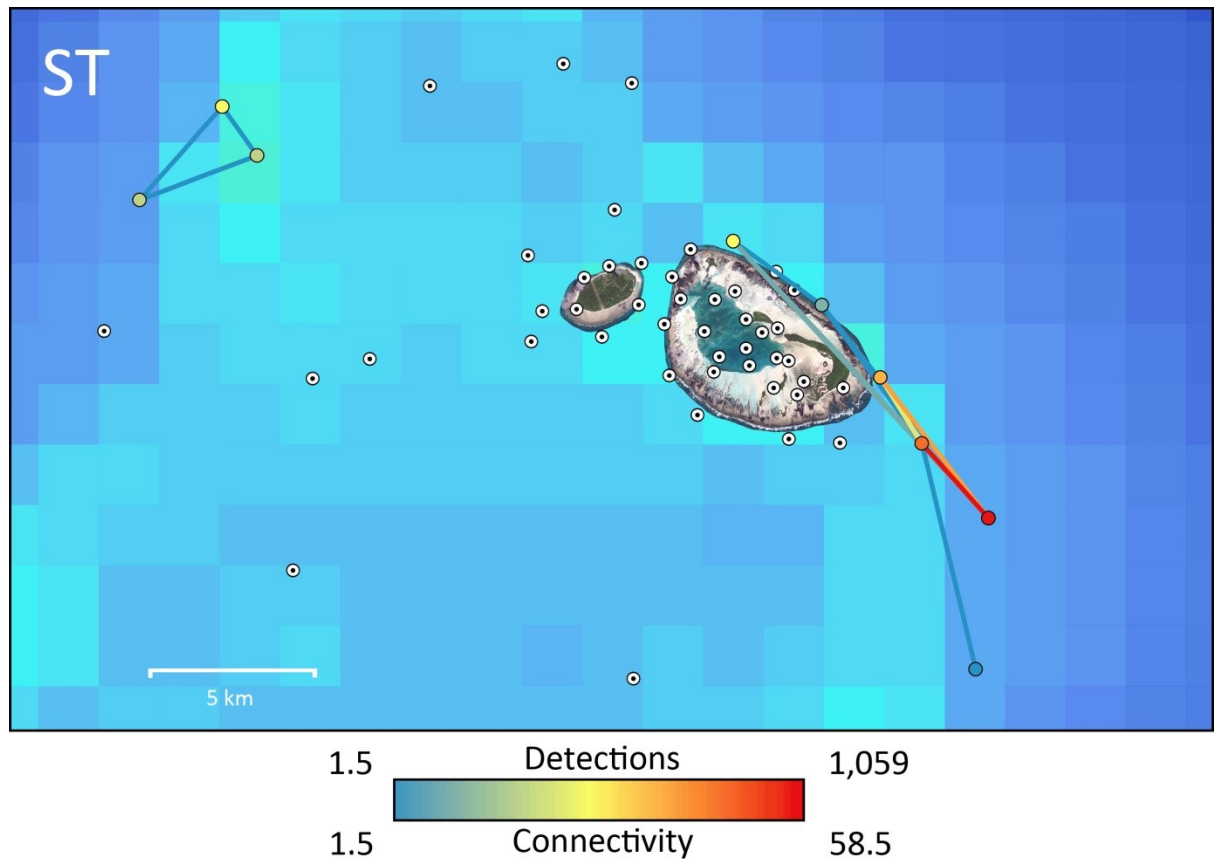


Figure 33: Network displaying silvertip shark detection frequency at each receiver (node colour) and how often each receiver was connected by subsequent detections (edge colour). Receivers with no detections marked with \emptyset . Maps created in ArcGIS, using satellite imagery from LAND INFO Worldwide Mapping and ETOPO2v2 bathymetry data.

All metrics of the real networks of all species were statistically different from those generated by the random networks (Table 8; Table 9). Apart from silvertip sharks along drop-offs, all real networks displayed lower connectivity in all habitats than random networks for all species, suggesting that all tracked individuals displayed more directed movement between nodes than their random counterparts. This is also consistent with the universally low edge densities for all

species (Table 9). The large standard error bars on positive results in Figure 34 reveal large variation even within habitat type, showing highly focused use of particular areas within a habitat, e.g. the eastern lagoon for blacktip reef sharks, and patches of high coral cover near the drop-off for grey reef sharks.

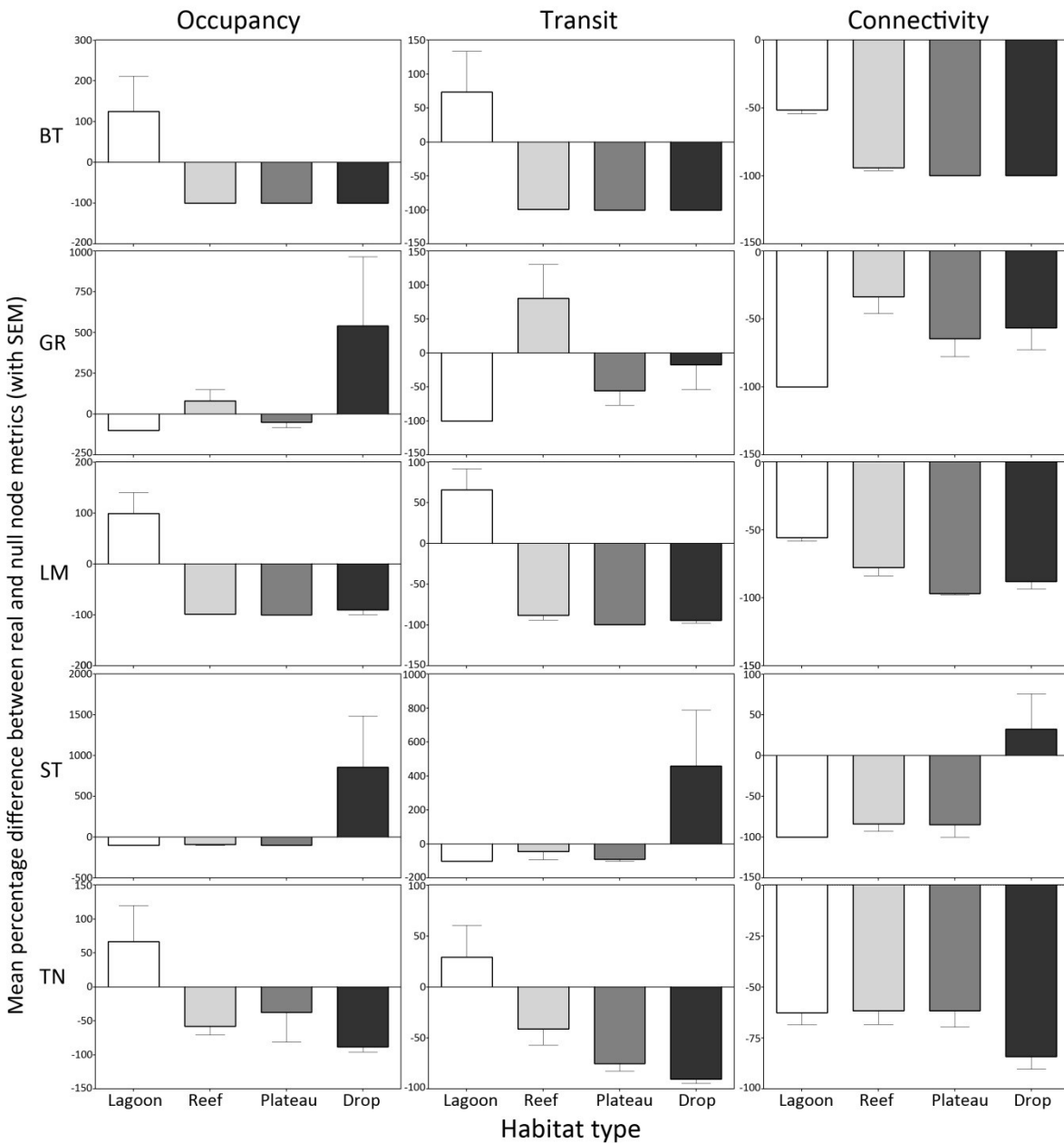


Figure 34: Charts showing, for each species, the mean percentage difference between the actual node metric and those from the randomly generated networks ($n = 100$ per species), with nodes grouped by habitat type. BT = blacktip reef, LM = lemon, GR = grey reef, TN = tawny nurse, ST = silvertip. Error bars represent the standard error of the mean.

Table 8: Results of Wilcoxon signed rank tests comparing node metrics (strength, betweenness, centrality) between real and randomly generated networks. BT = blacktip reef, LM = lemon, GR = grey reef, TN = tawny nurse, ST = silvertip.

Species	Metric	<i>n</i>	Z	p
BT	Strength	67	4.304	<0.001
BT	Betweenness	67	4.623	<0.001
BT	Centrality	67	7.115	<0.001
GR	Strength	67	2.942	0.003
GR	Betweenness	67	2.53	0.012
GR	Centrality	67	5.36	<0.001
LM	Strength	67	3.098	0.002
LM	Betweenness	67	3.198	0.001
LM	Centrality	67	7.102	<0.001
ST	Strength	67	5.959	<0.001
ST	Betweenness	67	5.485	<0.001
ST	Centrality	67	5.578	<0.001
TN	Strength	67	2.624	0.009
TN	Betweenness	67	2.561	0.011
TN	Centrality	67	7.009	<0.001

Table 9: Results of one-sample signed rank tests comparing the node and edge densities of the randomly generated networks to those of the real networks. BT = blacktip reef, LM = lemon, GR = grey reef, TN = tawny nurse, ST = silvertip.

Species	Density	Actual	Random (mean)	<i>n</i>	Z	p
BT	Node	0.522	0.989	100	8.843	<0.001
BT	Edge	0.086	0.722	100	8.682	<0.001
GR	Node	0.448	0.979	100	8.762	<0.001
GR	Edge	0.038	0.535	100	8.682	<0.001
LM	Node	0.836	0.988	100	8.836	<0.001
LM	Edge	0.150	0.720	100	8.683	<0.001
ST	Node	0.134	0.928	100	8.727	<0.001
ST	Edge	0.005	0.207	100	8.683	<0.001
TN	Node	0.761	0.974	100	8.762	<0.001
TN	Edge	0.120	0.516	100	8.683	<0.001

5.4 Discussion

This chapter has revealed that the habitats of D'Arros and St Joseph provide important, potentially nursery, habitats for sharks within the Amirantes and across the Seychelles. Juveniles of blacktip reef, sicklefin lemon, grey reef and tawny nurse sharks were all found to display long-term, perennial use of the lagoon and coastal reef habitats, fulfilling previously established nursery criteria, whereby a nursery should: contain juveniles more frequently than elsewhere, be used regularly for extended periods, and be used repeatedly across years (Heupel *et al.* 2007). The confined, access-restricted habitat provided by the lagoon presumably provides refuge from predation alongside foraging opportunities, as suggested for similar shark nurseries in the Bahamas (Guttridge *et al.* 2011). The potential importance of D'Arros and St Joseph as a nursery supporting regional recruitment is emphasised by the fact that such access restricted lagoon habitat, so strongly favoured by the majority of sharks here, is particularly rare in Seychelles. Only a few other locations in the Seychelles appear to offer such habitat as nursery refuges (e.g. the atolls of St Francois, Cosmoledo, and Aldabra), yet all of them are a considerable distance from D'Arros and St Joseph (200–1,000 km) and involve crossing very deep water (>1,000 m). Consequently D'Arros and St Joseph may form an important part of a small, isolated network of nurseries that support recruitment into the local reef shark populations.

5.4.1 *Species-specific Habitat Preferences*

Blacktip reef sharks (juveniles and adults) displayed a marked preference for the lagoon habitats of St Joseph Atoll, with comparatively limited use of the coastal reefs. The blacktip reef shark movements recorded here are consistent with those reported from other regions. In Aldabra Atoll blacktip reef sharks were recorded predominantly in the lagoon, with the highest catch rates near the mangroves at high tide (Stevens 1984). This is similar to the blacktips in the present study preferring the eastern end of the lagoon near sheltered flats and mangroves.

Blacktip reef sharks at Palmyra Atoll in the Pacific also displayed very restricted use of lagoon habitats, with smaller individuals more frequently using shallow sand flats (Papastamatiou *et al.* 2009). At Palmyra, 81% of blacktip reef shark movements occurred at a core receiver, while at Aldabra 81% of recaptures occurred within 1 km of the tagging location (Stevens 1984), both of which are also consistent with the predominant restriction of movements to the eastern end of the lagoon observed here. Such fine-scale spatial dynamics make the blacktip reef sharks particularly vulnerable to rapid depletion from relatively limited fishing exposure.

In Moorea, French Polynesia, female blacktip reef sharks preferentially use lagoon habitats while males more frequently use the fore-reef, overlapping with grey reef sharks (Mourier, Mills & Planes 2013). Consequently, the female bias in the tracked individuals of the present study may have emphasised the importance of the St Joseph lagoon, although individuals of both sexes were recorded over the long-term both within the lagoon and on the surrounding reefs. Despite the majority of blacktip reef shark movements being highly focused, they have also been recorded to move reasonable distances (>250 km, (Speed *et al.* 2015)), suggesting there may be some capacity for them to move more broadly across the Amirantes plateau, albeit not observed here, perhaps due to the relative isolation of D'Arros and St Joseph.

Data from Aldabra revealed that the largest blacktip reef shark caught there (140 cm; (Stevens 1984)) was small in comparison to other areas of the Indo-Pacific (up to 160 cm; (Chin *et al.* 2013)), suggesting that growth rates for this species may be comparatively limited in the Seychelles, perhaps due to food limitation. In the present study the largest blacktip reef shark was only 130 cm, suggesting growth may also be limited at D'Arros and St Joseph. Growth rates for hawksbill turtles at D'Arros and St Joseph have been recorded as amongst the slowest for the species in the world, perhaps due to sparse food availability or high competition, but

this may be an acceptable cost for the refuge from predators provided by the access restriction of the atoll lagoon (von Brandis *et al.* 2010).

Sicklefin lemon sharks also displayed extensive use of the lagoon, but also more frequent use of the coastal reefs and Amirantes plateau than the blacktip reef sharks. Consistent with the present study, previous acoustic tracking of juvenile and sub-adult lemon sharks in the lagoon of St Joseph revealed perennial high fidelity to the lagoon, with over 99.9% of detections occurring in lagoon habitats, particularly in the east (Filmlalter *et al.* 2013). The present study, however, also tracked adult lemon sharks as well as juveniles and across a much larger array of acoustic receivers. This showed that larger lemon sharks (>1.8 m total length), visited the lagoon frequently, but also started to adopt broader movements across the Amirantes plateau, including to other islands such as Marie-Louise (80 km away) and Bird Island (300 km away). Meanwhile individuals <1.8 m remained almost exclusively within the confines of the lagoon. This is consistent with the findings from Aldabra, whereby lemon sharks were overall most common in the lagoon, but those over approximately 1.8 m were more likely to be caught outside the lagoon in channels and on the surrounding reefs (Stevens 1984). In western Australia, lemon sharks also only remained within the apparent nursery area of Shark Bay until they started to mature (White & Potter 2004).

Similar to the blacktip reef sharks, the lemon sharks at D'Arros and St Joseph appear smaller than elsewhere in the Indian Ocean: the largest individual caught in the present study was a 241 cm mature male, while individuals have been recorded up to 310 cm in French Polynesia (Clua *et al.* 2010). The largest individual caught in Aldabra was also only 240 cm (Stevens 1984), consistent with the interpretation that sharks around D'Arros and St Joseph may have comparatively limited growth rates. Tawny nurse sharks displayed very similar movements to the lemon sharks, with smaller individuals (<2 m) preferring lagoon habitats, while sharks >2 m

more frequently used and aggregated on plateau habitat. Very few reports on tawny nurse shark could be found in the literature: in Aldabra nurse sharks were also found primarily in the lagoon, with larger individuals mostly recorded in the channels and on the outer reefs (Stevens 1984), while along the Great Barrier Reef, tawny nurse sharks were predominantly encountered along shallow reef flats (Rizzari, Frisch & Magnenat 2014).

Habitat preferences of grey reef sharks differed from the other species in that most adults favoured particular drop-off habitats, while the few smaller grey reef sharks tracked appeared to prefer the coastal reefs along the northern edge of St Joseph, spending the majority of their time patrolling there. The habitat use of grey reef sharks recorded here is consistent with that reported elsewhere, typically showing high fidelity to offshore reef slopes (Barnett *et al.* 2012; Vianna *et al.* 2013; Heupel & Simpfendorfer 2015; Espinoza *et al.* 2015b). For instance grey reef sharks at the remote Indian Ocean atolls of Rowley Shoals had over 99% of their detections occur on the outer reef slope (Field *et al.* 2011), while at Aldabra grey reef sharks were mainly caught along the outer reef and channel edges (Stevens 1984). The grey reefs in the present study also displayed high fidelity to particular regions, resulting in fragmentation of their network as those tagged nearer offshore drop-offs did not cross to coastal reefs and *vice versa*.

The strong female bias in the tagged grey reef sharks also highlights that only a subset of the local population was tracked, with the movements of males remaining largely unaccounted for. This may in part reflect the fact that tagging efforts predominantly fished at depths <20 m, while male grey reef sharks in the Red Sea have been recorded to favour depths ~35 m (Hussey *et al.* 2013), perhaps causing the fishing techniques used here to have selectively excluded males. However, given the large expanse of unmonitored, continuous plateau and drop-off habitat, the poor representation of grey reef shark movements may also be indicative

of them undertaking wider ranging movements in the Amirantes than when at other isolated atolls: in the Great Barrier Reef grey reef sharks have been recorded to move up to 134 km between reefs (Heupel, Simpfendorfer & Fitzpatrick 2010).

Similar to the nurse sharks, very little information on the behaviour of silvertip sharks seems to be available in the literature, with the present study among some the first reported tracks for the species (Barnett *et al.* 2012; Bond *et al.* 2015; Espinoza *et al.* 2015a), and seemingly the first for juveniles. The juvenile silvertip sharks tracked at D'Arros and St Joseph displayed a very strong preference for drop-off habitats, with limited movements towards the coastal reefs. This is largely comparable to catch data from Aldabra, where most silvertip sharks were caught within 1 km of the reef, with the majority also being small, immature individuals <120 cm (Stevens 1984). Most recaptures of individuals also only occurred within 2 km of their tagging location (Stevens 1984). It may be that silvertip sharks at Aldabra were recorded closer to coastal habitats because there the coastal reefs descend directly into the drop-off, whereas in the Amirantes the drop-off is removed from the coastal reefs by the expanse of plateau habitat.

In this chapter, the application of network analysis has revealed the dynamics of movement within and between the various habitats of D'Arros and St Joseph in an accessible and intuitive way. Moreover, comparing the observed networks to randomised null networks made it possible to determine actual shark habitat preferences, as opposed to simply describing where the tracked individuals spent more time. Doing so illustrated how various shark species using the coastal habitats of D'Arros and St Joseph showed a strong preference for the lagoon (e.g. blacktip reef, lemon sharks), while others displayed a marked preference for drop-off habitats further offshore (e.g. grey reef, silvertip sharks). The highly focused use of D'Arros and St Joseph by a multi-species assemblage of sharks, including the strong indication of its function

as an important nursery area, highlight that its protection through the designation of a marine protected area (MPA) may help promote recruitment into regional populations, particularly if larger individuals of certain species disperse broadly upon reaching maturity. The potential for different MPA options to protect the local shark species is evaluated in Chapter 7.

6 Influence of environmental temporal cycles on shark spatial dynamics at D'Arros and St Joseph, Seychelles

6.1 Introduction

The previous chapter revealed the habitat preferences of five shark species around D'Arros and St Joseph in the Amirantes, Seychelles. However, the use of these habitats may be dynamic across a variety of temporal scales, influenced by changing environmental conditions. For instance, in the Seychelles there are contrasting monsoonal seasons, where from May–October strong winds (15–30 kts) blow consistently from the southeast, during which there is little rainfall (~80 mm per month; (Walsh 1984)). During November through March, the wind blows from the northwest, but generally not as strongly or consistently, and during this period there is generally heavy, extended rainfall (~400 mm per month; (Walsh 1984)). Water temperatures vary between the two seasons, from ~26 °C during the southeast monsoon to ~28 °C in the northwest, and salinity may also vary given the contrasting rainfall. In the months between the monsoons as the winds change, there is often little wind and the seas can be very calm. Given such seasonal variation in environmental conditions, it is reasonable to hypothesise that this may have some influence on shark spatial dynamics, as was revealed for tiger sharks in the Atlantic in Chapters 3 and 4.

At a finer temporal scale, shark behaviour may also vary with the diel cycle – numerous studies have revealed contrasting behaviours between nocturnal and diurnal periods, with, for instance, higher nocturnal activity sometimes being related to foraging (Sundström *et al.* 2001; Sims 2010). At an even finer temporal resolution, there is another environmental cycle that may have a particularly strong influence at D'Arros and St Joseph: the tidal cycle. St Joseph atoll has a large (~15 km²), complex expanse of flats habitat surrounding the lagoon, access to

which is strictly controlled by the tides. The flats possess large beds of seagrass, are fringed by mangroves and contain shallow pools that become cut off at low tide. These areas are used by an abundance of marine life, including various reef sharks (see Chapter 5), rays, bonefish *Albula oligolepis*, carangids (e.g. permit *Trachinotus falcatus*), and green *Chelonia mydas* and hawksbill turtles *Eretmochelys imbricata*. Consequently habitat like this may provide profitable foraging and refuge opportunities (Carlisle & Starr 2010; Guttridge *et al.* 2011), but its use would be governed entirely by the tides.

To assess how dynamic shark space-use at D'Arros and St Joseph might be, this chapter investigates: 1) how presence in the array varies with the contrasting monsoon seasons, both within and between species; 2) at a finer scale, how diel cycles affect shark behaviour; and 3) how shark habitat use in St Joseph atoll varies over the course of the tidal cycle.

6.2 Methods

The study site for this chapter was D'Arros and St Joseph Atoll, as described in the General Methods (Chapter 2). Shark movements were tracked using acoustic telemetry as described in the General Methods, using the same tags, array and study period (November 2013 to November 2015) as outlined in the Methods of Chapter 5.

6.2.1 Seasonal Variation

The first step to assess broad temporal patterns was a visual inspection of the detection record by plotting presence/absence in the array over time for each shark. Seasonal variation was investigated using plots of mean proportion of pings per month for the three species with enough data to assess seasonal patterns (>20 tags for each of blacktip reef *Carcharhinus melanopterus*, sicklefin lemon *Negaprion acutidens*, grey reef shark *Carcharhinus amblyrhynchos*). Mean monthly water temperature was calculated from the temperature loggers attached to each receiver, grouped by whether they were inside (lagoon) or outside (reefs) the atoll – there was a suspected difference based on reduced flow of lagoon shallows versus deeper reefs circulated by upwellings. Apparent variation in ping frequency between the seasons was tested using Mann Whitney-U tests (due to non-normality of the data; SigmaPlot, Systat Software, San Jose, CA) on the proportion of pings in the northwest monsoon (NWM) versus the southeast monsoon (SEM) for each species. Lemon sharks were further split into individuals smaller and larger than 177 cm, based on the habitat use analysis in Chapter 5, where individuals ≥ 177 cm adopted broader movements across the Amirantes.

Apparent significance of seasonal variation in blacktip reef sharks was further investigated by testing for seasonal sex segregation, as most individuals remained within the array despite varying ping frequency (~21 tags active in both NWM and SEM). This was achieved using a grid occupancy analysis, whereby the study area was split into grid cells of 0.25 km² and the

presence/absence of male and female blacktip reef sharks within each cell was calculated on a daily basis. Only individuals over 100 cm were included in this analysis, to avoid inclusion of juvenile movements that may not be driven by reproductive factors. Calculating the proportion of grid cells that overlapped between males and females on a daily basis provided a daily overlap coefficient between 0 and 1, where 0 indicated no overlap for that day and 1 was complete overlap. The overlap coefficient was then plotted over time to reveal any seasonal variation. This procedure was also repeated for only the receivers installed at the very beginning of the study period ($n = 51$) to see if any patterns persisted over a longer period (3 years, November 2012 to November 2015). Any statistical differences in mean overlap between the seasons were tested for using Mann-Whitney U tests (SigmaPlot, Systat Software, San Jose, CA). The hypothesis that any observed sex-biased seasonal variation may be explained by thermal preferences was tested by comparing the temperatures experienced by each sex in each season, as determined by the receiver-linked temperature loggers. Temperature variation between the sexes for each season was also tested using Mann-Whitney U tests (SigmaPlot, Systat Software, San Jose, CA). Any differences in space use between the sexes and seasons were visualised using the network analysis outlined in General Methods (Chapter 2), with connection frequency limited to one hour so that only fine-scale, directed movements were displayed.

6.2.2 Diel Variation

To test whether sharks were present more frequently in the array during day versus night, the ratio of diurnal (06:00–18:00) to nocturnal (18:00–06:00) pings was calculated and plotted for each species, where a ratio of 1 represented equal diel ping distribution, >1 signified more pings during the day, and <1 more at night. Whether the ratio deviated significantly from 1 was tested using one-sample signed rank tests of day to night ping ratios, tested against the hypothesised null median of 1 (SigmaPlot, Systat Software, San Jose, CA). Furthermore, the

percentage of diurnal and nocturnal pings was calculated for each of the habitat types described in Chapter 5 (lagoon, coastal reef, plateau, drop-off) to see if shark habitat use changed with the diel cycle.

6.2.3 *Tidal Variation*

In order to evaluate the influence of the tidal cycle on the habitat use of sharks in the atoll, the analysis was restricted to only those receivers in the deep lagoon (mean depth 4.6 m, $n = 8$) and on the atoll flats (mean depth 1.1 m, $n = 9$). The analysis also only included blacktip reef and sicklefin lemon sharks, as these were the only species to frequent the lagoon and have >20 individuals tagged. First it was necessary to obtain high resolution tidal information to be able to match each shark ping to an absolute tidal height in metres. A pressure logger (HOBO Water Level Data Logger, Onset, Bourne, USA) was used to measure water pressure in the lagoon over a six month period. This was calibrated using the known depth of the logger to produce a depth in metres. Tidal cycles were also modelled using the Oregon State University Tidal Model Driver (Egbert & Erofeeva 2002) based on the harmonics for St Joseph Atoll's location, outputting predicted tidal heights in metres every 10 mins. The tidal heights of the logger and model were compared and found to differ by only 1.96%. Consequently the tidal heights from the model were used to estimate a tidal height for every ping in the database, with each ping being assigned the tidal height closest to it, temporally.

The proportion of blacktip reef and lemon shark tracks spent in the deep lagoon versus the lagoon flats was calculated across the tidal cycle by binning the number of pings into 10 cm tidal height bins. Due to the uneven distribution of tidal heights across the range (0–2 m) of the tidal cycle, it was necessary to correct the number of pings in each bin for bias prior to calculating the proportion of pings. This was achieved by first using the tidal model across the whole study period to calculate the absolute frequency of each tidal height during that period

(a). What proportion of the cycle each height bin would occupy if they were equally represented was then calculated (b). A correction factor was then calculated ($= b/a$), which was used to multiply the number of pings in each bin and normalised the representation of each bin in the cycle prior to calculating the proportions.

For blacktip reef and lemon sharks differences in normalised ping frequency between the deep and shallow lagoon for each tidal bin were tested using Mann-Whitney U tests (SigmaPlot, Systat Software, San Jose, CA), performed on the proportion of pings in the deep versus shallow receivers for each tidal bin. The threshold tidal height above which each species could more frequently access the lagoon flats was taken to be the height at which the shallow ping frequency was consistently, significantly greater than the deep ping frequency. These thresholds were used to construct low- and high-tide networks for each species, to determine how their habitat use changed with the higher tides (with connections restricted to one hour to prevent connections between individual tidal cycles).

6.3 Results

As with Chapter 5, over 41,655 tracking days were obtained from the five shark species (blacktip reef, sicklefin lemon, grey reef, tawny nurse *Nebrius ferrugineus*, silvertip *Carcharhinus albimarginatus*) tracked between November 2013 and November 2015: the same tracks are used for analysis here (Table 7).

6.3.1 Seasonal Variation

During the two years of data used for analysis, 257,486 verified pings were recorded across all sharks. Plotted over time, no immediate temporal patterns are apparent, apart from most individuals and species displaying long-term, perennial residence in the study area (Figure 35). There may be some indication of several grey reef sharks being absent from the array around August–November, but this is not apparent in all individuals. However, when the mean proportion of pings per month is plotted there does appear to be some variation in pings between the NWM and SEM seasons (Figure 36). For both lemon and blacktip reef sharks there is a slight but significant decrease in their detection frequency during the SEM (see Table 10, which shows the results for all tests), when temperatures are ~ 2 °C lower than during the NWM (Figure 36). Grey reef shark detection frequency, on the other hand, is somewhat more erratic, with no clear or significant difference between the seasons (Table 10; Figure 36).

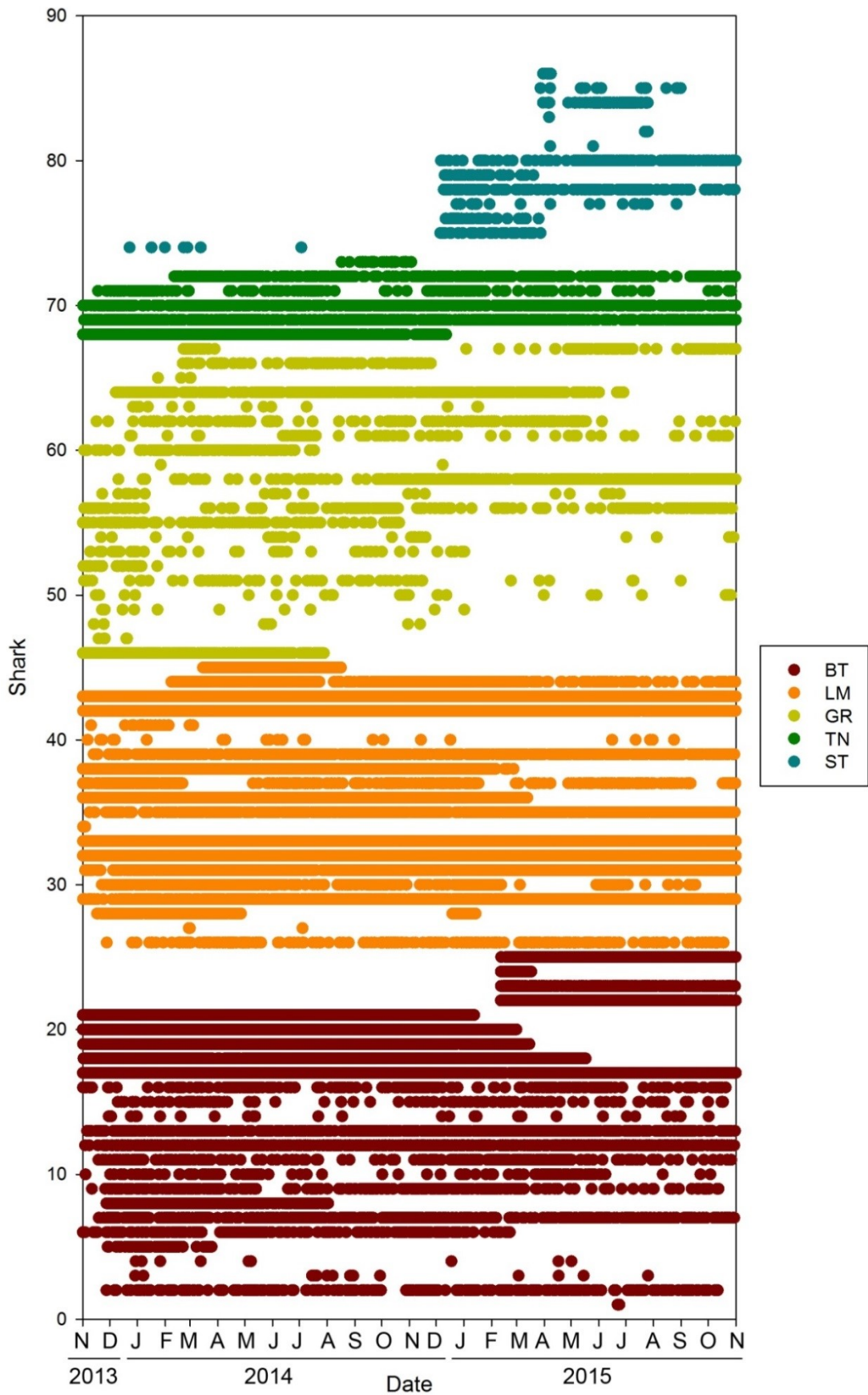


Figure 35: Presence plot of each individual shark in the D'Arros and St Joseph array, revealing regular presence in the array for the duration of the study for all species. BT = blacktip reef shark; LM = sicklefin lemon shark; GR = grey reef shark; TN = tawny nurse shark; ST = silvertip.

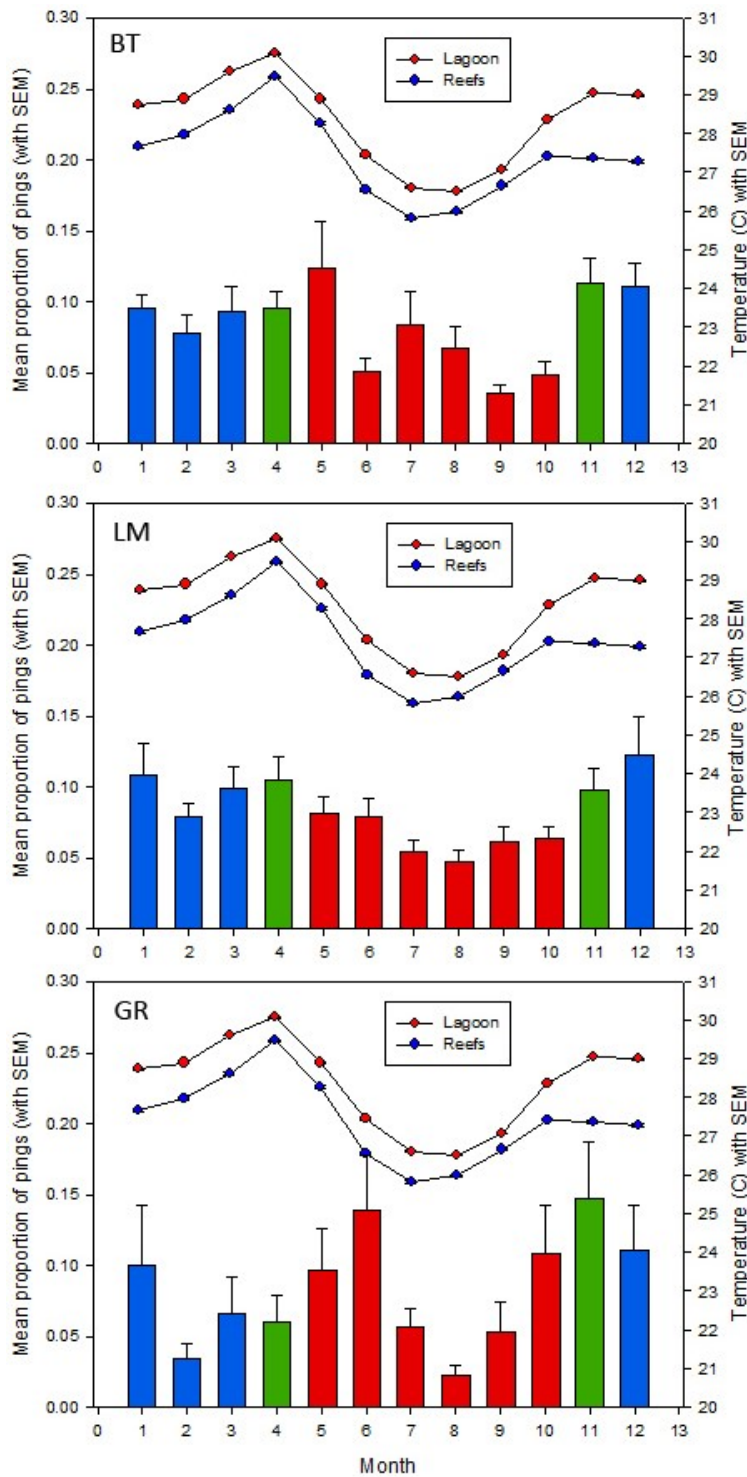


Figure 36: Monthly variation in detections for three most abundant species (histograms: blue = northwest monsoon, red = southeast monsoon, green = changing monsoons) with monthly water temperatures in the lagoon and on the outer reefs overlaid, revealing seasonal dips in ping frequency for blacktip reef and lemon sharks during the SE. BT = blacktip reef shark; LM = sicklefin lemon shark; GR = grey reef shark. Error bars represent the standard error of the mean.

Seasonal changes in movement may be more complex than suggested by overall changes in ping frequency. As demonstrated in the previous chapter (5), larger lemon sharks adopt wider

ranging movements than smaller individuals, with smaller lemon sharks remaining in the atoll. Consequently the test on seasonal differences in ping frequency was repeated for lemon sharks both larger and smaller than 177 cm. Seasonal differences were only found to be significant for the wider ranging larger lemon sharks (Table 10).

Table 10: Mann-Whitney results testing proportion of pings in the northwest monsoon versus southeast. BT = blacktip reef shark; LM = sicklefin lemon shark; GR = grey reef shark.

	U	T	n1	n2	p
BT	2412.5	7991.5	72	108	<0.001
GR	2626	4456	60	90	0.776
LM	2102	6122	64	96	<0.001
LM<177	659.5	1404.5	32	48	0.289
LM>177	430.5	1633.5	32	48	<0.001

Although for blacktip reef sharks fewer pings are recorded in the SEM, most individuals are still recorded in the array in both seasons (Figure 35). This implies the sharks are still within the study area, but are being picked up by the array less frequently during the SEM.

To investigate this further, blacktip reef shark movements were tested for sexual segregation using grid occupancy analysis, which revealed marked seasonal segregation (Figure 37). The mean overlap coefficient between males ($n = 2$) and females ($n = 15$) over 100 cm in the NWM was 0.324 ± 0.183 (S.D.), but only 0.0431 ± 0.0966 (S.D.) in the SEM, a difference that proved statistically significant (Table 11). Due to the low number of males when the study period is restricted to November 2013–November 2015, the analysis was also performed for the full, unrestricted study period (November 2012–November 2015), although this meant the array was restricted to the 51 receivers originally installed (Figure 38). During this period, the mean overlap coefficient between males ($n = 5$) and females ($n = 17$) was 0.310 ± 0.231 (S.D.) in the NWM and 0.0884 ± 0.156 (S.D.) in the SEM, providing highly comparable results to the previous analysis. Regardless of the array used for analysis, the overlap coefficient between males and females was significantly higher during the NWM than the SEM (Table 11).

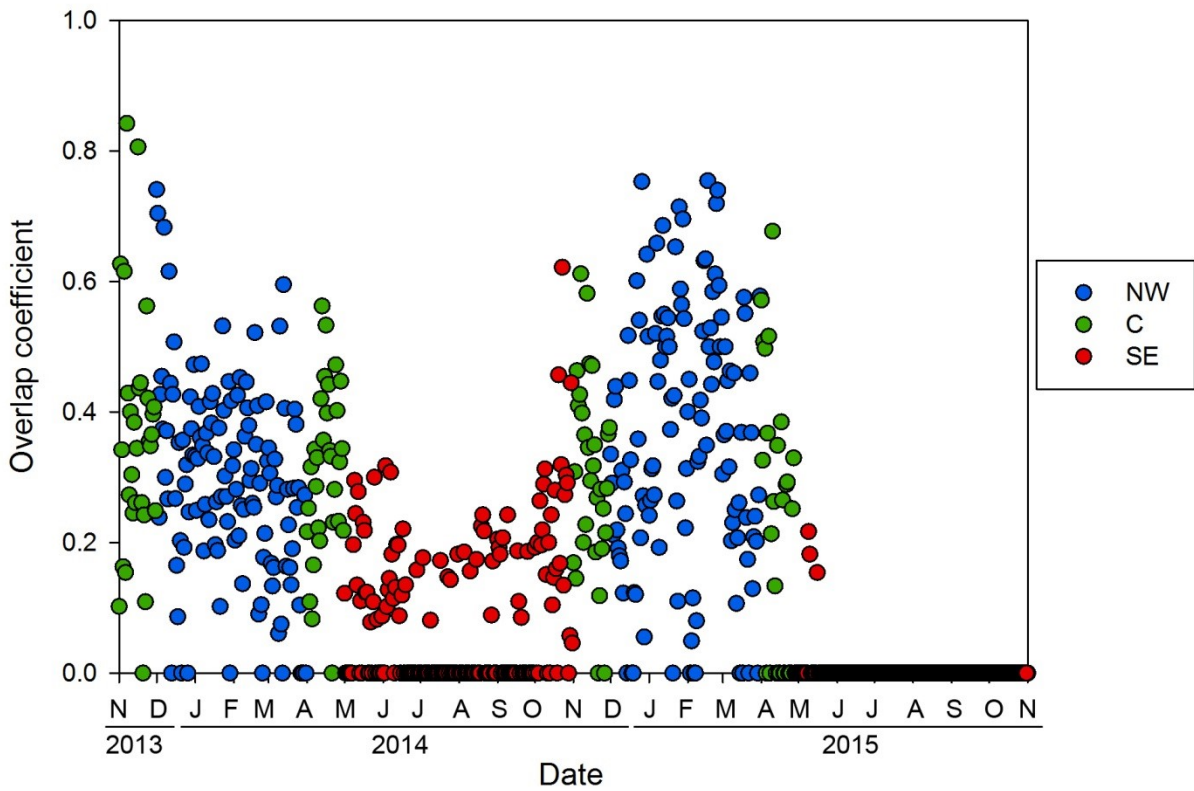


Figure 37: Daily overlap coefficient between mature male and female blacktip reef sharks. NW = northwest monsoon; C = changing season; SE = southeast monsoon.

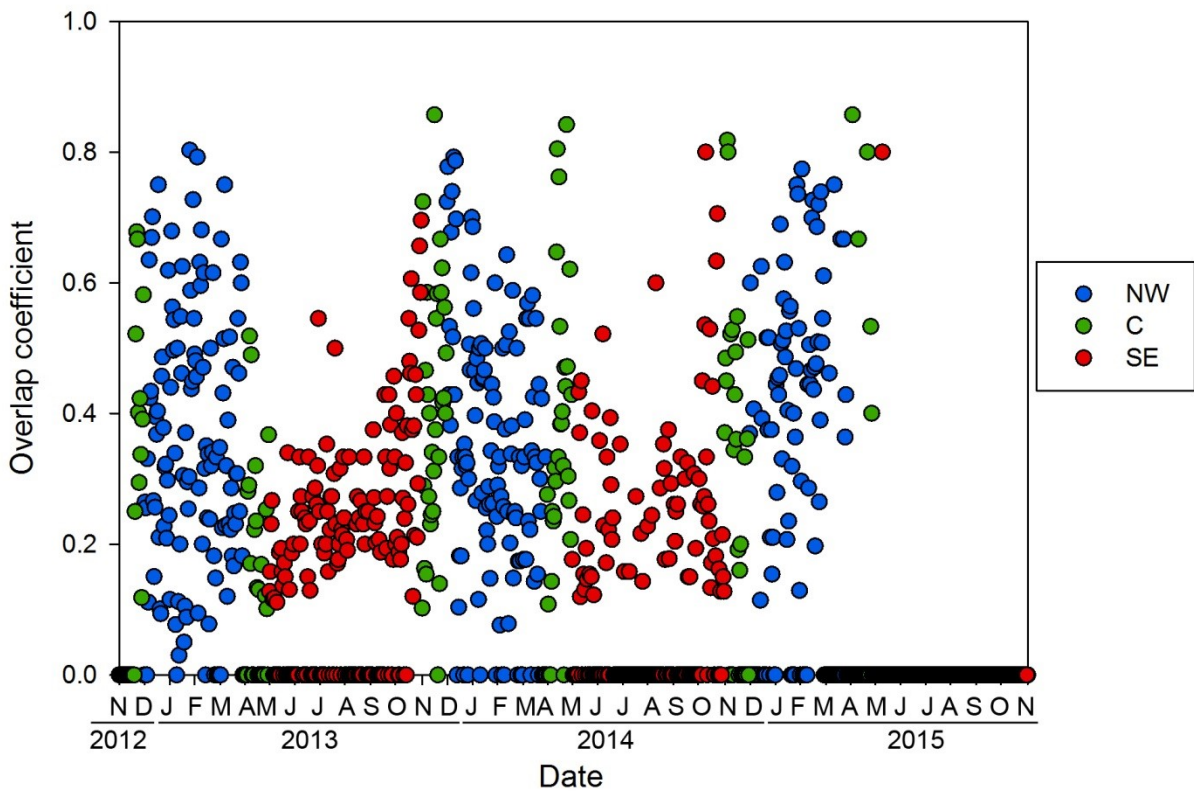


Figure 38: Daily overlap coefficient between mature male and female blacktip reef sharks (51-receiver original array). NW = northwest monsoon; C = changing season; SE = southeast monsoon.

Table 11: Mann-Whitney test results of male and female blacktip reef shark overlap coefficients between seasons for both the study array (67) and the original (51). NWM = northwest monsoon; SEM = southeast monsoon.

Test	U	T	n1	n2	p
NWM vs. SEM: 67	8078.5	110380.5	242	368	<0.001
NWM vs. SEM: 51	50202	243828	363	628	<0.001

To visualise how the movements of each sex differed according to the season, relative one hour restricted networks were constructed (Figure 39). Within each network all node and edge strengths were calculated as a proportion of their overall value, to make the scales comparable between maps. This revealed female movements to be largely similar between seasons, with focused use of the eastern lagoon habitats. Males, however, predominantly used other areas of the lagoon during the SEM, but frequently moved to the eastern region favoured by the females during the NWM. Consequently seasonal male movements are driving the seasonal segregation, which occurs over a fine geographical scale of ~1.5 km.

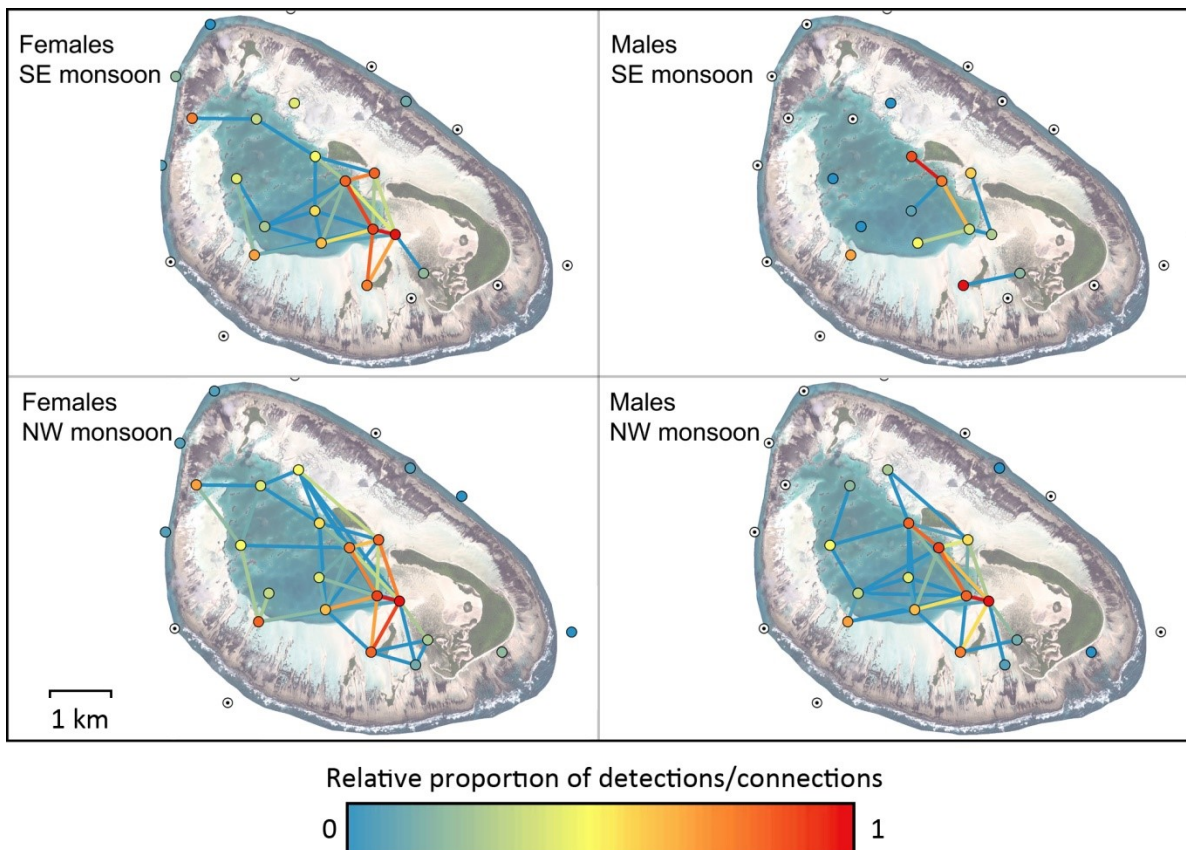


Figure 39: Relative one hour networks of male and female blacktip reef shark movements in each season.

The observed sexual segregation may be driven by contrasting thermal preferences of the two sexes. However, there is no evidence for this scenario from the present data: both male and female blacktip reef sharks experienced similar temperatures in both seasons (29.1 vs. 29.1 °C in NWM, 27.5 vs. 27.5 °C in SEM), as determined by pairing logger temperatures with detections and comparing the temperatures each sex experienced in each season (Table 12).

Table 12: Mann-Whitney test results comparing water temperatures experienced by male and female blacktip reef sharks in each season. NWM = northwest monsoon; SEM = southeast monsoon.

Test	U	T	n1	n2	p
m vs. f: NWM	18894570	22132228	2373	16102	0.386
m vs. f: SEM	28612209	34405342	3207	18046	0.311

6.3.2 Diel Variation

Having compared the observed ratio of diurnal to nocturnal pings to the expected ratio of 1, it was revealed that no diel variation in ping frequency was detected for blacktip reef sharks,

whereas lemon sharks were detected significantly more frequently at night (Table 13; Figure 40). In contrast, grey reef sharks were present in the array much more frequently during the day (although some individuals did show a strong nocturnal presence), with silvertip sharks detected almost exclusively during the day (Table 13; Figure 40). Similar to the blacktip reef sharks, tawny nurse sharks displayed no difference in ping frequency between day and night (Table 13; Figure 40).

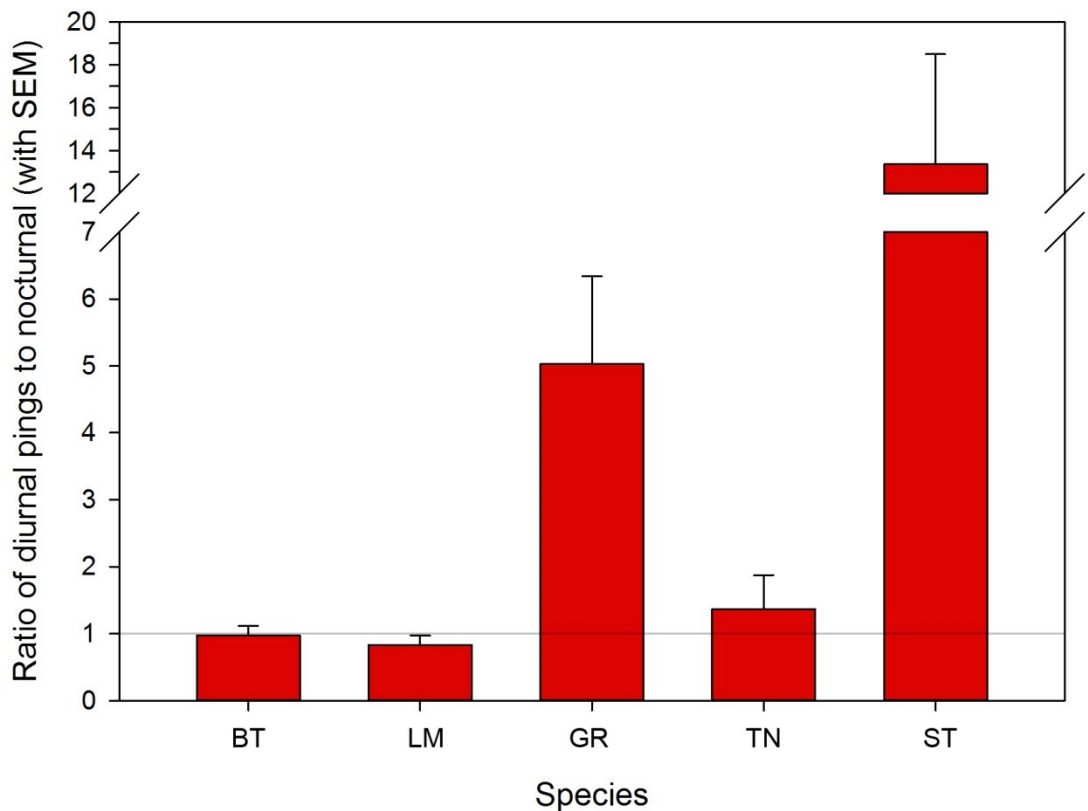


Figure 40: Ratio of diurnal to nocturnal ping frequencies for each species. A ratio of 1 indicates equal number of detections during day and night. BT = blacktip reef shark; LM = sicklefin lemon shark; GR = grey reef shark; TN = tawny nurse shark; ST = silvertip. Error bars represent the standard error of the mean.

Table 13: One-sample signed rank tests of day to night ping ratios (tested against hypothesised median of 1). BT = blacktip reef shark; LM = sicklefin lemon shark; GR = grey reef shark; TN = tawny nurse shark; ST = silvertip.

Test	Z	n	p
BT	-0.686	25	0.501
LM	-2.203	20	0.027
GR	3.285	22	<0.001
TN	0.105	6	1
ST	3.059	13	<0.001

However, this may mask diel changes in behaviour if movements during both day and night still occur within the detection field of the array. For instance for blacktip reef sharks 57.9% of pings in the lagoon occurred during the night, whereas 83.7% of the coastal reef pings were during the day (Figure 41). For lemon sharks, 54.7% of pings in the lagoon occurred at night, whereas 82.9% of coastal reef pings were during the day. Grey reef sharks showed the starkest contrast, with 80.7% of pings on coastal reefs occurring at night, whilst 85.4% of pings across the plateau and drop-off were during the day.

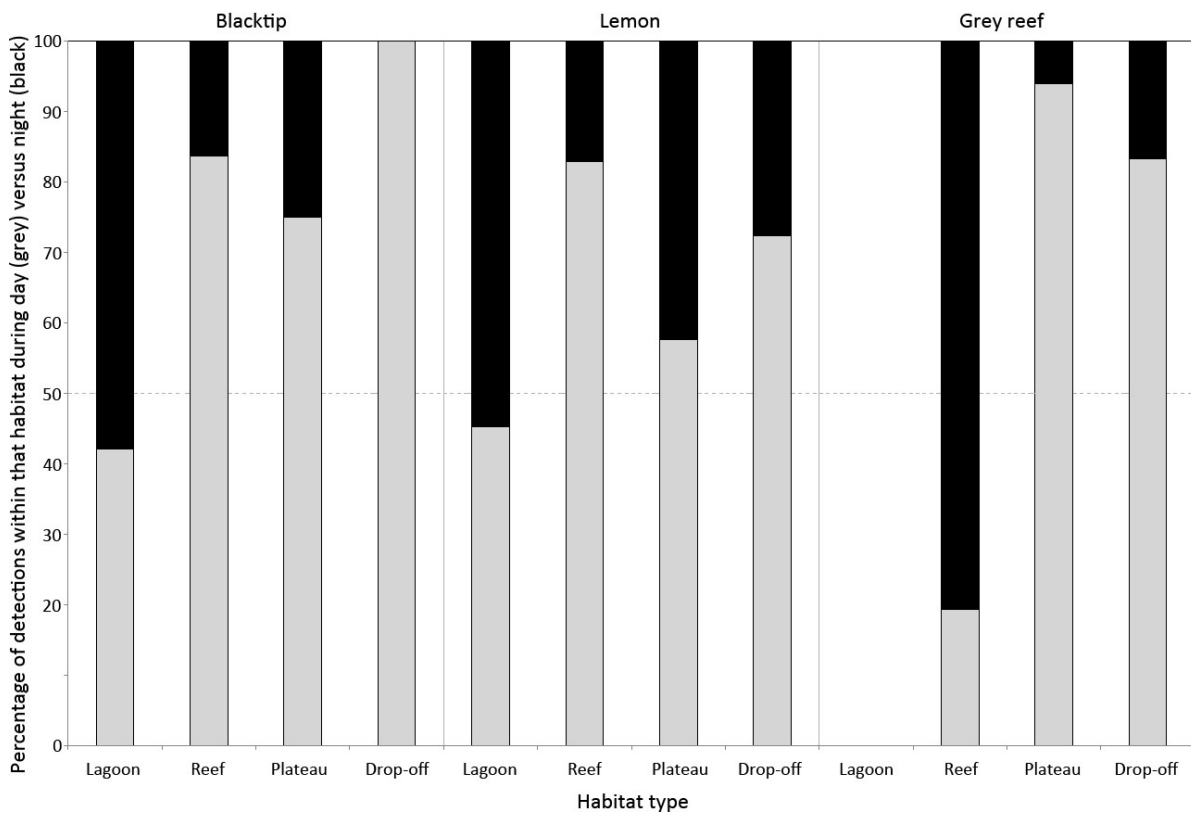


Figure 41: Diel difference in percentage of detections within each habitat type, for species with ≥ 20 tags.

6.3.3 *Tidal Variation*

Allocation of ping proportion by tidal bins for both blacktip reef and lemon sharks revealed that both species move into shallower lagoon habitats at higher tides (Figure 42), but that blacktip reef sharks can exploit them sooner in the tidal cycle than the lemon sharks (~0.5 m versus ~1.4 m, respectively), as determined by the significance thresholds of the ping-proportion comparisons (Table 14). The dip in ping frequency at higher tides can be accounted for by blacktip reef and lemon sharks moving even further into the shallows at extreme spring highs: 56.1% of blacktip reef shark pings at tides >1.8 m occurred at newer, shallower receivers not included in the present analysis due to their brief deployments (44.3% for lemon sharks).

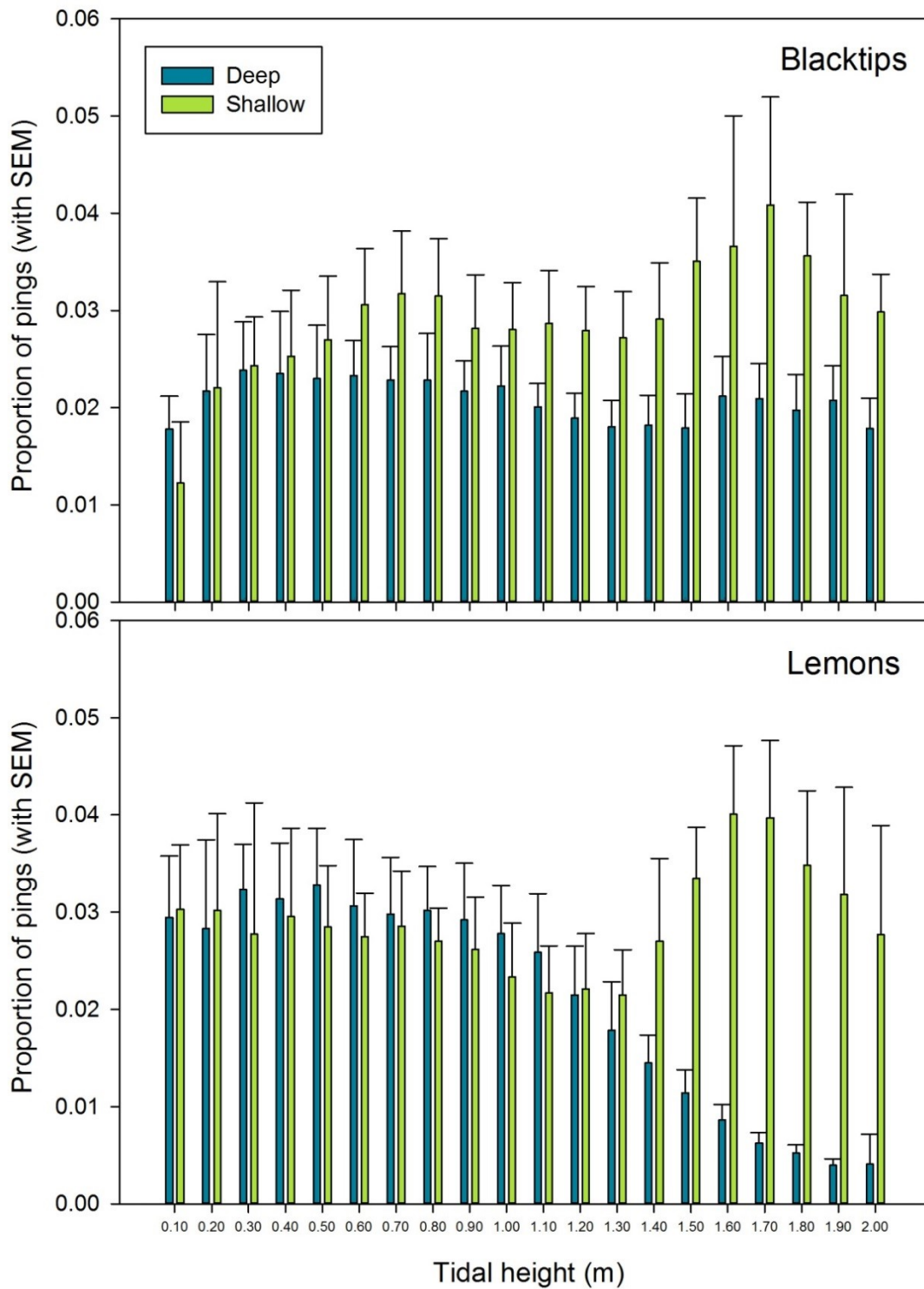


Figure 42: Proportion of pings for blacktip reef and lemon sharks in deep and shallow areas of the lagoon across the tidal cycle. Error bars represent the standard error of the mean.

Table 14: Mann-Whitney test results of proportion of pings at deep versus shallow areas of the lagoon for each tidal bin (BT = blacktip reef sharks, LM = lemon sharks).

BT						LM					
Tidal height	U	T	N1	N2	p	Tidal height	U	T	N1	N2	p
0.1	235	466	21	23	0.884	0.1	168.5	339.5	18	19	0.951
0.2	163	394	21	23	0.066	0.2	144	369	18	19	0.417
0.3	206.5	437.5	21	23	0.417	0.3	160	353	18	19	0.75
0.4	180	411	21	23	0.152	0.4	163.5	349.5	18	19	0.831
0.5	155	386	21	23	0.043	0.5	168	345	18	19	0.939
0.6	135	366	21	23	0.013	0.6	160.5	352.5	18	19	0.761
0.7	117	348	21	23	0.004	0.7	152.5	360.5	18	19	0.584
0.8	152	383	21	23	0.037	0.8	144	369	18	19	0.421
0.9	121.5	352.5	21	23	0.005	0.9	146.5	366.5	18	19	0.466
1.0	144.5	375.5	21	23	0.023	1.0	161	352	18	19	0.773
1.1	126.5	357.5	21	23	0.007	1.1	159	354	18	19	0.727
1.2	125.5	356.5	21	23	0.007	1.2	127.5	385.5	18	19	0.191
1.3	92.5	323.5	21	23	<0.001	1.3	107	406	18	19	0.054
1.4	104.5	335.5	21	23	0.001	1.4	72	441	18	19	0.003
1.5	98	329	21	23	<0.001	1.5	36	477	18	19	<0.001
1.6	90	321	21	23	<0.001	1.6	18	495	18	19	<0.001
1.7	61	292	21	23	<0.001	1.7	34	479	18	19	<0.001
1.8	134.5	365.5	21	23	0.011	1.8	27.5	485.5	18	19	<0.001
1.9	162.5	393.5	21	23	0.059	1.9	45	468	18	19	<0.001
2.0	194.5	425.5	21	23	0.227	2.0	87.5	425.5	18	19	0.008

One hour restricted networks were constructed to illustrate the difference in habitat use between the high and low tide for each species, with the thresholds for high versus low determined by when the difference in deep versus shallow usage became significant (0.5 m for blacktip reef sharks, 1.4 m for lemon sharks; Table 14). Both blacktip reef and lemon sharks use the shallow reef flats more at higher tides, particularly in the eastern end of the lagoon (Figure 43). However, the pattern is much more pronounced for lemon sharks, which appear to patrol the edge of the deep lagoon at lower tides, before targeting the flats almost exclusively at higher tides.

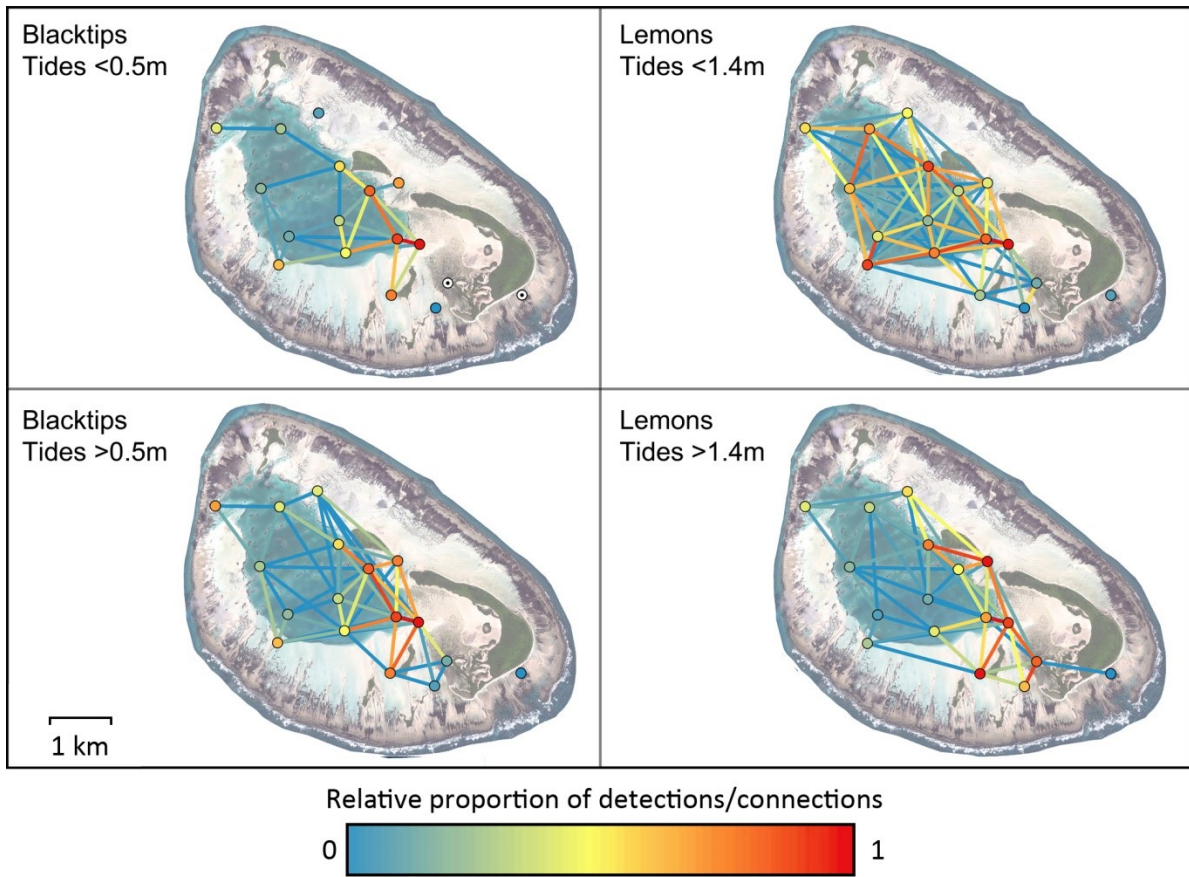


Figure 43: Relative one hour networks of blacktip reef and lemon shark movements at species-specific low and high tides (determined by the statistical cut-offs in Table 6.5).

6.4 Discussion

Although the majority of tracked sharks were present in the array throughout the year, the results presented here revealed some marked temporal variation in detection frequency at several different scales.

6.4.1 *Seasonal Variation*

Seasonal patterns in detection frequency were apparent for both blacktip reef and lemon sharks, which appeared to be detected more frequently during the NWM (December–March) than the SEM (May–October), when water temperatures are typically lower. For the blacktip reef sharks, this seasonal variation may be related to reproductive behaviour causing fine-scale changes in distribution. Elsewhere in the Seychelles at the remote atoll of Aldabra, blacktip reef sharks were caught most frequently in December (lowest catch rates in June), with mating peaking around October, at the start of the NWM (Stevens 1984). Similarly, blacktip reef sharks in French Polynesia mate in November through March, with each female following her own temporal cycle synchronised with the season (Porcher 2005).

These results are consistent with the interpretation that the seasonal variation in blacktip reef shark detections in the present study may reflect reproductive patterns: blacktip detections were more frequent during November through March, when both males and females were also shown to overlap more frequently, whilst remaining largely segregated during the SEM. It appears as though the males migrate to the eastern end of the lagoon during the SEM, where they overlap with the females, presumably to mate. Although occurring at a much finer scale of ~1.5 km, these migrations reflect those of the tiger sharks tracked in Chapter 3, where males were shown to undertake seasonal migrations, thought to be between foraging and mating grounds. Perhaps the seasonal change in ping frequency for blacktip reef sharks reflects these fine-scale changes in movement behaviour. The lagoon is a complex

environment with shallow pools and mangrove channels beyond the range of receivers, making it easy for detections to change significantly with small changes in range. This is emphasised by the detections on some of the shallower receivers installed later in the study and excluded from present analyses. These shallow, reef flat receivers recorded individuals isolated in shallow pools more frequently at lower tides.

The sexual segregation of blacktip reef sharks over such a fine scale is notable. Sexual segregation is a phenomenon recorded widely across the animal kingdom (Wearmouth & Sims 2008, 2010), with various explanatory hypotheses proposed including contrasting thermal preferences between the sexes (Economakis & Lobel 1998; Hight & Lowe 2007; Robbins 2007), differing foraging requirements (Wearmouth & Sims 2008), and females avoiding male harassment (Carrier, Pratt Jr & Martin 1994; Wearmouth *et al.* 2012). In ectothermic elasmobranchs, the thermal niche hypothesis suggests that females may prefer warmer habitats to promote embryonic development rates and facilitate gestation, while males may favour slightly cooler temperatures to promote spermatogenesis (Wearmouth & Sims 2008). While sex biases in thermal preferences have been reported for other elasmobranchs (Economakis & Lobel 1998; Robbins 2007), there is no evidence for it here as both sexes experienced similar temperatures in both seasons. There is the caveat, however, that comparatively few male blacktip reef sharks were tracked – it could be that males are more abundant on the reefs outside the lagoon, where temperatures are cooler, as has been recorded for blacktip reef sharks in French Polynesia (Mourier, Mills & Planes 2013). It may also be that, to avoid costly harassment from males, female blacktip reef sharks select suboptimal habitat – perhaps poorer foraging opportunities, or higher predation risk – that males usually avoid, unless moving in to mate.

It appears the seasonal patterns in detection frequency for the lemon sharks may also be influenced by reproductive factors. Smaller lemon sharks displayed no seasonal patterns in detection frequency, whereas larger individuals (≥ 177 cm) were detected more frequently during the NWM. Previous tracking work on juvenile lemon sharks at D'Arros and St Joseph found no seasonal patterns, but did note that the largest tracked individual (163 cm) was the first to leave the study area (Filmalter, Dagorn & Cowley 2013). Moreover, lemon sharks in Aldabra displayed the same reproductive cycle as the blacktip reef sharks, with pupping starting during October (Stevens 1984). So the higher ping frequency in the NWM, which was only observed for the larger lemon sharks, may reflect adults returning to the atoll for parturition and to mate. Juvenile lemon sharks, without the motivation to mate or pup, simply remain within the refuge of the atoll throughout the year. Although anecdotal, pups of both blacktip reef and lemon sharks appear to be most prevalent in the lagoon during the NWM (pers. obs.), consistent with the interpretation that the observed seasonal patterns are driven by reproductive factors. Atlantic lemon sharks *Negaprion brevirostris* show strong philopatry to nursery areas, and individuals may rely entirely on a single nursery for parturition (Feldheim, Gruber & Ashley 2002). If comparable to St Joseph, this emphasises its importance as a nursery habitat for regional recruitment.

Variation in grey reef shark detections over the year is more complex, with no clear seasonal pattern. The high number of detections in October/November coincides with the peak pupping time of October observed at Aldabra (Stevens 1984), suggesting parturition may be a factor as most tracked individuals were female. The strong sex bias in tagged grey reef sharks towards females may be a reflection of contrasting depth preferences between the sexes – in the Red Sea grey reef sharks have been shown to segregate in the water column, with females shallower (~20 m) than males (~35 m; (Hussey *et al.* 2013)). During tagging efforts the present study predominantly fished at 0–20 m depth, which may have inadvertently targeted females.

A potential explanation for the peaks in June and November is that tagging effort was largely focused in April and November due to the calmer weather. However, grey reef sharks were on average tracked for over 470 days, and most individuals ($n = 17$) were tagged prior to the start of the study period (November 2013), suggesting tagging effort is unlikely to have driven the observed patterns. Elsewhere grey reef sharks have shown clearer seasonal patterns, such as being more frequent on the reef during summer in Palau (Vianna *et al.* 2013), or seasonal aggregations of females in the shallows of Johnston Atoll (Economakis & Lobel 1998). Given the expanse of available habitat across the Amirantes plateau – as revealed by their association with drop-off habitats in the previous chapter – perhaps the array in the present study provided insufficient coverage of the grey reef sharks' range to reliably determine seasonal movements, as further suggested by the lack of male representation in the study.

In addition, receiver detection efficiency has been shown to change over time in response to various environmental factors that may attenuate signal transmission (e.g. wind, rain, receiver depth; (Gjelland & Hedger 2013)). As such it is possible that the contrasting conditions of the different monsoon seasons (e.g. higher wind and wave action during SEM, more rain during NWM) may have affected the detection probability of tagged animals and warrants further investigation with more rigorous range testing (including sentinel tags). This would be consistent with the observation that while detection frequencies varied between the seasons, the majority of individuals (particularly blacktip reef and lemon sharks) were still regularly detected in both seasons.

6.4.2 *Diel Variation*

Diel variation in behaviour has been reported for many species of elasmobranchs across numerous habitats (Klimley *et al.* 1988; Sims *et al.* 2005; Andrews *et al.* 2009; Cartamil *et al.* 2010; Heupel, Simpfendorfer & Fitzpatrick 2010). Such changes in behaviour between day and

night can often be attributed to factors such as foraging activity (Sims *et al.* 2005, 2006), predation risk (Morrissey & Gruber 1993), and thermal regulation (Sims *et al.* 2006). The present study revealed marked interspecific variation in diel presence in the array, with grey reef and silvertip sharks being detected significantly more frequently during the day, lemon sharks more at night, and blacktip reef and nurse sharks showing no difference. This is consistent with blacktip reef shark movements in French Polynesia, where no diel difference in activity space or location was recorded (Papastamatiou *et al.* 2009). However, diel presence/absence in the array may mask finer scale movements within the array: for instance, the majority of blacktip reef shark detections on coastal reefs occurred during the day, which is in contrast to Aldabra where blacktip reef sharks visited the reef flats more frequently at night (Stevens 1984). Although lemon sharks were detected mostly at night, the majority of reef pings were during the day, suggesting there may be some diurnal movements between the reef and the lagoon.

Grey reef shark pings during the day were considerably more abundant than those at night, which is consistent with grey reef shark tracks in Palau, where they were detected on reefs more during the day than at night (Vianna *et al.* 2013). But there was high intraspecific variation, with some individuals displaying a stronger nocturnal bias. Such variation was also apparent in grey reef sharks tracked in the Great Barrier Reef, where some were present more at night, others during the day (Heupel *et al.* 2010). While the overall pattern for grey reef sharks at D'Arros and St Joseph may be increased presence in the array during the day, there may be a pattern of grey reef sharks moving between coastal reefs at night and offshore drop-off habitats during the day, as revealed by the percentage of pings at day versus night in each habitat, perhaps related to foraging opportunities.

The lack of diel variation in tawny nurse sharks is notable, as Atlantic nurse sharks *Ginglymostoma cirratum* are typically more active at night and rest during the day (Compagno 2001). Such activity may be hidden by reasonable array coverage, or indeed the metrics used – despite equal ping frequency, one nurse shark was recorded to remain near one receiver to the south of D’Arros during the day, but patrolled back and forth along the north of D’Arros at night. This repeated pattern is consistent with the behaviour reported for *G. cirratum* (Compagno 2001), and suggests that tawny nurse sharks around D’Arros may also rest during the day and forage at night.

The fact that silvertip sharks were detected almost exclusively during the day is an interesting result, but there are limited reports on silvertip shark spatial dynamics in the literature to compare it to. Adult silvertip sharks have been tracked on the Great Barrier Reef, where some long-term residence was shown, but the authors excluded the silvertip sharks from their temporal analyses due to small sample size (Barnett *et al.* 2012). More recent tracks of adult silvertip sharks on the Great Barrier Reef reported detections to be higher at night, along with a strong diel shift in the recorded depth profiles (Espinoza *et al.* 2015). Given that all of the tracked silvertip sharks were juvenile, perhaps the presence on drop-offs during the day may represent some form of refuging behaviour, but equally it may simply represent a shift in diving behaviour: it was not possible to determine from the present study.

6.4.3 Tidal Variation

At D’Arros and St Joseph the tidal cycle dictates access to a considerable area of habitat: the flats of St Joseph (~15 km²) are largely exposed at low tide, but may provide productive foraging and refuge opportunities at higher tides. Analysis revealed that both blacktip reef and lemon sharks exploit shallower habitats at higher tides, but that blacktip reef sharks can exploit them much sooner in the tidal cycle than lemon sharks. This could simply be an artefact

of body size – mean blacktip reef shark length was 106.8 cm, lemon sharks 174.5 cm – with the larger lemon sharks physically only able to access the lagoon flats at higher tides compared to the blacktip reef sharks.

Movement into the flats may reflect exploitation of temporally discrete foraging opportunities: various species of ray, along with teleosts like bonefish and permit, are abundant on the lagoon flats, and are potential prey for blacktip reef and lemon sharks (pers. obs.; (Compagno 2001)) that may be inaccessible at lower tides. Similarly, leopard sharks *Triakis semifasciata* have been shown to exploit the tidal cycle in estuarine habitats to target high prey abundance in intertidal mudflats (Carlisle & Starr 2009, 2010). Blacktip reef sharks have also been shown to move into tidal flats at high tides in French Polynesia (Papastamatiou *et al.* 2009). Stevens (1984) found that the best place to catch blacktip reef sharks at Aldabra was around the mangroves at high tide, and in the drainage channels at low tide. Previous work on lemon sharks at St Joseph also found that pings in the deep lagoon were more frequent at lower tides, with a 12 hr Fast Fourier Transformation peak suggesting a strong tidal signal (Filmlalter *et al.* 2013).

Another reason for the sharks moving into the shallows at high tide, which may be more applicable to the smaller blacktip reef sharks, is refuge from predation risk, afforded by the access restriction of the shallow water. Juvenile Atlantic lemon sharks have been shown to use mangrove inlets for longer at deeper high-tide depths, coinciding with higher predator presence in the surrounding area (Guttridge *et al.* 2011), and mangroves at high tide have been suggested as important refuges for sharks in western Australia (White & Potter 2004). Perhaps the blacktip reef sharks at St Joseph use the flats as a refuge from predators such as lemon sharks, bull sharks *Carcharhinus leucas* and great hammerhead sharks *Sphyrna mokarran*, all of which are known to visit the lagoon. But blacktip reef sharks can avoid overlap

with these predators by using the flats even from relatively low tides (~0.5 m) before they become accessible to the larger sharks (at tides ~1.4 m). It may even be a combination of both foraging and refuging opportunities that drives use of the flats, as has been suggested for sea snakes *Hydrophis elegans* in western Australia, which only use a foraging area while the tide restricts shark access (Kerford *et al.* 2008). Being able to exploit the reef flats at tides the lemon sharks are less able to may also help promote habitat partitioning between the lemon and blacktip reef sharks (Speed *et al.* 2011). Thermal preferences may also play a role if shallow reef flat waters are warmer than the rest of the lagoon (they can reach temperatures over 35 °C), perhaps facilitating growth and digestion.

Overall a variety of different temporal cycles seem to affect shark spatial dynamics at D'Arros and St Joseph at several different scales. Broadly there are the contrasting NWM and SEM seasons that appear to dictate the breeding seasons in several species. Meanwhile the continuous alternation between day and night influences the different shark species in contrasting ways. At an even finer scale, the tidal cycle controls access to a considerable expansive of lagoon flat habitat that may provide both foraging opportunities and act as a refuge from predation.

7 Power of reef shark telemetry to enhance MPA design in the Amirantes, Seychelles

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7.1 Introduction

Fishing pressure on sharks has increased to the point where an estimated 63–273 million sharks are caught each year for the shark fin trade alone (Worm *et al.* 2013), with some populations appearing to have undergone significant declines (Ferretti *et al.* 2008; Dulvy *et al.* 2014). A common tool to combat overfishing, especially in tropical ecosystems like the Seychelles, is the designation of marine protected areas (MPAs), which can be very effective depending on their size, level of restriction and associated enforcement (Edgar *et al.* 2014). The initial design of an MPA should be informed by the movements and habitat preferences of the targets species, to ensure it covers sufficient critical habitat to be effective (Heupel & Simpfendorfer 2005; Speed *et al.* 2015). Yet such information is often unavailable and MPA boundaries can be established with limited information or even relatively arbitrarily, making them less likely to succeed (Brown *et al.* 2015; Costello & Ballantine 2015; Speed *et al.* 2015). MPA design should consider multiple species (Mouillot *et al.* 2016), as efficacy will likely vary between species with different behaviours, life history traits and vulnerability to fishing pressure (Osgood & Baum 2015; White *et al.* 2015).

Most declines in shark populations have been inferred from Atlantic and Pacific fisheries, which have historically kept the most comprehensive catch records (Ferretti *et al.* 2010; Worm *et al.* 2013; Clarke *et al.* 2013). For instance, catch rates for some shark species in the Atlantic Ocean have been estimated to have declined by over 90% (Baum & Myers 2004; Shepherd & Myers 2005; Ferretti *et al.* 2008), with similar declines (>70%) also indicated for the Pacific Ocean (Ward & Myers 2005; Nadon *et al.* 2012; Clarke *et al.* 2013; White *et al.* 2015). Data on Indian Ocean shark populations are severely deficient by comparison, but available reports suggest declines in this region may be similarly severe (van der Elst *et al.* 2005; Nevill *et al.* 2007; Graham, Spalding & Sheppard 2010; Tremblay-Boyer *et al.* 2011). For instance, visual surveys of reefs in the Chagos Archipelago, recently designated an MPA, indicate that reef shark populations there may have been reduced to levels less than 10% of those recorded in 1975 (Graham *et al.* 2010; Sheppard *et al.* 2012). In the Seychelles, shark fishing has long been of strong socio-economic importance but has intensified in recent years, following a temporary European Union (EU) ban on import of local swordfish *Xiphias gladius*, and persecution of sharks after two fatal shark attacks on humans in 2011 (Nevill *et al.* 2007; Seychelles Nation 2015). Yet the relative importance of shark to Seychelles fisheries has decreased by an order of magnitude in the past 70 years (Nevill *et al.* 2007). Although during the 1940's sightings of tiger *Galeocerdo cuvier*, white *Carcharodon carcharias*, and hammerhead *Sphyrna spp.*, sharks were apparently still common, sightings of larger sharks had become exceptionally rare by the end of the 1960's (Smith & Smith 1969). Thus, even now with stocks seemingly depleted, there is intense, unregulated fishing pressure on sharks in the Seychelles (Nevill *et al.* 2007), and associated impacts to their ecosystem services could be severe. Consequently shark populations in Seychelles require some level of precautionary management to promote their sustainability.

In the Seychelles existing MPAs have been established mostly to protect seabird colonies, coral reefs and nesting turtle species (Anon 2012) – the beaches of Seychelles host one of the world's largest nesting populations of the critically endangered hawksbill turtle *Eretmochelys imbricata* (Mortimer & Collie 1998). However, the largest MPA in the Seychelles extends only 1 km from Mean High Water (MHW) and others to only 400 m, and may be ineffective for protecting other vulnerable groups such as sharks, which may be exposed to exploitation over much larger areas (Jennings, Marshall & Polunin 1996). Therefore, while these MPAs may be effective in protecting the target species, they may not achieve the wider goal of sustaining ecosystem functionality in the long-term (Jennings *et al.* 1996).

Presently there is insufficient data concerning the behavioural ecology of sharks in the Seychelles (Filmalter, Dagorn & Cowley 2013), to predict whether an MPA designed for turtles or reefs would also be effective for predators such as sharks. A combined appreciation of shark behaviour, habitat use and population structure can help frame the scale at which management efforts may be required (Duncan *et al.* 2006). Consequently this chapter analysed detailed, long-term movements of multiple shark species at D'Arros and St Joseph in the Amirantes, Seychelles, specifically investigating whether an MPA designed for reefs and turtles would also be sufficient for the local sharks, and if not how could it be adjusted to accommodate them.

7.2 Methods

The study site for this chapter was D'Arros and St Joseph Atoll, as described in the General Methods (Chapter 2). Shark movements were tracked using acoustic telemetry as described in the General Methods, using the same tags, array and study period (November 2013 to November 2015) as outlined in the Methods of Chapter 5.

7.2.1 *Grid occupancy analysis*

The tracks analysed in Chapters 5 and 6 were further used to evaluate the potential efficacy of two MPA designs. Each design had its boundary radius restricted to 1 km as this matches the current best in Seychelles for the UNESCO World Heritage Site of Aldabra Atoll. The first MPA model, the null MPA, matches the Aldabra designation, with the boundary being formed by 1 km from the beach at MHW (Figure 44). The second, proposed MPA keeps the same boundary radius of 1 km, but instead measures it from the edge of the reef flat at the lowest astronomical tide (Figure 44). Due to the extensive reef flats at D'Arros and St Joseph, that are exposed at low tide and can exceed 1 km width, this forces the boundary to include all of the lagoon and coastal reefs, some of which remain exposed in the null MPA (Figure 44). The smaller null MPA encompassed an area of approximately 42.3 km², while the larger proposed MPA covers approximately 64.9 km² (~50% increase in area).

The potential efficacy of both MPAs was determined using a grid occupancy analysis. In order to account for bias that may stem from the uneven distribution of acoustic receivers, each track was interpolated across all gaps shorter than 24 hrs (longer gaps were ignored to limit erroneous interpolation). The array was then divided into 0.5 km grid squares, and the number of days each individual occurred within each grid square was summed. Using the boundaries of the null and proposed MPAs, it was then possible to sum the number of days each individual would have spent within the boundaries of each, based on which grid cells were in which MPA.

The number of days inside/outside was then used to calculate the proportion of each individual's recorded array occupancy that was inside each MPA. Proportion of time inside each MPA was then plotted using box plots, to see how much time each species spent within each MPA. The significance of differences in time spent inside each MPA was tested for each species using Wilcoxon matched-pairs signed rank tests, with Monte Carlo p values calculated after 10,000 permutations (IBM SPSS Statistics, IBM Corp. USA).

In addition to the grid occupancy analysis, maps of MPA boundaries were also overlaid on movement networks for two example species (blacktip reef *Carcharhinus melanopterus* and grey reef sharks *Carcharhinus amblyrhynchos*) to illustrate the difference in coverage between the two MPAs.

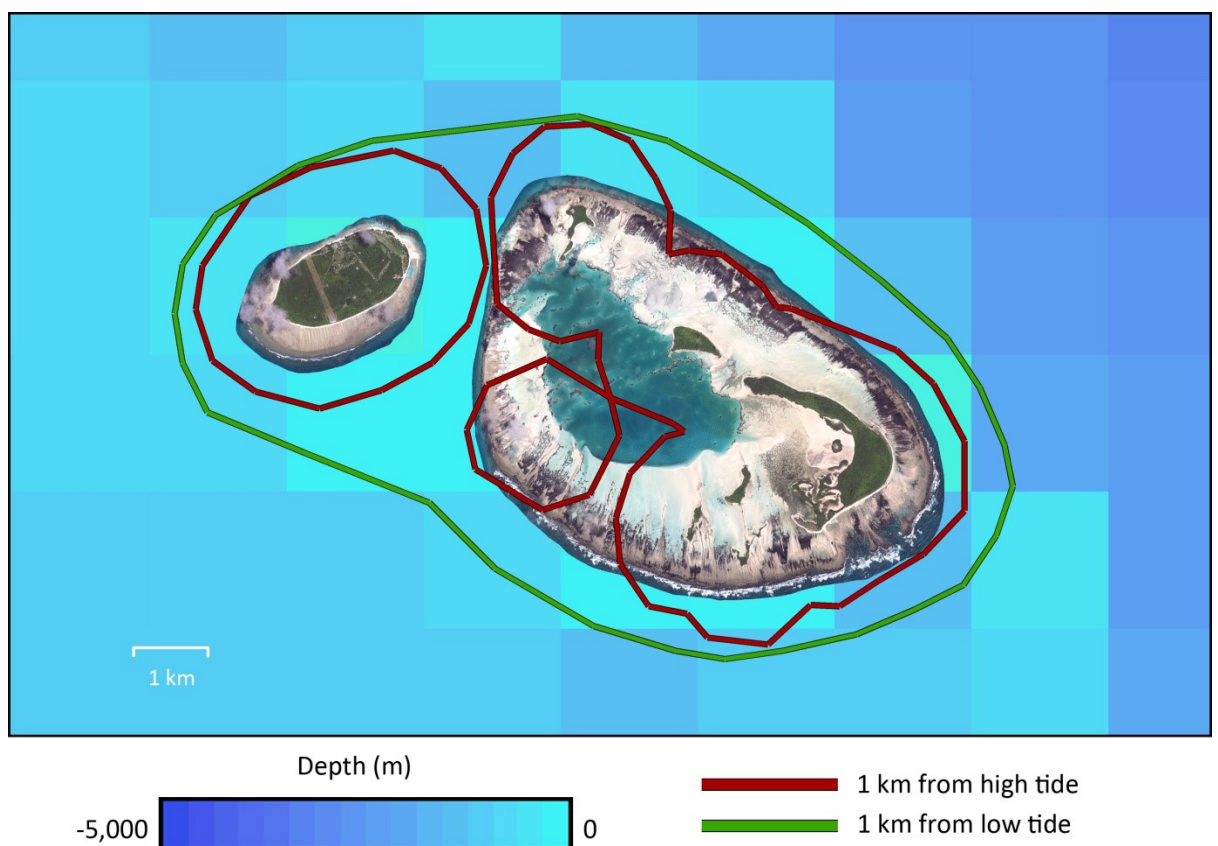


Figure 44: A map to show the borders of two potential MPAs: 1 km from the high tide mark (red) and 1 km from the low tide mark (green). Map created in ArcGIS, using satellite imagery from LAND INFO Worldwide Mapping and ETOPO2v2 bathymetry data.

7.3 Results

As with Chapters 5 and 6, over 41,655 tracking days were obtained from the five shark species (blacktip reef, sicklefin lemon *Negaprion acutidens*, grey reef, silvertip *Carcharhinus albimarginatus*, tawny nurse shark *Nebrius ferrugineus*) tracked between November 2013 and November 2015: the same tracks are used for analysis here (cross-ref to Chapter 5 table when linked).

7.3.1 MPA Use

Grid occupancy analysis revealed that overall the proposed (larger) MPA increased coverage of shark movements by 18.7% \pm 31.9 (S.D.) compared to the null (smaller) MPA, with all species apart from silvertip sharks displaying a significant increase in coverage from the larger MPA (Table 15). Grid occupancy analysis revealed that 89.9% of the blacktip reef shark tracks occurred within the boundaries of the smaller MPA, compared to 98.7% occurring within the larger MPA (Figure 45; $Z = 4.015$, $p < 0.001$; Table 15). As can be seen in Figure 46, the larger MPA encompasses all of the blacktip reef shark movements that occur within the lagoon and across the channel, for which the null MPA would only provide partial coverage. Lemon sharks received a similar increase in coverage from the larger MPA, with 83.5% of recorded tracks occurring within the smaller MPA versus 96.5% for the larger MPA (Figure 45; $Z = 3.621$, $p < 0.001$; Table 15). Larger lemon sharks spent more time outside both MPAs than smaller individuals, attributable to their wider movements (see Chapter 5).

Grey reef sharks overall received very poor coverage from both MPAs, but still received a significant increase in coverage from the larger MPA (26.6% of time in the smaller versus 32.8% inside the larger; Figure 45; $Z = 2.521$, $p = 0.006$; Table 15). Predominantly larger individuals along drop-offs receive no benefit. Smaller individuals receive high coverage from the larger MPA but very little from the smaller – attributable to their frequent movements

along the northern coastal reefs (Figure 47), which are barely covered by the smaller MPA. This drives the apparent large increase in MPA coverage for grey reef sharks evident in Figure 45 (although the median remains low): two of the smallest grey reef sharks (79 cm and 99 cm) both had their coverage more than double from ~47% to ~98%.

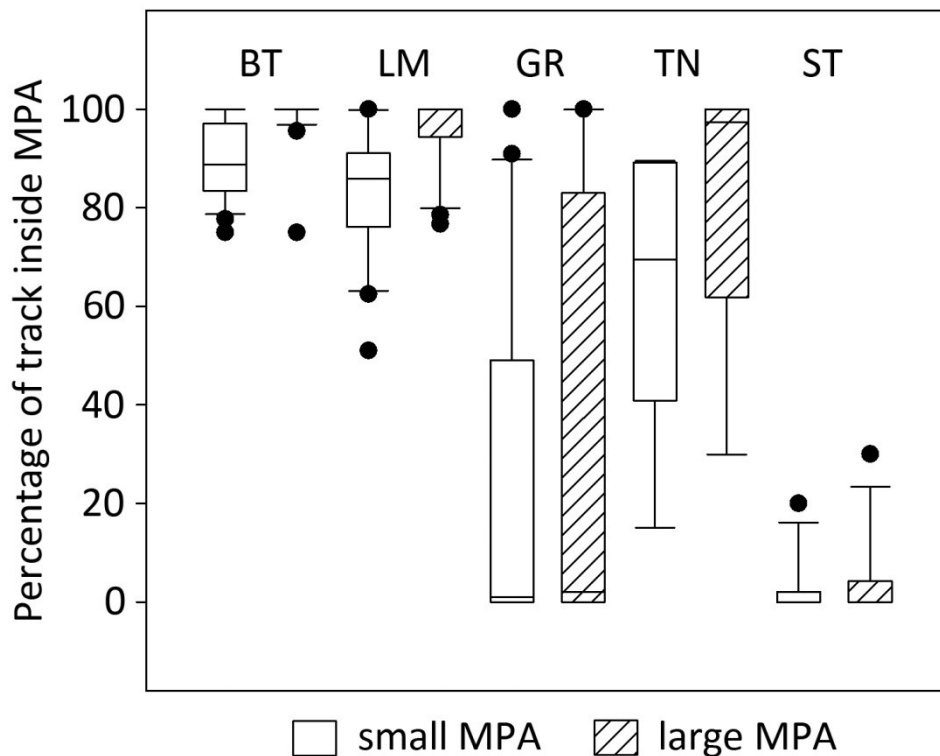


Figure 45: Box plots of the proportion of their recorded track each species spent inside the small MPA (white, 1 km from high tide) and the larger MPA (hatched, 1 km from low tide). BT = blacktip reef, LM = lemon (a: fine-scale, b: broad-scale), GR = grey reef, TN = tawny nurse, ST = silvertip.

Nurse sharks also receive a significant increase in coverage from the small MPA to the larger MPA (from 63.7% to 82.9%; $Z = 2.201$, $p = 0.019$; Table 15), but larger individuals still frequently travel outside across the plateau. Silvertip sharks spend very little time in either MPA (2.7% and 4.0%), with no significant difference between the two (Table 15), as movements are largely focused along the offshore drop-offs (see Chapter 5).

Table 15: Results of Wilcoxon matched-pairs signed rank tests comparing the time spent inside the two different MPAs, with Monte Carlo p values calculated after 10,000 permutations.

Species	<i>n</i>	Z	p
Blacktip	25	4.015	<0.001
Grey	22	2.521	0.006
Lemon	20	3.621	<0.001
Nurse	6	2.201	0.019
Silvertip	13	1.826	0.073

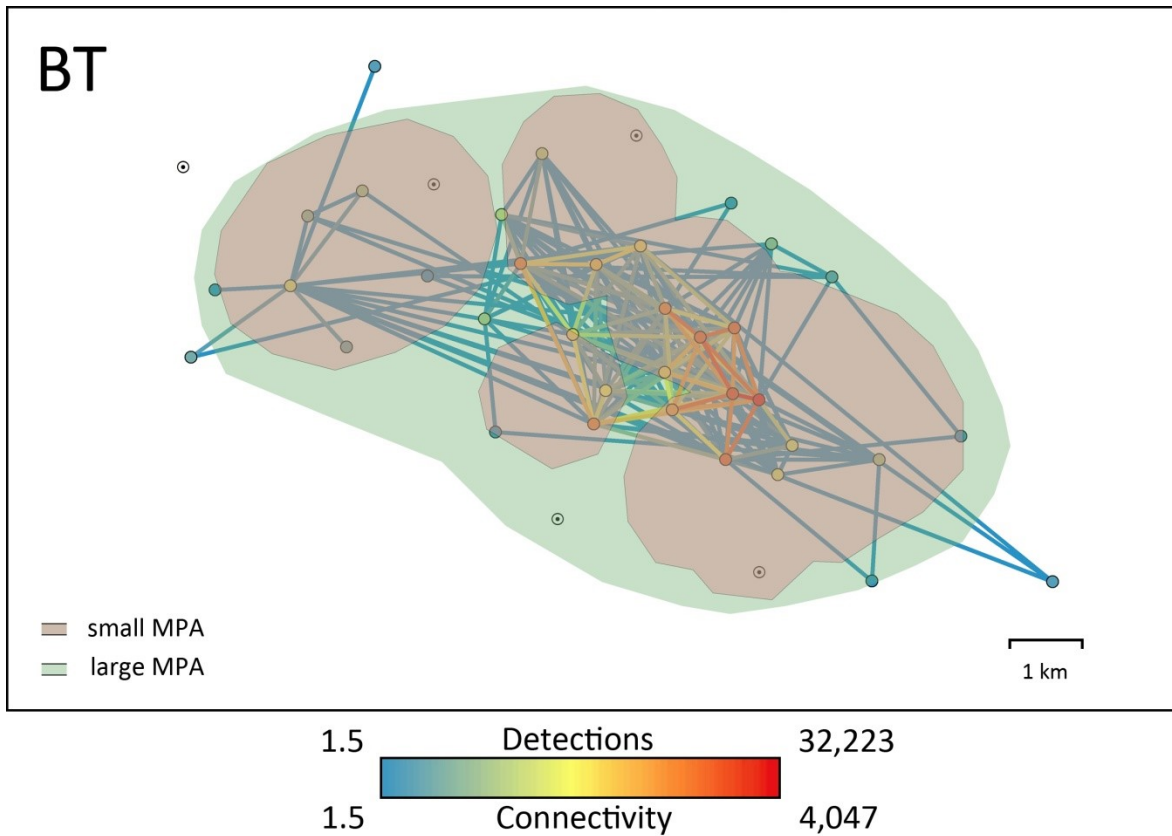


Figure 46: Map showing which blacktip reef shark movements are included in the large MPA (1 km from low tide) over the small MPA (1 km from MHW). Map created in ArcGIS.

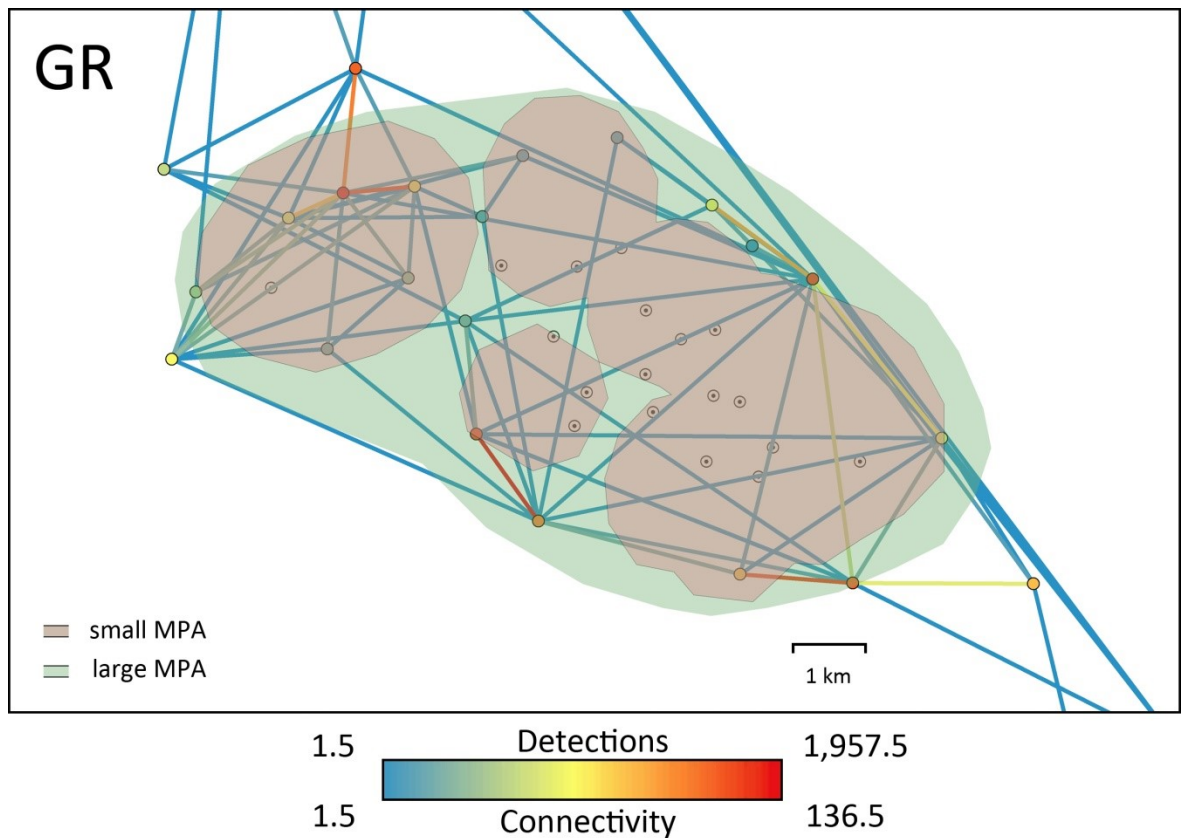


Figure 47: Map showing which grey reef shark movements are included in the large MPA (1 km from low tide) over the small MPA (1 km from MHW). Map created in ArcGIS.

7.3.2 MPA management

An early form of the habitat use analysis in Chapter 5 and the MPA results presented here were communicated to the Ministry of Environment, Energy and Climate Change, Seychelles, in order to demonstrate the importance of the habitat provided by D’Arros and St Joseph, and to indicate the potential efficacy of the larger MPA for protecting sharks. The results in part contributed to the Seychelles government formally adopting the larger MPA and declaring D’Arros and St Joseph a Special Reserve (International Union for the Conservation of Nature, IUCN, Category 1a) with a no-take zone extending 1 km from the low tide mark, effective from 14th July 2014 (Payet 2014). An implementation plan was also agreed where the Save Our Seas Foundation would also provide facilities (e.g. a patrol boat) to help enforce the protection. In response to this management outcome at D’Arros and St Joseph, there has also been a

proposal by the Ministry of Environment, Energy and Climate Change to extend the 400 m MPA of Aride Island on the Mahe plateau to 1 km.

7.4 Discussion

While efforts have been made to assess the efficacy of existing MPAs for certain species (e.g. (Jennings *et al.* 1996; Bond *et al.* 2012; Edgar *et al.* 2014; Espinoza *et al.* 2015; Speed *et al.* 2015; Belo *et al.* 2016)), this chapter is novel in using data on the dynamic habitat use of sharks to inform the design of an MPA at a remote atoll in the Indian Ocean. In particular, the telemetry-based network and grid occupancy analyses allowed complex animal movements to be collapsed into a few axes that could be more easily interpreted within and between species in relation to spatial areas. An early form of the data presented here and in Chapter 5 was used not only to emphasise the importance of D'Arros and St Joseph as critical nursery habitat worthy of protection, but also to justify having a boundary beyond the 1 km from MHW used elsewhere in the Seychelles, informing the subsequent adoption of the larger MPA. In July 2014 D'Arros and St Joseph were designated a 'Special Reserve' (IUCN Category 1a) by the Ministry of Environment, Energy and Climate Change, Seychelles, prohibiting all fishing within 1 km of the outer reef flat, measured at low tide (Payet 2014). Moreover, there has since been a proposal to extend the MPA around Aride Island in the Seychelles from 400 m offshore to 1 km (Seychelles News Agency 2015).

In light of global threats to marine ecosystems, conservation efforts are increasingly turning to spatial management options, with over 9,000 MPAs having been declared to date (Costello & Ballantine 2015). A recent review of MPAs that have successfully increased biomass found that the chances of MPA success increased with the designation of a no-take zone, effective enforcement, age, size and isolation (Edgar *et al.* 2014). Yet boundaries are often declared based on limited information, while over 90% of MPAs still permit some level of fishing, and the median size is only 4.5 km² (Costello & Ballantine 2015). By comparison the D'Arros and St Joseph Special Reserve is isolated, will not permit any fishing, will be over 65 km², and will have effective enforcement, all of which suggest it has the potential to be effective.

Although an MPA of 1 km from MHW at D'Arros and St Joseph may have still been effective in protecting some species or certain life stages, a change in definition to delineate the boundary according to the low tide mark predicts a significant increase in protection for all tracked species bar the silvertip shark. This increase can be explained by an understanding of movements and local topography – extending the boundary from the low tide means it starts at the edge of the wide reef flats that surround the islands, forcing the boundary out beyond the coastal reefs and covering the lagoon, the two habitats used most frequently by the majority of tracked species (see Chapter 5). The smaller MPA would not have covered all of the lagoon or outer reefs, leaving sharks frequently exposed to fishing pressure. Indeed, shark finning has been recently recorded in the lagoon (Vejarano & Engelhardt 2008). Given the potential nursery status of D'Arros and St Joseph, as described in Chapter 5, their protection through the designation of a more effective MPA is particularly important and may help promote survival and recruitment into regional populations, especially if larger individuals of certain species disperse broadly upon reaching maturity.

The differences in habitat use between the different shark species observed in Chapter 5 correspond with the varied efficacy of the MPA between species, highlighting the importance of understanding movements of multiple species in order for MPA design to be effective. Nevertheless, much of the literature on MPAs has focused on retrospective MPA assessments as opposed to efforts to inform their design, without which MPAs may prove costly and ineffective (Costello & Ballantine 2015).

Given that the larger MPA encompasses the entire lagoon and coastal reefs, it provides better coverage for blacktip reef sharks than if a smaller MPA intended solely for nesting turtles or coral reefs had been implemented. Sicklefins also displayed extensive use of the

lagoon, but also more frequent use of the coastal reefs and Amirantes plateau than the blacktip reef sharks, with the larger MPA also providing more significant coverage of these habitats. Better management of sicklefin lemon shark populations is particularly important as they are considered *Vulnerable* on the IUCN Red List and in several areas have been exploited to the point of extirpation, including India, Thailand and Southeast Asia (Pillans 2003). Consistent with previous work on lemon sharks in Seychelles (Stevens 1984; Filmlalter *et al.* 2013), the present study revealed perennial high fidelity to lagoon habitats in individuals <1.8 m (almost exclusively within the larger MPA), but also that individuals >1.8 m adopted broader movements across the Amirantes plateau, including to other islands such as Marie-Louise (80 km away) and Bird Island (300 km away). Similarly, larger tawny nurse sharks (>2 m) frequently use plateau habitat and spend a greater proportion of time beyond the MPA boundaries.

Most grey reef sharks favoured particular drop-off habitats beyond the confines of either MPA, and the few juvenile silvertip sharks tracked also favoured drop-off habitats, receiving almost no coverage from either MPA. This is of concern given that 21% of tagged silvertip sharks are known to have been caught by fishermen. No adult silvertip sharks have yet been encountered in the study area, suggesting management for their population is likely to be required at greater, perhaps regional scales.

The more extensive distribution of larger lemon, grey reef and nurse sharks means that certain individuals remain exposed to fishing exploitation, and reveals the need for alternative management strategies. Potential nurseries such as St Joseph Atoll may be maintained by relatively few mature females; in Atol das Rocas off Brazil it is estimated that a population of ~100 juvenile Atlantic lemon sharks *Negaprion brevirostris* could be maintained by as few as 5–7 mature females (Freitas *et al.* 2009). Consequently, even infrequent shark finning events, as have been reported within St Joseph Atoll (Vejarano & Engelhardt 2008), pose significant

risk to shark population stability. Over three days in January 2008 the D'Arros Research Centre recorded shark finning activities in and around St Joseph Atoll, subsequently noting multiple carcasses of large lemon sharks washed up on beaches, several of which were mature (Vejarano & Engelhardt 2008). Although the MPA should prevent finning events in the lagoon, the risk is further realised by the capture of tagged lemon sharks at Marie-Louise and Bird Island. These captures emphasise that for wider ranging species management tools like the MPA need to be coupled with broader fisheries management strategies in order to reduce mortality of wider ranging adults and be effective at promoting recruitment (Kinney & Simpfendorfer 2009; Osgood & Baum 2015), such as catch quotas, size limits, time/area closures, or even a larger shark sanctuary that covers at least the Amirantes.

Furthermore, MPAs need to be linked with reduced fishing capacity to ensure that effort is not simply displaced (Kinney & Simpfendorfer 2009). Indeed, the mean increase in coverage of $18.7\% \pm 31.9$ (S.D.) across all individuals comes at the expense of a 50% increase in area, which may incur a greater cost to local fishing capacity. However, this masks the fact that while some species (e.g. silvertip) receive little to no increase in coverage, the absolute coverage of the larger MPA for other species (e.g. blacktip reef, lemon) starts to approach 100% for most individuals, suggesting the change in boundary may be particularly valuable for the species using the atoll as a refuge or nursery, with recruitment benefits potentially outweighing the raw ratio of increase between coverage and MPA size.

In summary, this chapter reveals how a detailed understanding of shark spatial dynamics was used to inform the design of a no-take MPA at the point of inception, defining its boundaries to enhance its efficacy significantly. This highlights the importance of an evidence-driven approach to MPA design, and the value of incorporating multiple species over the long-term. This study emphasises how an MPA designed for one species (e.g. turtles) may not be as

effective for others (e.g. sharks), and will therefore fall short of protecting the ecosystem as a whole. Even when the larger MPA in this study is in place, however, broader management efforts will likely need to be framed at regional scales, as movements of certain species and size classes continue to traverse MPA boundaries, political boundaries, and the high seas.

8 An unexpected journey: long-distance, return migration across open ocean by a pregnant female bull shark *Carcharhinus leucas* between Seychelles and Madagascar

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8.1 Introduction

The declines in Seychelles shark populations described in Chapter 7 have been further exacerbated by increased targeting of large sharks following two fatal attacks on tourists in 2011, at least one of which can be attributed to a bull shark *Carcharhinus leucas* through genetic analysis of a tooth fragment (Seychelles Nation 2015). Consequently the movement behaviour of larger sharks, especially bull sharks, is now of particular interest in Seychelles, both from a fisheries management perspective and due to concerns of potential risks to human safety.

Apart from its presence in local waters, little is known about the ecology of the bull shark in the Seychelles. The bull shark is a large predatory shark (up to 4 m), found worldwide in tropical and warm temperate coastal waters, making seasonal appearances in cool temperate waters (Compagno 2001). The bull shark has been assessed as *Near Threatened* on the IUCN

Red List, mostly escaping targeted fisheries but kept as lucrative bycatch for their large fins (Simpfendorfer & Burgess 2009). Unlike other carcharhinids, bull sharks are able to tolerate fresh water, with females pupping in rivers or estuaries (Springer 1963), which the juveniles use as nurseries (Snelson, Mulligan & Williams 1984). Bull sharks have been found thousands of kilometres inland up rivers (Thorson 1972; Thomerson 1977), but to date the majority of recorded movements have remained coastal. Towards the end of the fieldwork conducted for Chapters 5–7, it was possible to also capture and tag several bull sharks near D’Arros Island in the Amirantes. While their movement data were obtained too late to include in Chapters 5–7, they form the basis of some future work aiming to determine the movement patterns of bull sharks in the Seychelles to aid management efforts, and this chapter presents an early result deemed of sufficient novelty and relevance to be included in the thesis.

8.2 Methods

The study site for this chapter was D'Arros and St Joseph Atoll, as described in the General Methods (Chapter 2). A 3 m female bull shark was caught on 21st August 2014 and tagged with an acoustic transmitter (V16 120 s nominal delay, Vemco Ltd, Bedford, Canada) as described in the General Methods. However, the shark was also tagged with a pop-up satellite-linked archival transmitter (PSAT) (Mk 10 PAT tag, Wildlife Computers, Redmond, Washington, USA). The PSAT was set to record depth every 10 seconds, with temperature and light levels being recorded every 5 minutes, and was attached to the shark via a monofilament tether through the first dorsal fin, set to pop-off after six months.

The presence of the acoustic tag was recorded across the same array of acoustic receivers as described in Chapter 5. As part of ongoing, long-term assessments of predator relative abundance and diversity in the area, underwater visual surveys were also performed at various locations in the Amirantes, whereby scuba divers released chum and recorded the abundance and diversity of shark species encountered, along with estimated size, sex, distinguishing marks, and notable behaviour. The tagged shark was encountered during one such survey on 19th January 2015 and came close enough for the divers to remove the PSAT, allowing retrieval of the raw archival data for analysis.

8.2.1 *Light-level Geolocation*

While the acoustic data reveals when the shark was recorded at particular receivers, reconstructing movements outside the array, based on the PSAT archival data, relied on light-based geolocation. The light-based geolocation was performed with Wildlife Computers' Global Position Estimator (<http://wildlifecomputers.com/support/downloads/>), which uses tag-recorded light levels to estimate local time at midday and midnight and day length to provide approximate longitudes and latitudes respectively. However, these Global Position

Estimates (GPE) have large error fields and perform poorly in estimating latitude near the equator or close to equinoxes. The GPE longitude outputs had a mean error of 107.46 km (range 25.30–798.12 km), while the GPE latitude outputs had a mean error of 493.90 km (range 27.80–3,333.68 km). Consequently, to improve on these raw estimates, the locations were filtered and refined by using a swim speed (diffusivity) filter and by matching sea surface temperature pixels and bathymetry. The process involves two steps. The first is to generate a ‘cloud’ of possible waypoints at each reachable location; the second is to select the ‘best’ waypoint at each location to produce a final, most probable path.

The process begins at the known deployment location by attempting to route to the first (target) GPE location. Based on documented swim speeds (Daly *et al.* 2014), a swim speed limit of 2 ms^{-1} together with the time to the target location is used to define a circle representing the theoretically reachable area. This circle is intersected with the ellipse defined by the GPE error estimate at the target location. If no intersection is possible then the target location is considered unreachable and is rejected. The process then continues with subsequent locations until a valid intersection is achieved. Pixels within the intersection where the bathymetry (from GEBCO, 30 second resolution, <http://www.gebco.net/>) is deeper than the maximum depth recorded on that day from the tag archive data and where the daily Sea Surface Temperature estimate (from OSTIA, http://ghrsst-pp.metoffice.com/pages/latest_analysis/ostia.html) is within 0.5°C of the recorded tag temperature, are selected as possible ‘waypoints’. If no matching pixels are identified then the location is rejected.

The process then continues by attempting to route in the same manner from each waypoint at the prior location to the next location, generating a collection of potential waypoints at each reachable location, until all locations have been processed. Any known, rather than estimated,

locations, such as those from the acoustic array, the deployment and pop-up locations are considered to be 'locked', are always routed to and have a single waypoint.

To determine the 'best' path through the reachable locations the process again begins at the first location, which being known and locked comprises a single waypoint. Waypoints at the next reachable location are scored according to the distance to the estimated location coordinates, the SST difference and the distance from the prior waypoint. A 'best' waypoint is selected by choosing a waypoint at random using a distribution constructed from the waypoint scores to bias the selection to the higher scoring waypoints. Note, that if there is a large spread of points at the two locations, that it is possible for no way point at a given location to be reachable from the selected waypoint at a prior location, given the 2 ms^{-1} swim speed. In these cases the location is rejected from this path. Waypoint selection is repeated in this way at each reachable location. The result is a path which is then assigned a score equal to the sum of the scores of the waypoints.

The process of path generation is continued, with better scoring paths being selected as the 'best' path until 500 new paths have been generated without improving on the score. The 'best' path points had reduced error fields, particularly for latitude: filtered latitude outputs had a mean error of 199.64 km (range 5.53–1,084.10 km), with filtered longitude outputs having a mean error of 147.52 km (5.34–798.65 km). The 'best' path locations also had low standard deviations, with ± 34.14 km latitude and ± 24.28 km for longitude. This 'best' path represented the final track used to plot the shark's movements. Estimating where the shark was and when also allowed time-at-depth profiles to be assigned to particular locations or portions of the track. Time-at-depth profiles were calculated as the proportion of time spent within a particular depth range, either on a daily basis or across a particular portion of the track (e.g. when migrating).

8.3 Results

In total the movements of this large female bull shark (300 cm total length) were tracked for 151 days from 21st August 2014. The final track consisted of 263 locations, comprising the tagging location, 194 acoustic detections, 67 filtered light-based geolocations, and the location of tag retrieval. During tagging the shark was notably gravid, presenting with considerable girth, and the writhing movement of pups could be felt through the ventral surface. The shark was then encountered again on 17th and 19th January 2015 during underwater visual surveys, appearing slender and with fresh bite marks on the left side.

Over the course of the track the shark is estimated to have travelled over 10,670 km at an average speed of 0.82 ms⁻¹. The shark is known to have remained within the Amirantes until at least 20th October 2014, which represents the last detection on the Amirantes acoustic array (at Marie-Louise). After this the shark's movements inferred from the light-based geolocation revealed a long-distance migration to the southeast coast of Madagascar (Figure 48), approximately 1,960 km away from the tagging location in the Amirantes. Between 20th October 2014 and approximately 19th November 2014, the shark travelled south from the Amirantes and across open ocean to the northern tip of Madagascar, passing near the Farquhar group of islands. The majority of geolocations available around Madagascar are focused along the south-eastern coast. Around 29th December 2014 the shark started to head north again, reaching the tagging area around 17th January 2015, having completed a roundtrip migration of approximately 4,000 km.

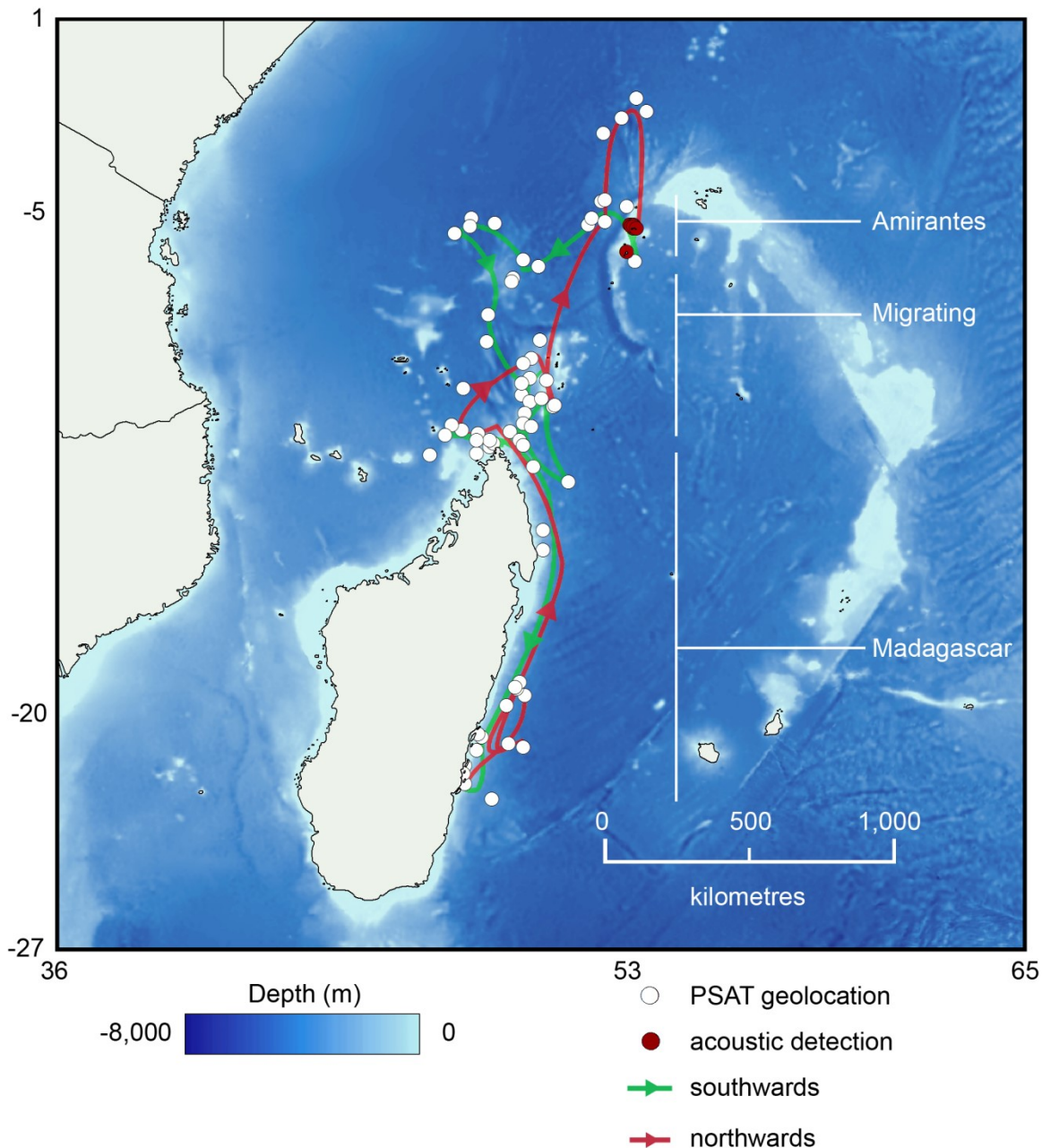


Figure 48: Map to show the ‘best’ path for the 3 m female bull shark tracked between 21st August 2014 and 19th January 2015. Points denote the processed track locations (red = receiver detections, white = PSAT geolocations), with a Bezier curve to illustrate the direction of travel (green = outbound, red = return). Map created in ArcGIS using ETOPO2v2 bathymetry data.

The shark displayed relatively restricted vertical movements, with the deepest dive during the entire track being to 164 m (Figure 49). The shark only experienced temperatures in excess of 20°C, ranging from 21°C at 164 m to 29°C at the surface, although the majority of time was spent around 26°C. Whilst in the Amirantes the shark’s depth profile appears restricted by bathymetry. The Amirantes plateau barely gets deeper than 60–70m, and before leaving the

Amirantes in mid-October the shark spent 86.3% of its time shallower than 50 m, with 56.6% of time spent at 30–50 m (Figure 50). Despite this preference for deeper water, the shark performed occasional rapid ascents to the surface (from ~60 m) at speeds of up to 4.3 ms^{-1} .

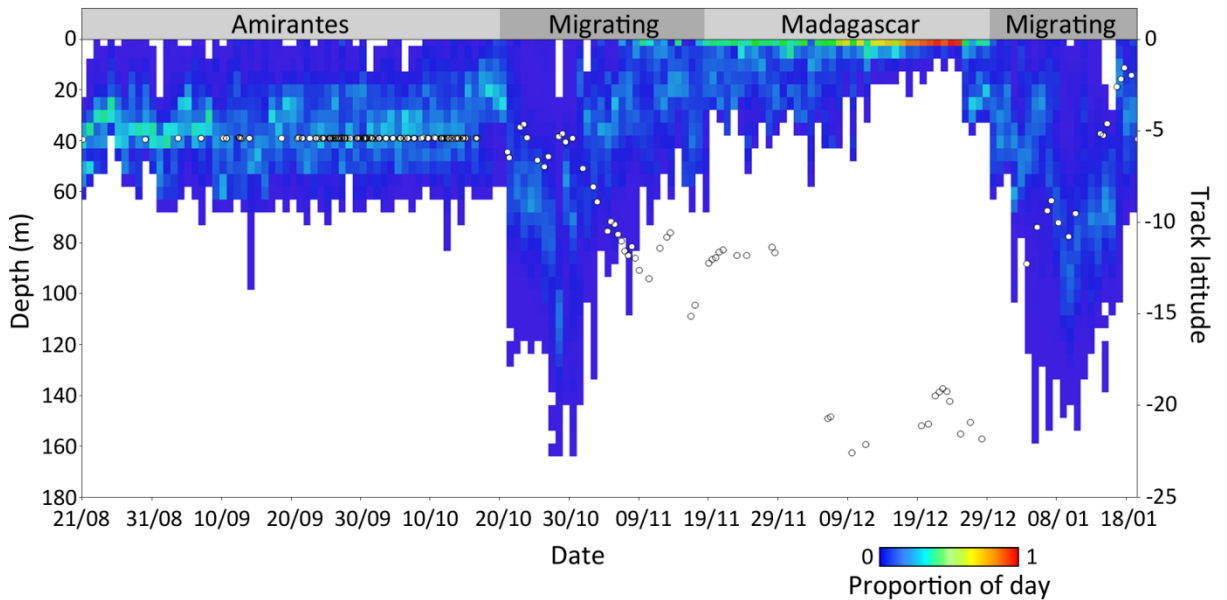


Figure 49: Plot of daily time-at-depth, overlaid with track latitude. Warmer colour denotes greater time spent at that depth. The string of detections around -5 degrees towards the start of the track are from the Amirantes acoustic array.

When migrating across open ocean (both to and from Madagascar), the shark displayed a much broader range of depth use and tended to stay deeper than when on the Amirantes (Figure 49), spending over a third of its time below 100 m (Figure 50). The shark regularly dived to depths of up to 164 m, often oscillating between 50 and 100 m. On several occasions the shark made some marked accelerations to the surface, including one from 130 m to the surface over the course of 60 s.

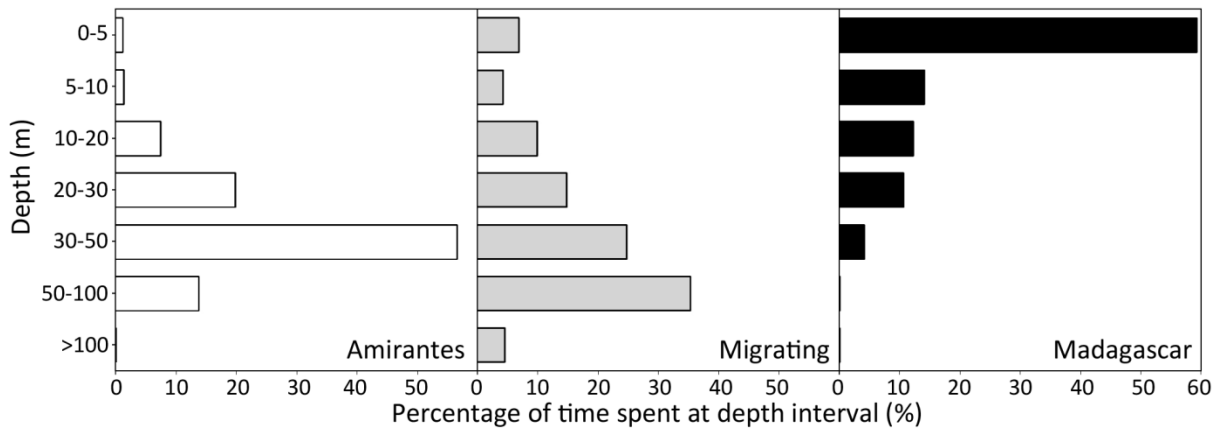


Figure 50: Time spent at depth while on the Amirantes plateau in Seychelles, during migration and at Madagascar.

Once along the coast of Madagascar the shark displayed a marked change in depth use (Figure 49), with 59.2% of time spent shallower than 5 m (Figure 50). This is predominantly attributable to the latter half of December, once the shark was along the southeast coast and remained almost exclusively shallower than 5 m (Figure 49).

8.4 Discussion

This large, female bull shark travelled from a remote chain of islands in the Seychelles to southeast Madagascar, approximately 2,000 km away, before returning back to the Seychelles. Previous tracking studies on bull sharks have generally reported relatively restricted coastal movements (Kohler, Casey & Turner 1998; Brunnschweiler, Queiroz & Sims 2010; Hammerschlag *et al.* 2012), with juveniles often being perennial residents in estuarine nurseries (Heupel & Simpfendorfer 2008). Some large movements have been recorded, such as 1,500 km along the coast of the United States (Carlson *et al.* 2010), and 2,000 km along the coast of South Africa to Mozambique (SOSF 2015). Bull sharks have been recorded moving over deeper water for short periods in the Gulf of Mexico, the Gulf Stream, and Reunion Island near Madagascar (Carlson *et al.* 2010; Brunnschweiler *et al.* 2010), but sustained, directed migration across open ocean as presented here has not previously been reported. Consequently this return migration is believed to be the first reported of its kind for bull sharks, being long-distance across deep, open ocean (similar to the tiger sharks in Chapter 3), and also represents the longest known PSAT track of a bull shark (151 days, previously 85 (Carlson *et al.* 2010)).

This shark could have travelled to Madagascar for parturition. At the time of tagging the shark was notably gravid, and the area of Madagascar it travelled to near Manakara has several large rivers and estuaries in the vicinity. As previously mentioned, female bull sharks preferentially pup in riverine and estuarine habitats (Springer 1963). Moreover, when in this area of Madagascar, the shark displayed a marked change in diving behaviour, remaining almost exclusively shallower than 5 m for several days, consistent with entering a river or estuary system. Immediately after leaving the shallower habitat, the shark resumed regular diving behaviour all the way back to the Seychelles, where it was observed as slender and no longer gravid. Consequently the shark must have pupped during the intervening absence from the

Seychelles, and the shallow depth profile in the vicinity of estuarine habitats in Madagascar is therefore a plausible candidate for its pupping ground.

This result is particularly surprising given that juvenile bull sharks are encountered coastally around Mahe in the Seychelles (pers. obs.), just over 200 km from the Amirantes. This raises the question as to why this shark would migrate 2,000 km away if suitable habitat was much nearer. Elsewhere female bull sharks are suspected of high reproductive philopatry, as evidenced by highly restricted maternal gene flow between different nursery areas (Karl *et al.* 2011; Tillett *et al.* 2012). Some shark species even show natal philopatry, returning to their own place of birth for parturition (Feldheim *et al.* 2014). Consequently this shark may simply have exhibited strong, possibly natal, philopatry to a particular nursery area. Alternatively, individual condition and the associated cost/benefit ratio may play a role in migration propensity (Chapman *et al.* 2012). There is little suitable estuarine habitat around Mahe, so perhaps the estuaries of Madagascar offer more favourable nursery habitat, and this individual may have been of sufficient body condition to afford the costs of migration to seek better habitat and survival odds for its offspring.

These data suggest that bull shark life cycles in the southwest Indian Ocean may play out over large geographical scales that cross international boundaries and the high seas, perhaps constituting a single population. This highlights the need for international cooperation on potential management efforts. How such collaboration can be achieved is exemplified by the Memorandum of Understanding on the Conservation and Management of Marine Turtles and their Habitats in the Indian Ocean and South-East Asia (IOSEA Marine Turtle MoU), whereby signatory states have agreed to protect a network of sites important to marine turtles (Hays *et al.* 2014). It is proposed that southwest Indian Ocean states adopt a similar initiative for migratory sharks in the region, with signatories agreeing to share data and collectively manage

areas deemed of particular importance to regional populations, such as potential nursery habitats for bull sharks in Madagascar. Madagascar may be an important pupping habitat for bull sharks regionally, with genetic analysis also indicating gene flow between Madagascar and Reunion Island 870 km to the east (Soria *et al.* 2015).

Further investigation incorporating genetics, shark condition and a larger sample size will be required to fully understand the migratory behaviour of bull sharks in the Seychelles. In the meantime, discovery of this novel, long-distance reproductive migration across open ocean highlights a potentially important pupping and nursery area for bull sharks regionally, and that management of this species will need to be considered across the ocean basin and not just locally. Finally, this also suggests that potential risks to beachgoers may also vary seasonally, and that southwest Indian Ocean states should collaborate on strategies to mitigate risk.

9 General Discussion

Through the application of remote telemetry, the present work has characterised the detailed, long-term movements of different shark species at contrasting geographical scales. Tiger sharks *Galeocerdo cuvier* were revealed to undertake broad-scale, annually repeated seasonal migrations that span an ocean basin, while reef sharks in the Seychelles were shown to display long-term residency to a small, relatively isolated atoll. Such a detailed understanding of movement behaviour and space use will be crucial when considering the implementation of management options to combat threats to shark population sustainability. A recent assessment of management strategy development concluded that characterising the long-term spatial dynamics of the target species in detail should be the first step of any decision making process (Allen & Singh 2016). Yet such assessments are often performed retrospectively (Chapman *et al.* 2005; Field *et al.* 2011; Speed *et al.* 2015; Allen & Singh 2016; Graham *et al.* 2016), the risks of which are emphasised by the reduced efficacy of certain management initiatives that neglected to consider animal spatial dynamics at the point of inception (Thirgood *et al.* 2004; Moffitt *et al.* 2009). This final chapter will discuss the findings of the present work in a broader context of population spatial dynamics for each species, with particular reference to how the results may inform and be incorporated into conservation strategies, and a more general synthesis of how migratory behaviour may in part be governed by an individual's body size.

9.1 Tiger Shark Population Dynamics

The first two data chapters (3 and 4) revealed previously unknown predictability in the migratory behaviour of male tiger sharks in the Atlantic Ocean. The sharks migrated between individually philopatric coral reef locations in winter and offshore pelagic areas near the mid-

Atlantic ridge and Gulf Stream in summer, up to 3,500 km away (Lea *et al.* 2015b). This pattern was repeated by individuals across multiple years, apart from for those smaller than ~270 cm, revealing that the repeated migratory behaviour was only adopted by adults. Relating the movements to environmental variation emphasised this ontogenetic disparity in behaviour even further: larger individuals associated with particular thermal niches and areas of high productivity more so than smaller individuals. This ontogenetic shift, combined with the strong philopatry within individuals but broad variation in migration targets between individuals, suggest individual ability and experience may play a significant role in the success of locating productive foraging areas through migration. Indeed, for various turtle species, the ontogeny of migration targets appears to be informed by individual experience, with adults migrating to regions they encountered as drifting hatchlings (Scott, Marsh & Hays 2014). It may be that individual tiger sharks adopt foraging targets informed by their encounters when switching to the migratory habit as they mature.

Repeated, long-distance migrations between highly contrasting habitats have rarely been reported among sharks (Weng *et al.* 2008; Domeier & Nasby-Lucas 2013; Howey-Jordan *et al.* 2013), and may seem at odds with the existing literature on tiger sharks, which tends to suggest high variation in movement patterns (Heithaus *et al.* 2007; Meyer *et al.* 2009; Hazin *et al.* 2013; Werry *et al.* 2014; Ferreira *et al.* 2015), that do not reflect the clear migratory behaviour observed here. Such an apparent lack of similarity in reported tiger shark movements from different regions across their range presents a particular management problem, in that a lack of predictability makes it difficult to determine how limited management resources should be allocated.

However, it is possible that tiger shark movements, while complex, may adhere more to a predictable pattern than the existing literature may suggest. The lack of a general pattern and

predictability in some locations could be an artefact of sample size and study duration: due to the costs and logistical difficulties of working in the marine environment (Gruber & Myrberg 1977), telemetry studies often suffer from small sample sizes and comparatively brief tracks (Sims 2010; Hussey *et al.* 2015). This presents a problem when studying a species that seems to adopt complex partial migration patterns across ocean basins, as there is the risk that individual studies may not be fully representative of population movements, which could in turn hinder effective management of the population as a whole (Chapter 3; (Papastamatiou *et al.* 2013)). For instance, while the present work achieved a mean track duration of 514 days, it is mainly limited to adult male tiger sharks.

In contrast, another study in the Atlantic predominantly tracked large females in the Bahamas, but only attained an average track duration of ~100 days (largely restricted to winter/early spring) and reported predominant reef association in the Bahamas with only some long-distance dispersal offshore (Hammerschlag *et al.* 2012). These female tiger sharks were also reported to spend significant portions of time within the Bahamian Exclusive Economic Zone (EEZ), where shark fishing is prohibited, and the authors suggested that if the coastal waters of the eastern USA also prohibited tiger shark catches then this species would spend the majority of its time within protected waters (Graham *et al.* 2016). But the brevity of such tracks hinders a study's capacity to determine long-term movements and migratory behaviour, suggesting that the findings should be interpreted with caution and within the limitations of the study.

Indeed, combining the results of the present work with the tracks of the Bahamas females suggests that the population spatial dynamics of tiger sharks in the northwest Atlantic, and hence the management situation, may be somewhat more complicated than either reveals in isolation. The spatio-temporal overlap of the male and female tiger sharks between the two studies in winter in areas of the Bahamas and Caribbean (Hammerschlag *et al.* 2012), when a

seasonal peak in mating scars is observed (Sulikowski *et al.* 2016), suggests they form part of the same basin-wide population. As few females were caught in the present study when tagging efforts were focused offshore at Challenger Bank, it may be that females migrate less frequently than males, perhaps due to skipped breeding partial migrations, as suggested for female tiger sharks in Hawaii; there, gravid individuals may skip migration and remain within warmer waters to facilitate gestation (Papastamatiou *et al.* 2013). In addition to sex bias in partial migration, ontogenetic partial migration is also apparent, with smaller sub-adult tiger sharks (~170–270 cm) favouring long-term residency at offshore insular habitats over migration. Yet new-born and juvenile tiger sharks <170 cm are not encountered in these habitats, but in shallow coastal waters along the coast of the USA and Caribbean reefs (Driggers III *et al.* 2008).

Taken together the differing findings in each study indicate there may be a complex, but predictable, pattern of tiger shark movement in the northwest Atlantic (Figure 51). Initially new-borns and juveniles may associate with shallow coastal habitats in the USA and Caribbean prior to dispersing to offshore foraging habitats (e.g. Challenger Bank) to mature. Once mature or maturing, the larger sharks then adopt the migratory habit between individual offshore foraging areas (perhaps discovered during dispersal) and warm insular reefs, where mating presumably occurs (Sulikowski *et al.* 2016) – perhaps even displaying natal philopatry, as suggested for Atlantic lemon sharks *Negaprion brevirostris* (Feldheim *et al.* 2014). Males, without the restrictions imposed by parturition, may be able to undertake these migrations annually, as observed in Chapter 3, while females only migrate depending on their reproductive state, remaining resident to parturition grounds if need be. This appears to be a reasonable model of tiger shark population structure and movement behaviour in the Atlantic based upon the available published reports for the area (Driggers III *et al.* 2008; Hammerschlag *et al.* 2012; Fu *et al.* 2016), but also suggests that studies restricted to a particular population

unit, location, or window of time may allow broader patterns and dynamic structure to go unnoticed. This absence of movement details may in turn severely impact the efficacy of population assessments and planned management initiatives (see section 9.2).

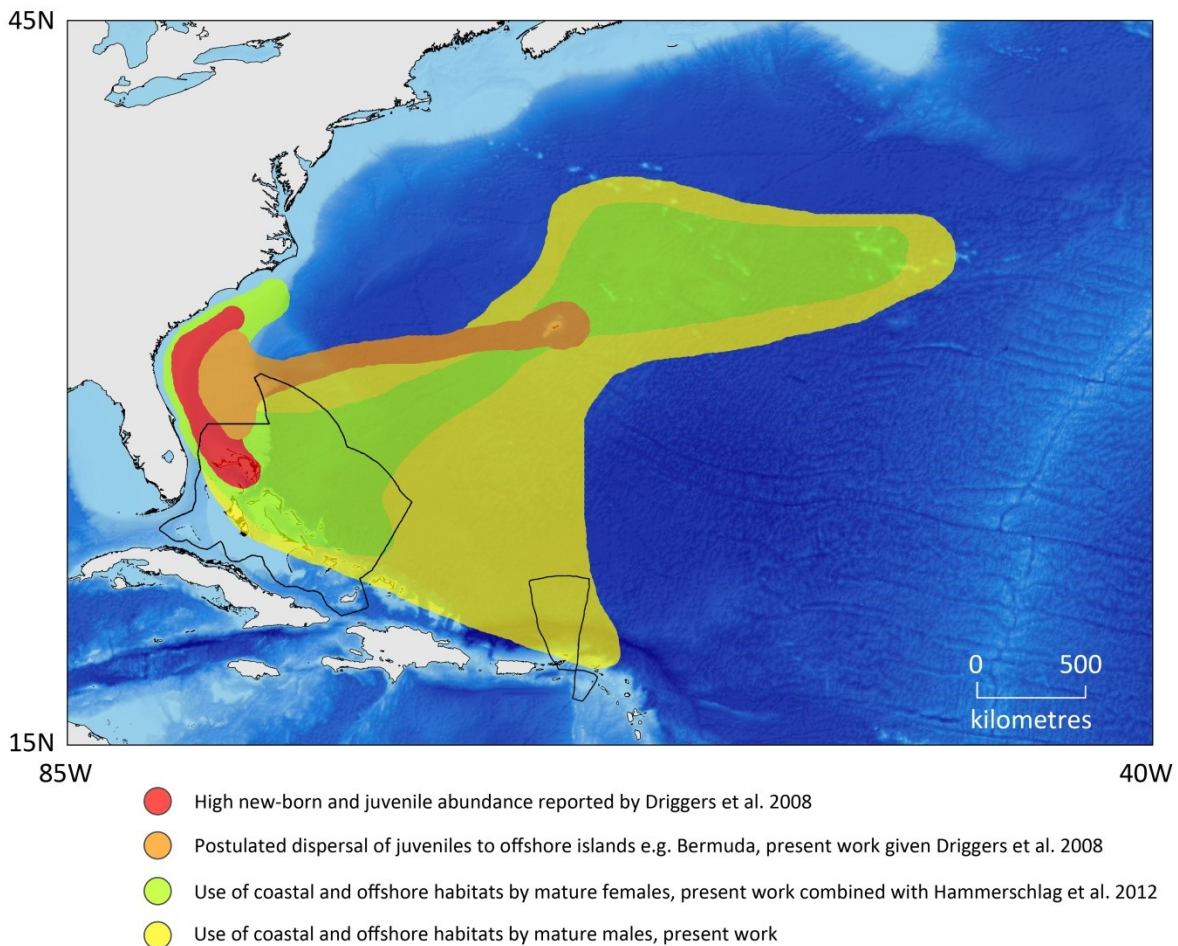


Figure 51: Proposed, simplified model of tiger shark population structure in the northwest Atlantic. High incidence of new-borns and juveniles in coastal regions (red), combined with the larger juveniles recorded at Bermuda in Chapter 3, suggest a dispersal to offshore insular habitats as individuals approach ≥ 170 cm (orange). As individuals > 270 cm start to approach maturity they then adopt a migratory habit between offshore foraging areas and insular breeding areas, with adult males (yellow) more regularly migrating offshore than adult females (green), due to skipped breeding partial migration. The black borders denote the shark sanctuaries of Bahamas, British Virgin Islands and Saba. Map created in ArcGIS, using GSHHG coastline data and ETOPO2v2 bathymetry data.

It is possible that this model, or a variation of it, could also apply to tiger shark populations elsewhere in their range, such as the Pacific or Indian Oceans. Indeed, while tiger sharks have traditionally been considered a coastal species, recent examination of pelagic catch records reveals them to be caught across the Atlantic high seas (Domingo *et al.* 2016), which with the

present study support the assertion that tiger sharks may adopt long distance migrations across pelagic habitats far more frequently than previously thought – they have just gone unrecorded. If only a subset of the population is observed, different individuals may perform markedly different movements depending on their individual condition and experience, without the overall pattern becoming apparent, impeding a full appreciation of their population ecology. The most comprehensive description of tiger shark movements from a single study is for individuals off Hawaii in the Pacific (Papastamatiou *et al.* 2013). Here, long-term acoustic telemetry was used to reveal skipped breeding partial migration in adult females, which may or may not migrate over 1,000 km along the chain of Hawaiian islands, depending on their reproductive state (Papastamatiou *et al.* 2013). In addition, and consistent with the present work, larger individuals exhibited greater ranging behaviour than smaller individuals (Papastamatiou *et al.* 2013). However the latter study was limited to large females, and the lack of long-term satellite telemetry (some brief tracks were reported) restricts inference to when the sharks were present in the acoustic array around Hawaii, leaving potential offshore movements unaccounted for. Nonetheless, the available information suggests that, while high intraspecific variation remains, the overall pattern of movement by tiger sharks in Hawaii is not inconsistent with the proposed dispersal – skipped breeding partial migration model. Elsewhere tiger sharks have been found to display perennial residency, seasonal patterns or long-distance movements (Heithaus 2001; Heithaus *et al.* 2007; Werry *et al.* 2014; Ferreira *et al.* 2015), but given either the lack of full representation in the sample or brevity of tracks, it was not possible to resolve broader patterns of population spatial dynamics.

It could be that the prevalence of migratory, resident and nomadic behaviours within a given population may depend on regional variation in habitat and resource availability, as well as environmental gradients in relation to the physiological needs of the individual. For instance,

migration propensity in moose *Alces alces* increases at higher latitudes, with more southerly individuals more likely to display a range of movement behaviours, attributable to contrasting variability in environmental factors along the latitudinal gradient (e.g. snow depth, predation risk): those in the more stable environment appear less likely to migrate (Singh *et al.* 2012). Nonetheless, without all population units being considered together it is not possible to determine whether populations elsewhere may reflect the model proposed here for the northwest Atlantic, but the potential for complex population structure over such a large geographical range should be investigated further, given the pertinent management implications.

9.2 Management of Broad-scale Migration

The highly complex nature of tiger shark population structure and migratory behaviour in the northwest Atlantic has significant implications for their fisheries interactions and sustainable management. Available data report considerable fishing pressure across the north Atlantic (Queiroz *et al.* 2016), with tiger sharks caught regularly in longline fisheries and now considered *Near Threatened* on the IUCN Red List (Simpfendorfer 2009; Domingo *et al.* 2016). The migratory behaviour of this species predicts significant overlap with these fisheries (Queiroz *et al.* 2016). The offshore foraging targets of the migratory individuals reported here puts them at much higher risk of overlap and exploitation (Figure 52). In order to illustrate the potential risk of interaction between tiger sharks and tuna longline fisheries during the study period, reported fishing effort (number of hooks set per 5° × 5° grid cell) during 2009–2012 was obtained from The International Commission for the Conservation of Atlantic Tunas (ICCAT) website (<https://www.iccat.int/en/>) and was multiplied by the corresponding tiger shark occupancy for that cell (recalculated to match the 5° × 5° of the fishing effort). This provides an estimate of where high tiger shark occupancy overlapped with high fishing effort more frequently, with the scale normalised from 0–1 to represent the relative interaction

strength (Figure 52). The strongest overlap occurred offshore in open ocean habitat, revealing that management strategies for migratory adults should perhaps primarily focus on mitigating mortality in high seas fisheries.

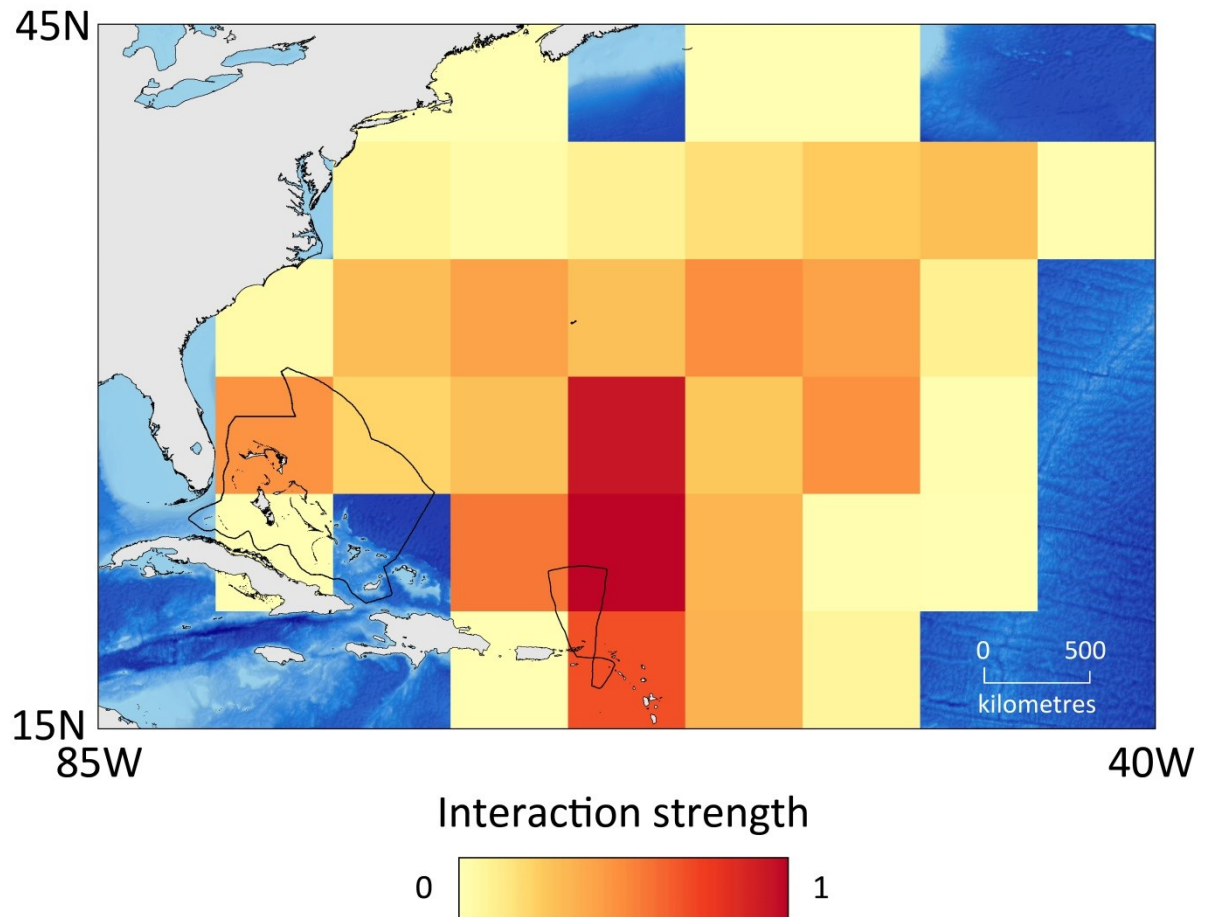


Figure 52: Map displaying the strength of interactions between tiger sharks and tuna longliners during 2009–2012 at a $5^\circ \times 5^\circ$ resolution. Interaction strength reveals where high tiger shark occupancy overlapped with high fishing effort. The black borders denote the shark sanctuaries of the Bahamas, British Virgin Islands and Saba. Maps created in ArcGIS, using GSHHG coastline data, ETOPO2v2 bathymetry data and ICCAT data on tuna longline fishing effort for the study period (hooks set per $5^\circ \times 5^\circ$ cell, 2009–2012).

At present the only firm protection for tiger sharks in the northwest Atlantic are the shark sanctuaries of the Bahamas, British Virgin Islands and Saba, as well as certain small MPAs and seasonal restrictions to sport fishers along the USA coast (Graham *et al.* 2016). This may at least afford some juveniles and non-migrating females with reasonable protection (Figure 51), but management of the population must be considered as a whole to ensure it remains a functional unit. Selective depletion of males, females or juveniles, as may be the case given the

apparent complex structure in the northwest Atlantic, may have severe cascading impacts that could still cause populations to decline even if certain units receive reasonable protection (Wearmouth & Sims 2008; Mucientes *et al.* 2009). For example, juveniles and females along the USA coast largely remain exposed to fishing pressure at present, as do migratory individuals and larger juveniles at offshore insular stages such as Bermuda (Figure 51; Figure 52). In the US Atlantic and Gulf of Mexico capture of sharks in the 'Aggregated Large Coastal Sharks' group (which includes tiger sharks and six other species) is limited to a total allowable catch each year (85.5 mt in 2016), but there are no specific conservation or management measures in place for the tiger shark (NOAA 2016). Given the comparatively restricted movements of subunits along the USA coast and around Bermuda, reasonable levels of protection for them could be achieved with spatial management options such as MPAs or shark sanctuaries that prohibit shark fishing. Apparent high interactions with fisheries for migrants near the Caribbean islands of Puerto Rico, Virgin Islands and Antigua and Barbuda (Figure 52), where some individuals overwintered, suggest that similar spatial management options could be considered in these areas to extend protection of tiger shark overwintering sites beyond the existing shark sanctuaries.

More complicated is how to manage fisheries interactions during the pelagic phase of migrants. Due to the broad geographical scale and intensive fishing pressure, static spatial management options such as high seas MPAs may have limited efficacy (Game *et al.* 2009; Allen & Singh 2016). One alternative might be time-area closures that track the routes and timings of tiger shark migrations, as has been proposed for leatherback turtles *Dermochelys coriacea*, which undertake similarly large migrations and are also severely threatened by fishing pressure (Shillinger *et al.* 2008). However, the broad variability in routes adopted by individual tiger sharks may limit the effectiveness of such a technique. Another option may be time-area closure of the offshore foraging area during summer, where the tiger sharks

displayed high overlap with the loggerhead turtles *Caretta caretta* and high interaction with longliners (Figure 52). If this does represent an offshore foraging area, then capture risk may be even higher if individuals are more likely to take hooked baits than when they are migrating, when station-keeping responses may be inhibited (Dingle & Drake 2007). This area also appears important for a variety of other large marine predators (Queiroz *et al.* 2016), so time-area closure here may benefit a wide variety of species. Such an approach has been suggested for offshore pupping areas for the porbeagle shark *Lamna nasus* in the Sargasso Sea (Campana, Joyce & Fowler 2010).

However, such time-area closure would still need to encompass a relatively large area (evident in Figure 52) that may be difficult to enforce and may conflict with preferred tuna and swordfish *Xiphias gladius* fishing grounds (Queiroz *et al.* 2016). Changing fishing techniques may be another option, as suggested for thresher sharks *Alopias vulpinus*, whereby setting hooks at different depths may reduce overlap between fishing effort and thresher shark diving behaviour, yet maintain overlap with tuna movements (Cartamil *et al.* 2010). Tiger sharks in the northwest Atlantic, however, are known to display highly varied diving behaviour (Vaudo *et al.* 2014), making it difficult to determine fishing depths that may reduce bycatch without impacting tuna or swordfish catches. Perhaps, as has been proposed for blue sharks *Prionace glauca* in the eastern Atlantic (Queiroz *et al.* 2012), a more appropriate method may be the introduction of quotas specific to tiger sharks, above which they must be released. This may prove effective given the reasonably high post release survival of most large shark species, including tiger sharks (Musyl *et al.* 2011; Gallagher *et al.* 2014; Afonso & Hazin 2014), and the comparative ease of compliance and enforcement with on-board observers and monitoring of landings.

Combined, the results of the present work in the context of other tiger shark studies in the region, suggest that management strategies targeting the population as a whole may need to adopt an array of approaches that will require a significant degree of international cooperation: the offshore areas used are all fished by the USA, Canadian, Japanese, Chinese, Taiwanese, Russian and European fleets, and use of coastal areas spans the USA, Bahamas, Bermuda and various Caribbean EEZs (Driggers III *et al.* 2008; Graham *et al.* 2016). It is suggested that the primary focus should be easily managed targets, such as a shark sanctuary for Bermuda and certain Caribbean islands, where even adult migrants stopover for significant periods, and expanding the protection received in USA waters to support existing protection in the Bahamas. Further quantitative assessment is needed to inform the best management for offshore movements, but imposition of release practices and quotas specific to tiger sharks should be considered, combined with time-area closures along migration routes and in offshore foraging areas. Such measures would need to be implemented through an appropriate body such as ICCAT, which already performs stock assessments and provides management recommendations for a variety of pelagic shark species (Cortés *et al.* 2015). However, despite identification that stocks of shortfin mako *Isurus oxyrinchus* and porbeagle shark may be overfished, ICCAT has yet to establish management strategies for these species (Cortés *et al.* 2015). It may be more appropriate to seek alternative interventions, such as prohibition of landing tiger and other pelagic sharks in certain countries, as implemented for porbeagle sharks in the European Union (Ellis *et al.* 2016).

Given the observed significant association between tiger shark movements and environmental features (e.g. water temperature, see Chapter 4), future management efforts may also need to consider how tiger shark distributions may shift with the changing climate (Edwards & Richardson 2004; Roessig *et al.* 2004; Cheung *et al.* 2009; Hoegh-Guldberg & Bruno 2010). Population performance may depend on individual ability to adapt to environmental change,

such as adapting foraging movements to habitat loss (McNamara *et al.* 2011). Variation in water temperature may in part cue tiger shark migration and facilitate location of productive foraging patches by synchronising movements with peak food availability. The use of changing temperatures to cue migration and target peak food availability is considered a pertinent adaptation among various bird species, although those without such behavioural plasticity appear to be declining due to the timing of breeding becoming mismatched with peak food (Møller, Rubolini & Lehikoinen 2008). Consequently as sea temperatures rise and the severity of climate events such as El Niño may increase (Cobb *et al.* 2003; Van Oldenborgh, Philip & Collins 2005; Meehl *et al.* 2007), shifts in shark distribution may occur that will require dynamic modification of management strategies (Perry *et al.* 2005). For instance, modelling of 23 different marine predators in the Pacific under increasing SST and changing chlorophyll- α distributions predicted a change of up to 35% in core habitat, which may increase migration times, exacerbate declines and inhibit recovery (Hazen *et al.* 2013). If applicable to tiger sharks in the Atlantic, foraging patches may be pushed further north under increasing SST landscapes as productive isotherms shift northward, forcing foraging migrations away from overwintering sites to be longer, potentially stressing the metabolic costs of migration and affecting population viability.

9.3 Reef Shark Population Dynamics

The present work also evaluated the habitat use of five different reef shark species around a remote coral atoll in the Indian Ocean, including how this varied over time and influenced the efficacy of potential spatial management options. In stark contrast to the broad, long-distance movements of the tiger sharks, the majority of reef sharks displayed highly restricted movements, particularly focused around the lagoon habitat provided by St Joseph Atoll (Lea *et al.* 2016). Such a detailed understanding of habitat use, as evaluated in Chapters 5–7, is invaluable for assessing population dynamics and the potential effectiveness of existing and

planned management initiatives (Allen & Singh 2016). Identifying habitat use patterns helps define areas of critical importance for survival and recruitment, as well as determining the likelihood of both direct and indirect interspecific interactions, which can influence community structure and stability (Brown 1999; Hansen *et al.* 1999; Allen & Singh 2016). However, the protection provided by the MPAs assessed in Chapter 7 varied significantly between species and size classes, reflecting varied habitat use and population structure that may influence the likelihood of increased recruitment supported by such an MPA (Lea *et al.* 2016). Consequently it is important to interpret the observed patterns in habitat use in a broader context of population dynamics in order to understand how an MPA such as the D'Arros and St Joseph Special Reserve may support recovery and stability of local shark populations.

Blacktip reef sharks *Carcharhinus melanopterus* displayed the most focused use of D'Arros and St Joseph, with almost all detections occurring within the lagoon or on the coastal reefs (Chapter 5). Connectivity even within this area was restricted, with individuals not even recorded to cross the 1 km channel between D'Arros and St Joseph for the first eight months of the study, providing another example of how time, or sampled-limited, studies can allow rarer movements to go unnoticed. Both juveniles and adults of both sexes displayed this perennial site fidelity, although there were some disparities in the sex ratio and size classes observed. Similarly, the tracked sicklefin lemon sharks *Negaprion acutidens* remained almost exclusively within lagoon habitats, with dispersals to other islands across the Amirantes only performed by individuals greater than ~180 cm (Chapter 5). No blacktip reef or lemon sharks smaller than ~70 cm were tracked, leaving the movements of the youngest individuals unaccounted for. This could be due to fishing techniques, as the size of hook used (19–20/0 circle hooks) may have reduced the chance of capturing smaller individuals. Moreover, even the smallest tags used (V13) would have been too large to use on the smaller sharks. As such their lack of capture does not necessarily signify absence: during field work in the lagoon

neonate blacktip reef and lemon sharks were regularly seen patrolling the extreme shallows (<20 cm) along the flats and coastal mangroves (pers. obs.). In addition, regular survey work in the area using gillnets reveals high abundance of neonate blacktip reef and lemon sharks in the lagoon (O. Weideli, pers. comms.). Consequently size classes smaller than those tracked here are also present in the lagoon, and may even display similar site fidelity among mangrove habitats.

Male blacktip reef sharks were also represented poorly in the recorded tracks. While this may suggest that males occur more frequently elsewhere (male blacktip reef sharks have in fact been suggested to roam more widely than females (Mourier & Planes 2013)), it is possible that fishing procedures may have biased the proportion of males tagged. Although efforts were made to homogenise tagging effort, a disproportionate number of tags on blacktip reef sharks were deployed in the lagoon due to the higher catch rates there. If males and females structure their habitat use over scales of only a few kilometres (as seen in Chapter 6), the precise fishing location may have affected the observed sex ratio. This is supported by observations of blacktip reef sharks at the remote island of Moorea in French Polynesia, Pacific, where males displayed high residency, but favoured reef habitats more than females (Mourier, Mills & Planes 2013). As such it may be reasonable to assume that while males were underrepresented, they too could display high fidelity to D'Arros and St Joseph, as the few tracked males did.

The focused use of D'Arros and St Joseph by all life history stages of blacktip reef sharks may be a combination of the suitability of available habitat for all size classes and the relative isolation of the islands. At similarly remote locations, such as Palmyra and Moorea in the Pacific, blacktip reef sharks have shown comparably restricted movements and high fidelity, as well as high genetic population structure, indicative of isolation and low connectivity

(Papastamatiou *et al.* 2009; Mourier *et al.* 2013; Mourier & Planes 2013). Conversely, in areas with more contiguous coastline, such as western or eastern Australia, wider dispersals and ranging seasonal movements of over 100 km have been reported (Speed *et al.* 2011; Chin *et al.* 2016). The lack of observed connectivity and dispersal across the Amirantes plateau may be a combination of the strong suitability of the lagoon habitat provided by D'Arros and St Joseph and favoured by blacktip reef sharks, combined with the risks of traversing deeper waters that may be frequented by predators. The last detection of one individual occurred quite suddenly along the south eastern drop-off having previously shown long-term residence in the lagoon. While this may have represented a rare dispersal (two other individuals have in fact now been recorded moving up to 15 km away from D'Arros), it could also reflect predation by a larger ranging shark species (e.g. bull).

Further work will be required to determine the relative isolation of D'Arros and St Joseph's blacktip reef sharks (e.g. population genetics, more tracking of all size classes and sexes, survey work), but the potential that it may support all life stages of blacktip reef sharks and consequently represent a reasonably isolated population suggest that it may be particularly vulnerable to exploitation and rapid depletion, even from relatively limited fishing pressure, as there may be limited capacity for the population to be replenished from other nearby populations (Osgood & Baum 2015).

In contrast to blacktip reef sharks, while the lagoon habitats are evidently still important, sicklefin lemon sharks start to undertake significant dispersals away from D'Arros and St Joseph as they mature. This represents an ontogenetic shift in ranging behaviour, similar to the tiger sharks in chapters 3 and 4, perhaps due to size-related changes in foraging targets/ability or reproductive needs (Heupel *et al.* 2014). Larger lemon sharks were detected over 90 km away from D'Arros on the most southern tip of the Amirantes, while one male was caught 300

km away at Bird Island north of Mahe. This switch in behaviour is also apparent in the seasonal pattern in presence observed for larger lemon sharks (Chapter 6), perhaps as females return to the lagoon for parturition, which may also be when males return to find mates. Consequently overall distribution of the local lemon shark population may be far greater than the local blacktip reef sharks, attributable to the switch to more ranging behaviour as individuals mature.

Similar shifts in behaviour have been reported for the Atlantic lemon shark, which remains within particular lagoon habitat for the first few years of life before dispersing to adopt a wider ranging habit as they grow over ~130 cm, but eventually returning to their own nursery for parturition as adults (Sundström *et al.* 2001; Feldheim, Gruber & Ashley 2002; Feldheim *et al.* 2014; Chapman *et al.* 2009). The main contrast with observed sicklefin lemon shark behaviour (both in the present study and at Aldabra; (Stevens 1984)) is the almost exclusive use of lagoon nursery habitat such as St Joseph Atoll until they start to approach maturity (~180 cm; (Stevens 1984)). This extended use of nursery habitat in the Seychelles could be due to the comparative isolation and low availability of suitable habitat: shallow lagoon refuges are rare in the dispersed archipelago of islands and atolls in the Seychelles, contrasting the clustered collection of shallow islands in the Bahamas that are also close to the long, continuous coastline of the USA (Feldheim *et al.* 2002, 2014). Consequently nurseries such as St Joseph may be very important for survival and recruitment, as they are comparatively rare and cover a greater duration of development through to maturity (Kinney & Simpfendorfer 2009). Nonetheless, the ranging behaviour of larger individuals implies that the local lemon shark population may be structured at a more regional scale, with management strategies beyond the application of local MPAs required to sustain both survival and recruitment.

Habitat use of grey reef sharks *Carcharhinus amblyrhynchos* was in stark contrast to blacktip reef and lemon sharks, with no use of the lagoon observed for any individual (Chapter 5). Rather, grey reef sharks favoured particular areas along the plateau drop-off and the coastal reefs of D'Arros and St Joseph, particularly at night (Chapter 6). However, the majority of tracked individuals were large females, severely reducing the capacity to obtain a more general understanding of the movements and space use of males and juveniles. Given the strong association with drop-off habitat, and the comparatively low coverage of such available habitat in the array, it is possible that grey reef shark movements may be distributed across the entire Amirantes plateau. While in particularly isolated locations grey reef sharks tend to display highly focused residency (Field *et al.* 2011; Espinoza *et al.* 2015b), in other regions grey reef sharks have been shown to be capable of movements greater than the length of the Amirantes chain (~150 km; (Heupel, Simpfendorfer & Fitzpatrick 2010)). Indeed, grey reef sharks display low genetic structuring across the Great Barrier Reef, indicative of high local connectivity and movement throughout the reef system (Momigliano *et al.* 2015). In addition, analysis of grey reef shark diets using stable isotope signatures at Palmyra Atoll in the Pacific revealed that, despite frequenting coral reefs, pelagic resources constituted a significant component of their diet (McCauley *et al.* 2012), suggesting broader movement and consistent with the coastal reef/drop-off habitat switching observed here.

Consequently, without further supporting information, it may be that the local grey reef shark population is distributed at least across the Amirantes chain, where a long, continuous stretch of drop-off habitat may be used by adults, with the coastal reefs of various islands providing refuge for juveniles. Another study tracking grey reef shark movements around the Mahe plateau – 230 km away, separated by deep water (>1,000 m) – has yet to detect any of the sharks tracked in the present study, and *vice versa* (R. Govinden, pers. comms.). This suggests that grey reef sharks in the Amirantes may be relatively confined to the plateau, although

further tracking of males and smaller individuals at other locations in the Amirantes and over longer periods will be required to determine whether the area does support all population units of the grey reef shark.

For tawny nurse sharks *Nebrius ferrugineus* only six individuals were tracked, reducing the study's capacity to represent population movements, and there is little information on tawny nurse shark space use in the literature to compare these to (Rizzari, Frisch & Magnenat 2014). While the juveniles displayed marked preferences for lagoon habitat, no individuals less than ~120 cm have been observed in the study area. If tawny nurse sharks do use the lagoon for parturition, small individuals may not have been caught due to the selective nature of the larger hooks used, and may not have been seen if favouring more turbid, deeper sections of the lagoon, but ultimately the local pupping grounds for this species remain unknown. The few large individuals tracked displayed varied, wide ranging movements beyond D'Arros and St Joseph, suggesting the local population encompasses at least the Amirantes. The potential importance of the Amirantes is inferred from chance encounters with aggregations of 50+ adult male and female tawny nurse sharks, both along the drop-off and coast of D'Arros (Figure 53; N. Filmalter, pers. comms.; C. Vaughn-Jones, pers. comms.). Given that sexual segregation is typical of most shark species (Wearmouth & Sims 2008), the co-occurrence of adult male and female sharks suggest these may be mating aggregations (Pratt Jr & Carrier 2001). Due to limited tracks and the concealing nature of the marine environment, it has not been possible to determine any spatio-temporal pattern in these aggregations, apart from that they broadly seem to occur towards the end of the northwest monsoon (~March). Despite limited data for tawny nurse sharks, parallels in the observed patterns with those for lemon sharks suggest that larger individuals may also disperse to other island groups in the Seychelles, further complicating planning of management interventions.



Figure 53: Image of tawny nurse shark aggregation near the drop-off ~15 km north of D'Arros. Photograph by Nick Filmalter.

For the silvertip sharks *Carcharhinus albimarginatus*, an appreciation of population spatial dynamics remains severely limited as only small juveniles were tracked, which associated almost exclusively with drop-off habitat during the day (Chapters 5 and 6). Silvertip shark tracks were also comparatively short in duration, with at least 20% of tagged individuals being caught by fishermen. Such high mortality is concerning given how data deficient this species is both locally and globally – there appear to be only three published studies tracking silvertip shark movements (Barnett *et al.* 2012; Bond *et al.* 2015; Espinoza *et al.* 2015a), only one of which attained $n > 4$ and it focused on adults (Espinoza *et al.* 2015a). While adult sharks may visit the Amirantes for parturition, their distribution may cover a much larger, regional scale: their movements remain unaccounted for in the present work and pelagic movements have been reported in the Pacific (Bond *et al.* 2015). Adult silvertip sharks are known to occur at depths of 40–50 m in the mouth of the main channel at Aldabra atoll, over 900 km away (D. Beecham, pers. comms.), consistent with adults being caught at depths of 75–150 m at Aldabra (Stevens 1984). If there is life history segregation by depth, the present study may have excluded larger silvertip sharks from being caught by predominantly fishing at 0–20 m

depth. Nonetheless, despite their paucity the available data support the precautionary interpretation that the silvertip shark population in Seychelles is structured regionally and will require management at a similar scale.

9.4 Management of Fine-scale Spatial Dynamics

Where marine ecosystems are under threat and the exploited species display fine-scale, focused use of particular habitats or locations (e.g. nurseries), conservation efforts are increasingly turning to spatial management options. Indeed, over 9,000 MPAs have been declared to date (Costello & Ballantine 2015), with an increasing trend amongst shark conservation for the establishment of shark sanctuaries, specifically prohibiting shark fishing in the designated area (Hoyt 2014). A recent review of MPA attributes that promoted increased biomass found that the chances of MPA success increased with the designation of a no-take zone, effective enforcement, increased age, size and isolation (Edgar *et al.* 2014). Yet few MPAs achieve these criteria, with boundaries often declared without a full appreciation of the spatial dynamics of the target species, while over 90% of MPAs still permit some level of fishing, and the median size is only 4.5 km² (Costello & Ballantine 2015). The need for effective enforcement is emphasised by the ongoing decline of reef shark populations in MPAs such as Cocos Island and parts of the Great Barrier Reef, where limited surveillance facilitates poaching activities (Robbins *et al.* 2006; White *et al.* 2015). By comparison, as described in Chapter 7, the D'Arros and St Joseph Special Reserve implemented to protect the local reef shark assemblage is isolated, will not permit any fishing, will be over 65 km², and will have effective enforcement through provision of a patrol boat, all of which suggest it may promote the sustainability of this important ecosystem. However, in the context of the broader population dynamics discussed above, the efficacy of the MPA to sustain both survival and recruitment of the local reef shark populations may vary considerably depending on the species and life history stage, requiring complementary management strategies for population units not

covered by the MPA to ensure sustainable management of the population as a whole (Kinney & Simpfendorfer 2009; Osgood & Baum 2015; Allen & Singh 2016).

Despite the increased vulnerability of an isolated population of blacktip reef sharks at D'Arros and St Joseph, it does mean that spatial management options, such as the D'Arros and St Joseph Special Reserve, may be effective at promoting population stability (Osgood & Baum 2015). As revealed by analysis in Chapter 7, the D'Arros and St Joseph Special Reserve would cover almost all blacktip reef shark movements, which is beneficial considering the *Near Threatened* status of blacktip reef sharks on the IUCN Red List (Heupel 2009). If all population units are represented within the MPA, as suggested above, then it may prove particularly effective at conserving the local blacktip reef shark population without any further management intervention.

Similarly restricted movements of juvenile lemon, tawny nurse and grey reef sharks suggest that the discrete spatial management of the MPA may also be effective for these species prior to maturity, but the more complex movement behaviour of adults in the Amirantes requires their management to be considered at multiple scales beyond just the D'Arros and St Joseph MPA. Effective management of lemon shark populations in Seychelles is particularly important given the extirpation of this species in other regions (e.g. Thailand, India) and its listing as *Vulnerable* along with the tawny nurse shark on the IUCN Red List (Pillans 2003a; b). For grey reef sharks, also *Near Threatened* on the IUCN Red List (Smale 2009), the D'Arros MPA appears to only provide substantial cover for the movements of relatively small individuals, with sub-adults and adults remaining largely exposed to local fishing pressure (Chapter 7), which is of note given that grey reef sharks are the most common component of the Seychelles artisanal shark fishery (Nevill *et al.* 2007). The tracked silvertip sharks received almost no benefit from the D'Arros and St Joseph MPA (Chapter 7), and although adult silvertip sharks may frequent

the Amirantes, the limited information available combined with observed high mortality of tagged juveniles implies the need for urgent further work and precautionary management in the meantime.

The broader distribution of larger, mature lemon, tawny nurse and grey reef sharks across at least the Amirantes plateau is a primary management concern as evidence suggests that for late maturing species such as the sicklefin lemon shark, survival of maturing and mature individuals may be the most important factor for sustaining recruitment rates (Prince 2005; Gallucci, Taylor & Erzini 2006; Kinney & Simpfendorfer 2009). This is due to the recruitment curve of elasmobranchs, where recruitment rates are directly proportional to the number of breeding adults (Kinney & Simpfendorfer 2009). Consequently, irrespective of juvenile survival, relatively limited exploitation of adults may perpetuate decline of the whole population as even those that do mature may not get the opportunity to reproduce (Prince 2005; Kinney & Simpfendorfer 2009).

Population declines mediated by adult mortality have been reported for various fish species (Birkeland & Dayton 2005), and is thought to be what happened in the southern Australian fishery for school sharks *Galeorhinus galeus* (Prince 2005). The population there experienced severe declines despite strict, focused protection of nursery grounds, as ongoing exploitation of adults broke the recruitment cycle prior to parturition (Prince 2005). In contrast, exploitation of smaller size classes for the gummy shark *Mustelus antarcticus*, with limited exploitation of adults, appears to have been relatively sustainable thus far (Prince 2005). This has led to the suggestion of a 'gauntlet fishery' as a management option for long-lived elasmobranchs, whereby smaller size classes are preferentially exploited over mature and maturing individuals, with a reduced focus on spatial management of nurseries (Birkeland & Dayton 2005; Prince 2005; Kinney & Simpfendorfer 2009).

While the D'Arros and St Joseph MPA will still support survival and recruitment, especially for lemon sharks where individuals receive coverage up until they start to mature, the risks outlined above emphasise that this MPA must be coupled with measures to mitigate adult mortality within the Seychelles, to ensure parturition is maintained and the populations remain viable. Given the cultural significance of sharks such as grey reef and lemon sharks to the Seychelles artisanal fishery (Nevill *et al.* 2007), strategies beyond MPAs around critical habitats such as D'Arros and St Joseph will need to incorporate the needs of a broad range of stakeholders. One option may be for the Seychelles government to enforce species-specific quotas or size limits within the EEZ, such that sharks above a certain size are released or only a few captures are permitted. Combined with nursery MPAs this may ensure sufficient survival and recruitment for population stability. Given the seasonal variation in use of the atoll by adult lemon sharks, perhaps the imposition of such size limits could vary seasonally for this species, possibly only being enforced during the southeast monsoon when larger individuals are less likely to be inside nursery MPAs such as St Joseph lagoon.

However, without detailed information on the catch rates of sharks in Seychelles fisheries, and a comprehensive understanding of movements beyond the array (perhaps addressed via satellite telemetry), it is not possible to reliably suggest what management strategies may be effective, but given the apparent limited connectivity between the Amirantes and Mahe for most species (albeit based on comparatively limited tracking effort), perhaps a precautionary measure that may prove effective in the interim would be designation of the Amirantes plateau as a shark sanctuary by the Seychelles government. Such initiatives are being increasingly adopted in areas where shark tourism is being identified as a greater, and more sustainable, source of income than directed fisheries, such as for grey reef sharks in Palau (Vianna *et al.* 2012). Perhaps preventing the capture of sharks in the Amirantes, incorporating

the entirety of available drop-off habitat, while promoting tourism in the area, may provide a reasonable starting point for management given the lack of available information.

Of somewhat broader management significance, and more comparable to the tiger shark situation discussed above, is the long-distance, return migration of a pregnant bull shark *Carcharhinus leucas* from the Amirantes to Madagascar and back (Chapter 8 (Lea *et al.* 2015a)). This reveals that, regardless of any management initiatives imposed in the Seychelles, the larger sharks such as bull sharks (*Near Threatened* on the IUCN Red List; (Simpfendorfer & Burgess 2009)) will still be vulnerable to exploitation in other countries and across the high seas. This is further emphasised by the deployment of additional satellite tags (PSATs, $n = 3$) since the present work, one of which revealed another return migration to Madagascar, while the other two remained in the Seychelles (J. Lea, unpublished data). Consequently there appears to be potential high connectivity of bull sharks in the western Indian Ocean, with eastern Madagascar provisionally identified as an important pupping site. Such migration is similar in scale to the repeated, long-distance migrations observed in the tiger sharks, and may also be partial in nature considering not all have gone to Madagascar. In contrast to the tiger shark migrations, however, the bull shark migration appears to be considerably more direct: long-term residence was observed in the Amirantes for ~9–10 months, followed by direct dispersal to Madagascar (3–4 weeks), where parturition presumably occurred late December, followed by rapid (2 weeks), direct dispersal back to the Amirantes. This appears to be a classic migration pattern between foraging (Amirantes) and breeding grounds (Madagascar), but due to the skewed timing and directed nature of the migration, may prove easier to manage than those of the tiger sharks, subject to international collaboration.

Given the relatively restricted movements shown in the Amirantes, spatial management options such as the D'Arros MPA or an Amirantes shark sanctuary may provide reasonable

coverage of bull shark movements for a reasonable proportion of the year. As the migration to Madagascar was so directed and brief, comparatively little time was spent exposed to high seas fisheries, perhaps negating the need to apply any management initiatives that may be difficult to enforce in the open ocean, such as time-area closures that track migrations. Bull sharks may also be less likely to be caught during migration motivated by parturition due to reduced motivation to feed and take baits as a consequence of inhibition of station-keeping responses that promote dispersal to pupping areas (Dingle & Drake 2007). Most of the migration duration was spent at Madagascar, presumably to pup, potentially revealing another spatial management target: the coastal nurseries of Madagascar, which could again be reasonably covered by an MPA or shark sanctuary. Complications arise, however, both from the need for international cooperation and that it has already been revealed that some females use other locations in the Seychelles for parturition (e.g. Mahe; J. Lea, unpublished data), where fishing effort for bull sharks remains high. Moreover, no male bull sharks have yet been recorded in the study area – perhaps they are more frequently encountered around Madagascar, from where migrating females have returned with apparent mating scars (pers. obs.). Consequently, integrating the broad-scale migrations of species like bull sharks into the fine-scale spatial dynamics of other shark species is an important issue that will be incorporated into future work, moving towards a comprehensive, holistic understanding of shark movement behaviour and population ecology that may be used to inform effective management strategies that can be reliably enforced.

9.5 Migration Propensity – Does Size Matter?

A common theme running through the thesis is the scale of individual shark movement and to what extent they tend towards residency or migration, which has been demonstrated to vary both within and between species (Chapters 3–8). Assuming there must be a compromise of

costs and benefits as to whether an individual adopts a resident or migratory habit (Dingle & Drake 2007; Chapman *et al.* 2011, 2015), what factors may cause a shark to tend towards one over the other? Based on the present work and existing literature (Peters 1986; Clarke & Johnston 1999; Chapman *et al.* 2011; Jacoby *et al.* 2015; Iosilevskii & Papastamatiou 2016), a significant factor dictating an individual's dispersal ability and migration propensity appears to be body size and its effects on an individual's metabolic rate and energy budget. Sharks are ectothermic and, unlike most other taxa, are somewhat unique in that the majority of species must keep swimming in order to respire through ram ventilation (Compagno 2001), meaning that the cost of continuous swimming must be incorporated into minimum energy budgets. Moreover, the relative cost of transport for sharks may be greater than other fish species because they lack a swim bladder and so are negatively buoyant – it has been estimated that the metabolic cost of transport for negatively buoyant fish is 40% greater than for neutrally buoyant fish (Iosilevskii & Papastamatiou 2016). Consequently sharks must work to maintain a constant depth, produced through a combination of up thrust from swimming and buoyancy provided by the low density lipids within a comparatively enlarged liver (Del Raye & Jorgensen 2013).

So given the unusual situation of sharks having to move continuously, how might variations in body size influence whether a shark is migratory or not? Why can't smaller sharks disperse as much as larger sharks if they already have to swim constantly? The observed movement behaviour will be the product of various intrinsic and extrinsic factors, but one of the most important impacts of body size is how it affects metabolic rate and the overall cost of transport (summarised in Figure 54) (Weihs 1977; Iosilevskii & Papastamatiou 2016). Although the absolute metabolic cost of transport will increase with size as more energy is required to push more mass through a viscous fluid, the relative cost of swimming actually decreases for a variety of reasons (Weihs 1977; Iosilevskii & Papastamatiou 2016). Due to a lower surface area

to volume ratio, increased body size is associated with a lower relative metabolic rate per unit mass, along with lower relative drag and increased momentum (Weihs 1977; Peters 1986). Larger sharks also typically receive greater lift from their fins and body due to allometric scaling of morphology as they grow, and larger individuals of many species (including tiger sharks) possess comparatively larger livers than smaller conspecifics, meaning they are generally more buoyant and have to put less effort into maintaining depth (Baldrige 1970; Weihs 1977). In addition larger, thereby older, sharks have to invest less energy in somatic growth, contributing to a lower basal metabolic rate (Chapman *et al.* 2015). Combined this means that the relative energetic cost of transport decreases with increasing body size, such that for the same metabolic rate larger sharks are able to travel faster than smaller sharks, both within and between species (Iosilevskii & Papastamatiou 2016).

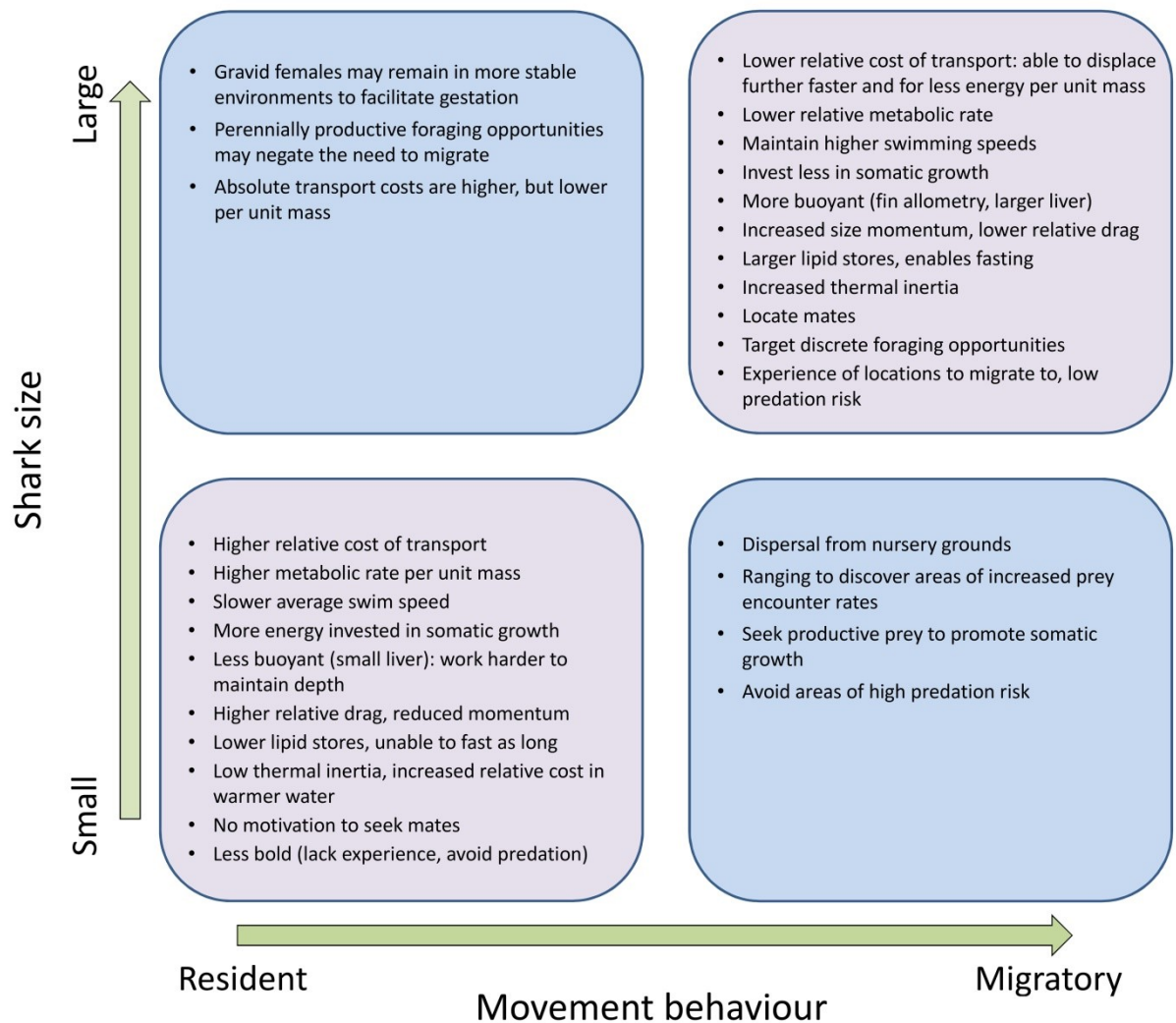


Figure 54: A summary of physiological factors and behavioural motivations that may determine whether sharks of differing size adopt a more resident or migratory habit.

Indeed, this pattern of maintaining greater speeds with larger body size is evident in the present work: plotting of average speed against total length for all sharks tracked across all chapters, from 0.77 m blacktip reef sharks to 3.96 m tiger sharks, reveals a significant increase in average speed with size ($R^2 = 0.58$, $F = 190$, $p < 0.001$; Figure 55). This reflects, for example, ontogenetic development of migratory behaviour in tiger sharks in Chapters 3 and 4, and adoption of long range dispersals by adult lemon sharks in Chapters 5 and 6. Being able to travel faster for less energy will intrinsically make it easier for larger sharks to undertake long distance migrations than it would be for smaller sharks. Moreover, it has been suggested that some sharks may fast during long distance dispersals and subsist on energy stores (Del Raye &

Jorgensen 2013), again making it an advantage to be larger when migrating due to the increased relative size of the liver. Given that most sharks are ectothermic (Compagno 2001), body size will also affect how quickly body temperature, and consequently metabolic rate, changes in relation to temperature gradients in the surrounding water (Peters 1986; Clarke & Johnston 1999). Due to a lower surface area to volume ratio, and subsequently increased thermal inertia, the body temperature and metabolic rate of larger sharks will change at lower rate than for smaller sharks faced with the same gradient (Mehner & Kasprzak 2011). Consequently if, for example, a migration involves occupying warmer water than residency, as it does for the Bermuda tiger sharks (Chapters 3 and 4), then larger individuals may pay a reduced metabolic cost versus smaller individuals.

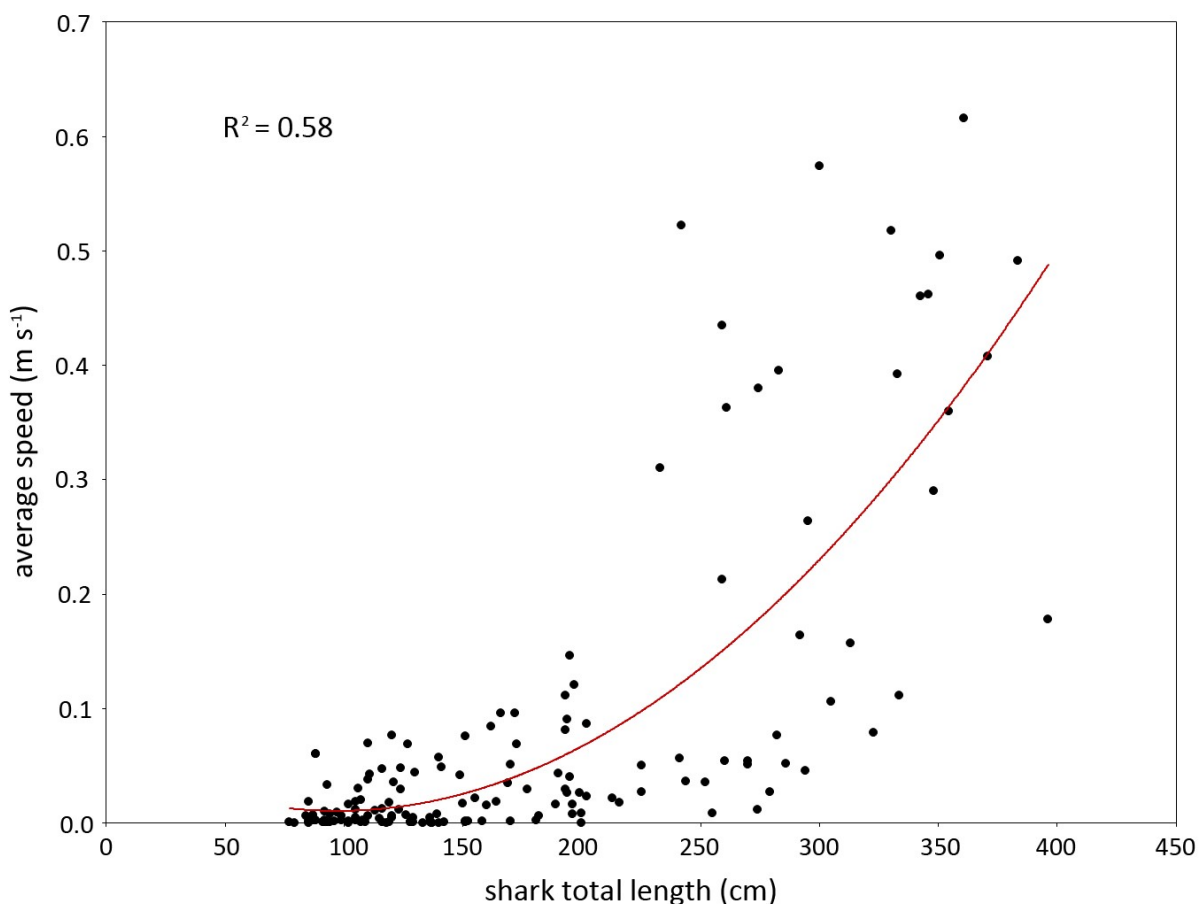


Figure 55: Scatter plot to show how average speed increases with shark total length ($n = 152$). The plot includes all sharks tracked for the thesis, apart from those detected at only one acoustic receiver, as well as some additional sharks tagged in Seychelles since the chapter analyses. Incremental polynomial regression was performed to reveal the best fit was a square function, shown in red: $y = 0.000005x^2 - 0.001x + 0.0611$.

In addition to contrasting ability to disperse and travel at speed, changes in body size may also confer different motivations and ability to forage. A significant implication of increased body size is maturation: reproduction provides additional incentives to move or not, such as finding mates, gestating and parturition. Reproduction is interesting as obviously only mature, large individuals reproduce, but it may promote both migration and residency, depending on the circumstances (Chapman *et al.* 2012, 2015). For instance, as suggested for tiger sharks in Chapter 3, individuals may migrate to find mates (often required as sexual segregation is very common in sharks (Wearmouth & Sims 2008)), but mature females may opt to switch between migration and residency depending on whether they are gravid or not (Papastamatiou *et al.* 2013). Gravid females may favour residency in warmer waters to increase metabolic rate and facilitate embryonic development, while also avoiding spending energy reserves on migration (Economakis & Lobel 1998; Papastamatiou *et al.* 2013). Size may also influence decisions to migrate based on ontogenetic shifts in diet – as sharks grow their extendable gape allows them to consume larger (and typically more calorific) prey (Wilga, Motta & Sanford 2007). Consequently larger sharks may migrate to target productive prey that smaller individuals may not be able to exploit, such as white sharks *Carcharodon carcharias* seasonally travelling to exploit naïve, young-of-the-year pinnipeds (Jorgensen *et al.* 2009). In contrast it has been suggested that in some locations where productive foraging opportunities are perennially available that otherwise migratory species may tend towards residency, such as tiger sharks remaining in the Chesterfield Islands, Australia (Werry *et al.* 2014). Given that larger sharks within a species will also be older, as well as having to invest less in somatic growth they will have a greater wealth of experience that may inform migration targets and promote subsequent migration based on memory of foraging success (Sims *et al.* 2006b; Papastamatiou *et al.* 2011).

This combination of intrinsic and extrinsic factors, governed by individual size, suggests that longer distance displacements may be more energetically efficient for larger individuals (both within and between species), perhaps contributing to increased prevalence of migratory behaviour in larger sharks (Figure 54).

9.6 Concluding Remarks and Future Work

This thesis has characterised the migratory behaviour and spatial dynamics of different shark species at contrasting geographical scales, in order to determine how spatio-temporal variation in movement behaviour might drive population distribution and dynamics. This is particularly important in the context of global declines in shark populations and the important ecological roles sharks fulfil as trophically well-connected predators. A detailed appreciation of movement behaviour is essential when evaluating the potential efficacy of proposed management strategies and how population distributions may change over time in response to both environmental perturbations and human disturbance.

To this end, the first portion of the thesis focused on elucidating the migration patterns of large tiger sharks encountered offshore in the northwest Atlantic – a species that has traditionally been assumed to be restricted to continental shelves. Application of satellite telemetry revealed previously unknown repeated, long-distance migrations between Caribbean reefs in winter and offshore areas of the Atlantic in summer, up to 3,500 km away (Lea *et al.* 2015b). Putative motivations behind these migrations are exploitation of productive offshore foraging areas in summer, followed by returning to tropical reefs to mate in winter. Where sharks spent more time, and performed more tortuous movements, was also strongly influenced by underwater topography, sea surface temperature, chlorophyll concentrations and thermal fronts. This is indicative of increased foraging activity in more productive areas

and suggests that tiger sharks may to some extent use particular environmental cues to direct their movements.

The revelation of such distinct, broad-scale migratory behaviour has significant management implications for this species: a considerable portion of the population spends the majority of their time exposed to fishing pressure in international waters due to their dispersed use of the high seas. While discrete units may be targeted with spatial management options (e.g. the sub-adults resident near Bermuda), the migratory adults may require imposition of size limits or time-area closures for their management to be effective. If such closures are applied, they may also need to be dynamic in time and space to accommodate for tiger sharks responding to environmental variation as climates change.

Further work is required to address a variety of different deficits in the current understanding to help further refine an appreciation of tiger shark population structure and migration behaviour. For instance, it would be informative to conduct further tracking work across a suite of locations and size classes, particularly targeting individuals that may bridge ontogenetic shifts in behaviour to test the proposed links between population subunits. It would also be useful to employ other biologging techniques, such as accelerometry or 'daily diary' tags, to determine how energy expenditure may change with body size, and identify behaviours such as mating or foraging at particular locations (Wilson, Shepard & Liebsch 2008; Gleiss *et al.* 2009). Conducting blood analysis and abdominal ultrasounds of migratory versus resident females could also help assess the proposed skipped breeding partial migration by revealing any correlations between migration and gestation. Comparing stable isotope signatures of shark body tissues to those of potential prey and regional isoscapes may also help reveal when and where foraging occurred in particular habitats, thereby helping test the proposed foraging targets of migration (McMahon, Hamady & Thorrold 2013). In addition,

further analysis of the tracks in relation to fishing vessel behaviour would be highly beneficial, and useful for determining quantitatively the dynamic overlap between sharks and vessels, allowing assessment of potential management strategies such as time-area closures.

At a much finer geographical scale, the latter part of the thesis characterised the fine-scale habitat selection patterns of reef sharks at a remote Indian Ocean atoll, revealing that in certain circumstances (focused, long-term, predictable use of particular locations) the application of spatial management options may prove particularly effective. Indeed, the demonstration of the high importance of lagoon habitats in the atoll to a variety of different species was in part used to justify the adoption of the D'Arros and St Joseph Special Reserve, highlighting how an appreciation of shark spatial dynamics can directly influence policy that enhances shark conservation measures (Lea *et al.* 2016). However, the MPA coverage was not exhaustive, with adults of some species displaying broader dispersals away from the atoll that will require incorporation of further management tools such as quotas and size limits to ensure the cycle of recruitment is not broken beyond the confines of the MPA.

However, there were a number of limitations with the present work that need to be addressed to ensure the observed shark populations are managed effectively as a whole, thereby maintaining their ecosystem functions. While blacktip reef sharks were reasonably represented, further tracking should aim to include more juveniles and mature males (at least 10–20 of each) to ensure their movements are incorporated into the MPA as expected. For lemon sharks, satellite telemetry and genetic analyses to determine population structuring and connectivity could be employed to evaluate the geographical scale over which the adults may truly range. This would allow formation of targeted management responses to their exploitation. Indeed, the local artisanal fisheries require detailed, quantitative monitoring to track changes in shark relative abundance and diversity in the fishery, although this is already

partly being addressed on Mahe (J. Nevill, pers. comms.). Genetic analyses could also be applied to blacktip reef and lemon shark populations in order to further investigate their breeding and mating behaviour, as well as estimating how many females may support the St Joseph atoll nursery.

The extent of grey reef shark ranging behaviour also needs to be characterised in full. Given the predicted broad use of the Amirantes plateau, perhaps a practical step would be to increase coverage of this habitat in the receiver array by deploying more receivers, combined with tagging efforts further afield and at different depths, in an attempt to track the underrepresented population units. Modifying fishing techniques should also help increase samples sizes of tawny nurse and silvertip sharks, as well as the elusive whitetip reef shark *Triaenodon obesus*. Tawny nurse sharks were often seen on the reefs but were rarely caught – a new capture method of hooking them underwater on SCUBA without bait may prove more effective, helping to address the small sample size and thus relatively poor representation here. Further exploratory fishing, including at deeper depths, is required to target other silvertip size classes, with satellite telemetry potentially worthwhile if any larger individuals are caught. Whitetip reef sharks continue to be seen in the study area, but have not yet been caught. Consequently future efforts should endeavour to target this species to determine its use of the D'Arros and St Joseph Special Reserve, with alternative capture methods already being explored (e.g. fish traps). Isotope analysis of each species in this multi-species assemblage, combined with characterising the isotopic landscape of potential prey, may also help determine how niche partitioning occurs between the sympatric reef shark species.

A variety of further work is already underway for the bull sharks in the area, now that a reliable capture technique has been developed. Ongoing tagging with both acoustic and satellite tags will be required to characterise the full nature of their apparent pupping

migrations and it would be beneficial to ultrasound tagged females to confirm whether they are gravid, which will be more reliable than the simple manual abdominal palpation used thus far. Exploratory surveys should also be conducted along the east Madagascan coast to verify the observed link, perhaps extending the array there to monitor potential pupping and nursery habitats. Genetic analysis of individuals both in Madagascar and Seychelles may help further clarify the degree of connectivity, and potentially provide direct evidence for parturition in Madagascar by the Seychelles females. In addition to isotope analyses, plans are already in place to fin-mount video cameras and accelerometers to help determine the foraging behaviour of the bull sharks.

All of this will help better frame the scales at which management strategies should be adopted, and the types of management tools that should be applied. Another aspect of particularly important further work that is already underway is comprehensive, long-term survey work of shark, reef fish and coral relative abundance and diversity around D'Arros and St Joseph, both inside and outside the MPA as well as before and after its implementation, in order to document whatever impact the MPA may have on the local fish assemblages and marine ecosystem over time.

Overall, the present work provides novel insights to shark migratory behaviour and spatial dynamics that have significant management implications that can, and have, helped target conservation initiatives. Yet many important questions remain unanswered that can only be addressed through ongoing, expanded effort that strives towards the comprehensive, multi-faceted understanding of shark population ecology and dynamics required to truly appreciate their ecological significance and manage their populations sustainably.

References

- Abascal, F.J., Quintans, M., Ramos-Cartelle, A. & Mejuto, J. (2011) Movements and environmental preferences of the shortfin mako, *Isurus oxyrinchus*, in the southeastern Pacific Ocean. *Marine Biology*, **158**, 1175–1184.
- Afonso, A.S. & Hazin, F.H.V. (2014) Post-release survival and behavior and exposure to fisheries in juvenile tiger sharks, *Galeocerdo cuvier*, from the South Atlantic. *Journal of Experimental Marine Biology and Ecology*, **454**, 55–62.
- Allen, A.M. & Singh, N. (2016) Linking movement ecology with wildlife management and conservation. *Frontiers in Ecology and Evolution*, **3**, 155.
- Anderson, R.C. & Ahmed, H. (1993) The shark fisheries of the Maldives. *FAO, Rome, and Ministry of Fisheries, Male, Maldives*.
- Andrews, K.S., Williams, G.D., Farrer, D., Tolimieri, N., Harvey, C.J., Bargmann, G. & Levin, P.S. (2009) Diel activity patterns of sixgill sharks, *Hexanchus griseus*: the ups and downs of an apex predator. *Animal Behaviour*, **78**, 525–536.
- Anon. (2012) *National Parks and Nature Conservancy Act*. Ministry of Environment, Energy and Climate Change, Victoria, Seychelles.
- Baldrige, H.D. (1970) Sinking factors and average densities of Florida sharks as function of liver buoyancy. *Copeia*, **1970**, 744–754.
- Barnett, A., Abrantes, K.G., Seymour, J. & Fitzpatrick, R. (2012) Residency and spatial use by reef sharks of an isolated seamount and its implications for conservation. *PLoS ONE*, **7**, e36574.
- Barnett, A., Payne, N.L., Semmens, J.M. & Fitzpatrick, R. (2016) Ecotourism

- increases the field metabolic rate of whitetip reef sharks. *Biological Conservation*, **199**, 132–136.
- Bascompte, J., Melián, C.J. & Sala, E. (2005) Interaction strength combinations and the overfishing of a marine food web. *Proceedings of the National Academy of Sciences*, **102**, 5443–5447.
- Baum, J.K. & Blanchard, W. (2010) Inferring shark population trends from generalized linear mixed models of pelagic longline catch and effort data. *Fisheries Research*, **102**, 229–239.
- Baum, J.K. & Myers, R.A. (2004) Shifting baselines and the decline of pelagic sharks in the Gulf of Mexico. *Ecology Letters*, **7**, 135–145.
- Baum, J.K., Myers, R.A., Kehler, D.G., Worm, B., Harley, S.J. & Doherty, P.A. (2003) Collapse and conservation of shark populations in the Northwest Atlantic. *Science*, **299**, 389–392.
- Belo, A.F., Pereira, T.J., Quintella, B.R., Castro, N., Costa, J.L. & de Almeida, P.R. (2016) Movements of *Diplodus sargus* (Sparidae) within a Portuguese coastal marine protected area: are they really protected? *Marine Environmental Research*, **114**, 80–94.
- Beschta, R.L. & Ripple, W.J. (2009) Large predators and trophic cascades in terrestrial ecosystems of the western United States. *Biological Conservation*, **142**, 2401–2414.
- Bestley, S., Patterson, T.A., Hindell, M.A. & Gunn, J.S. (2010) Predicting feeding success in a migratory predator: integrating telemetry, environment, and modeling techniques. *Ecology*, **91**, 2373–2384.
- Beyer, H.L. (2011) Geospatial modelling environment. *Spatial Ecology*. Available at www.spatial ecology.com/gme.

- Birkeland, C. & Dayton, P.K. (2005) The importance in fishery management of leaving the big ones. *Trends in Ecology & Evolution*, **20**, 356–358.
- Block, B.A., Jonsen, I.D., Jorgensen, S.J., Winship, A.J., Shaffer, S.A., Bograd, S.J., Hazen, E.L., Foley, D.G., Breed, G.A., Harrison, A.-L., Ganong, J.E., Swithenbank, A., Castleton, M., Dewar, H., Mate, B.R., Shillinger, G.L., Schaefer, K.M., Benson, S.R., Weise, M.J., Henry, R.W. & Costa, D.P. (2011) Tracking apex marine predator movements in a dynamic ocean. *Nature*, **475**, 86–90.
- Bond, M.E., Babcock, E.A., Pikitch, E.K., Abercrombie, D.L., Lamb, N.F. & Chapman, D.D. (2012) Reef sharks exhibit site-fidelity and higher relative abundance in marine reserves on the Mesoamerican Barrier Reef. *PLoS ONE*, **7**, e32983.
- Bond, M.E., Tolentino, E., Mangubhai, S. & Howey, L.A. (2015) Vertical and horizontal movements of a silvertip shark (*Carcharhinus albimarginatus*) in the Fijian archipelago. *Animal Biotelemetry*, **3**.
- Bonfil, R., Meÿer, M., Scholl, M.C., Johnson, R., O'Brien, S., Oosthuizen, H., Swanson, S., Kotze, D. & Paterson, M. (2005) Transoceanic migration, spatial dynamics, and population linkages of white sharks. *Science*, **310**, 100–103.
- Von Brandis, R. (2011) *The Foraging Ecology of Hawksbill Turtles at D'Arros Island, Republic of Seychelles*. Doctoral Thesis, Department of Nature Conservation, Faculty of Natural Science, Tshwane.
- Von Brandis, R.G., Mortimer, J.A. & Reilly, B.K. (2010) In-water observations of the diving behaviour of immature hawksbill turtles, *Eretmochelys imbricata*, on a coral reef at D'Arros Island, Republic of Seychelles. *Chelonian Conservation and Biology*, **9**, 26–32.

- Branstetter, S., Musick, J. & Colvocoresses, J. (1987) A comparison of the age and growth of the tiger shark, *Galeocerdo cuvier*, from off Virginia and from the northern Gulf of Mexico. *Fishery Bulletin*, **85**, 269–279.
- Brena, P.F., Mourier, J., Planes, S. & Clua, E. (2015) Shark and ray provisioning: functional insights into behavioral, ecological and physiological responses across multiple scales. *Marine Ecology Progress Series*, **538**, 273–283.
- Brodersen, J., Nilsson, P.A., Hansson, L.-A., Skov, C. & Brönmark, C. (2008) Condition-dependent individual decision-making determines cyprinid partial migration. *Ecology*, **89**, 1195–1200.
- Brooks, E.J., Sloman, K.A., Liss, S., Hassan-Hassanein, L., Danylchuk, A.J., Cooke, S.J., Mandelman, J.W., Skomal, G.B., Sims, D.W. & Suski, C.D. (2011) The stress physiology of extended duration tonic immobility in the juvenile lemon shark, *Negaprion brevirostris* (Poey 1868). *Journal of Experimental Marine Biology and Ecology*, **409**, 351–360.
- Brown, J.S. (1999) Vigilance, patch use and habitat selection: foraging under predation risk. *Evolutionary Ecology Research*, **1**, 49–71.
- Brown, C.J., White, C., Beger, M., Grantham, H.S., Halpern, B.S., Klein, C.J., Mumby, P.J., Tulloch, V.J., Ruckelshaus, M. & Possingham, H.P. (2015) Fisheries and biodiversity benefits of using static versus dynamic models for designing marine reserve networks. *Ecosphere*, **6**, 1–14.
- Brunnschweiler, J.M. & Baensch, H. (2011) Seasonal and long-term changes in relative abundance of bull sharks from a tourist shark feeding site in Fiji. *PLoS ONE*, **6**, e16597.
- Brunnschweiler, J.M., Queiroz, N. & Sims, D.W. (2010) Oceans apart?: Short-term movements and behaviour of adult bull sharks *Carcharhinus leucas* in

- Atlantic and Pacific Oceans determined from pop-off satellite archival tagging. *Journal of Fish Biology*, **77**, 1343–1358.
- Burgess, G.H., Beerkircher, L.R., Cailliet, G.M., Carlson, J.K., Cortés, E., Goldman, K.J., Grubbs, R.D., Musick, J.A., Musyl, M.K. & Simpfendorfer, C.A. (2005) Is the collapse of shark populations in the Northwest Atlantic Ocean and Gulf of Mexico real? *Fisheries*, **30**, 19–26.
- Camhi, M.D., Valenti, S.V., Fordham, S.V., Fowler, S.L. & Gibson, C. (2009) The conservation status of pelagic sharks and rays: Report of the IUCN shark specialist group pelagic shark red list workshop. *IUCN Species Survival Commission Shark Specialist Group, Newbury, UK*.
- Campana, S.E., Joyce, W. & Fowler, M. (2010) Subtropical pupping ground for a cold-water shark. *Canadian Journal of Fisheries and Aquatic Sciences*, **67**, 769–773.
- Carey, F.G., Scharold, J.V., Kalmijn, A.J. (1990) Movements of blue sharks (*Prionace glauca*) in depth and course. *Marine Biology*, **106**, 329–342.
- Carlisle, A.B. & Starr, R.M. (2009) Habitat use, residency, and seasonal distribution of female leopard sharks *Triakis semifasciata* in Elkhorn Slough, California. *Marine Ecology Progress Series*, **380**, 213–228.
- Carlisle, A.B. & Starr, R.M. (2010) Tidal movements of female leopard sharks (*Triakis semifasciata*) in Elkhorn Slough, California. *Environmental Biology of Fishes*, **89**, 31–45.
- Carlson, J.K., Ribera, M.M., Conrath, C.L., Heupel, M.R. & Burgess, G.H. (2010) Habitat use and movement patterns of bull sharks *Carcharhinus leucas* determined using pop-up satellite archival tags. *Journal of Fish Biology*, **77**, 661–675.

- Carrier, J.C., Pratt Jr, H.L. & Martin, L.K. (1994) Group reproductive behaviors in free-living nurse sharks, *Ginglymostoma cirratum*. *Copeia*, **1994**, 646–656.
- Cartamil, D., Wegner, N.C., Aalbers, S., Sepulveda, C.A., Baquero, A. & Graham, J.B. (2010) Diel movement patterns and habitat preferences of the common thresher shark (*Alopias vulpinus*) in the Southern California Bight. *Marine and Freshwater Research*, **61**, 596–596.
- Carwardine, M. & Watterson, K. (2002) *The Shark Watcher's Handbook: A Guide to Sharks and Where to See Them*. BBC Worldwide, UK.
- Chapman, D.D., Babcock, E.A., Gruber, S.H., Dibattista, J.D., Franks, B.R., Kessel, S.A., Guttridge, T., Pikitch, E.K. & Feldheim, K.A. (2009a) Long-term natal site-fidelity by immature lemon sharks (*Negaprion brevirostris*) at a subtropical island. *Molecular Ecology*, **18**, 3500–3507.
- Chapman, B.B., Brönmark, C., Nilsson, J.-Å. & Hansson, L.-A. (2011) The ecology and evolution of partial migration. *Oikos*, 1764–1775.
- Chapman, D.D., Feldheim, K., Papastamatiou, Y. & Hueter, R.E. (2015) There and back again: a review of residency and return migrations in sharks, with implications for population structure and management. *Annual Review of Marine Science*, **7**, 547–570.
- Chapman, B.B., Hulthén, K., Brodersen, J., Nilsson, P.A., Skov, C., Hansson, L.-A. & Brönmark, C. (2012a) Partial migration in fishes: causes and consequences. *Journal of Fish Biology*, **81**, 456–478.
- Chapman, B.B., Hulthén, K., Brodersen, J., Nilsson, P.A., Skov, C., Hansson, L.-A. & Brönmark, C. (2012b) Partial migration in fishes: causes and consequences. *Journal of Fish Biology*, **81**, 456–478.
- Chapman, D.D., Pikitch, E.K., Babcock, E. & Shivji, M.S. (2005) Marine reserve

- design and evaluation using automated acoustic telemetry: a case-study involving coral reef-associated sharks in the Mesoamerican Caribbean. *Marine Technology Society Journal*, **39**, 42–55.
- Chapman, D.D., Pinhal, D. & Shivji, M.S. (2009b) Tracking the fin trade: genetic stock identification in western Atlantic scalloped hammerhead sharks *Sphyrna lewini*. *Endangered Species Research*, 221–228.
- Cheung, W.W., Lam, V.W., Sarmiento, J.L., Kearney, K., Watson, R. & Pauly, D. (2009) Projecting global marine biodiversity impacts under climate change scenarios. *Fish and Fisheries*, **10**, 235–251.
- Chin, A., Heupel, M.R., Simpfendorfer, C.A. & Tobin, A.J. (2016) Population organisation in reef sharks: new variations in coastal habitat use by mobile marine predators. *Marine Ecology Progress Series*, **544**, 197–211.
- Chin, A., Tobin, A.J., Heupel, M.R. & Simpfendorfer, C.A. (2013) Population structure and residency patterns of the blacktip reef shark *Carcharhinus melanopterus* in turbid coastal environments. *Journal of Fish Biology*, **82**, 1192–1210.
- Clarke, A., Johnston, N.M. (1999) Scaling of metabolic rate with body mass and temperature in teleost fish. *Journal of Animal Ecology*, **68**, 893–905.
- Clarke, S.C., Harley, S.J., Hoyle, S.D. & Rice, J.S. (2013) Population trends in Pacific Oceanic sharks and the utility of regulations on shark finning. *Conservation Biology*, **27**, 197–209.
- Clarke, C.R., Karl, S.A., Horn, R.L., Bernard, A.M., Lea, J.S., Hazin, F.H., Prodöhl, P.A. & Shivji, M.S. (2015) Global mitochondrial DNA phylogeography and population structure of the silky shark, *Carcharhinus falciformis*. *Marine Biology*, **162**, 945–955.

- Clarke, C., Lea, J.S.E. & Ormond, R.F.G. (2011) Reef-use and residency patterns of a baited population of silky sharks, *Carcharhinus falciformis*, in the Red Sea. *Marine and Freshwater Research*, **62**, 668–675.
- Clarke, C., Lea, J. & Ormond, R. (2012) Comparative abundance of reef sharks in the Western Indian Ocean. *Proceedings of the 12th International Coral Reef Symposium*, Cairns, Australia pp. 9–13.
- Clarke, C.R., Lea, J.S.E. & Ormond, R.F.G. (2013) Changing relative abundance and behaviour of silky and grey reef sharks baited over 12 years on a Red Sea reef. *Marine and Freshwater Research*, **64**, 909–919.
- Clarke, S.C., McAllister, M.K., Milner-Gulland, E.J., Kirkwood, G.P., Michielsens, C.G.J., Agnew, D.J., Pikitch, E.K., Nakano, H. & Shivji, M.S. (2006) Global estimates of shark catches using trade records from commercial markets. *Ecology Letters*, **9**, 1115–1126.
- Clarke, S., Milner-Gulland, E.J. & Bjørndal, T. (2007) Social, economic, and regulatory drivers of the shark fin trade. *Marine Resource Economics*, **22**, 305–327.
- Cline, W. (2008) Shark diving overview for the islands of the Bahamas. *Economic report prepared for the Bahamas Dive Association and the Ministry of Tourism*. p, **36**.
- Clua, E., Buray, N., Legendre, P., Mourier, J. & Planes, S. (2010) Behavioural response of sicklefin lemon sharks *Negaprion acutidens* to underwater feeding for ecotourism purposes. *Marine Ecology Progress Series*, **414**, 257–266.
- Clua, E., Buray, N., Legendre, P., Mourier, J. & Planes, S. (2011) Business partner or simple catch? The economic value of the sicklefin lemon shark in French Polynesia. *Marine and Freshwater Research*, **62**, 764–770.

- Cobb, K.M., Charles, C.D., Cheng, H. & Edwards, R.L. (2003) El Niño/Southern Oscillation and tropical Pacific climate during the last millennium. *Nature*, **424**, 271–276.
- Compagno, L.J. (2001) *Sharks of the World: An Annotated and Illustrated Catalogue of Shark Species Known to Date*. Food & Agriculture Org., Rome.
- Cooke, S.J. & Suski, C.D. (2004) Are circle hooks an effective tool for conserving marine and freshwater recreational catch-and-release fisheries? *Aquatic Conservation: Marine and Freshwater Ecosystems*, **14**, 299–326.
- Cortés, E. (1999) Standardized diet compositions and trophic levels of sharks. *ICES Journal of Marine Science: Journal du Conseil*, **56**, 707–717.
- Cortés, E., Domingo, A., Miller, P., Forselledo, R., Mas, F., Arocha, F., Campana, S., Coelho, R., Da Silva, C. & Hazin, F.H.V. (2015) Expanded ecological risk assessment of pelagic sharks caught in Atlantic pelagic longline fisheries. *Collective Volume of Scientific Papers ICCAT*, **71**, 2637–2688.
- Costello, M.J. & Ballantine, B. (2015) Biodiversity conservation should focus on no-take Marine Reserves: 94% of Marine Protected Areas allow fishing. *Trends in Ecology & Evolution*, **30**, 507–509.
- Daly, R., Smale, M.J., Cowley, P.D., Froneman, P.W. (2014) Residency patterns and migrations dynamics of adult bull sharks (*Carcharhinus leucas*) on the east coast of Southern Africa. *PLoS ONE*, **9**, e109357.
- De la Cruz Modino, R., Esteban, A., Crilly, R. & Pascual-Fernandez, J. (2010) Bucear con tiburones y rayas en España. *Análisis de su potencial en España y en las Islas Canarias.*, Instituto Universitario de Ciencias Políticas y Sociales NEF-The New Economics Foundation, 8–16.
- Davis, D., Banks, S., Birtles, A., Valentine, P. & Cuthill, M. (1997) Whale sharks in

- Ningaloo Marine Park: managing tourism in an Australian marine protected area. *Tourism Management*, **18**, 259–271.
- Del Raye, G., Jorgensen, S.J. (2013) Travelling light: white sharks (*Carcharodon carcharias*) rely on lipid stores to power ocean-basin scale migration. *Proceedings of the Royal Society B: Biological Sciences*, **280**, 21030836.
- Díaz, S., Fargione, J., Chapin, F.S. & Tilman, D. (2006) Biodiversity loss threatens human well-being. *PLoS Biology*, **4**, 1300–1305.
- Dicken, M.L. & Hosking, S.G. (2009) Socio-economic aspects of the tiger shark diving industry within the Aliwal Shoal Marine Protected Area, South Africa. *African Journal of Marine Science*, **31**, 227–232.
- Dingle, H. & Drake, V.A. (2007) What is migration? *Bioscience*, **57**, 113–121.
- Domeier, M.L. & Nasby-Lucas, N. (2013) Two-year migration of adult female white sharks (*Carcharodon carcharias*) reveals widely separated nursery areas and conservation concerns. *Animal Biotelemetry*, **1**, 1–10.
- Domingo, A., Coelho, R., Cortes, E., Garcia-Cortes, B., Mas, F., Mejuto, J., Miller, P., Ramos-Cartelle, A., Santos, M.N. & Yokawa, K. (2016) Is the tiger shark *Galeocerdo cuvier* a coastal species?: Expanding its distribution range in the Atlantic Ocean using at-sea observer data. *Journal of Fish Biology*, **88**, 1223–1228.
- Driggers III, W.B., Ingram Jr, G.W., Grace, M.A., Gledhill, C.T., Henwood, T.A., Horton, C.N. & Jones, C.M. (2008) Pupping areas and mortality rates of young tiger sharks *Galeocerdo cuvier* in the western North Atlantic Ocean. *Aquatic Biology*, **2**, 161–170.
- Dulvy, N.K., Baum, J.K., Clarke, S., Compagno, L.J., Cortes, E., Domingo, A., Fordham, S., Fowler, S., Francis, M.P. & Gibson, C. (2008) You can swim but

you can't hide: the global status and conservation of oceanic pelagic sharks and rays. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **18**, 459–482.

Dulvy, N.K., Fowler, S.L., Musick, J.A., Cavanagh, R.D., Kyne, P.M., Harrison, L.R., Carlson, J.K., Davidson, L.N., Fordham, S.V., Francis, M.P., Pollock, C.M., Simpfendorfer, C.A., Burgess, G.H., Carpenter, K.E., Compagno, L.J., Ebert, D.A., Gibson, C., Heupel, M.R., Livingstone, S.R., Sanciangco, J.C., Stevens, J.D., Valenti, S. & White, W.T. (2014) Extinction risk and conservation of the world's sharks and rays. *eLife*, **3**.

Dulvy, N.K., Freckleton, R.P. & Polunin, N.V. (2004) Coral reef cascades and the indirect effects of predator removal by exploitation. *Ecology Letters*, **7**, 410–416.

Duncan, K.M., Martin, A.P., Bowen, B.W. & De Couet, H.G. (2006) Global phylogeography of the scalloped hammerhead shark (*Sphyrna lewini*). *Molecular Ecology*, **15**, 2239–2251.

Eckert, S.A. & Stewart, B.S. (2001) Telemetry and satellite tracking of whale sharks, *Rhincodon typus*, in the Sea of Cortez, Mexico, and the north Pacific Ocean. *Environmental Biology of Fishes*, **60**, 299–308.

Economakis, A.E. & Lobel, P.S. (1998) Aggregation behavior of the grey reef shark, *Carcharhinus amblyrhynchos*, at Johnston Atoll, Central Pacific Ocean. *Environmental Biology of Fishes*, **51**, 129–139.

Edgar, G.J., Stuart-Smith, R.D., Willis, T.J., Kininmonth, S., Baker, S.C., Banks, S., Barrett, N.S., Becerro, M.A., Bernard, A.T.F., Berkhout, J., Buxton, C.D., Campbell, S.J., Cooper, A.T., Davey, M., Edgar, S.C., Försterra, G., Galván, D.E., Irigoyen, A.J., Kushner, D.J., Moura, R., Parnell, P.E., Shears, N.T.,

- Soler, G., Strain, E.M.A. & Thomson, R.J. (2014) Global conservation outcomes depend on marine protected areas with five key features. *Nature*, **506**, 216–220.
- Edwards, M. & Richardson, A.J. (2004) Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature*, **430**, 881–884.
- Egbert, G. & Erofeeva, S. (2002) Efficient inverse modeling of barotropic ocean tides. *Journal of Atmospheric and Oceanic Technology*, **19**, 183–204.
- Ellis, J., Farrell, E., Jung, A., McCully, S., Sims, D. & Soldo, A. (2016) *Lamna nasus*. The IUCN Red List of Threatened Species 2016.
- Van der Elst, R., Everett, B., Jiddawi, N., Mwatha, G., Afonso, P.S. & Boulle, D. (2005) Fish, fishers and fisheries of the Western Indian Ocean: their diversity and status. A preliminary assessment. *Philosophical Transactions of the Royal Society of London A: Mathematical, Physical and Engineering Sciences*, **363**, 263–284.
- Emery, S.H. (1986) Hematological comparisons of endothermic vs ectothermic elasmobranch fishes. *Copeia*, 700–705.
- Espinoza, M., Heupel, M.R., Tobin, A.J. & Simpfendorfer, C.A. (2015a) Movement patterns of silvertip sharks (*Carcharhinus albimarginatus*) on coral reefs. *Coral Reefs*, **34**, 807–821.
- Espinoza, M., Heupel, M.R., Tobin, A.J. & Simpfendorfer, C.A. (2015b) Residency patterns and movements of grey reef sharks (*Carcharhinus amblyrhynchos*) in semi-isolated coral reef habitats. *Marine Biology*, **162**, 343–358.
- Espinoza, M., Lédée, E.J., Simpfendorfer, C.A., Tobin, A.J. & Heupel, M.R. (2015c) Contrasting movements and connectivity of reef-associated sharks using acoustic telemetry: implications for management. *Ecological Applications*, **25**,

2101–2118.

Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J., Carpenter, S.R., Essington, T.E., Holt, R.D., Jackson, J.B.C., Marquis, R.J., Oksanen, L., Oksanen, T., Paine, R.T., Pikitch, E.K., Ripple, W.J., Sandin, S.A., Scheffer, M., Schoener, T.W., Shurin, J.B., Sinclair, A.R.E., Soule, M.E., Virtanen, R. & Wardle, D.A. (2011) Trophic downgrading of planet Earth. *Science*, **333**, 301–306.

Estes, J.A., Tinker, M.T., Williams, T.M. & Doak, D.F. (1998) Killer whale predation on sea otters linking oceanic and nearshore ecosystems. *Science*, **282**, 473–476.

Feldheim, K.A., Gruber, S.H. & Ashley, M.V. (2002) The breeding biology of lemon sharks at a tropical nursery lagoon. *Proceedings of the Royal Society of London B: Biological Sciences*, **269**, 1655–1661.

Feldheim, K.A., Gruber, S.H., Dibattista, J.D., Babcock, E.A., Kessel, S.T., Hendry, A.P., Pikitch, E.K., Ashley, M.V. & Chapman, D.D. (2014) Two decades of genetic profiling yields first evidence of natal philopatry and long-term fidelity to parturition sites in sharks. *Molecular Ecology*, **23**, 110–117.

Ferreira, L.C., Thums, M., Meeuwig, J.J., Vianna, G.M., Stevens, J., McAuley, R. & Meekan, M.G. (2015) Crossing latitudes—long-distance tracking of an apex predator. *PLoS ONE*, **10**, e0116916.

Ferretti, F., Myers, R.A., Serena, F. & Lotze, H.K. (2008) Loss of large predatory sharks from the Mediterranean Sea. *Conservation Biology*, **22**, 952–964.

Ferretti, F., Worm, B., Britten, G.L., Heithaus, M.R. & Lotze, H.K. (2010) Patterns and ecosystem consequences of shark declines in the ocean. *Ecology Letters*, **13**, 1055–1071.

- Field, I.C., Meekan, M.G., Buckworth, R.C. & Bradshaw, C.J. (2009) Susceptibility of sharks, rays and chimaeras to global extinction. *Advances in Marine Biology*, **56**, 275–363.
- Field, I.C., Meekan, M.G., Speed, C.W., White, W. & Bradshaw, C.J.A. (2011) Quantifying movement patterns for shark conservation at remote coral atolls in the Indian Ocean. *Coral Reefs*, **30**, 61–71.
- Filmalter, J.D., Dagorn, L. & Cowley, P.D. (2013) Spatial behaviour and site fidelity of the sicklefin lemon shark *Negaprion acutidens* in a remote Indian Ocean atoll. *Marine Biology*, **160**, 2425–2436.
- Fitzpatrick, R., Abrantes, K.G., Seymour, J. & Barnett, A. (2011) Variation in depth of whitetip reef sharks: does provisioning ecotourism change their behaviour? *Coral Reefs*, **30**, 569–577.
- Ford, E. (1921) A contribution to our knowledge of the life-histories of the dogfishes landed at Plymouth. *Journal of the Marine Biological Association of the United Kingdom*, **12**, 468–505.
- Frank, K.T., Petrie, B., Choi, J.S. & Leggett, W.C. (2005) Trophic cascades in a formerly cod-dominated ecosystem. *Science*, **308**, 1621–1623.
- Freitas, R.H.A. de, Rosa, R.S., Wetherbee, B.M. & Gruber, S.H. (2009) Population size and survivorship for juvenile lemon sharks (*Negaprion brevirostris*) on their nursery grounds at a marine protected area in Brazil. *Neotropical Ichthyology*, **7**, 205–212.
- Frisk, M.G., Miller, T.J. & Dulvy, N.K. (2005) Life histories and vulnerability to exploitation of elasmobranchs: inferences from elasticity, perturbation and phylogenetic analyses. *Journal of Northwest Atlantic Fishery Science*, **35**, 27–45.

- Fu, A.L., Hammerschlag, N., Lauder, G.V., Wilga, C.D., Kuo, C. & Irschick, D.J. (2016) Ontogeny of head and caudal fin shape of an apex marine predator: The tiger shark (*Galeocerdo cuvier*). *Journal of Morphology*, **277**, 556–564.
- Gallagher, A.J. & Hammerschlag, N. (2011) Global shark currency: the distribution, frequency, and economic value of shark ecotourism. *Current Issues in Tourism*, **14**, 797–812.
- Gallagher, A.J., Serafy, J.E., Cooke, S.J. & Hammerschlag, N. (2014) Physiological stress response, reflex impairment, and survival of five sympatric shark species following experimental capture and release. *Marine Ecology Progress Series*, **496**, 207–218.
- Gallucci, V.F., Taylor, I.G. & Erzini, K. (2006) Conservation and management of exploited shark populations based on reproductive value. *Canadian Journal of Fisheries and Aquatic Sciences*, **63**, 931–942.
- Game, E.T., Grantham, H.S., Hobday, A.J., Pressey, R.L., Lombard, A.T., Beckley, L.E., Gjerde, K., Bustamante, R., Possingham, H.P. & Richardson, A.J. (2009) Pelagic protected areas: the missing dimension in ocean conservation. *Trends in Ecology and Evolution*, **24**, 360–369.
- Gifford, A., Compagno, L.J., Levine, M. & Antoniou, A. (2007) Satellite tracking of whale sharks using tethered tags. *Fisheries Research*, **84**, 17–24.
- Gjelland, K.Ø. & Hedger, R.D. (2013) Environmental influence on transmitter detection probability in biotelemetry: developing a general model of acoustic transmission. *Methods in Ecology and Evolution*, **4**, 665–674.
- Gleiss, A.C., Norman, B., Liebsch, N., Francis, C. & Wilson, R.P. (2009) A new prospect for tagging large free-swimming sharks with motion-sensitive dataloggers. *Fisheries Research*, **97**, 11–16.

- Goldman, K.J. & Anderson, S.D. (1999) Space utilization and swimming depth of white sharks, *Carcharodon carcharias*, at the South Farallon Islands, central California. *Environmental Biology of Fishes*, **56**, 351–364.
- González-Solís, J., Croxall, J.P., Oro, D. & Ruiz, X. (2007) Trans-equatorial migration and mixing in the wintering areas of a pelagic seabird. *Frontiers in Ecology and the Environment*, **5**, 297–301.
- Gore, M.A., Rowat, D., Hall, J., Gell, F.R. & Ormond, R.F. (2008) Transatlantic migration and deep mid-ocean diving by basking shark. *Biology Letters*, **4**, 395–398.
- Graham, R.T., Roberts, C.M. & Smart, J.C. (2006) Diving behaviour of whale sharks in relation to a predictable food pulse. *Journal of the Royal Society Interface*, **3**, 109–116.
- Graham, F., Rynne, P., Estevanez, M., Luo, J., Ault, J.S. & Hammerschlag, N. (2016) Use of marine protected areas and exclusive economic zones in the subtropical western North Atlantic Ocean by large highly mobile sharks. *Diversity and Distributions*, **22**, 534–546.
- Graham, N.A., Spalding, M.D. & Sheppard, C.R. (2010) Reef shark declines in remote atolls highlight the need for multi-faceted conservation action. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **20**, 543–548.
- Griffiths, A.M., Sims, D.W., Cotterell, S.P., El Nagar, A., Ellis, J.R., Lynghammar, A., McHugh, M., Neat, F.C., Pade, N.G. & Queiroz, N. (2010) Molecular markers reveal spatially segregated cryptic species in a critically endangered fish, the common skate (*Dipturus batis*). *Proceedings of the Royal Society of London B: Biological Sciences*, rspb20092111.
- Grubbs, R.D., Carlson, J.K., Romine, J.G., Curtis, T.H., McElroy, W.D., McCandless,

- C.T., Cotton, C.F. & Musick, J.A. (2016) Critical assessment and ramifications of a purported marine trophic cascade. *Scientific Reports*, **6**.
- Gruber, S.H. & Myrberg, A.A. (1977) Approaches to the study of the behavior of sharks. *American Zoologist*, **17**, 471–486.
- Gurarie, E., Andrews, R.D. & Laidre, K.L. (2009) A novel method for identifying behavioural changes in animal movement data. *Ecology Letters*, **12**, 395–408.
- Gurshin, C.W. & Szedlmayer, S.T. (2004) Short-term survival and movements of Atlantic sharpnose sharks captured by hook-and-line in the north-east Gulf of Mexico. *Journal of Fish Biology*, **65**, 973–986.
- Guttridge, T.L., Gruber, S.H., Franks, B.R., Kessel, S.T., Gledhill, K.S., Uphill, J., Krause, J. & Sims, D.W. (2011) Deep danger: intra-specific predation risk influences habitat use and aggregation formation of juvenile lemon sharks *Negaprion brevirostris*. *Marine Ecology Progress Series*, **445**, 279–291.
- Guttridge, T.L., Myrberg, A.A., Porcher, I.F., Sims, D.W. & Krause, J. (2009) The role of learning in shark behaviour. *Fish and Fisheries*, **10**, 450–469.
- Guzner, B., Novplansky, A., Shalit, O. & Chadwick, N.E. (2010) Indirect impacts of recreational scuba diving: patterns of growth and predation in branching stony corals. *Bulletin of Marine Science*, **86**, 727–742.
- Hammerschlag, N., Gallagher, A.J. & Lazarre, D.M. (2011) A review of shark satellite tagging studies. *Journal of Experimental Marine Biology and Ecology*, **398**, 1–8.
- Hammerschlag, N., Gallagher, A.J., Wester, J., Luo, J. & Ault, J.S. (2012a) Don't bite the hand that feeds: assessing ecological impacts of provisioning ecotourism on an apex marine predator. *Functional Ecology*, **26**, 567–576.
- Hammerschlag, N., Luo, J., Irschick, D.J. & Ault, J.S. (2012b) A comparison of

- spatial and movement patterns between sympatric predators: bull sharks (*Carcharhinus leucas*) and atlantic tarpon (*Megalops atlanticus*). *PLoS ONE*, **7**, e45958.
- Hansen, A.J., Rotella, J.J., Kraska, M.P.V. & Brown, D. (1999) Dynamic habitat and population analysis: an approach to resolve the biodiversity manager's dilemma. *Ecological Applications*, **9**, 1459–1476.
- Hara, M., Maharaj, I. & Pithers, L. (2003) Marine-based tourism in Gansbaai: A socio-economic study. *Final report for the Department of Environmental Affairs and Tourism (DEAT), South Africa. 55pp.*
- Hawkes, L.A., Witt, M.J., Broderick, A.C., Coker, J.W., Coyne, M.S., Dodd, M., Frick, M.G., Godfrey, M.H., Griffin, D.B., Murphy, S.R., Murphy, T.M., Williams, K.L. & Godley, B.J. (2011) Home on the range: spatial ecology of loggerhead turtles in Atlantic waters of the USA. *Diversity and Distributions*, **17**, 624–640.
- Hays, G.C., Åkesson, S., Godley, B.J., Luschi, P. & Santidrian, P. (2001) The implications of location accuracy for the interpretation of satellite-tracking data. *Animal Behaviour*, **61**, 1035–1040.
- Hays, G.C., Hobson, V.J., Metcalfe, J.D., Righton, D. & Sims, D.W. (2006) Flexible foraging movements of leatherback turtles across the North Atlantic Ocean. *Ecology*, **87**, 2647–2656.
- Hays, G.C. & Scott, R. (2013) Global patterns for upper ceilings on migration distance in sea turtles and comparisons with fish, birds and mammals. *Functional Ecology*, **27**, 748–756.
- Hays, G.C., Mortimer, J.A., Ierodiaconou, D. & Esteban, E. (2014). Use of long-distance migration patterns of an endangered species to inform conservation

- planning for the world's largest marine protected area. *Conservation Biology*, **28**, 1636–1644.
- Hazel, J. (2009) Evaluation of fast-acquisition GPS in stationary tests and fine-scale tracking of green turtles. *Journal of Experimental Marine Biology and Ecology*, **374**, 58–68.
- Hazen, E.L., Jorgensen, S., Rykaczewski, R.R., Bograd, S.J., Foley, D.G., Jonsen, I.D., Shaffer, S.A., Dunne, J.P., Costa, D.P. & Crowder, L.B. (2013) Predicted habitat shifts of Pacific top predators in a changing climate. *Nature Climate Change*, **3**, 234–238.
- Hazin, F.H., Afonso, A.S., Castilho, P.C., Ferreira, L.C. & Rocha, B.C. (2013) Regional movements of the tiger shark, *Galeocerdo cuvier*, off northeastern Brazil: inferences regarding shark attack hazard. *Anais da Academia Brasileira de Ciências*, **85**, 1053–1062.
- Heithaus, M.R. (2001) The biology of tiger sharks, *Galeocerdo cuvier*, in Shark Bay, Western Australia: sex ratio, size distribution, diet, and seasonal changes in catch rates. *Environmental Biology of Fishes*, **61**, 25–36.
- Heithaus, M.R., Frid, A., Wirsing, A.J., Dill, L.M., Fourqurean, J.W., Burkholder, D., Thomson, J. & Bejder, L. (2007a) State-dependent risk-taking by green sea turtles mediates top-down effects of tiger shark intimidation in a marine ecosystem. *Journal of Animal Ecology*, **76**, 837–844.
- Heithaus, M.R., Frid, A., Wirsing, A.J. & Worm, B. (2008) Predicting ecological consequences of marine top predator declines. *Trends in Ecology & Evolution*, **23**, 202–210.
- Heithaus, M.R., Vaudo, J.J., Kreicker, S., Layman, C.A., Krützen, M., Burkholder, D.A., Gastrich, K., Bessey, C., Sarabia, R. & Cameron, K. (2013) Apparent

- resource partitioning and trophic structure of large-bodied marine predators in a relatively pristine seagrass ecosystem. *Marine Ecology Progress Series*, **481**, 225–237.
- Heithaus, M.R., Wirsing, A.J., Burkholder, D., Thomson, J. & Dill, L.M. (2009) Towards a predictive framework for predator risk effects: the interaction of landscape features and prey escape tactics. *The Journal of animal ecology*, **78**, 556–562.
- Heithaus, M.R., Wirsing, A.J., Dill, L.M. & Heithaus, L.I. (2007b) Long-term movements of tiger sharks satellite-tagged in Shark Bay, Western Australia. *Marine Biology*, **151**, 1455–1461.
- Heupel, M. (2009) *Carcharhinus Melanopterus*. The IUCN Red List of Threatened Species 2009.
- Heupel, M.R., Carlson, J.K. & Simpfendorfer, C.A. (2007) Shark nursery areas: concepts, definition, characterization and assumptions. *Marine Ecology Progress Series*, **337**, 287–297.
- Heupel, M.R., Knip, D.M., Simpfendorfer, C.A. & Dulvy, N.K. (2014) Sizing up the ecological role of sharks as predators. *Marine Ecology Progress Series*, **495**, 291–298.
- Heupel, M.R. & Simpfendorfer, C.A. (2005) Quantitative analysis of aggregation behavior in juvenile blacktip sharks. *Marine Biology*, **147**, 1239–1249.
- Heupel, M.R. & Simpfendorfer, C.A. (2008) Movement and distribution of young bull sharks *Carcharhinus leucas* in a variable estuarine environment. *Aquatic Biology*, **1**, 277–289.
- Heupel, M.R. & Simpfendorfer, C.A. (2015) Long-term movement patterns of a coral reef predator. *Coral Reefs*, **34**, 679–691.

- Heupel, M.R., Simpfendorfer, C.A. & Fitzpatrick, R. (2010) Large-scale movement and reef fidelity of grey reef sharks. *PLoS ONE*, **5**, e9650.
- Hight, B.V. & Lowe, C.G. (2007) Elevated body temperatures of adult female leopard sharks, *Triakis semifasciata*, while aggregating in shallow nearshore embayments: evidence for behavioral thermoregulation? *Journal of Experimental Marine Biology and Ecology*, **352**, 114–128.
- Hoegh-Guldberg, O. & Bruno, J.F. (2010) The impact of climate change on the world's marine ecosystems. *Science*, **328**, 1523–1528.
- Hoelzel, A.R., Shivji, M.S., Magnussen, J. & Francis, M.P. (2006) Low worldwide genetic diversity in the basking shark (*Cetorhinus maximus*). *Biology Letters*, **2**, 639–642.
- Holland, K.N., Wetherbee, B.M., Lowe, C.G. & Meyer, C.G. (1999) Movements of tiger sharks (*Galeocerdo cuvier*) in coastal Hawaiian waters. *Marine Biology*, **134**, 665–673.
- Holmlund, C.M. & Hammer, M. (1999) Ecosystem services generated by fish populations. *Ecological Economics*, **29**, 253–268.
- Horn, R.L. (2010) *Applying a Molecular Genetics Approach to Shark Conservation and Management: Assessment of DNA Barcoding in Hammerhead Sharks and Global Population Genetic Structuring in the Gray Reef Shark, Carcharhinus Amblyrhynchos*. Master's Thesis, Nova Southeastern University Oceanographic Center.
- Howey-Jordan, L.A., Brooks, E.J., Abercrombie, D.L., Jordan, L.K., Brooks, A., Williams, S., Gospodarczyk, E. & Chapman, D.D. (2013) Complex movements, philopatry and expanded depth range of a severely threatened pelagic shark, the oceanic whitetip (*Carcharhinus longimanus*) in the Western

North Atlantic. *PLoS ONE*, **8**, 56588.

Hoyt, E. (2014) The role of marine protected areas and sanctuaries. *Sharks: Conservation, Governance and Management* pp. 236–261. Routledge, Oxford, New York.

Humphries, N.E., Queiroz, N., Dyer, J.R.M., Pade, N.G., Musyl, M.K., Schaefer, K.M., Fuller, D.W., Brunnschweiler, J.M., Doyle, T.K., Houghton, J.D.R., Hays, G.C., Jones, C.S., Noble, L.R., Wearmouth, V.J., Southall, E.J. & Sims, D.W. (2010) Environmental context explains Lévy and Brownian movement patterns of marine predators. *Nature*, **465**, 1066–1069.

Hussey, N.E., Kessel, S.T., Aarestrup, K., Cooke, S.J., Cowley, P.D., Fisk, A.T., Harcourt, R.G., Holland, K.N., Iverson, S.J. & Kocik, J.F. (2015) Aquatic animal telemetry: a panoramic window into the underwater world. *Science*, **348**, 1221–1232.

Hussey, N.E., Stroh, N., Klaus, R., Chekchak, T. & Kessel, S.T. (2013) SCUBA diver observations and placard tags to monitor grey reef sharks, *Carcharhinus amblyrhynchos*, at Sha'ab Rumi, The Sudan: assessment and future directions. *Journal of the Marine Biological Association of the United Kingdom*, **93**, 299–308.

Hutchings, J.A., Myers, R.A., García, V.B., Lucifora, L.O. & Kuparinen, A. (2012) Life-history correlates of extinction risk and recovery potential. *Ecological Applications*, **22**, 1061–1067.

The International Commission for the Conservation of Atlantic Tunas (ICCAT). (2009) Report of the 2008 shark stock assessments meeting. *Collective Volume of Scientific Papers*, **64**, 1343–1491.

The International Commission for the Conservation of Atlantic Tunas (ICCAT).

- (2012) *Report of the 2012 Shortfin Mako Stock Assessment and Ecological Risk Assessment Meeting*. Olhão, Portugal.
- Iglésias, S.P., Toulhoat, L. & Sellos, D.Y. (2010) Taxonomic confusion and market mislabelling of threatened skates: important consequences for their conservation status. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **20**, 319–333.
- Iosilevskii G., Papastamatiou, Y.P. (2016) Relations between morphology, buoyancy and energetics of requiem sharks. *Royal Society Open Science*, **3**, 160406.
- Jacoby, D.M.P., Brooks, E.J., Croft, D.P. & Sims, D.W. (2012) Developing a deeper understanding of animal movements and spatial dynamics through novel application of network analyses. *Methods in Ecology and Evolution*, **3**, 574–583.
- Jacoby, D.M.P., Siriwat, P., Freeman, R., Carborne, C. (2015) Is the scaling of swim speed in sharks driven by metabolism? *Biology Letters*, **11**, 20150781.
- Jahn, A.E., Levey, D.J., Hostetler, J.A. & Mamani, A.M. (2010) Determinants of partial bird migration in the Amazon Basin. *Journal of Animal Ecology*, **79**, 983–992.
- Jennings, S., Marshall, S.S. & Polunin, N.V. (1996) Seychelles' marine protected areas: comparative structure and status of reef fish communities. *Biological Conservation*, **75**, 201–209.
- Jones, D.L., Walter, J.F., Brooks, E.N. & Serafy, J.E. (2010) Connectivity through ontogeny: fish population linkages among mangrove and coral reef habitats. *Marine Ecology Progress Series*, **401**, 245–258.
- Jonsen, I.D., Flemming, J.M. & Myers, R.A. (2005) Robust state-space modeling of animal movement data. *Ecology*, **86**, 2874–2880.

- Jonsen, I.D., Myers, R.A. & James, M.C. (2007) Identifying leatherback turtle foraging behaviour from satellite telemetry using a switching state-space model. *Marine Ecology Progress Series*, **337**, 255–264.
- Jorgensen, S.J., Reeb, C.A., Chapple, T.K., Anderson, S., Perle, C., Van Sommeran, S.R., Fritz-Cope, C., Brown, A.C., Klimley, A.P. & Block, B.A. (2009) Philopatry and migration of Pacific white sharks. *Proceedings of the Royal Society of London B: Biological Sciences*, 679–688.
- Juan-Jordá, M.J., Mosqueira, I., Cooper, A.B., Freire, J. & Dulvy, N.K. (2011) Global population trajectories of tunas and their relatives. *Proceedings of the National Academy of Sciences*, **108**, 20650–20655.
- Karl, S.A., Castro, A.L.F., Lopez, J.A., Charvet, P. & Burgess, G.H. (2011) Phylogeography and conservation of the bull shark (*Carcharhinus leucas*) inferred from mitochondrial and microsatellite DNA. *Conservation Genetics*, **12**, 371–382.
- Kerford, M.R., Wirsing, A.J., Heithaus, M.R. & Dill, L.M. (2008) Danger on the rise: diurnal tidal state mediates an exchange of food for safety by the bar-bellied sea snake *Hydrophis elegans*. *Marine Ecology Progress Series*, **358**, 289.
- Kinney, M.J. & Simpfendorfer, C.A. (2009) Reassessing the value of nursery areas to shark conservation and management. *Conservation Letters*, **2**, 53–60.
- Kitchell, J.F., Essington, T.E., Boggs, C.H., Schindler, D.E. & Walters, C.J. (2002) The role of sharks and longline fisheries in a pelagic ecosystem of the Central Pacific. *Ecosystems*, **5**, 202–216.
- Klimley, A.P. (1993) Highly directional swimming by scalloped hammerhead sharks, *Sphyrna lewini*, and subsurface irradiance, temperature, bathymetry, and geomagnetic field. *Marine Biology*, **117**, 1–22.

- Klimley, A.P., Butler, S.B., Nelson, D.R. & Stull, A.T. (1988) Diel movements of scalloped hammerhead sharks, *Sphyrna lewini* Griffith and Smith, to and from a seamount in the Gulf of California. *Journal of Fish Biology*, **33**, 751–761.
- Knip, D.M., Heupel, M.R. & Simpfendorfer, C.A. (2010) Sharks in nearshore environments: models, importance, and consequences. *Marine Ecology Progress Series*, **402**, 1–11.
- Knip, D.M., Heupel, M.R. & Simpfendorfer, C.A. (2012) Evaluating marine protected areas for the conservation of tropical coastal sharks. *Biological Conservation*, **148**, 200–209.
- Kohler, N., Casey, J. & Turner, P. (1998) NMFS cooperative shark tagging program, 1962-93: an atlas of shark tag and recapture data. *Marine Fisheries Review*, **60**, 1–87.
- Lack, M. & Sant, G. (2006) *Confronting Shark Conservation Head On!* TRAFFIC International, Cambridge (United Kingdom).
- Laidre, K.L., Heide-Jørgensen, M.P., Logsdon, M.L., Hobbs, R.C., Dietz, R. & VanBlaricom, G.R. (2004) Fractal analysis of narwhal space use patterns. *Zoology*, **107**, 3–11.
- Laroche, R., Kock, A., Dill, L. & Oosthuizen, W. (2007) Effects of provisioning ecotourism activity on the behaviour of white sharks *Carcharodon carcharias*. *Marine Ecology Progress Series*, **338**, 199–209.
- Lea, J.S., Humphries, N., von Brandis, R., Clarke, C. & Sims, D. (2016) Acoustic telemetry and network analysis reveal space-use of multiple reef predators and enhance MPA design. *Proceedings of The Royal Society of London B: Biological Sciences*, **283**
- Lea, J.S.E., Humphries, N.E., Clarke, C.R. & Sims, D.W. (2015a) To Madagascar and

- back: long-distance, return migration across open ocean by a pregnant female bull shark *Carcharhinus leucas*. *Journal of Fish Biology*, **87**, 1313–1321.
- Lea, J.S., Wetherbee, B.M., Queiroz, N., Burnie, N., Aming, C., Sousa, L.L., Mucientes, G.R., Humphries, N.E., Harvey, G.M. & Sims, D.W. (2015b) Repeated, long-distance migrations by a philopatric predator targeting highly contrasting ecosystems. *Scientific Reports*, **5**.
- Lippi, G., Targher, G. & Franchini, M. (2010) Vaccination, squalene and anti-squalene antibodies: facts or fiction? *European Journal of Internal Medicine*, **21**, 70–73.
- Lockyer, C.H. & Brown, S.G. (1981) The migration of whales. *Animal Migration* pp. 105–137. Cambridge University Press, Cambridge.
- Lowe, C.G., Wetherbee, B.M., Crow, G.L. & Tester, A.L. (1996) Ontogenetic dietary shifts and feeding behavior of the tiger shark, *Galeocerdo cuvier*, in Hawaiian waters. *Environmental Biology of Fishes*, **47**, 203–211.
- Lowe, C.G., Wetherbee, B.M. & Meyer, C.G. (2006) Using acoustic telemetry monitoring techniques to quantify movement patterns and site fidelity of sharks and giant trevally around French Frigate Shoals and Midway Atoll. *Atoll Research Bulletin*, **543**, 281–303.
- Lutcavage, M.E., Brill, R.W., Skomal, G.B., Chase, B.C. & Howey, P.W. (1999) Results of pop-up satellite tagging of spawning size class fish in the Gulf of Maine: do North Atlantic bluefin tuna spawn in the mid-Atlantic? *Canadian Journal of Fisheries and Aquatic Sciences*, **56**, 173–177.
- Maljković, A. & Côté, I.M. (2011) Effects of tourism-related provisioning on the trophic signatures and movement patterns of an apex predator, the Caribbean reef shark. *Biological Conservation*, **144**, 859–865.

- Mansfield, K.L., Saba, V.S., Keinath, J.A. & Musick, J.A. (2009) Satellite tracking reveals a dichotomy in migration strategies among juvenile loggerhead turtles in the Northwest Atlantic. *Marine Biology*, **156**, 2555–2570.
- Mansfield, K.L., Wyneken, J., Porter, W.P. & Luo, J. (2014) First satellite tracks of neonate sea turtles redefine the “lost years” oceanic niche. *Proceedings of the Royal Society of London B: Biological Sciences*, **281**, 20133039.
- Martin, R.. & Hakeem, A.A.. (2006) Development of a sustainable shark diving ecotourism industry in the Maldives: Challenges and opportunities. *Maldives Marine Research Bulletin*, **8**, 1–53.
- Matich, P., Heithaus, M.R. & Layman, C.A. (2011) Contrasting patterns of individual specialization and trophic coupling in two marine apex predators. *Journal of Animal Ecology*, 294–305.
- McCauley, D.J., Pinsky, M.L., Palumbi, S.R., Estes, J.A., Joyce, F.H. & Warner, R.R. (2015) Marine defaunation: Animal loss in the global ocean. *Science*, **347**, 1255641.
- McCauley, D.J., Young, H.S., Dunbar, R.B., Estes, J.A., Semmens, B.X. & Micheli, F. (2012) Assessing the effects of large mobile predators on ecosystem connectivity. *Ecological Applications*, **22**, 1711–1717.
- McClellan, C.M. & Read, A.J. (2007) Complexity and variation in loggerhead sea turtle life history. *Biology Letters*, **3**, 592–594.
- McKinney, J.A., Hoffmayer, E.R., Wu, W., Fulford, R. & Hendon, J. (2012) Feeding habitat of the whale shark *Rhincodon typus* in the northern Gulf of Mexico determined using species distribution modelling. *Marine Ecology Progress Series*, **458**, 199–211.
- McMahon, K.W., Hamady, L.L. & Thorrold, S.R. (2013) A review of

- ecogeochemistry approaches to estimating movements of marine animals. *Limnology and Oceanography*, **58**, 697–714.
- McNamara, J.M., Barta, Z., Klaassen, M. & Bauer, S. (2011) Cues and the optimal timing of activities under environmental changes. *Ecology Letters*, **14**, 1183–1190.
- Medio, D., Ormond, R.F.G. & Pearson, M. (1997) Effect of briefings on rates of damage to corals by scuba divers. *Biological Conservation*, **79**, 91–95.
- Meehl, G.A., Stocker, T.F., Collins, W.D., Friedlingstein, P., Gaye, A.T., Gregory, J.M., Kitoh, A., Knutti, R., Murphy, J.M. & Noda, A. (2007) Global climate projections. *Climate change*, **3495**, 747–845.
- Mehner, T. & Kasprzak, P. (2011) Partial diel vertical migrations in pelagic fish. *Journal of Animal Ecology*, **80**, 761–770.
- Meyer, C.G., Dale, J.J., Papastamatiou, Y.P., Whitney, N.M. & Holland, K.N. (2009) Seasonal cycles and long-term trends in abundance and species composition of sharks associated with cage diving ecotourism activities in Hawaii. *Environmental Conservation*, **36**, 104–111.
- Moffitt, E.A., Botsford, L.W., Kaplan, D.M. & O’Farrell, M.R. (2009) Marine reserve networks for species that move within a home range. *Ecological Applications*, **19**, 1835–1847.
- Momigliano, P., Harcourt, R., Robbins, W.D. & Stow, A. (2015) Connectivity in grey reef sharks (*Carcharhinus amblyrhynchos*) determined using empirical and simulated genetic data. *Scientific Reports*, **5**.
- Morrissey, J.F. & Gruber, S.H. (1993) Habitat selection by juvenile lemon sharks, *Negaprion brevirostris*. *Environmental Biology of Fishes*, **38**, 311–319.
- Mortimer, J.A., Camille, J.-C. & Boniface, N. (2011) Seasonality and status of nesting

- hawksbill (*Eretmochelys imbricata*) and green turtles (*Chelonia mydas*) at D'Arros Island, Amirantes Group, Seychelles. *Chelonian Conservation and Biology*, **10**, 26–33.
- Mortimer, J.A. & Collie, J. (1998) Status and conservation of sea turtles in the Republic of Seychelles. *Epperly SE, Braun J (compilers). Proc 17th Annu Sea Turtle Symp. NOAA Tech Memo NMFS-SEFSC-415* pp. 74–75.
- Mouillot, D., Parravicini, V., Bellwood, D.R., Leprieur, F., Huang, D., Cowman, P.F., Albouy, C., Hughes, T.P., Thuiller, W. & Guilhaumon, F. (2016) Global marine protected areas do not secure the evolutionary history of tropical corals and fishes. *Nature Communications*, **7**.
- Mourier, J., Mills, S.C. & Planes, S. (2013) Population structure, spatial distribution and life-history traits of blacktip reef sharks *Carcharhinus melanopterus*. *Journal of Fish Biology*, **82**, 979–993.
- Mourier, J. & Planes, S. (2013) Direct genetic evidence for reproductive philopatry and associated fine-scale migrations in female blacktip reef sharks (*Carcharhinus melanopterus*) in French Polynesia. *Molecular Ecology*, **22**, 201–214.
- Mucientes, G.R., Queiroz, N., Sousa, L.L., Tarroso, P. & Sims, D.W. (2009) Sexual segregation of pelagic sharks and the potential threat from fisheries. *Biology Letters*, **5**, 156–159.
- Musick, J.A. (1999) *Life in the Slow Lane: Ecology and Conservation of Long-Lived Marine Animals. American Fisheries Society Symposium 23*. American Fisheries Society, Bethesda, Maryland, USA.
- Musyl, M.K., Brill, R.W., Curran, D.S., Fragoso, N.M., McNaughton, L.M., Nielsen, A., Kikkawa, B.S. & Moyes, C.D. (2011) Postrelease survival, vertical and

- horizontal movements, and thermal habitats of five species of pelagic sharks in the central Pacific Ocean. *Fishery Bulletin*, **109**, 341–368.
- Myers, R.A., Baum, J.K., Shepherd, T.D., Powers, S.P. & Peterson, C.H. (2007) Cascading effects of the loss of apex predatory sharks from a coastal ocean. *Science*, **315**, 1846–1850.
- Myers, R.A. & Worm, B. (2005) Extinction, survival or recovery of large predatory fishes. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **360**, 13–20.
- Møller, A.P., Rubolini, D. & Lehikoinen, E. (2008) Populations of migratory bird species that did not show a phenological response to climate change are declining. *Proceedings of the National Academy of Sciences*, **105**, 16195–16200.
- Nadon, M.O., Baum, J.K., Williams, I.D., McPherson, J.M., Zgliczynski, B.J., Richards, B.L., Schroeder, R. & Brainard, R. (2012) Re-creating missing population baselines for Pacific reef sharks. *Conservation Biology*, **26**, 493–503.
- Nagelkerken, I. (2009) Evaluation of nursery function of mangroves and seagrass beds for tropical decapods and reef fishes: patterns and underlying mechanisms. *Ecological connectivity among tropical coastal ecosystems* pp. 357–399. Springer, Netherlands.
- Natanson, L.J., Casey, J.G., Kohler, N.E. & Colket, T. (1999) Growth of the tiger shark, *Galeocerdo cuvier*, in the western North Atlantic based on tag returns and length frequencies; and a note on the effects of tagging. *Fishery Bulletin*, **97**, 944–953.
- Nelson, D.R. (1976) Ultrasonic telemetry of shark behavior. *The Journal of the*

Acoustical Society of America, **59**, 1004–1007.

- Nelson, D.R., McKibben, J.N., Strong Jr, W.R., Lowe, C.G., Sisneros, J.A., Schroeder, D.M. & Lavenberg, R.J. (1997) An acoustic tracking of a megamouth shark, *Megachasma pelagios*: a crepuscular vertical migrator. *Environmental Biology of Fishes*, **49**, 389–399.
- Nevill, J., Robinson, J., Giroux, F. & Isidore, M. (2007) *Seychelles National Plan of Action for the Conservation and Management of Sharks*. Seychelles Fishing Authority, Victoria, Seychelles.
- Newsome, D. & Rodger, K. (2008) To feed or not to feed: a contentious issue in wildlife tourism. *Too close for comfort* pp. 255–270. Royal Zoological Society of New South Wales.
- National Oceanic and Atmospheric Administration (NOAA). (2016) NOAA Fisheries a Final Rule Regarding the 2016 Atlantic Shark Commercial Fishing Season: Office of Sustainable Fisheries.
- Okey, T.A., Banks, S., Born, A.F., Bustamante, R.H., Calvopiña, M., Edgar, G.J., Espinoza, E., Fariña, J.M., Garske, L.E. & Reck, G.K. (2004) A trophic model of a Galápagos subtidal rocky reef for evaluating fisheries and conservation strategies. *Ecological Modelling*, **172**, 383–401.
- Van Oldenborgh, G.J., Philip, S.Y. & Collins, M. (2005) El Nino in a changing climate: a multi-model study. *Ocean Science*, **1**, 81–95.
- Oschlies, A. & Garçon, V. (1998) Eddy-induced enhancement of primary production in a model of the North Atlantic Ocean. *Nature*, **394**, 266–269.
- Osgood, G.J. & Baum, J.K. (2015) Reef sharks: recent advances in ecological understanding to inform conservation. *Journal of Fish Biology*, **87**, 1489–1523.

- O'Connor, S., Campbell, R., Cortez, H. & Knowles, T. (2009) Whale Watching Worldwide: tourism numbers, expenditures and expanding economic benefits, a special report from the International Fund for Animal Welfare. *Yarmouth MA, USA, prepared by Economists at Large*, **228**.
- Paine, R.T. (1966) Food web complexity and species diversity. *American Naturalist*, **100**, 65–75.
- Papastamatiou, Y.P., Cartamil, D.P., Lowe, C.G., Meyer, C.G., Wetherbee, B.M. & Holland, K.N. (2011) Scales of orientation, directed walks and movement path structure in sharks. *Journal of Animal Ecology*, **80**, 864–874.
- Papastamatiou, Y.P. & Lowe, C.G. (2012) An analytical and hypothesis-driven approach to elasmobranch movement studies. *Journal of Fish Biology*, **80**, 1342–1360.
- Papastamatiou, Y.P., Lowe, C.G., Caselle, J.E. & Friedlander, A.M. (2009) Scale-dependent effects of habitat on movements and path structure of reef sharks at a predator-dominated atoll. *Ecology*, **90**, 996–1008.
- Papastamatiou, Y.P., Meyer, C.G., Carvalho, F., Dale, J.J., Hutchinson, M.R. & Holland, K.N. (2013) Telemetry and random-walk models reveal complex patterns of partial migration in a large marine predator. *Ecology*, **94**, 2595–2606.
- Papastamatiou, Y.P., Meyer, C.G. & Holland, K.N. (2007) A new acoustic pH transmitter for studying the feeding habits of free-ranging sharks. *Aquatic Living Resources*, **20**, 287–290.
- Pauly, D., Christensen, V. & Walters, C. (2000) Ecopath, Ecosim, and Ecospace as tools for evaluating ecosystem impact of fisheries. *ICES Journal of Marine Science: Journal du Conseil*, **57**, 697–706.

- Pauly, D., Hilborn, R. & Branch, T.A. (2013) Fisheries: Does catch reflect abundance? *Nature*, **494**, 303–306.
- Payet, R. (2014) *National Parks (D'Arros and St Joseph Special Reserve) Designation Order*. National Parks and Nature Conservancy Act.
- Perry, A.L., Low, P.J., Ellis, J.R. & Reynolds, J.D. (2005) Climate change and distribution shifts in marine fishes. *Science*, **308**, 1912–1915.
- Peters, R.H. (1986) The ecological implications of body size. *Cambridge University Press*, Cambridge, UK.
- Pillans, R. (2003a) *Negaprion Acutidens*. The IUCN Red List of Threatened Species 2003.
- Pillans, R. (2003b) *Nebrius Ferrugineus*. The IUCN Red List of Threatened Species 2003.
- Pinhal, D., Shivji, M.S., Vallinoto, M., Chapman, D.D., Gadig, O.B.F. & Martins, C. (2012) Cryptic hammerhead shark lineage occurrence in the western South Atlantic revealed by DNA analysis. *Marine Biology*, **159**, 829–836.
- Polovina, J.J., Howell, E., Kobayashi, D.R. & Seki, M.P. (2001) The transition zone chlorophyll front, a dynamic global feature defining migration and forage habitat for marine resources. *Progress in Oceanography*, **49**, 469–483.
- Poonian, C., Davis, P.Z.R. & McNaughton, C.K. (2010) Impacts of recreational divers on Palauan coral reefs and options for management. *Pacific Science*, **64**, 557–565.
- Porcher, I.F. (2005) On the gestation period of the blackfin reef shark, *Carcharhinus melanopterus*, in waters off Moorea, French Polynesia. *Marine Biology*, **146**, 1207–1211.
- Pratt Jr, H.L. & Carrier, J.C. (2001) A review of elasmobranch reproductive behavior

- with a case study on the nurse shark, *Ginglymostoma cirratum*. *Environmental Biology of Fishes*, **60**, 157–188.
- Prince, J.D. (2005) Gauntlet fisheries for elasmobranchs—the secret of sustainable shark fisheries. *Journal of Northwest Atlantic Fishery Science*, **35**, 407–416.
- Queiroz, N., Humphries, N.E., Mucientes, G., Hammerschlag, N., Lima, F.P., Scales, K.L., Miller, P.I., Sousa, L.L., Seabra, R. & Sims, D.W. (2016) Ocean-wide tracking of pelagic sharks reveals extent of overlap with longline fishing hotspots. *Proceedings of the National Academy of Sciences*, **113**, 1582–1587.
- Queiroz, N., Humphries, N.E., Noble, L.R., Santos, A.M. & Sims, D.W. (2010) Short-term movements and diving behaviour of satellite-tracked blue sharks *Prionace glauca* in the northeastern Atlantic Ocean. *Marine Ecology Progress Series*, **406**, 265–279.
- Queiroz, N., Humphries, N.E., Noble, L.R., Santos, A.M. & Sims, D.W. (2012) Spatial dynamics and expanded vertical niche of blue sharks in oceanographic fronts reveal habitat targets for conservation. *PLoS ONE*, **7**.
- Ripple, W.J. & Beschta, R.L. (2007) Restoring Yellowstone’s aspen with wolves. *Biological Conservation*, **138**, 514–519.
- Ripple, W.J., Larsen, E.J., Renkin, R.A. & Smith, D.W. (2001) Trophic cascades among wolves, elk and aspen on Yellowstone National Park’s northern range. *Biological Conservation*, **102**, 227–234.
- Rizzari, J.R., Frisch, A.J. & Magnenat, K.A. (2014) Diversity, abundance, and distribution of reef sharks on outer-shelf reefs of the Great Barrier Reef, Australia. *Marine Biology*, **161**, 2847–2855.
- Robbins, R.L. (2007) Environmental variables affecting the sexual segregation of great white sharks *Carcharodon carcharias* at the Neptune Islands South

- Australia. *Journal of Fish Biology*, **70**, 1350–1364.
- Robbins, W.D., Hisano, M., Connolly, S.R. & Choat, J.H. (2006) Ongoing collapse of coral-reef shark populations. *Current Biology*, **16**, 2314–2319.
- Robichaud, D. & Rose, G.A. (2001) Multiyear homing of Atlantic cod to a spawning ground. *Canadian Journal of Fisheries and Aquatic Sciences*, **58**, 2325–2329.
- Roessig, J.M., Woodley, C.M., Cech Jr, J.J. & Hansen, L.J. (2004) Effects of global climate change on marine and estuarine fishes and fisheries. *Reviews in Fish Biology and Fisheries*, **14**, 251–275.
- Rowat, D. & Engelhardt, U. (2007) Seychelles: A case study of community involvement in the development of whale shark ecotourism and its socio-economic impact. *Fisheries Research*, **84**, 109–113–109–113.
- Rowat, D. & Gore, M. (2007) Regional scale horizontal and local scale vertical movements of whale sharks in the Indian Ocean off Seychelles. *Fisheries Research*, **84**, 32–40.
- Scales, K.L., Miller, P.I., Hawkes, L.A., Ingram, S.N., Sims, D.W. & Votier, S.C. (2014) Review: On the Front Line: frontal zones as priority at-sea conservation areas for mobile marine vertebrates. *Journal of Applied Ecology*, **51**, 1575–1583.
- Schofield, G., Hobson, V.J., Fossette, S., Lilley, M.K., Katselidis, K.A. & Hays, G.C. (2010) Biodiversity Research: fidelity to foraging sites, consistency of migration routes and habitat modulation of home range by sea turtles. *Diversity and Distributions*, **16**, 840–853–840–853.
- Scott, R., Marsh, R. & Hays, G.C. (2014) Ontogeny of long distance migration. *Ecology*, **95**, 2840–2850–2840–2850.
- Seychelles Nation. (2015) Bull shark killed British honeymooner in Seychelles. URL

<http://sharkyear.com/2011/bull-shark-killed-british-honeymooner-in-seychelles.html> [accessed 10 April 2015]

Seychelles News Agency. (2015) Proposed extension of Aride's boundaries aims for more protection of the Seychelles special reserve. URL <http://www.seychellesnewsagency.com/articles/4160/Proposed+extension+of+Arides+boundaries+aims+for+more+protection+of+the+Seychelles+special+reserve> [accessed 14 December 2015]

Shaffer, S.A., Tremblay, Y., Weimerskirch, H., Scott, D., Thompson, D.R., Sagar, P.M., Moller, H., Taylor, G.A., Foley, D.G. & Block, B.A. (2006) Migratory shearwaters integrate oceanic resources across the Pacific Ocean in an endless summer. *Proceedings of the National Academy of Sciences*, **103**, 12799–12802.

Shepard, E.L., Ahmed, M.Z., Southall, E.J., Witt, M.J., Metcalfe, J.D. & Sims, D.W. (2006) Diel and tidal rhythms in diving behaviour of pelagic sharks identified by signal processing of archival tagging data. *Marine Ecology Progress Series*, **328**, 205–213–205–213.

Shepherd, T.D. & Myers, R.A. (2005) Direct and indirect fishery effects on small coastal elasmobranchs in the northern Gulf of Mexico. *Ecology Letters*, **8**, 1095–1104.

Sheppard, C.R.C., Ateweberhan, M., Bowen, B.W., Carr, P., Chen, C.A., Clubbe, C., Craig, M.T., Ebinghaus, R., Eble, J., Fitzsimmons, N., Gaither, M.R., Gan, C.-H., Gollock, M., Guzman, N., Graham, N.A.J., Harris, A., Jones, R., Keshavmurthy, S., Koldewey, H., Lundin, C.G., Mortimer, J.A., Obura, D., Pfeiffer, M., Price, A.R.G., Purkis, S., Raines, P., Readman, J.W., Riegl, B., Rogers, A., Schleyer, M., Seaward, M.R.D., Sheppard, A.L.S., Tamelander, J.,

- Turner, J.R., Visram, S., Vogler, C., Vogt, S., Wolschke, H., Yang, J.M.-C., Yang, S.-Y. & Yesson, C. (2012) Reefs and islands of the Chagos Archipelago, Indian Ocean: why it is the world's largest no-take marine protected area. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **22**, 232–261.
- Shillinger, G.L., Palacios, D.M., Bailey, H., Bograd, S.J., Swithenbank, A.M., Gaspar, P., Wallace, B.P., Spotila, J.R., Paladino, F.V., Piedra, R., Eckert, S.A. & Block, B.A. (2008) Persistent leatherback turtle migrations present opportunities for conservation. *PLoS Biology*, **6**.
- Shivji, M.S., Chapman, D.D., Pikitch, E.K. & Raymond, P.W. (2005) Genetic profiling reveals illegal international trade in fins of the great white shark, *Carcharodon carcharias*. *Conservation Genetics*, **6**, 1035–1039.
- Shivji, M., Clarke, S., Pank, M., Natanson, L., Kohler, N. & Stanhope, M. (2002) Genetic identification of pelagic shark body parts for conservation and trade monitoring. *Conservation Biology*, **16**, 1036–1047.
- Simpfendorfer, C. (2009) *Galeocerdo cuvier*. The IUCN Red List of Threatened Species 2009
- Simpfendorfer, C. & Burgess, G.H. (2009) *Carcharhinus leucas*. The IUCN Red List of Threatened Species 2009.
- Simpfendorfer, C.A., Goodreid, A.B. & McAuley, R.B. (2001) Size, sex and geographic variation in the diet of the tiger shark, *Galeocerdo cuvier*, from Western Australian waters. *Environmental Biology of Fishes*, **61**, 37–46.
- Simpfendorfer, C.A., Heupel, M.R., White, W.T. & Dulvy, N.K. (2011) The importance of research and public opinion to conservation management of sharks and rays: a synthesis. *Marine and Freshwater Research*, **62**, 518–527.

- Sims, D.W. (2010) Tracking and analysis techniques for understanding free-ranging shark movements and behavior. *Sharks and their relatives II: biodiversity, adaptive physiology, and conservation*. CRC Press, Boca Raton, Florida pp. 351–392. CRC Press, Boca Raton.
- Sims, D.W., Humphries, N.E., Bradford, R.W. & Bruce, B.D. (2012) Lévy flight and Brownian search patterns of a free-ranging predator reflect different prey field characteristics. *Journal of Animal Ecology*, **81**, 432–442.
- Sims, D.W. & Quayle, V.A. (1998) Selective foraging behaviour of basking sharks on zooplankton in a small-scale front. *Nature*, **393**, 460–464.
- Sims, D.W., Southall, E.J., Richardson, A.J., Reid, P.C. & Metcalfe, J.D. (2003) Seasonal movements and behaviour of basking sharks from archival tagging: no evidence of winter hibernation. *Marine Ecology Progress Series*, **248**, 187–196.
- Sims, D.W., Southall, E.J., Tarling, G.A. & Metcalfe, J.D. (2005) Habitat-specific normal and reverse diel vertical migration in the plankton-feeding basking shark. *Journal of Animal Ecology*, **74**, 755–761.
- Sims, D.W., Wearmouth, V.J., Southall, E.J., Hill, J.M., Moore, P., Rawlinson, K., Hutchinson, N., Budd, G.C., Righton, D. & Metcalfe, J.D. (2006a) Hunt warm, rest cool: bioenergetic strategy underlying diel vertical migration of a benthic shark. *Journal of Animal Ecology*, **75**, 176–190.
- Sims, D.W., Witt, M.J., Richardson, A.J., Southall, E.J. & Metcalfe, J.D. (2006b) Encounter success of free-ranging marine predator movements across a dynamic prey landscape. *Proceedings of the Royal Society of London B: Biological Sciences*, **273**, 1195–1201.
- Singh, N.J., Börger, L., Dettki, H., Bunnefeld, N. & Ericsson, G. (2012) From

- migration to nomadism: movement variability in a northern ungulate across its latitudinal range. *Ecological Applications*, **22**, 2007–2020.
- Skomal, G.B., Zeeman, S.I., Chisholm, J.H., Summers, E.L., Walsh, H.J., McMahon, K.W. & Thorrold, S.R. (2009) Transequatorial migrations by basking sharks in the western Atlantic Ocean. *Current Biology*, **19**, 1019–1022.
- Smale, M.. (2009) *Carcharhinus Amblyrhynchos*. The IUCN Red List of Threatened Species 2009.
- Smith, J.L.B. & Smith, M.M. (1969) *The Fishes of Seychelles*. J.L.B. Smith Institute of Ichthyology.
- Snelson, F.F., Mulligan, T.J. & Williams, S.E. (1984) Food habits, occurrence, and population structure of the bull shark, *Carcharhinus Leucas*, in Florida coastal lagoons. *Bulletin of Marine Science*, **34**, 71–80.
- Soria, M., Jaquemet, S., Trystram, C., Chabanet, P., Bourjea, J., Jean, C., Ciccione, S., Dalleau, M., Bigot, L., Hemery, A., Blaison, A., Lemahieu, A., Dulau, V., Estrade, V., Magalon, H., Révillion, C., Pennober, G., Goutorbe, S., Cambert, H., Turquet, J., Cotel, P., Pirog, A. & Verlinden, N. (2015). Rapport scientifique final du programme CHARC (Connaissances de l'écologie et de l'habitat de deux espèces de requins côtiers sur la côte ouest de La Réunion). *Technical Report*. Available at <http://www.la-reunion.ird.fr/le-programme-charc/> [Accessed 27 June 2015].
- Sousa, L.L., Queiroz, N., Mucientes, G., Humphries, N.E., Simds, D.W. (2016). Environmental influence on the seasonal movements of satellite-tracked ocean sunfish *Mola mola* in the north-east Atlantic. *Animal Biotelemetry*, **4**, 1.
- Save Our Seas Foundation (SOSF). (2015) Sensational findings on Breede River bull shark migration. URL

http://saveourseas.com/press/sensational_findings_on_breede_river_bull_shark_migration [accessed 10 April 2015]

- Southall, E.J., Sims, D.W., Witt, M.J. & Metcalfe, J.D. (2006) Seasonal space-use estimates of basking sharks in relation to protection and political–economic zones in the North-east Atlantic. *Biological Conservation*, **132**, 33–39.
- Speed, C.W., Meekan, M.G., Field, I.C., McMahon, C.R., Harcourt, R.G., Stevens, J.D., Babcock, R.C., Pillans, R.D. & Bradshaw, C.J.A. (2015) Reef shark movements relative to a coastal marine protected area. *Regional Studies in Marine Science*, **3**, 58–66.
- Speed, C.W., Meekan, M.G., Field, I.C., McMahon, C.R., Stevens, J.D., McGregor, F., Huveneers, C., Berger, Y. & Bradshaw, C.J. (2011) Spatial and temporal movement patterns of a multi-species coastal reef shark aggregation. *Marine Ecology Progress Series*, **429**, 261–275.
- Springer, S. (1963) Field observations on large sharks of the Florida-Caribbean region. *Sharks and survival* pp. 95–113. D. C. Heath Co., Boston.
- Stamps, J. (1995) Motor learning and the value of familiar space. *American Naturalist*, **146**, 41–58.
- Stevens, J.D. (1984) Life-history and ecology of sharks at Aldabra Atoll, Indian Ocean. *Proceedings of the Royal Society of London B: Biological Sciences*, **222**, 79–106.
- Stevens, J.D., Bonfil, R., Dulvy, N.K. & Walker, P.A. (2000) The effects of fishing on sharks, rays, and chimaeras (chondrichthyans), and the implications for marine ecosystems. *ICES Journal of Marine Science: Journal du Conseil*, **57**, 476–494.
- Stokesbury, M.J., Harvey-Clark, C., Gallant, J., Block, B.A. & Myers, R.A. (2005)

- Movement and environmental preferences of Greenland sharks (*Somniosus microcephalus*) electronically tagged in the St. Lawrence Estuary, Canada. *Marine Biology*, **148**, 159–165.
- Stone, G., Florez-Gonzalez, L. & Katona, S. (1990) Whale migration record. *Nature*, **346**, 705–705.
- Sulikowski, J.A., Wheeler, C.R., Gallagher, A.J., Prohaska, B.K., Langan, J.A. & Hammerschlag, N. (2016) Seasonal and life-stage variation in the reproductive ecology of a marine apex predator, the tiger shark *Galeocerdo cuvier*, at a protected female-dominated site. *Aquatic Biology*, **24**, 175–184.
- Sundström, L.F., Gruber, S.H., Clermont, S.M., Correia, J.P., de Marignac, J.R., Morrissey, J.F., Lowrance, C.R., Thomassen, L. & Oliveira, M.T. (2001) Review of elasmobranch behavioral studies using ultrasonic telemetry with special reference to the lemon shark, *Negaprion brevirostris*, around Bimini Islands, Bahamas. *Environmental Biology of Fishes*, **60**, 225–250.
- Tada, K., Sakai, K., Nakano, Y., Takemura, A., Montani, S. (2003). Size-fractionated phytoplankton biomass in coral reef waters off Sesoko Island, Okinawa, Japan. *Journal of Plankton Research*, **25**, 991–997.
- Taylor, D.S., Reyier, E.A., Davis, W.P. & McIvor, C.C. (2007) Mangrove removal in the Belize cays: effects on mangrove-associated fish assemblages in the intertidal and subtidal. *Bulletin of Marine Science*, **80**, 879–890.
- Thirgood, S., Mosser, A., Tham, S., Hopcraft, G., Mwangomo, E., Mlengeya, T., Kilewo, M., Fryxell, J., Sinclair, A.R.E. & Borner, M. (2004) Can parks protect migratory ungulates? The case of the Serengeti wildebeest. *Animal Conservation*, **7**, 113–120.
- Thomerson, J.E. (1977) The bull shark, *Carcharhinus leucas*, from the upper


- Mississippi River near Alton, Illinois. *Copeia*, **1**, 166–168.
- Thorson, T.B. (1972) The status of the bull shark, *Carcharhinus leucas*, in the Amazon River. *Copeia*, **1972**, 601–605.
- Tillett, B.J., Meekan, M.G., Field, I.C., Thorburn, D.C. & Ovenden, J.R. (2012) Evidence for reproductive philopatry in the bull shark *Carcharhinus leucas*. *Journal of Fish Biology*, **80**, 2140–2158.
- Tremblay-Boyer, L., Gascuel, D., Watson, R., Christensen, V. & Pauly, D. (2011) Modelling the effects of fishing on the biomass of the world's oceans from 1950 to 2006. *Marine Ecology Progress Series*, **442**, 169–185.
- Vandeperre, F., Aires-da-Silva, A., Fontes, J., Santos, M., Serrão Santos, R. & Afonso, P. (2014) Movements of blue sharks (*Prionace glauca*) across their life history. *PLoS ONE*, e103538–e103538.
- Vaudo, J.J. & Heithaus, M.R. (2009) Spatiotemporal variability in a sandflat elasmobranch fauna in Shark Bay, Australia. *Marine Biology*, **156**, 2579–2590.
- Vaudo, J.J., Wetherbee, B.M., Harvey, G., Nemeth, R.S., Aming, C., Burnie, N., Howey-Jordan, L.A. & Shivji, M.S. (2014) Intraspecific variation in vertical habitat use by tiger sharks (*Galeocerdo cuvier*) in the western North Atlantic. *Ecology and Evolution*, **4**, 1768–1786.
- Vejarano, C.C. & Engelhardt, U. (2008) *Report on Shark-Finching Incidents at St Joseph Atoll, Amirantes from 24-26 January 2008*. D'Arros Research Centre, Seychelles.
- Vianna, G.M.S., Meekan, M.G., Meeuwig, J.J. & Speed, C.W. (2013) Environmental influences on patterns of vertical movement and site fidelity of grey reef sharks (*Carcharhinus amblyrhynchos*) at aggregation sites. *PLoS ONE*, **8**.

- Vianna, G.M.S., Meekan, M.G., Pannell, D.J., Marsh, S.P. & Meeuwig, J.J. (2012) Socio-economic value and community benefits from shark-diving tourism in Palau: A sustainable use of reef shark populations. *Biological Conservation*, **145**, 267–277.
- Voegeli, F.A., Smale, M.J., Webber, D.M., Andrade, Y. & O’Dor, R.K. (2001) Ultrasonic telemetry, tracking and automated monitoring technology for sharks. *Environmental Biology of Fishes*, **60**, 267–282.
- Walsh, R.P.D. (1984) Climate of the Seychelles. *Biogeography and ecology of the Seychelles islands* pp. 39–62. Dr W. Junk Publishers.
- Ward, P. & Myers, R.A. (2005) Shifts in open-ocean fish communities coinciding with the commencement of commercial fishing. *Ecology*, **86**, 835–847.
- Watsky, M.A. & Gruber, S.H. (1990) Induction and duration of tonic immobility in the lemon shark, *Negaprion brevirostris*. *Fish Physiology and Biochemistry*, **8**, 207–210.
- Wearmouth, V.J. & Sims, D.W. (2008) Sexual segregation in marine fish, reptiles, birds and mammals: behaviour patterns, mechanisms and conservation implications. *Advances in Marine Biology*, **54**, 107–170.
- Wearmouth, V. & Sims, D. (2010) Sexual segregation in elasmobranchs. *Biologia Marina Mediterranea*, **17**, 236–239.
- Wearmouth, V.J., Southall, E.J., Morritt, D., Thompson, R.C., Cuthill, I.C., Partridge, J.C. & Sims, D.W. (2012) Year-round sexual harassment as a behavioral mediator of vertebrate population dynamics. *Ecological Monographs*, **82**, 351–366.
- Weihs, D. (1977) Effects of size on sustained swimming speeds of aquatic organisms. *Scale Effects in Animal Locomotion* pp. 333–338. Academic Press, New York.

- Weng, K.C., Castilho, P.C., Morrissette, J.M., Landeira-Fernandez, A.M., Holts, D.B., Schallert, R.J., Goldman, K.J. & Block, B.A. (2005) Satellite tagging and cardiac physiology reveal niche expansion in salmon sharks. *Science*, **310**, 104–106.
- Weng, K.C., Foley, D.G., Ganong, J.E., Perle, C., Shillinger, G.L. & Block, B.A. (2008) Migration of an upper trophic level predator, the salmon shark *Lamna ditropis*, between distant ecoregions. *Marine Ecology Progress Series*, **372**, 253–264.
- Werry, J.M., Planes, S., Berumen, M.L., Lee, K.A., Braun, C.D. & Clua, E. (2014) Reef-fidelity and migration of tiger sharks, *Galeocerdo cuvier*, across the Coral Sea. *PLoS ONE*, **9**, e83249.
- Whatmough, S., Putten, I.V. & Chin, A. (2011) From hunters to nature observers: a record of 53 years of diver attitudes towards sharks and rays and marine protected areas. *Marine and Freshwater Research*, **62**, 755–763.
- White, E.R., Myers, M.C., Flemming, J.M. & Baum, J.K. (2015) Shifting elasmobranch community assemblage at Cocos Island--an isolated marine protected area. *Conservation Biology*, **29**, 1186–1197.
- White, W.T. & Potter, I.C. (2004) Habitat partitioning among four elasmobranch species in nearshore, shallow waters of a subtropical embayment in Western Australia. *Marine Biology*, **145**, 1023–1032.
- Wilga, C.D., Motta, P.J. & Sanford, C.P. (2007) Evolution and ecology of feeding in elasmobranchs. *Integrative and Comparative Biology*, **47**, 55–69.
- Wilson, S.G., Polovina, J.J., Stewart, B.S. & Meekan, M.G. (2006) Movements of whale sharks (*Rhincodon typus*) tagged at Ningaloo Reef, Western Australia. *Marine Biology*, **148**, 1157–1166.

- Wilson, R.P., Shepard, E.L.C. & Liebsch, N. (2008) Prying into the intimate details of animal lives: use of a daily diary on animals. *Endangered Species Research*, **4**, 123–137.
- Wirsing, A.J. & Heithaus, M.R. (2009) Olive-headed sea snakes *Disteria major* shift seagrass microhabitats to avoid shark predation. *Marine Ecology Progress Series*, **387**, 287–293.
- Wirsing, A.J., Heithaus, M.R. & Dill, L.M. (2006) Tiger shark (*Galeocerdo cuvier*) abundance and growth in a subtropical embayment: evidence from 7 years of standardized fishing effort. *Marine Biology*, **149**, 961–968.
- Wolanski, E. & Hamner, W.M. (1988) Topographically controlled fronts in the ocean and their biological influence. *Science*, **241**, 177–181.
- Wong, M.Y.L. (2009) Ecological constraints and benefits of philopatry promote group-living in a social but non-cooperatively breeding fish. *Proceedings of the Royal Society of London B: Biological Sciences*, **277**, 353–358.
- Wood, S. (2006) *Generalized Additive Models: An Introduction with R*. CRC press.
- Worm, B. & Branch, T.A. (2012) The future of fish. *Trends in Ecology and Evolution*, **27**, 594–599.
- Worm, B., Davis, B., Kettner, L., Ward-Paige, C.A., Chapman, D., Heithaus, M.R., Kessel, S.T. & Gruber, S.H. (2013) Global catches, exploitation rates, and rebuilding options for sharks. *Marine Policy*, **40**, 194–204.
- Worm, B., Lotze, H.K. & Myers, R.A. (2003) Predator diversity hotspots in the blue ocean. *Proceedings of the National Academy of Sciences*, **100**, 9884–9888.
- Zuur, A., Ieno, E., Walker, N., Saveliev, A. & Smith, G. (2009) *Mixed Effects Models and Extensions in Ecology with R*. Springer, New York.

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Repeated, long-distance migrations by a philopatric predator targeting highly contrasting ecosystems

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Long-distance movements of animals are an important driver of population spatial dynamics and determine the extent of overlap with area-focused human activities, such as fishing. Despite global concerns of declining shark populations, a major limitation in assessments of population trends or spatial management options is the lack of information on their long-term migratory behaviour. For a large marine predator, the tiger shark *Galeocerdo cuvier*, we show from individuals satellite-tracked for multiple years (up to 1101 days) that adult males undertake annually repeated, round-trip migrations of over 7,500 km in the northwest Atlantic. Notably, these migrations occurred between the highly disparate ecosystems of Caribbean coral reef regions in winter and high latitude oceanic areas in summer, with strong, repeated philopatry to specific overwintering insular habitat. Partial migration also occurred, with smaller, immature individuals displaying reduced migration propensity. Foraging may be a putative motivation for these oceanic migrations, with summer behaviour showing higher path tortuosity at the oceanic range extremes. The predictable migratory patterns and use of highly divergent ecosystems shown by male tiger sharks appear broadly similar to migrations seen in birds, reptiles and mammals, and highlight opportunities for dynamic spatial management and conservation measures of highly mobile sharks.

Migration is typically identified as persistent, straightened movement that requires temporary inhibition of station-keeping behaviour, and is recognised as an adaptation driven by the transitory availability and location of resources¹. In this context, migration is ubiquitous across animal taxa and its elucidation has been an important component in a wider understanding of animal population ecology¹. Generally, this

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is because temporal change in the density of a population at a specific geographic location is not only a function of births and deaths but also of movements, including migration². However, long-term tracking studies have focused largely on terrestrial and aerial species, with the most commonly identified ('classical') form of migration involving seasonal movements between a breeding and non-breeding area¹. The availability of remote marine telemetry systems in recent years has enabled increasing studies tracking marine predators, such as turtles, seabirds and marine mammals, many of which reveal long-distance movements consistent with population-level migration^{3–5}. By comparison, a general understanding of migratory behaviour in large sharks is less well developed, in part due to still few studies achieving multi-year tracks to detect repeated seasonal patterns^{4,6–11}. Determining the timing, repeatability and potential motivations for annual movements of large sharks is necessary to understand the ecological and evolutionary role of such behaviour more generally in marine predators.

Global exploitation of large pelagic fish by industrialised fisheries has resulted in dwindling catches of important stocks despite increasing fishing effort¹², emphasising the urgent need for enhanced management and conservation efforts¹³. Management action ideally necessitates evidence of population-wide declines but there is controversy^{14,15} over whether reported declines in shark catch rates within analysed regions reflect decreasing population abundance over entire ranges^{16,17}, or are confounded by shifts in shark movements and habitat selection and changes in the areas exploited by fisheries¹⁸. More reliable interpretation of population size trends from shark fishery catch data will benefit from identifying the migratory ranges, routes and residency patterns of exploited species, particularly in the Atlantic where there is little appreciation of the spatial dynamics of overlap between sharks and fishing fleets despite fishing exploitation being exceptionally high^{19,20}. With few exceptions^{4,6,7,9,10}, detailed, long-term movement information remains sparse for many large shark species, making it very difficult to assess the potential efficacy of oceanic Marine Protected Areas (MPAs) for these highly mobile species²¹.

The tiger shark *Galeocerdo cuvier* (Péron & Lesueur, 1822) is an interesting and suitable species to investigate migratory patterns because it is one of the largest predatory sharks, reaching up to ~5.5 m in length and ~600 kg in mass, and is found circumglobally in tropical and warm temperate coastal/pelagic waters²². It is captured in commercial fisheries, and is listed as 'near threatened' in the Red List of the International Union for Conservation of Nature (IUCN)²³. The tiger shark typically occupies the highest trophic level available where it occurs, often being the sole predator on a wide range of other large, highly mobile marine vertebrates (e.g. marine mammals, turtles, other elasmobranchs)^{24–27}. Moreover, tiger sharks have a very cosmopolitan diet and, consequently, are highly connected in marine food webs, displaying a wide niche breadth that is mostly attributable to high individual variation in prey consumed and depth utilisation^{26,28}. A wide niche breadth of a predator could indicate an adaptation allowing it to remain within relatively localised areas, thus foregoing the necessity for seasonal migration to specific foraging grounds to feed on seasonally abundant prey. But several studies have documented long-distance movements for individual tiger sharks^{8,28–34}. Additionally, seasonal variation in movement behaviour has been inferred from non-continuously tracked animals in acoustic telemetry-based presence/absence studies^{8,35}. However, detailed spatial behaviour observed by continuous tracking over multiple years consistent with more classical, seasonal migratory patterns between discrete focal habitats has not been described.

In this study we use long-term satellite tracking of tiger sharks to determine movement patterns across multiple years, including examination of whether a large, marine predator with high intraspecific variability in diet and vertical habitat use shows any predictable migratory behaviour.

Results

We tagged a total of 24 tiger sharks, 20 of which were male, varying in total length (TL) from 1.73 to 3.96 m (mean 3.03 m; Supporting Information, table S1). Overall, tiger shark movements were tracked for a total of 411 months (mean 17.1 months), covering an estimated distance of 356,085 m (mean 14,836 km), averaging 865.3 km month⁻¹. Tracking periods for individual sharks ranged from 41 to 1101 days (mean 514 d), generating between 19 and 2,404 geolocations (mean 821) of varied Argos location class. Four individuals experienced intermediate transmission absences of 100 days or more. None of the sharks showed evidence from their SPOT transmissions of being captured during their tracks (e.g. a sudden sequence of LC3s).

Repeated, long-distance migration. Tiger sharks tagged at Bermuda displayed extensive space-use throughout the northwest Atlantic, ranging between latitudes of 17–40°N and longitudes of 48–79°W (Fig. 1), covering 6.7 million km², as determined by the 95% isopleth of a kernel density plot for all sharks. This space-use varied seasonally, however, revealing long-distance north-south migrations (Fig. 1). Locations occupied during winter were primarily associated with coral reef-bound islands in the Bahamas, Turks and Caicos Islands, and Anguilla/Saint Martin. None of the tiger sharks was recorded entering the Caribbean Sea, nor crossing the mid-Atlantic Ridge. In contrast, during summer the majority of sharks adopted a temperate, oceanic habit, with most occupying open water north/northeast of Bermuda. There was a more dispersed distribution of locations in both spring (sharks generally moving north) and autumn (generally moving south), representing migratory transitions between the winter insular and summer oceanic phases.

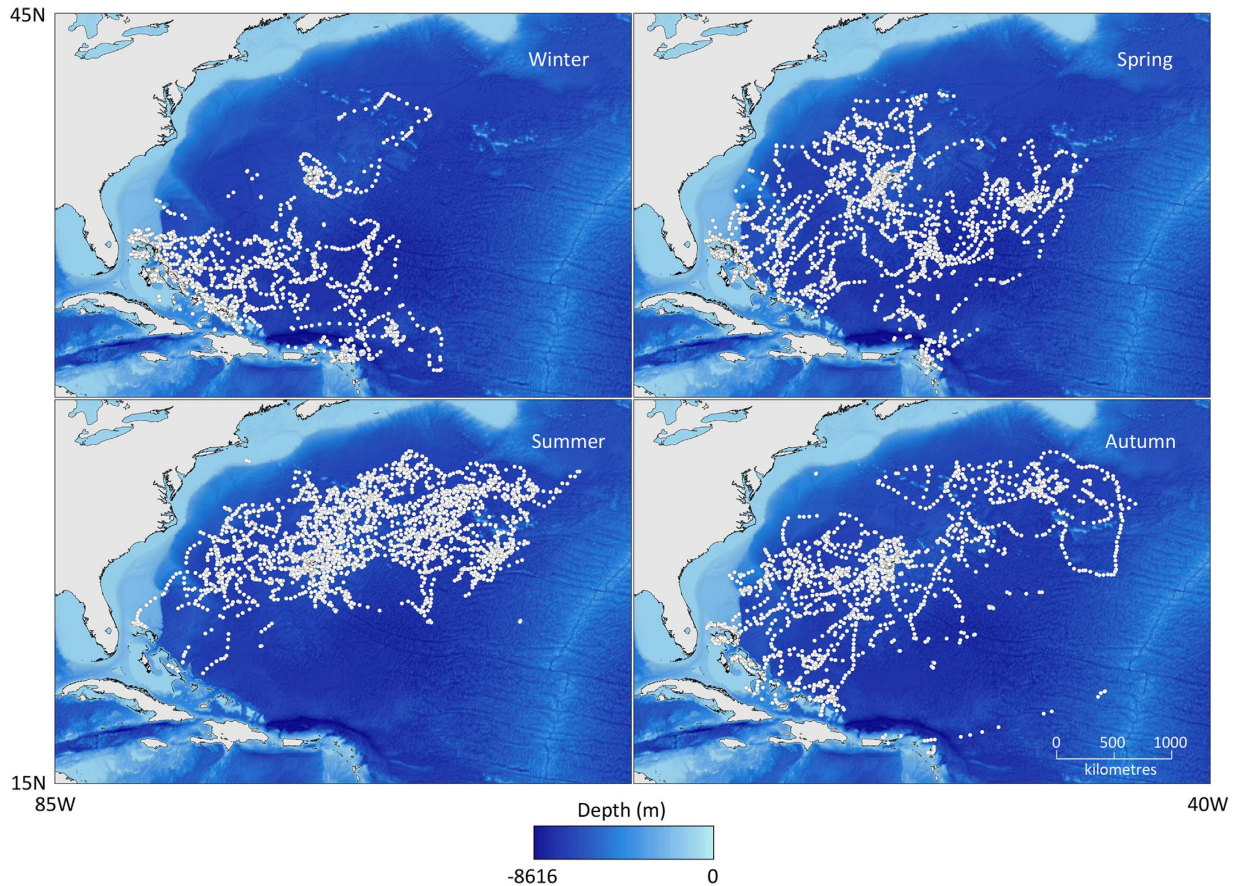


Figure 1. SSM adjusted geolocations for all tiger sharks separated by season and overlaid on bathymetry. Maps created in ArcGIS, using GSHHG coastline data and ETOPO2v2 bathymetry data.

Partial migration. The majority of tiger sharks (16; 273–396 cm TL) displayed a seasonal pattern of considerable latitudinal displacement (up to 2,500 km), between southern islands in winter and northern oceanic areas in summer (Fig. 2). The precise timing and duration of these migrations varied both between years and individuals. Notably, the five smallest tagged sharks (two females and three males: sharks 5, 12, 13, 15, and 20; 173–259 cm TL; table S1) did not conform to this general seasonal migratory pattern, staying in the vicinity of Bermuda over winter (Figs. 1,2). The two largest of these Bermuda overwintering residents (12 and 13, both 259 cm TL at tagging) did eventually undertake longer distance movements, but not until eight and eleven months after tagging, respectively, and neither migrated in the first winter season of their tracks. Overall, larger sharks tended to travel at increased rates (Spearman rank correlation between mean number of kilometres travelled per month and shark total length: $r_s = 0.58$, $p < 0.01$). Although only four female sharks were tracked, both patterns – seasonal migrations and Bermuda winter residence – were displayed by both sexes.

During winter, migratory individuals occupied the warmer, southern waters of the northwest Atlantic, and the expansion in range north during the summer coincides with warmer waters ($>25^\circ\text{C}$) extending up to the Gulf Stream (Fig. 3). The mean sea surface temperature (SST) of the southern insular regions exceeds that of the northern oceanic area throughout the year; however only during late summer and early autumn (July, August, September) does the mean SST in the north exceed the mean winter SST in the southern extent (Supporting Information, Fig. S3). Consequently, the individuals that undertook the annual north-south migrations occupied waters with surface temperatures of approximately $24\text{--}26^\circ\text{C}$ in both winter and summer, whereas those remaining near Bermuda over winter experienced lower surface temperatures ($18\text{--}20^\circ\text{C}$).

Despite the large range of movements by most tiger sharks, high occupancy was spatially restricted while in insular southern areas: up to 6–12 weeks within a given $0.5^\circ \times 0.5^\circ$ cell (Supporting Information, Fig. S4a). In contrast, occupancy in oceanic areas was considerably more transient: little time was spent in any given oceanic cell, although there was elevated space-use around Bermuda, especially Challenger Bank, in the northeast of their tracked range.

Philopatry. There were nine individuals with enough data to investigate seasonal migratory philopatry across two or more years, six of which displayed distinct repeatability in the locality of their space-use.

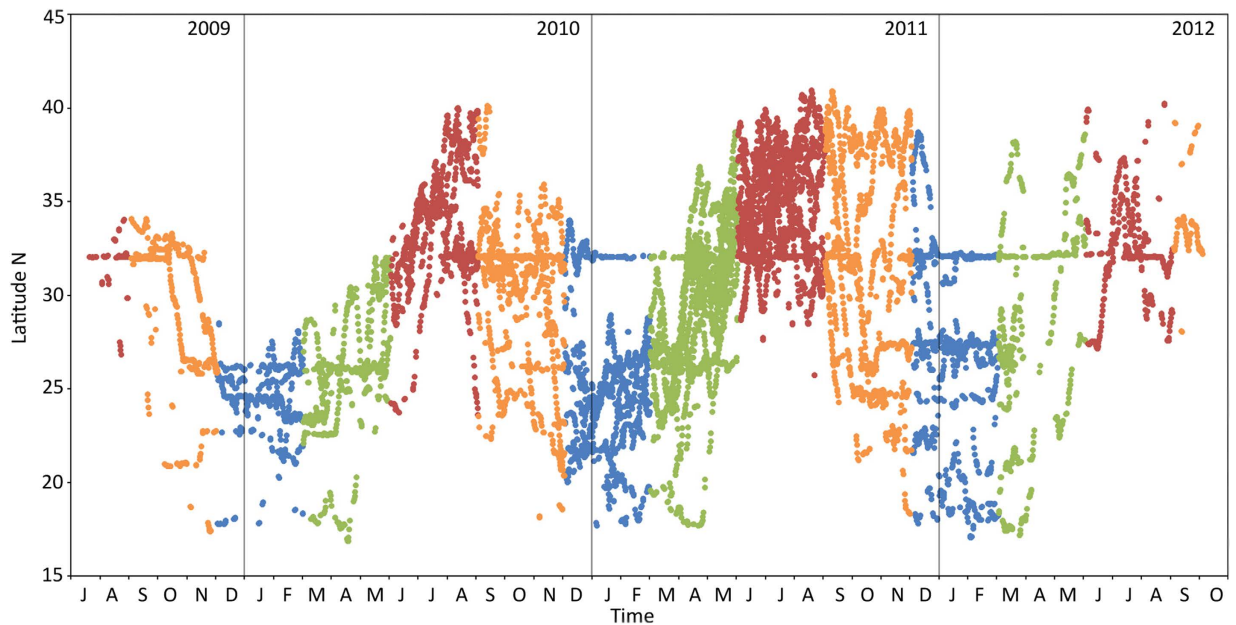


Figure 2. Latitude of all tiger shark locations over time (2009–2012), colour coded by season (blue = winter; green = spring; red = summer; orange = autumn).

Winter philopatry was high, whilst summer philopatry appeared low (Fig. 4). The mean winter-to-winter centroid displacement was 191.4 km (ranging 12.4–1036.2 km, SD 331.6 km), whereas the mean summer-to-summer centroid displacement was 756.1 km (ranging 51.0–1308.2 km, SD 386.2 km). The repeated, philopatric migration pattern is exemplified by shark 7, which displayed spatially restricted use of a particular insular region and offshore oceanic regions over 3,500 km away, punctuated by relatively direct dispersals (Fig. 5). In both years of its two year track, shark 7 occupied the same area in the Bahamas during winter, displaying a winter-to-winter centroid displacement of only 65.7 km, although its centroid displacement between summers was 819.2 km. Over a three year track, shark 1 displayed similar insular winter philopatry (centroid displacements of 24.3 and 56.2 km), but also some degree of philopatry to offshore areas over 2,500 km away across consecutive summers, with summer-to-summer centroid displacements of 51.0 km and 545.3 km. In contrast, use of insular areas by shark 4 was comparatively dispersed, spending no more than 13 days within any given cell and providing multiple centroids for each season (Supporting Information, Fig. S5).

Straightness of movement. Analysis of the comparative straightness of shark movements revealed overall reduced straightness around the southern islands, and also on the northern edge of the recorded range adjacent to the Gulf Stream. In contrast, shark movements were more directed in the oceanic environment in between these locations (Supporting Information, Fig. S4b). Despite lower occupancy compared to insular regions, the north-eastern area of the tracked sharks' range (south of the Flemish Cap and in the general proximity of the Corner Rise Seamounts) is an area of particularly high turning frequency. Considering only summer straightness of movement emphasises this high turning frequency further (Supporting Information, Fig. S6). Overlaid with the juvenile loggerhead turtle *Caretta caretta* tracks of McClelland and Read (2007) and Mansfield *et al.* (2009), this area of high tiger shark turning overlaps with the pelagic distribution of *C. caretta* both in summer and year round (Supporting Information, Fig. S6). These turtle tracks overlapped with 37.6% of the $0.5^\circ \times 0.5^\circ$ cells in which the tiger sharks were recorded during summer. Moreover, the stomachs of four out of five tiger sharks opportunistically sampled from a commercial long-lining vessel contained *C. caretta*, including small juveniles consumed whole (Supporting Information, table 2; Fig. S6).

Discussion

Our study is one of only a handful in obtaining multi-year, continuous, high resolution tracks of individual fish migrations^{4,6–8,10,11}, and provides the first report of annually repeated, distinct seasonal migrations for tiger sharks in the Atlantic. The satellite tracks are also the longest reported for individual tiger shark movements to date throughout their distribution (up to 1101 days, previously 517 days³⁴). This apex marine predator displays remarkable plasticity in ecosystem use, accomplished by extensive, seasonal migrations between insular, coral reef ecosystems in winter and temperate oceanic, potentially foraging areas in summer. These round-trip migrations span over 7,500 km annually, with individuals displaying marked philopatry to overwintering areas. These migrations are also partial in nature: the five sharks

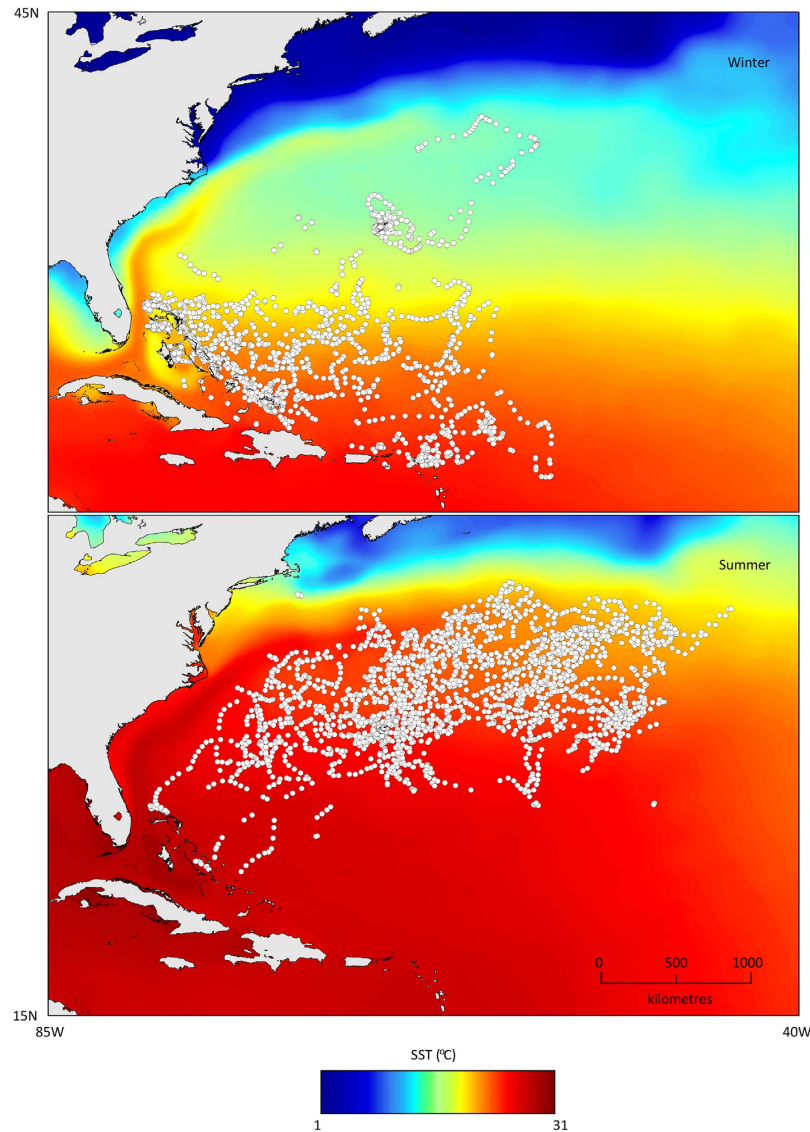


Figure 3. SSM corrected geolocations for all tiger sharks in winter and summer, overlaid on mean seasonal sea surface temperature (SST). Maps created in ArcGIS, using GSHHG coastline data and OSTIA SST data.

that remained close to Bermuda over winter were all juveniles (including both sexes), whilst all migrants were large males, with the exception of the single mature female tracked.

Use of disparate, contrasting habitats is common among diadromous fish, but the repeated switching between such markedly different ecosystems (in terms of thermal regime, bathymetry, structural complexity and insular coral reef to oceanic ecosystems) as we show here for the tiger shark is not commonly reported for marine fish species. Consequently it is particularly notable that the sharks we tracked invested in dual strategies, switching between highly focused use of insular reef systems and dynamic use of open ocean, in addition to exhibiting strong, repeated migratory philopatry to overwintering sites. Philopatry may improve foraging success and be less costly than searching for other suitable habitat elsewhere, potentially enhancing individual fitness³⁶.

Few marine fish have been shown to adopt such marked behavioural plasticity in ecosystem use, in particular repeated within individuals across years. The closest parallel reported among elasmobranchs is for endothermic sharks in contrast to the ectothermic tiger shark. For example, the white shark *Carcharodon carcharias* in the Pacific and Indian Oceans switches between high fidelity to particular coastal areas and long-distance migrations to oceanic areas^{7,9,37}. The closely related salmon shark *Lamna ditropis* also makes long-distance migrations offshore in the Pacific Ocean, before returning to specific regions of the Alaskan coast⁶. For ectothermic sharks, philopatry to tropical insular regions has been shown for the sympatric oceanic whitetip shark *Carcharhinus longimanus*, which returns to

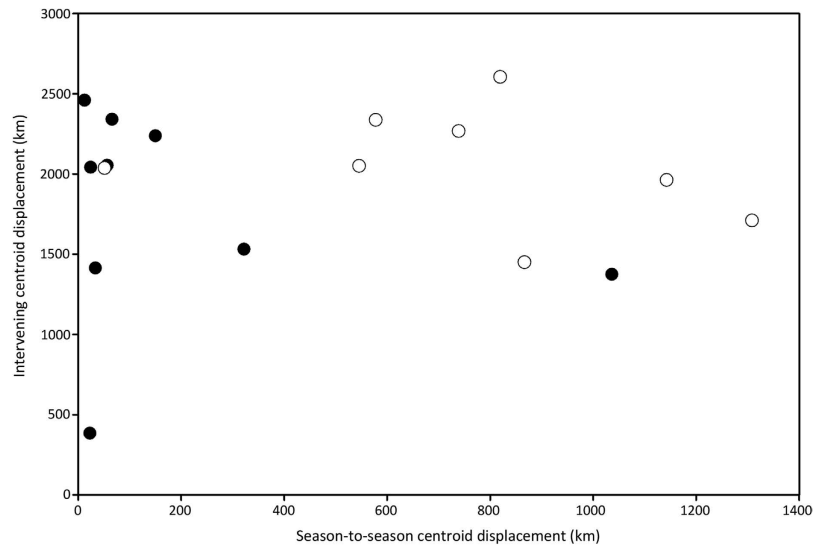


Figure 4. The relation between season-to-season centroid displacement (‘●’ = winter; ‘○’ = summer) and the intervening centroid displacement for both successive winters and summers, from sharks with tracks of two years or more.

particular areas of the Bahamas after movements into the Atlantic³⁸, however this behaviour has not been demonstrated across multiple years nor across as vast oceanic distances as displayed by the tiger sharks. Among teleosts, some large, temperate, demersal species such as Atlantic cod *Gadus morhua* are known to return to within a few kilometres of the previous year’s spawning sites, despite long-distance migrations in between to foraging grounds³⁹. However, the behaviours displayed by the tiger sharks migrating between tropical islands and distant, higher latitude, temperate oceanic zones are seemingly more similar to some turtle, bird and mammal movements than to other fish. For instance, loggerhead turtles display a marked dichotomy of ranging behaviours, switching between coastal and oceanic habits, often returning to within a few kilometres of previous foraging sites^{36,40}. Leatherback turtles *Dermochelys coriacea* display similar seasonal movements, associating with aggregations of gelatinous zooplankton in the Irish Sea in summer⁴¹. Among birds, Cory’s shearwaters *Calonectris diomedea* in the Atlantic undertake long-distance, trans-equatorial, round-trip migrations between particular nesting sites and foraging areas³, as do sooty shearwaters *Puffinus griseus* in the Pacific⁴². Baleen whales, such as the humpback whale, *Megaptera novaeangliae*, exemplify similarly substantial repeat migrations in mammals, which move thousands of kilometres seasonally between near-polar feeding grounds and tropical breeding grounds⁴³. Southern elephant seals *Mirounga leonina* have also been demonstrated to show very high fidelity to offshore foraging areas in the Antarctic between years⁴⁴.

Understanding the motivations behind such migrations will better enable prediction of how movements might respond to environmental changes. However, despite a number of tracking studies correlating animal movements with environmental variables^{4,8,45,46}, the motivation for migration often remains unknown^{7,8,32}. The tracked tiger sharks migrated north in spring and summer as sea surface temperatures increase, displaying very high turning frequencies in the north and north eastern extent of their range, which may reflect potential foraging activity⁴⁷. Another ocean migrant, the leatherback turtle, displays similarly high foraging activity at higher latitudes, following extended migration from tropical waters⁴¹. In addition, the northerly limit of tiger shark movements may be driven by thermal preferences, as it appears from comparisons with seasonal SST that their movements are contained within an isotherm of approximately 24 °C. Isotherms are thought to drive range limits of other ectothermic species, such as leatherback turtles, which also undertakes large north-south movements in the Atlantic⁴⁸. Consequently a conceivable motivation for the sharks to migrate in the summer may be foraging opportunities in the area, including on juvenile turtles, cued by increasing sea surface temperature. Elsewhere turtles make up a significant portion of the diets of larger individual tiger sharks^{24,25}, so it is possible that the tracked tiger sharks may migrate to exploit an abundance of preferred prey in the summer, connecting the trophic ecologies of disparate coral reef and oceanic ecosystems. However, this hypothesis remains untested and requires further investigation; for instance turtles may simply appear more prevalent in a diet if their shells digest more slowly than other items.

As the majority of sharks tagged in our study were mature males, a possible reason for them to return from foraging to their overwintering areas is to find mates. Consistent with our study, some large female tiger sharks tracked from the Bahamas have also travelled long distances into the Sargasso Sea, but most remained relatively close to the Bahamas and Florida²⁹, where there is an apparent peak in pupping

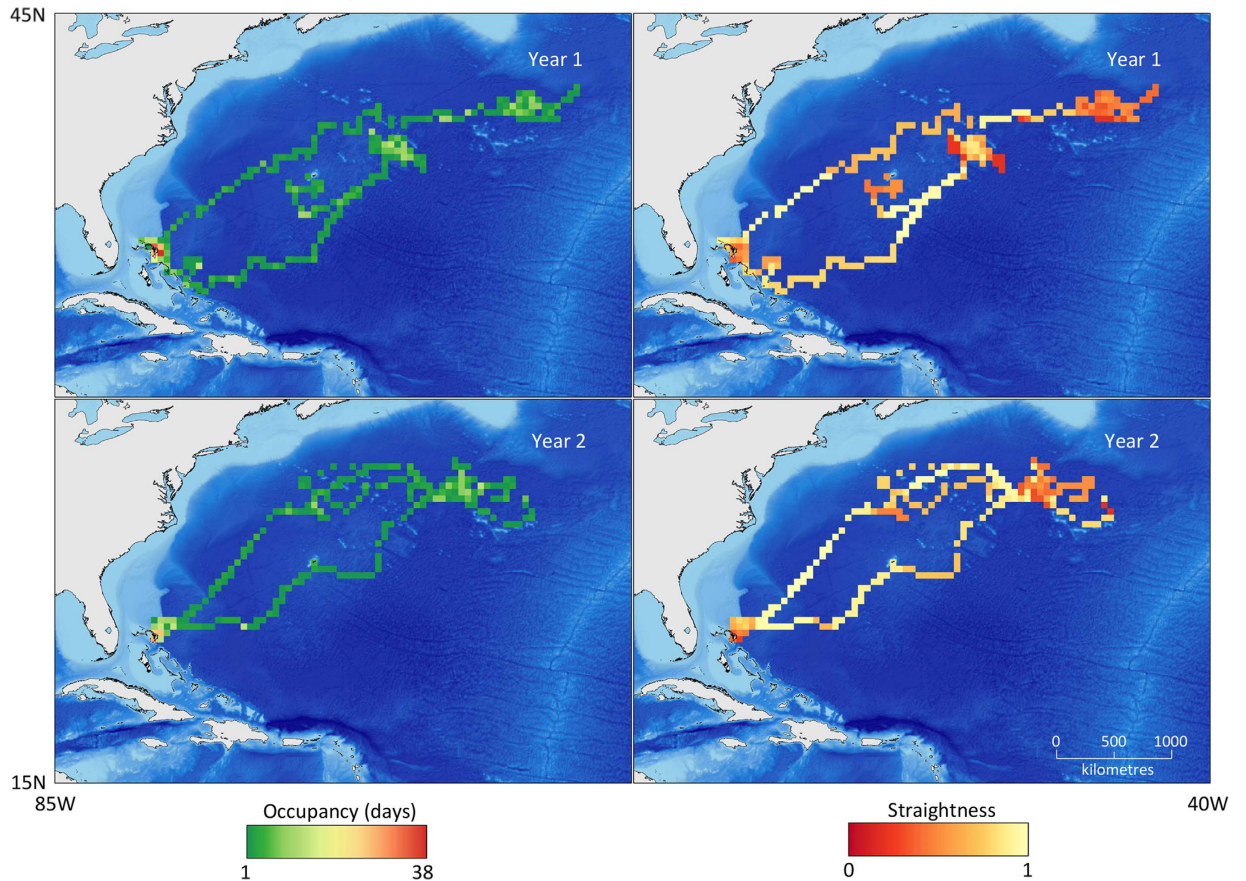


Figure 5. The occupancy and mean straightness of movement for shark 7 (384 cm male) for the first and second year of its track (measured from tagging date). Maps created in ArcGIS, using GSHHG coastline data and ETOPO2v2 bathymetry data.

during early summer⁴⁹. Given that tiger sharks in the northwest Atlantic have a 13–16 month gestation period⁵⁰, mating should have peaked in late winter/early spring, when adults of both sexes are known to be in tropical insular regions. Although other factors may be involved, including foraging and thermal preferences, given the available information it is reasonable to hypothesise that a driver of winter philopatry is returning for mating opportunities.

Complex population structure and extensive movements by a segment of the population can result in regional fishing activity having disproportionate effects on different population components¹⁹. Thus, understanding potential demographic segregation and partial migration patterns – who goes where, when and why – is crucial for the sustainable management of any population. Partial migration is widespread across taxa, although the driving processes often remain unclear, with animal size, sex, condition and personality (e.g. boldness) all reported as factors contributing towards the propensity to migrate or not⁵¹. Partial migration has been reported for female tiger sharks in Hawaii based on presence/absence data from acoustic telemetry, where seasonal presence appears to be associated with reproductive state and individual foraging targets⁸. From work on other species it has been suggested that swim speed and migration propensity and ability may be linked to size-related dispersal ability^{51,52}. This is consistent with the observation in the present study that distance travelled per month increased with tiger shark length and, furthermore, that all individuals observed overwintering around Bermuda were comparatively small and immature⁵⁰. Similarly in Hawaii larger tiger sharks were also more likely to undertake long range movements⁸, and year-round residency has been reported for sub-adult tiger sharks at the Chesterfield Islands in the Coral Sea³². Work on salmonids *Coregonus* spp. suggests that smaller individual fish within an ectothermic species may incur a greater metabolic cost in warmer waters, potentially reducing the benefits of migration⁵³. If such a size-dependent limitation on long-distance dispersal were applicable to tiger sharks, it would be consistent with our observation of fewer smaller individuals migrating seasonally to exploit prey elsewhere and remaining within cooler water over winter. The overwintering of smaller, immature sharks in cooler waters is also consistent with the hypothesis of mating as a driver for southerly migrations of mature individuals.

Individual condition may therefore be a strong driver of migration propensity in tiger sharks: adults may be of sufficient condition to absorb the costs of migration to exploit disparate, but profitable, food

sources, with females possibly skipping migration if gravid, whilst juveniles may have to invest more in somatic growth.

Such segregated use of large oceanic areas by size, as shown here, combined with high fidelity to particular regions, can result in differential exploitation by spatially-focused fisheries and contribute towards rapid population declines^{19,54}. With the observed size-related migration differences in tiger sharks, such differential exploitation by long-line fisheries in summer could disrupt the age structure of the population, exacerbating any impact of fisheries-induced mortalities. Some overwintering sites are covered by the Bahamian Exclusive Economic Zone, where long-lining and commercial trade of shark is prohibited, whereas sharks migrating to oceanic areas may be at greater risk of fishing mortality. This highlights the need for informed, spatially dynamic, management and conservation measures, such as the designation of MPAs or time/area closures of fisheries in summer foraging areas, or for greater spatial protection of philopatric overwintering sites.

Our study reveals unexpected predictability in tiger shark horizontal movements in the northwest Atlantic, which contrasts with the high intraspecific variability observed in their vertical movement behaviour in the same region²⁸. They seasonally and repeatedly switch between coastal coral reef and temperate oceanic habitats, displacing thousands of kilometres in the process, yet also showing marked philopatry to overwintering sites. However, the expansive movements of tiger sharks throughout the northwest Atlantic leaves them exposed to international fisheries for extended periods of time. Understanding these migration patterns, particularly when partial in nature and size segregated, is crucial for future conservation efforts. Identifying where tiger sharks may focus their movements and use migration corridors will inform assessments of where, when and how high space-use areas overlap with commercial fisheries in the North Atlantic.

Methods

We tagged 24 tiger sharks with Argos satellite platform terminal transmitters, or PTTs (SPOT5, Wildlife Computers, Redmond, Washington, USA) between August 2009 and July 2012 at Challenger Bank (N 32°05', W 065°03') near Bermuda in the northwest Atlantic (Supporting Information, table S1). All field work was approved by, and conducted with the knowledge of, the Marine Resources Section of the Bermuda Department of Environmental Protection. The shark handling and tagging methods were performed in accordance with the approved guidelines of Nova Southeastern University. The SPOT5 tag location accuracy is determined by the timing and number of transmissions received by Argos satellites within a single overpass⁵⁵. The location classes (LCs) available are 3, 2, 1, 0, A and B, with LC3 providing the lowest errors and LCB the highest^{56,57}.

As Argos positions vary in frequency and quality it was necessary to process the data to obtain normalised positions that were comparable between individuals and over time. The raw Argos positions were processed in three steps, each adopted to address a specific issue. Firstly, it was necessary to avoid inclusion of steps between positions that were deemed too large to be biologically plausible, basing filter rules on previously documented swimming speeds for large sharks⁵⁸. To do this we analysed all raw positions point-to-point with a 3 m s⁻¹ swim speed filter and 20 km distance filter: any position separated from both adjacent positions by either too great a distance or speed were shifted to a linearly interpolated position between the two (i.e. the most parsimonious location). Positions where either the distance or speed to only one of the adjacent positions was too great were ignored. Secondly, because each raw position has a different error field according to its Argos location class, we needed to decide the most probable location for each point within its error field. We achieved this by using a Bayesian state-space model (SSM) that adjusted the filtered tracks by producing regular positions based on the Argos location class, mean turning angle, and autocorrelation in speed and direction, producing the most probable track through the error fields⁵⁹. Given that 80.1% of gaps between positions in our tracks were under 12 hours (Supporting Information, Fig. S1), we used a time step of 12 hours in the SSM to produce two positions per day for each shark's track. However, the SSM produces regular positions for the entire track, even on days where there were no raw positions. Consequently we deleted all positions for days on which there were no real Argos transmissions. This step resulted in our normalised track positions and formed the dataset used for the plotting of positions on maps by season and plotting latitude over time to display how the distribution of animals changes over time.

Argos tracks only have locations for when the sharks were at the surface; consequently there is high variability in the number of locations in a given area, as a result of the shark's varied surfacing behaviour rather than because of its actual location. This would introduce a bias into the analysis of time spent in different areas. To correct this bias, linear interpolation was used to normalise the transmission frequency by generating points at 12 hour intervals along track gaps of <20 days. Where gaps >20 days were encountered the track was split into sections to avoid spurious interpolation. Moreover, in order for these space-use analyses to be as conservative as possible, all were conducted at a grid resolution of 0.5° × 0.5°, greater than the reported errors of the worst location class (LCB, ~10 km^{56,57}). Examples of how track positions varied between each processing step can be found in Figure S2 of the Supporting Information.

To determine track sections with higher turning frequency from those with more directed movement, the 'straightness' of individual trajectories was calculated for successive 12 day portions of each SSM processed, linearly interpolated track, where:

$$\text{Straightness} = \text{displacement over 12 days} / \text{distance travelled over 12 days}$$

Values closer to 1 indicate periods of straighter movement, and values closer to 0 indicate periods of higher turning frequency, providing a proxy for station-keeping or area-restricted searching (foraging) behaviour⁴⁷. Straightness was calculated over 12 day periods as this was, on average, the time taken for the sharks to traverse a distance greater than the error of the worst location class (LCB, ~10 km^{56,57}). The mean distance travelled per month was also calculated for each individual, and correlated with individual total length using a Spearman rank correlation.

To perform analyses on space-use and movement behaviour, the SSM normalised, linear interpolated tracks were plotted on a 0.5° × 0.5° grid cell in ArcGIS (ESRI Inc., CA, USA). Coastline and bathymetry data were obtained from the U.S. Department of Commerce, National Oceanic and Atmospheric Administration (NOAA): coastlines from the Global Self-consistent, Hierarchical, High-resolution Geography Database (GSHHG) and bathymetry from the 2-minute Gridded Global Relief Data (ETOPO2v2). Computerised digital images and associated databases are available from the National Geophysical Data Center, NOAA, U.S. Department of Commerce, <http://www.ngdc.noaa.gov/>. Sea surface temperature (SST) data were obtained from the Operational Sea Surface Temperature and Sea Ice Analysis (OSTIA) system via the U.K. National Centre for Ocean Forecasting (Contains public sector information licensed under the Open Government Licence v3.0 <http://www.nationalarchives.gov.uk/doc/open-government-licence/version/3/>). All maps were created using the Plate Carrée projection.

The total time spent within each cell (occupancy) was calculated by summing the number of 12-hourly points located within cells. The mean straightness for each 0.5° × 0.5° cell was calculated by averaging the straightness values associated with points located within them. This was performed for all sharks combined as well as individuals, and for both complete tracks and tracks separated by season to address any seasonality in distribution. The seasons were defined as follows: Winter, Dec–Feb; Spring, Mar–May; Summer, Jun–Aug; Autumn, Sep–Nov. When occupancy was calculated for all sharks combined, the results were corrected for tagging location by dividing the occupancy value for each 0.5° × 0.5° cell by the number of tags active in that cell. The overall geographical range of tracked sharks was calculated in ArcGIS using the 95% isopleth of the kernel density estimate for all locations.

For qualitative comparison of seasonal distribution of locations with sea surface temperature (SST), track locations were overlaid in ArcGIS on seasonal SST means throughout the northwest Atlantic. In addition, the mean monthly SST for 5° × 2° areas at the northern and southern extents of the tracked sharks' range were calculated to examine the SSTs likely experienced by sharks at the surface when in those areas compared to the typical annual variation in SST. The bounding for the northern extent was 37–39°N by 62–57°W, and for the southern extent was 24–26°N by 76–71°W.

A number of sharks displayed focused space-use in both winter and summer, so potential philopatry was tested for in individuals with sufficiently long tracks to cover repeat seasons ($n = 9$ sharks). First, central locations were calculated for individuals for each winter and summer period, defined as the central point, or centroid, of the 5% isopleth of the kernel density estimate for that season, and calculated using Geospatial Modelling Environment⁶⁰. Season-to-season centroid displacement was then plotted against intervening centroid displacement for both successive winters and summers to test the spatial resolution at which sharks returned to a particular location given the intervening long-distance migration.

One of the authors (GRM) was opportunistically able to retain the stomachs of the five tiger sharks caught by a Spanish commercial long-lining vessel operating in the northwest Atlantic in 2012 for contents analysis whilst acting as a scientific observer on-board. The stomachs appeared to predominantly contain juvenile loggerhead turtles *Caretta caretta* (Linnaeus, 1758), and so maps of spatial and temporal variation in the straightness index were compared to the locations of juvenile loggerhead turtles as determined by satellite tracks reported in McClellan and Read (2007) and Mansfield *et al.* (2009). The loggerhead tracks were digitised using ArcGIS, where they were projected to the correct spatial reference and had their features recreated manually. To quantify any spatial overlap, the percentage of 0.5° × 0.5° grid cells in which both tiger sharks and loggerhead turtles were tracked was calculated in ArcGIS.

All shark tracks used in the present study are available for viewing on the Nova Southeastern University website: <http://www.nova.edu/ocean/ghri/tracking/>. However, given the tiger shark is listed as 'near threatened' in the IUCN Red List, the raw, detailed location data are considered sensitive information. Consequently the raw tracks are not freely available at present so as not to encourage further fisheries interactions.

References

- Dingle, H. & Drake, V. A. What is migration? *Bioscience* **57**, 113–121 (2007).
- Turchin, P. *Quantitative Analysis of Movement: measuring and modeling population redistribution in plants and animals*. (Sinauer Associates, Sunderland, MA, 1998).
- González-Solis, J., Croxall, J. P., Oro, D. & Ruiz, X. Trans-equatorial migration and mixing in the wintering areas of a pelagic seabird. *Front. Ecol. Environ.* **5**, 297–301 (2007).
- Block, B. A. *et al.* Tracking apex marine predator movements in a dynamic ocean. *Nature* **475**, 86–90 (2011).
- Hays, G. C. & Scott, R. Global patterns for upper ceilings on migration distance in sea turtles and comparisons with fish, birds and mammals. *Funct. Ecol.* **27**, 748–756 (2013).
- Weng, K. C. *et al.* Migration of an upper trophic level predator, the salmon shark *Lamna ditropis*, between distant ecoregions. *Mar. Ecol. Prog. Ser.* **372**, 253–264 (2008).
- Jorgensen, S. J. *et al.* Philopatry and migration of Pacific white sharks. *Proc. B: Biol. Sci.* **277**, 679–688 (2010).
- Papastamatiou, Y. P. *et al.* Telemetry and random-walk models reveal complex patterns of partial migration in a large marine predator. *Ecology* **94**, 2595–2606 (2013).

9. Domeier, M. L. & Nasby-Lucas, N. Two-year migration of adult female white sharks (*Carcharodon carcharias*) reveals widely separated nursery areas and conservation concerns. *Animal Biotelemetry* **1**, 1–10 (2013).
10. Vandeperre, F. *et al.* Movements of blue sharks (*Prionace glauca*) across their life history. *PLoS ONE* **9**, e103538 (2014).
11. Chapman, D. D., Feldheim, K., Papastamatiou, Y. & Hueter, R. E. There and back again: a review of residency and return migrations in sharks, with implications for population structure and management. *Annu. Rev. Mar. Sci.* **7**, 547–570 (2015).
12. Worm, B. & Branch, T. A. The future of fish. *Trends Ecol. Evol.* **27**, 594–599 (2012).
13. Ferretti, F., Worm, B., Britten, G. L., Heithaus, M. R. & Lotze, H. K. Patterns and ecosystem consequences of shark declines in the ocean. *Ecol. Lett.* **13**, 1055–1071 (2010).
14. Burgess, G. H. *et al.* Is the collapse of shark populations in the Northwest Atlantic Ocean and Gulf of Mexico real? *Fisheries* **30**, 19–26 (2005).
15. Baum, J. K., Kehler, D. & Myers, R. A. Robust estimates of decline for pelagic shark populations in the northwest Atlantic and Gulf of Mexico. *Fisheries* **10**, 26–28 (2005).
16. Ferretti, F., Myers, R. A., Serena, F. & Lotze, H. K. Loss of large predatory sharks from the Mediterranean Sea. *Conserv. Biol.* **22**, 952–964 (2008).
17. Baum, J. K. *et al.* Collapse and conservation of shark populations in the northwest Atlantic. *Science* **299**, 389–392 (2003).
18. International Commission for the Conservation of Atlantic Tuna (ICCAT). *Report of the 2008 shark stock assessments meeting. Collective Volume of Scientific Papers* 1343–1491 (2009).
19. Mucientes, G. R., Queiroz, N., Sousa, L. L., Tarroso, P. & Sims, D. W. Sexual segregation of pelagic sharks and the potential threat from fisheries. *Biol. Lett.* **5**, 156–159 (2009).
20. Queiroz, N., Humphries, N. E., Noble, L. R., Santos, A. M. & Sims, D. W. Spatial dynamics and expanded vertical niche of blue sharks in oceanographic fronts reveal habitat targets for conservation. *PLoS ONE* **7**, e32374 (2012).
21. Game, E. T. *et al.* Pelagic protected areas: the missing dimension in ocean conservation. *Trends Ecol. Evol.* **24**, 360–369 (2009).
22. Compagno, L. J. Sharks of the world: an annotated and illustrated catalogue of shark species known to date. *FAO Species Catalogue for Fishery Purposes* **2**, 269 (Food & Agriculture Org., 2001).
23. Simpfendorfer, C. *Galeocerdo cuvier*. IUCN Red List of Threatened Species. (2013). Available at: www.iucnredlist.org (Date of access: 13/06/2014).
24. Lowe, C. G., Wetherbee, B. M., Crow, G. L. & Tester, A. L. Ontogenetic dietary shifts and feeding behavior of the tiger shark, *Galeocerdo cuvier*, in Hawaiian waters. *Environ. Biol. Fish.* **47**, 203–211 (1996).
25. Simpfendorfer, C. A., Goodreid, A. B. & McAuley, R. B. Size, sex and geographic variation in the diet of the tiger shark, *Galeocerdo cuvier*, from Western Australian waters. *Environ. Biol. Fish.* **61**, 37–46 (2001).
26. Matich, P., Heithaus, M. R. & Layman, C. A. Contrasting patterns of individual specialization and trophic coupling in two marine apex predators. *J. Anim. Ecol.* **80**, 294–305 (2011).
27. Heithaus, M. R. *et al.* Apparent resource partitioning and trophic structure of large-bodied marine predators in a relatively pristine seagrass ecosystem. *Mar. Ecol. Prog. Ser.* **481**, 225–237 (2013).
28. Vaudo, J. J. *et al.* Intraspecific variation in vertical habitat use by tiger sharks (*Galeocerdo cuvier*) in the western North Atlantic. *Ecol. Evol.* **4**, 1768–1786 (2014).
29. Hammerschlag, N., Gallagher, A. J., Wester, J., Luo, J. & Ault, J. S. Don't bite the hand that feeds: assessing ecological impacts of provisioning ecotourism on an apex marine predator. *Funct. Ecol.* **26**, 567–576 (2012).
30. Kohler, N., Casey, J. & Turner, P. NMFS cooperative shark tagging program, 1962–93: An atlas of shark tag and recapture data. *Mar. Fish. Rev.* **60**, 1–87 (1998).
31. Heithaus, M. R., Wirsing, A. J., Dill, L. M. & Heithaus, L. I. Long-term movements of tiger sharks satellite-tagged in Shark Bay, Western Australia. *Mar. Biol.* **151**, 1455–1461 (2007).
32. Werry, J. M. *et al.* Reef-fidelity and migration of tiger sharks, *Galeocerdo cuvier*, across the Coral Sea. *PLoS ONE* **9**, e83249 (2014).
33. Holmes, B. J. *et al.* Tiger shark (*Galeocerdo cuvier*) movement patterns and habitat use determined by satellite tagging in eastern Australian waters. *Mar. Biol.* **161**, 2645–2658 (2014).
34. Ferreira, L. C. *et al.* Crossing latitudes—long-distance tracking of an apex predator. *PLoS ONE* **10**, e0116916 (2015).
35. Heithaus, M. R. The biology of tiger sharks, *Galeocerdo cuvier*, in Shark Bay, Western Australia: sex ratio, size distribution, diet, and seasonal changes in catch rates. *Environ. Biol. Fish.* **61**, 25–36 (2001).
36. Schofield, G. *et al.* Biodiversity Research: fidelity to foraging sites, consistency of migration routes and habitat modulation of home range by sea turtles. *Divers. Distrib.* **16**, 840–853 (2010).
37. Sims, D. W., Humphries, N. E., Bradford, R. W. & Bruce, B. D. Lévy flight and Brownian search patterns of a free-ranging predator reflect different prey field characteristics. *J. Anim. Ecol.* **81**, 432–442 (2012).
38. Howey-Jordan, L. A. *et al.* Complex movements, philopatry and expanded depth range of a severely threatened pelagic shark, the oceanic whitetip (*Carcharhinus longimanus*) in the Western North Atlantic. *PLoS ONE* **8**, 56588 (2013).
39. Robichaud, D. & Rose, G. A. Multiyear homing of Atlantic cod to a spawning ground. *Can. J. Fish. Aquat. Sci.* **58**, 2325–2329 (2001).
40. Hawkes, L. A. *et al.* Home on the range: spatial ecology of loggerhead turtles in Atlantic waters of the USA. *Divers. Distrib.* **17**, 624–640 (2011).
41. Houghton, J. D. R., Doyle, T. K., Wilson, M. W., Davenport, J. & Hays, G. C. Jellyfish aggregations and leatherback turtle foraging patterns in a temperate coastal environment. *Ecology* **87**, 1967–1972 (2006).
42. Shaffer, S. A. *et al.* Migratory shearwaters integrate oceanic resources across the Pacific Ocean in an endless summer. *Proc. Natl. Acad. Sci.* **103**, 12799–12802 (2006).
43. Stone, G., Florez-Gonzalez, L. & Katona, S. Whale migration record. *Nature* **346**, 705 (1990).
44. Bradshaw, C. J. A., Hindell, M. A., Sumner, M. D. & Michael, K. J. Loyalty pays: potential life history consequences of fidelity to marine foraging regions by southern elephant seals. *Anim. Behav.* **68**, 1349–1360 (2004).
45. Hays, G. C., Hobson, V. J., Metcalfe, J. D., Righton, D. & Sims, D. W. Flexible foraging movements of leatherback turtles across the North Atlantic Ocean. *Ecology* **87**, 2647–2656 (2006).
46. Queiroz, N., Humphries, N. E., Noble, L. R., Santos, A. M. & Sims, D. W. Short-term movements and diving behaviour of satellite-tracked blue sharks *Prionace glauca* in the northeastern Atlantic Ocean. *Mar. Ecol. Prog. Ser.* **406**, 265–279 (2010).
47. Sims, D. W. Tracking and analysis techniques for understanding free-ranging shark movements and behaviour in *Sharks and their relatives II: biodiversity, adaptive physiology, and conservation* (eds Carrier, J. C., Musick, J. A., Heithaus, M. R.) Ch. 8, 351–392 (CRC Press, 2010).
48. McMahon, C. R. & Hays, G. C. Thermal niche, large-scale movements and implications of climate change for a critically endangered marine vertebrate. *Glob. Change Biol.* **12**, 1330–1338 (2006).
49. Natanson, L. J., Casey, J. G., Kohler, N. E. & Colket, T. Growth of the tiger shark, *Galeocerdo cuvier*, in the western North Atlantic based on tag returns and length frequencies; and a note on the effects of tagging. *Fish. Bull.* **97**, 944–953 (1999).
50. Branstetter, S., Musick, J. A. & Colvocoresses, J. A. A comparison of the age and growth of the tiger shark, *Galeocerdo cuvier*, from off Virginia and from the northern Gulf of Mexico. *Fish. Bull.* **85**, 269–279 (1987).

51. Chapman, B. B. *et al.* Partial migration in fishes: causes and consequences. *J. Fish Biol.* **81**, 456–478 (2012).
52. Weihs, D. Effects of size on sustained swimming speeds of aquatic organisms in *Scale Effects in Animal Locomotion* (ed Pedley, T. J.) 333–338 (New York: Academic Press, 1977).
53. Mehner, T. & Kasprzak, P. Partial diel vertical migrations in pelagic fish. *J. Anim. Ecol.* **80**, 761–770 (2011).
54. Ford, E. A contribution to our knowledge of the life-histories of the dogfishes landed at Plymouth. *J. Mar. Biol. Assoc. UK* **12**, 468–505 (1921).
55. Taillade, M. Animal tracking by satellite in *Wildlife telemetry: remote monitoring and tracking of animals* (eds Priede, I. G., Swift, S. M.) 149–160 (Ellis Horwood, Ltd, 1992).
56. Hazel, J. Evaluation of fast-acquisition GPS in stationary tests and fine-scale tracking of green turtles. *J. Exp. Mar. Biol. Ecol.* **374**, 58–68 (2009).
57. Hays, G. C., Åkesson, S., Godley, B. J., Luschi, P. & Santidrian, P. The implications of location accuracy for the interpretation of satellite-tracking data. *Anim. Behav.* **61**, 1035–1040 (2001).
58. Bruce, B. D., Stevens, J. D. & Malcolm, H. Movements and swimming behaviour of white sharks (*Carcharodon carcharias*) in Australian waters. *Mar. Biol.* **150**, 161–172 (2006).
59. Jonsen, I. D., Flemming, J. M. & Myers, R. A. Robust state-space modeling of animal movement data. *Ecology* **86**, 2874–2880 (2005).
60. Beyer, H. L. Geospatial modelling environment. *Spatial Ecology*. Available at www.spatial ecology.com/gme (2011). (Date of access: 28/03/2013)

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Author Contributions

N.B., C.A., G.M.H., B.M.W. and M.S.S. conceived the study and performed the field work. N.Q. and L.L.S. advised on, and assisted with, track analysis techniques. N.E.H. wrote software to automate track processing. D.W.S. oversaw the manuscript structure and analysis techniques. J.S.E.L. performed the analyses and created all figures. G.R.M. provided the stomach contents data. J.S.E.L., B.M.W., D.W.S. and M.S.S. wrote the manuscript.

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6

7 **To Madagascar and back: long-distance, return migration across open ocean by a**
8 **pregnant female bull shark *Carcharhinus leucas***

9

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21

22 *Lea et al.* Bull shark pupping migration

23 **Abstract**

24 A large, pregnant, female bull shark *Carcharhinus leucas* was tracked migrating from the
25 Seychelles across open ocean to southeast Madagascar, approximately 2,000 km away, and
26 back again. In Madagascar the shark spent a prolonged period shallower than 5 m, consistent
27 with entering estuarine habitat to pup, and upon return to Seychelles the shark was slender
28 and no longer gravid. This represents an unprecedented return migration across open ocean
29 for a *C. leucas*, and highlights the need for international collaboration to manage the regional
30 *C. leucas* population sustainably.

31

32 Keywords: geolocation, philopatry, PSAT, parturition, satellite telemetry

33 Animal migration and its underlying motivations are important factors in the understanding
34 of population ecology. Where animal populations experience threats that jeopardise their
35 sustainability, such as overfishing, an understanding is crucial for the development of
36 informed management strategies. Although the study of movement behaviour in marine
37 animals has traditionally lagged behind terrestrial species, increasing availability of remote
38 telemetry is fuelling a growing literature on the spatial dynamics of marine species (Block *et*
39 *al.* 2011). In particular several shark species have been shown to perform extensive
40 migrations (Chapman *et al.* 2015), which is of particular concern given reports of severe
41 declines in shark populations (Worm & Branch 2012), and the difficulties of managing
42 species that traverse international boundaries and the high seas (Game *et al.* 2009).

43

44 In contrast to some areas of the Atlantic and Pacific, information on shark populations in the
45 Indian Ocean remains comparatively limited. The available information suggests the outlook
46 is similarly poor. For example, in the Seychelles, from where large quantities of shark meat
47 were exported during the 19th and 20th centuries, surveys of local fishermen suggest that
48 shark populations have declined dramatically (Nevill *et al.* 2007), with sightings of larger
49 sharks becoming exceptionally rare (Smith & Smith 1969). Yet in 2003–2005 shark fishing
50 was intensified in the Seychelles, following the European Union ban on import of local
51 swordfish, a principal target species, due to their high cadmium levels (Nevill *et al.* 2007).
52 Declines have been further exacerbated by increased targeting of large sharks following two
53 fatal attacks on tourists in 2011, at least one of which can be attributed to a bull shark
54 *Carcharhinus leucas* (Müller & Henle, 1839) through genetic analysis of a tooth fragment
55 (Seychelles Nation 2011). Thus even now there is intense fishing pressure on sharks in the
56 Seychelles, putting populations at risk of severe declines. Consequently the movement
57 behaviour of sharks, especially *C. leucas*, is now of particular interest in Seychelles, both

58 from a fisheries management perspective and due to concerns of potential risks to human
59 safety.

60

61 Apart from its presence in local waters, little is known about the ecology of *C. leucas* in the
62 Seychelles. *C. leucas* is a large predatory shark (up to 4 m), found worldwide in tropical and
63 warm temperate coastal waters, making seasonal appearances in cool temperate waters
64 (Compagno 2001). *C. leucas* has been assessed as Near Threatened on the IUCN Red List,
65 mostly escaping targeted fisheries but kept as lucrative bycatch for their large fins
66 (Simpfendorfer & Burgess 2009). Unlike other carcharhinids, *C. leucas* is able to tolerate
67 fresh water, with females pupping in rivers or estuaries (Springer 1963), which the juveniles
68 use as nurseries (Snelson, Mulligan & Williams 1984). *C. leucas* has been found thousands of
69 kilometres inland up rivers (Thorson 1972; Thomerson 1977), but to date the majority of
70 recorded movements have remained coastal. The present study set out to determine the
71 movement patterns of *C. leucas* in the Seychelles to aid management efforts, and presents
72 here an early result deemed of sufficient novelty to warrant communication.

73

74 A 3 m female *C. leucas* was caught using a baited hand line and tagged with both an acoustic
75 transmitter (V16, Vemco Ltd, Canada, <http://vemco.com/>) and a pop-up satellite-linked
76 archival transmitter (PSAT) (Mk 10 PAT tag, Wildlife Computers, Redmond, Washington,
77 USA, <http://wildlifecomputers.com/>) on 21st August 2014 in the Amirantes, Seychelles (S
78 05°24', E 053°17'). The PSAT was set to record depth every 10 seconds, with temperature
79 and light levels being recorded every 5 minutes, and was attached to the shark via a
80 monofilament tether through the first dorsal fin, set to pop-off after six months. The acoustic
81 transmitter had a nominal delay of 60–180 seconds, and was surgically implanted into the
82 shark's coelom to prevent any risk of tag loss, while the shark lay in tonic immobility

83 alongside the research vessel. All field work was approved by, and conducted with the
84 knowledge of the Environment Department, Seychelles. The shark handling and tagging
85 methods were performed in accordance with the approved guidelines of the University of
86 Plymouth, UK.

87

88 The presence of the acoustic tag was recorded across the Amirantes by an array of 88
89 acoustic receivers (VR2W, Vemco Ltd, Canada, <http://vemco.com/>). Underwater visual
90 surveys were also performed at various locations in the Amirantes, whereby scuba divers
91 released chum and recorded the abundance and diversity of shark species encountered, along
92 with estimated size, sex, distinguishing marks, and notable behaviour. The tagged shark was
93 encountered during one such survey on 19/01/2015 and came close enough for the divers to
94 remove the PSAT, allowing retrieval of the raw archival data for analysis.

95

96 While the acoustic data reveals when the shark was recorded at particular receivers,
97 reconstructing movements outside the array, based on the PSAT archival data, relied on light-
98 based geolocation. The light-based geolocation was performed with Wildlife Computers'
99 Global Position Estimator (<http://wildlifecomputers.com/support/downloads/>), which uses tag
100 recorded light levels to estimate local time at midday and midnight and day length to provide
101 approximate longitudes and latitudes respectively. However, these Global Position Estimates
102 (GPE) have large error fields and perform poorly in estimating latitude near the equator or
103 close to equinoxes. The GPE longitude outputs had a mean error of 107.46 km (range 25.30–
104 798.12 km), while the GPE latitude outputs had a mean error of 493.90 km (range 27.80–
105 3,333.68 km). Consequently, to improve on these raw estimates, the locations were filtered
106 and refined by using a swim speed (diffusivity) filter and by matching sea surface
107 temperature pixels and bathymetry. The process involves two steps. The first is to generate a

108 'cloud' of possible waypoints at each reachable location; the second is to select the 'best'
109 waypoint at each location to produce a final, most probable path.

110

111 The process begins at the known deployment location by attempting to route to the first
112 (target) GPE location. A swim speed of 2 ms^{-1} together with the time to the target location is
113 used to define a circle representing the theoretically reachable area. This circle is intersected
114 with the ellipse defined by the GPE error estimate at the target location. If no intersection is
115 possible then the target location is considered unreachable and is rejected. The process then
116 continues with subsequent locations until a valid intersection is achieved. Pixels within the
117 intersection where the bathymetry (from GEBCO, 30 second resolution,
118 <http://www.gebco.net/>) is deeper than the maximum depth recorded on that day from the tag
119 archive data and where the daily Sea Surface Temperature estimate (from OSTIA,
120 http://ghrsst-pp.metoffice.com/pages/latest_analysis/ostia.html) is within 0.5°C of the
121 recorded tag temperature, are selected as possible 'waypoints'. If no matching pixels are
122 identified then the location is rejected.

123

124 The process then continues by attempting to route in the same manner from each waypoint at
125 the prior location to the next location, generating a collection of potential waypoints at each
126 reachable location, until all locations have been processed. Any known, rather than
127 estimated, locations, such as those from the acoustic array, the deployment and pop-up
128 locations are considered to be 'locked', are always routed to and have a single waypoint.
129 To determine the 'best' path through the reachable locations the process again begins at the
130 first location, which being known and locked comprises a single waypoint. Waypoints at the
131 next reachable location are scored according to the distance to the estimated location
132 coordinates, the SST difference and the distance from the prior waypoint. A 'best' waypoint

133 is selected by choosing a waypoint at random using a distribution constructed from the
134 waypoint scores to bias the selection to the higher scoring waypoints. Note, that if there is a
135 large spread of points at the two locations, that it is possible for no way point at a given
136 location to be reachable from the selected waypoint at a prior location, given the 2 ms^{-1} swim
137 speed. In these cases the location is rejected from this path. Waypoint selection is repeated in
138 his way at each reachable location. The result is a path which is then assigned a score equal to
139 the sum of the scores of the waypoints.

140

141 The process of path generation is continued, with better scoring paths being selected as the
142 'best' path until 500 new paths have been generated without improving on the score. The
143 'best' path points had reduced error fields, particularly for latitude: filtered latitude outputs
144 had a mean error of 199.64 km (range 5.53–1,084.10 km), with filtered longitude outputs
145 having a mean error of 147.52 km (5.34–798.65 km). The 'best' path locations also had low
146 standard deviations, with +/- 34.14 km latitude and +/- 24.28 km for longitude. This 'best'
147 path represented the final track used to plot the shark's movements. Estimating where the
148 shark was and when also allowed time-at-depth profiles to be assigned to particular locations
149 or portions of the track. Time-at-depth profiles were calculated as the proportion of time
150 spent within a particular depth range, either on a daily basis or across a particular portion of
151 the track (e.g. when migrating).

152

153 In total the movements of this large female *C. leucas* (300 cm total length) were tracked for
154 151 days from 21/08/2014. The final track consisted of 263 locations, comprising the tagging
155 location, 194 acoustic detections, 67 filtered light-based geolocations, and the location of tag
156 retrieval. During tagging the shark was notably gravid, presenting with considerable girth,
157 and the writhing movement of pups could be felt through the ventral surface. The shark was

158 then encountered again on 17/01/2015 and 19/01/2015 during underwater visual surveys,
159 appearing slender and with fresh bite marks on the left side.

160

161 Over the course of the track the shark is estimated to have travelled over 10,670 km at an
162 average speed of 0.82 ms^{-1} . The shark is known to have remained within the Amirantes until
163 at least 20/10/2014, which represents the last detection on the Amirantes acoustic array (at
164 Marie-Louise). After this the shark's movements inferred from the light-based geolocation
165 revealed a long-distance migration to the southeast coast of Madagascar (Fig. 1),
166 approximately 1,960 km away from the tagging location in the Amirantes. Between
167 20/10/2014 and approximately 19/11/2014, the shark travelled south from the Amirantes and
168 across open ocean to the northern tip of Madagascar, passing near the Farquhar group of
169 islands. The majority of geolocations available around Madagascar are focused along the
170 south-eastern coast. Around 29/12/2014 the shark started to head north again, reaching the
171 tagging area around 17/01/2015, having completed a roundtrip migration of approximately
172 4,000 km.

173

174 The shark displayed relatively restricted vertical movements, with the deepest dive during the
175 entire track being to 164 m (Fig. 2). The shark only experienced temperatures in excess of
176 20°C , ranging from 21°C at 164 m to 29°C at the surface, although the majority of time was
177 spent around 26°C . Whilst in the Amirantes the shark's depth profile appears restricted by
178 bathymetry. The Amirantes plateau barely gets deeper than 60–70m, and before leaving the
179 Amirantes in mid-October the shark spent 86.3% of its time shallower than 50 m, with 56.6%
180 of time spent at 30–50 m (Fig. 3). Despite this preference for deeper water, the shark
181 performed occasional rapid ascents to the surface (from ~ 60 m) at speeds of up to 4.3 ms^{-1} .

182

183 When migrating across open ocean (both to and from Madagascar), the shark displayed a
184 much broader range of depth use and tended to stay deeper than when on the Amirantes (Fig.
185 2), spending over a third of its time below 100 m (Fig. 3). The shark regularly dived to depths
186 of up to 164 m, often oscillating between 50 and 100 m. On several occasions the shark made
187 some marked accelerations to the surface, including one from 130 m to the surface over the
188 course of 60 s.

189

190 Once along the coast of Madagascar the shark displayed a marked change in depth use (Fig.
191 2), with 59.2% of time spent shallower than 5 m (Fig. 3). This is predominantly attributable
192 to the latter half of December, once the shark was along the southeast coast and remained
193 almost exclusively shallower than 5 m (Fig. 2).

194

195 This large, female *C. leucas* travelled from a remote chain of islands in the Seychelles to
196 southeast Madagascar, approximately 2,000 km away, before returning back to the
197 Seychelles. Previous tracking studies on *C. leucas* have generally reported relatively
198 restricted coastal movements (Kohler, Casey & Turner 1998; Brunnschweiler, Queiroz &
199 Sims 2010; Hammerschlag *et al.* 2012), with juveniles often being perennial residents in
200 estuarine nurseries (Heupel & Simpfendorfer 2008). Some large movements have been
201 recorded, such as 1,500 km along the coast of the United States (Carlson *et al.* 2010), and
202 2,000 km along the coast of South Africa to Mozambique (Save Our Seas Foundation, 2011).
203 *C. leucas* has been recorded moving over deeper water for short periods in the Gulf of
204 Mexico, the Gulf Stream, and Reunion Island near Madagascar (Carlson *et al.* 2010;
205 Brunnschweiler *et al.* 2010; Soria *et al.* 2015), but sustained, directed migration across open
206 ocean as presented here has not previously been reported. Consequently this return migration
207 is believed to be the first reported of its kind for *C. leucas*, being long-distance across deep,

208 open ocean, and also represents the longest known PSAT track of a *C. leucas* (151 days,
209 previously 85 (Carlson *et al.* 2010)).

210

211 This shark could have travelled to Madagascar for parturition. At the time of tagging the
212 shark was notably gravid, and the area of Madagascar it travelled to near Manakara has
213 several large rivers and estuaries nearby. As previously mentioned, female *C. leucas*
214 preferentially pup in riverine and estuarine habitats (Springer 1963). Moreover, when in this
215 area of Madagascar, the shark displayed a marked change in diving behaviour, remaining
216 almost exclusively shallower than 5 m for several days, consistent with entering a river or
217 estuary system. Immediately after leaving the shallower habitat, the shark resumed regular
218 diving behaviour all the way back to the Seychelles, where it was observed as slender and no
219 longer gravid. Consequently the shark must have pupped during the intervening absence from
220 the Seychelles, and the shallow depth profile in the vicinity of estuarine habitats in
221 Madagascar is therefore a plausible candidate for its pupping ground.

222

223 This result is particularly surprising given that juvenile *C. leucas* are encountered coastally
224 around Mahe in the Seychelles (pers. obs.), just over 200 km from the Amirantes. This raises
225 the question as to why this shark would migrate 2,000 km away if suitable habitat was much
226 nearer. Elsewhere female *C. leucas* are suspected of high reproductive philopatry, as
227 evidenced by highly restricted maternal gene flow between different nursery areas (Karl *et al.*
228 2011; Tillett *et al.* 2012). Some shark species even show natal philopatry, returning to their
229 own place of birth for parturition (Feldheim *et al.* 2014). Consequently this shark may simply
230 have exhibited strong, possibly natal, philopatry to a particular nursery area. Alternatively,
231 individual condition and the associated cost/benefit ratio may play a role in migration
232 propensity (Chapman *et al.* 2012). There is little suitable estuarine habitat around Mahe, so

233 perhaps the estuaries of Madagascar offer more favourable nursery habitat, and this
234 individual may have been of sufficient body condition to afford the costs of migration to seek
235 better habitat and survival odds for its offspring.

236

237 These data suggest that *C. leucas* life cycles in the southwest Indian Ocean may play out over
238 large geographical scales that cross international boundaries and the high seas, perhaps
239 constituting a single population. This highlights the need for international cooperation on
240 potential management efforts. How such collaboration can be achieved is exemplified by the
241 Memorandum of Understanding on the Conservation and Management of Marine Turtles and
242 their Habitats in the Indian Ocean and South-East Asia (IOSEA Marine Turtle MoU),
243 whereby signatory states have agreed to protect a network of sites important to marine turtles
244 (Hays *et al.* 2014). We propose that southwest Indian Ocean states adopt a similar initiative
245 for migratory sharks in the region, with signatories agreeing to share data and collectively
246 manage areas deemed of particular importance to regional populations, such as potential
247 nursery habitats for *C. leucas* in Madagascar. Madagascar may be an important pupping
248 habitat for *C. leucas* regionally, with genetic analysis also indicating gene flow between
249 Madagascar and Reunion Island 870 km to the east (Soria *et al.* 2015).

250

251 Further investigation incorporating genetics, shark condition and a larger sample size will be
252 required to fully understand the migratory behaviour of *C. leucas* in the Seychelles. In the
253 meantime, discovery of this novel, long-distance reproductive migration across open ocean
254 highlights a potentially important pupping and nursery area for *C. leucas* regionally, and that
255 management of this species will need to be considered across the ocean basin and not just
256 locally. Finally, this also suggests that potential risks to beachgoers may also vary seasonally,
257 and that southwest Indian Ocean states should collaborate on strategies to mitigate risk.

258

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264 **References**

265

266 Block, B.A., Jonsen, I.D., Jorgensen, S.J., Winship, A.J., Shaffer, S.A., Bograd, S.J.,
267 Hazen, E.L., Foley, D.G., Breed, G.A., Harrison, A.-L., Ganong, J.E., Swithenbank,
268 A., Castleton, M., Dewar, H., Mate, B.R., Shillinger, G.L., Schaefer, K.M., Benson,
269 S.R., Weise, M.J., Henry, R.W. & Costa, D.P. (2011) Tracking apex marine
270 predator movements in a dynamic ocean. *Nature*, **475**, 86–90.

271 Brunnschweiler, J.M., Queiroz, N. & Sims, D.W. (2010) Oceans apart? Short-term
272 movements and behaviour of adult bull sharks *Carcharhinus leucas* in Atlantic and
273 Pacific Oceans determined from pop-off satellite archival tagging. *Journal of Fish*
274 *Biology*, **77**, 1343–1358.

275 Carlson, J.K., Ribera, M.M., Conrath, C.L., Heupel, M.R. & Burgess, G.H. (2010) Habitat
276 use and movement patterns of bull sharks *Carcharhinus leucas* determined using
277 pop-up satellite archival tags. *Journal of Fish Biology*, **77**, 661–675.

278 Chapman, D.D., Feldheim, K., Papastamatiou, Y. & Hueter, R.E. (2015) There and back
279 again: a review of residency and return migrations in sharks, with implications for
280 population structure and management. *Annual Review of Marine Science*, **7**, 547–
281 570.

282 Chapman, B.B., Hulthén, K., Brodersen, J., Nilsson, P.A., Skov, C., Hansson, L.-A. &
283 Brönmark, C. (2012) Partial migration in fishes: causes and consequences. *Journal*
284 *of Fish Biology*, **81**, 456–478.

285 Compagno, L.J. (2001) *Sharks of the world: an annotated and illustrated catalogue of*
286 *shark species known to date*. Food & Agriculture Org., Rome.

287 Feldheim, K.A., Gruber, S.H., Dibattista, J.D., Babcock, E.A., Kessel, S.T., Hendry, A.P.,
288 Pikitch, E.K., Ashley, M.V. & Chapman, D.D. (2014) Two decades of genetic

289 profiling yields first evidence of natal philopatry and long-term fidelity to
290 parturition sites in sharks. *Molecular Ecology*, **23**, 110–117.

291 Game, E.T., Grantham, H.S., Hobday, A.J., Pressey, R.L., Lombard, A.T., Beckley, L.E.,
292 Gjerde, K., Bustamante, R., Possingham, H.P. & Richardson, A.J. (2009) Pelagic
293 protected areas: the missing dimension in ocean conservation. *Trends in Ecology*
294 *and Evolution*, **24**, 360–369.

295 Hammerschlag, N., Luo, J., Irschick, D.J. & Ault, J.S. (2012) A comparison of spatial and
296 movement patterns between sympatric predators: bull sharks (*Carcharhinus leucas*)
297 and Atlantic tarpon (*Megalops atlanticus*). *PLoS ONE* **7**, e45958

298 Hays, G.C., Mortimer, J.A., Ierodiaconou, D. & Esteban, E. (2014) Use of long-distance
299 migration patterns of an endangered species to inform conservation planning for the
300 world’s largest marine protected area. *Conservation Biology*, **28**, 1636–1644.

301 Heupel, M.R. & Simpfendorfer, C.A. (2008) Movement and distribution of young bull
302 sharks *Carcharhinus leucas* in a variable estuarine environment. *Aquatic Biology*, **1**,
303 277–289.

304 Karl, S.A., Castro, A.L.F., Lopez, J.A., Charvet, P. & Burgess, G.H. (2011)
305 Phylogeography and conservation of the bull shark (*Carcharhinus leucas*) inferred
306 from mitochondrial and microsatellite DNA. *Conservation Genetics*, **12**, 371–382.

307 Kohler, N., Casey, J. & Turner, P. (1998a) NMFS cooperative shark tagging program,
308 1962-93: An atlas of shark tag and recapture data. *Marine Fisheries Review*, **60**, 1–
309 87.

310 Nevill, J., Robinson, J., Giroux, F. & Isidore, M. (2007) *Seychelles National Plan of Action*
311 *for the Conservation and Management of Sharks*. Seychelles Fishing Authority,
312 Victoria, Seychelles.

313 Smith, J.L.B. & Smith, M.M. (1969) *The Fishes of Seychelles*. J.L.B. Smith Institute of

314 Ichthyology.

315 Snelson, F.F., Mulligan, T.J. & Williams, S.E. (1984) Food habits, occurrence, and
316 population structure of the bull shark, *Carcharhinus leucas*, in Florida coastal
317 lagoons. *Bulletin of Marine Science*, **34**, 71–80.

318 Springer, S. (1963) Field observations on large sharks of the Florida-Caribbean region.
319 *Sharks and survival* pp. 95–113. D. C. Heath Co., Boston.

320 Thomerson, J.E. (1977) The bull shark, *Carcharhinus leucas*, from the upper Mississippi
321 River near Alton, Illinois. *Copeia*, **1**, 166–168.

322 Thorson, T.B. (1972) The status of the bull shark, *Carcharhinus leucas*, in the Amazon
323 River. *Copeia*, 601–605.

324 Tillett, B.J., Meekan, M.G., Field, I.C., Thorburn, D.C. & Ovenden, J.R. (2012) Evidence
325 for reproductive philopatry in the bull shark *Carcharhinus leucas*. *Journal of Fish*
326 *Biology*, **80**, 2140–2158.

327 Worm, B. & Branch, T.A. (2012) The future of fish. *Trends in Ecology and Evolution*, **27**,
328 594–599.

329

330

331 **Electronic References**

332

333

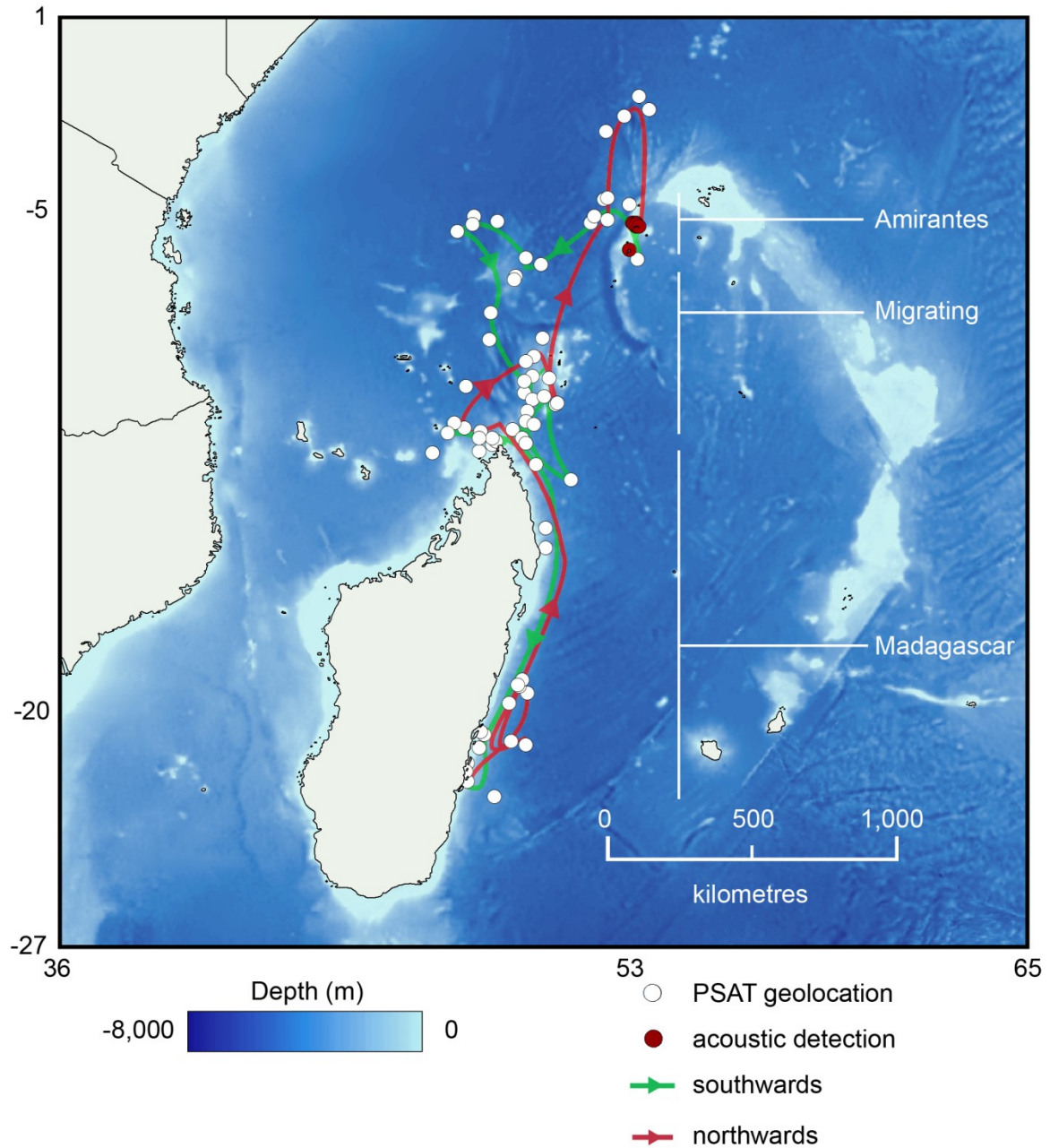
334 Save Our Seas Foundation. (2011) Sensational findings on Breede river bull shark
335 migration. URL
336 [http://saveourseas.com/press/sensational_findings_on_breede_river_bull_shark_mi](http://saveourseas.com/press/sensational_findings_on_breede_river_bull_shark_migration)
337 [gration](http://saveourseas.com/press/sensational_findings_on_breede_river_bull_shark_migration) [accessed 10 April 2015]

338 Seychelles Nation. (2011) Bull shark killed British honeymooner in Seychelles. URL

339 <http://sharkyear.com/2011/bull-shark-killed-british-honeymooner-in->
340 [seychelles.html](http://sharkyear.com/2011/bull-shark-killed-british-honeymooner-in-seychelles.html) [accessed 10 April 2015]

341 Simpfendorfer, C. & Burgess, G.H. (2009) *Carcharhinus leucas*. The IUCN Red List of
342 Threatened Species. Version 2014.3. URL www.iucnredlist.org [accessed 10 April
343 2015]

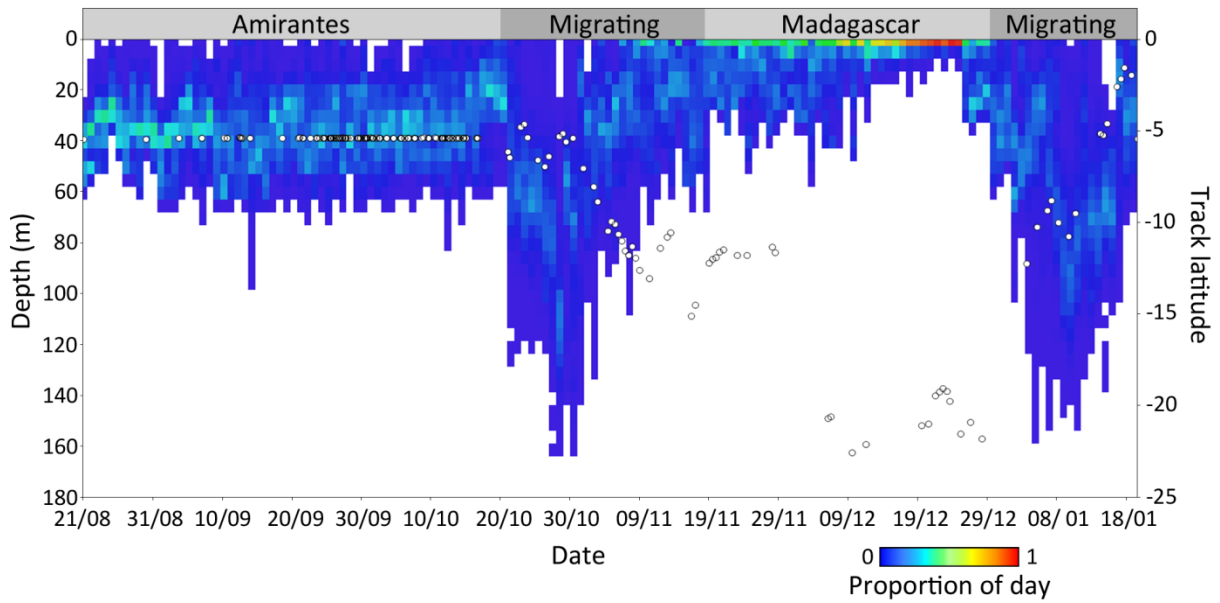
344 Soria, M., Jaquemet, S., Trystram, C., Chabanet, P., Bourjea, J., Jean, C., Ciccione, S.,
345 Dalleau, M., Bigot, L., Hemery, A., Blaison, A., Lemahieu, A., Dulau, V., Estrade,
346 V., Magalon, H., Révillion, C., Pennober, G., Goutorbe, S., Cambert, H., Turquet,
347 J., Cotel, P., Pirog, A. & Verlinden, N. (2015) Rapport scientifique final du
348 programme CHARC (Connaissances de l'écologie et de l'habitat de deux espèces
349 de requins côtiers sur la côte ouest de La Réunion). Technical Report, 130 pp. URL
350 <http://www.la-reunion.ird.fr/le-programme-charc> [accessed 27 June 2015]
351



352

353 Figure 1: Map to show the ‘best’ path for the 3 m female *Carcharhinus leucas* tracked
 354 between 21st August 2014 and 19th January 2015. Points denote the processed track
 355 locations (red = receiver detections, white = PSAT geolocations), with a Bezier curve to
 356 illustrate the direction of travel (green = outbound, red = return). Map created in ArcGIS
 357 (ESRI Inc., CA, USA, <http://www.esri.com/software/arcgis>) using ETOPO2v2 bathymetry
 358 data (<http://www.ngdc.noaa.gov/>).

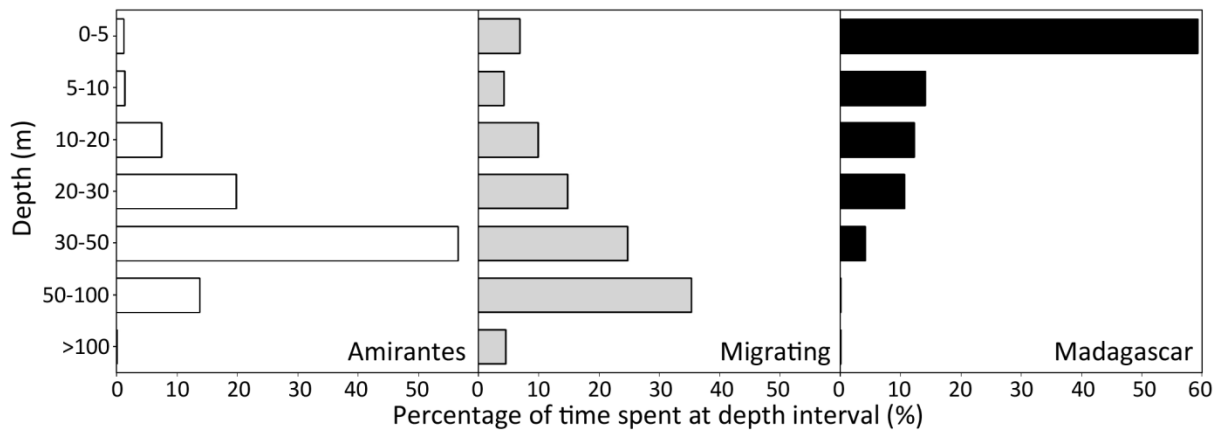
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360

361 Figure 2: Plot of daily time-at-depth, overlaid with track latitude. Warmer colour denotes
 362 greater time spent at that depth. The string of detections around -5 degrees towards the start
 363 of the track are from the Amirantes acoustic array.

364



365

366 Figure 3: Time spent at depth while on the Amirantes plateau in Seychelles, during migration
 367 and at Madagascar.

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5

6 **Acoustic telemetry and network analysis reveal space-use of multiple reef predators and**
7 **enhance MPA design**

8

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23

24 **Keywords**

25

26 Animal telemetry, conservation, management, ecology

27

28 **Abstract**

29

30 Marine protected areas (MPAs) are commonly employed to protect ecosystems from threats
31 like overfishing. Ideally, MPA design should incorporate movement data from multiple target
32 species to ensure sufficient habitat is protected. We used long-term acoustic telemetry and
33 network analysis to determine the fine-scale space-use of five shark and one turtle species at
34 a remote atoll in the Seychelles, Indian Ocean, and evaluate the efficacy of a proposed MPA.
35 Results revealed strong, species-specific habitat use in both sharks and turtles, with
36 corresponding variation in MPA use. Defining the MPA's boundary from the edge of the reef
37 flat at low tide instead of the beach at high tide (the current best in Seychelles) significantly
38 increased the MPA's coverage of predator movements by an average of 33.8%. Informed by
39 these results, the larger MPA was adopted by the Seychelles government, demonstrating how
40 telemetry data can improve shark spatial conservation by affecting policy directly.

41 **Introduction**

42

43 Marine ecosystems provide highly valuable services, including food production, climate
44 regulation and nutrient cycling [1,2]. However, the sustainability of these services is
45 threatened globally by factors such as overfishing, pollution, and habitat degradation [3,4].

46 Predators help promote ecosystem diversity and stability by exerting strong, top-down forces
47 that shape communities over large spatio-temporal scales [5–7]. Sharks, for instance, occupy
48 high trophic levels in most marine food webs, are typically well connected trophically, and
49 can elicit strong avoidance behaviours in prey [8–10]. Yet most fisheries target large
50 predators, potentially exacerbating the impacts of overfishing on ecosystem stability by
51 selectively removing influential predators like sharks and tuna [2].

52

53 Fishing pressure on sharks has increased to the point where an estimated 63–273 million
54 sharks are caught each year [11], with some populations appearing to have undergone
55 significant declines [12,13]. A common tool to combat overfishing, especially in tropical
56 ecosystems, is the designation of marine protected areas (MPAs), which can be very effective
57 depending on their size, level of restriction and associated enforcement [14,15]. The initial
58 design of an MPA should be informed by the movements and habitat use of the target
59 species, to ensure it covers sufficient critical habitat to be effective [16,17]. Yet such
60 information is rarely available at the point of inception and MPA boundaries can be
61 established with limited information, making them less likely to succeed [18,19]. To conserve
62 ecosystem services MPA design should also consider multiple species [20,21], as efficacy
63 will likely vary between species with different behaviours, life history traits and vulnerability
64 to fishing pressure [15].

65

66 Most declines in shark populations have been inferred from Atlantic and Pacific fisheries,
67 which have historically kept the most comprehensive catch records [7,11,22]. For instance,
68 catch rates for some shark species in the Atlantic Ocean are estimated to have declined by
69 over 90% [12,23], with similar declines (>70%) also indicated for the Pacific Ocean [22,24].
70 Data on Indian Ocean shark populations are severely deficient by comparison, but available
71 reports suggest declines in this region, for example in the Seychelles, may be similarly severe
72 [25,26]. Shark fishing in the Seychelles has long been of strong socio-economic importance,
73 but has intensified in recent years, following a temporary European Union (EU) ban on
74 import of local swordfish *Xiphias gladius*, and persecution of sharks after two fatal shark
75 attacks in 2011 [25,27]. Yet the relative importance of shark to Seychelles fisheries has
76 decreased by an order of magnitude in the past 70 years [25]. Thus, even now with stocks
77 seemingly depleted, there is intense, unregulated fishing pressure on sharks in the Seychelles
78 [25], and associated impacts to their ecosystem services could be severe. Consequently shark
79 populations in Seychelles require some level of precautionary management to promote their
80 sustainability.

81

82 In the Seychelles most MPAs have been established to protect seabird colonies, coral reefs or
83 turtle species [28] – the beaches of Seychelles host one of the world’s largest nesting
84 populations of the critically endangered hawksbill turtle *Eretmochelys imbricata* [29].

85 However, the largest MPA in the Seychelles currently extends only 1 km from Mean High
86 Water (MHW) and others to only 400 m, and may be ineffective for protecting vulnerable,
87 wide ranging groups such as sharks and turtles, which may be exposed to exploitation over
88 larger areas [30,31]. Therefore, while these MPAs may be effective in protecting some target
89 species, they may not achieve the wider goal of sustaining ecosystem functionality in the
90 long-term [30].

91

92 Presently there is insufficient data concerning the behavioural ecology of sharks in the
93 Seychelles [32] to predict whether an MPA designed for turtles or reefs would also be
94 effective for predators such as sharks. A combined appreciation of shark behaviour, habitat
95 use and population structure can help frame the scale at which management efforts may be
96 required [15]. Consequently the present study analysed detailed, long-term movements of
97 hawksbill turtles and five shark species at a remote atoll in the Seychelles, specifically
98 investigating whether an MPA designed for reefs and turtles would also be sufficient for the
99 local sharks, and if not how could it be adjusted to accommodate them.

100

101 **Methods**

102

103 *Study site*

104

105 The study focused on the islands of D'Arros and St Joseph in the Amirantes, Seychelles
106 (Supplementary Material, Fig. S1), where existing data suggest these islands may provide
107 rare, critical habitat in the Seychelles for a variety of species, including important nesting and
108 foraging habitat for the regions' recovering turtle populations [32–34]. D'Arros Island (S
109 05°24', E 53°17') is a small sand cay (~1.6 km²) situated on a patch reef (~3.6 km²), while St
110 Joseph (~22 km²; S 05°25', E 53°20') is one kilometre east, separated by a channel of 60–70
111 m depth. St Joseph Atoll has 16 small islands atop an uninterrupted reef flat that encloses a
112 shallow (3–9 m), access-restricted lagoon of ~5 km². The flats surrounding St Joseph lagoon
113 are largely exposed at low tide, causing temporary isolation of the lagoon from the outer reef.
114 Up to 2 m of water covers the flats at high tide.

115

116 *Animal telemetry*

117

118 Between August 2012 and March 2015 a total of 116 sharks of five different species (blacktip
119 reef *Carcharhinus melanopterus*, sicklefin lemon *Negaprion acutidens*, grey reef
120 *Carcharhinus amblyrhynchos*, tawny nurse *Nebrius ferrugineus*, silvertip shark *Carcharhinus*
121 *albimarginatus*) and 25 hawksbill turtles were tagged with acoustic transmitters (either V13
122 180 s nominal delay or V16 120 s nominal delay, Vemco Ltd, Bedford, Canada; see
123 Supplementary Material for details). Sharks and turtles were tracked using an array of 88
124 acoustic receivers (VR2W, Vemco Ltd) (Supplementary Material, Fig. S1), with tags
125 detected within $165 \text{ m} \pm 33 \text{ (SD)}$ of the receiver, as determined by range testing. However, to
126 accommodate the staggered deployment of acoustic receivers the study was restricted to 67
127 receivers active November 2013 – November 2015, providing an effective sample of 110
128 tagged individuals (see Supplementary Material for details).

129

130 *Network analysis*

131

132 Network analysis was used to determine animal space-use, with receivers being treated as
133 nodes and pairs of subsequent pings between nodes treated as a connection between those
134 nodes [35]. Several network metrics were used to describe each network (see Supplementary
135 Material for details). In brief, ‘occupancy’ provides a measure of how much time individuals
136 spent at each receiver location. ‘Connectivity’ is the proportion of other nodes to which there
137 is a connection. ‘Transit’ represents the extent to which a node is part of a corridor of
138 movement as opposed to an area of occupancy. ‘Node density’ measures the extent of the
139 array occupied, and ‘edge density’ provides a measure of mobility within the network, both
140 ranging 0–1.

141

142 To test whether the observed movements were different from random, random networks were
143 generated (see Supplementary Material for details) and their node metrics were tested against
144 those of the real tracks using Wilcoxon matched-pairs signed rank tests.

145

146 Each receiver location was designated a habitat type: lagoon (habitat within St Joseph Atoll,
147 including the flats), coastal reef (sloped reefs bordering islands), plateau (flat-bottomed areas
148 of patchy reef rubble and seagrass beds) or drop-off (the edge of the Amirantes plateau,
149 before it drops to hundreds of metres). To reveal differences in space use between habitats for
150 each species, node metrics were grouped according to habitat type and had their values
151 compared to those of the same habitat type in the random networks. This was achieved by
152 calculating a randomisation index:

$$Rnd_i = \frac{O_m - R_m}{R_m} \times 100$$

153 Where O_m is the observed and R_m the random metric. Mean values were then plotted for each
154 node metric in each habitat type, according to species. For each individual a residency index
155 was calculated, representing the percentage of days during its track that it was detected within
156 the array:

$$Res_i = \frac{D_d}{D_{al}} \times 100$$

157 Where D_d is days detected and D_{al} is days at liberty.

158

159 *Grid occupancy analysis*

160

161 The data were further used to evaluate the potential efficacy of two MPA designs. Each
162 design had its boundary radius restricted to 1 km as this matches the current best in

163 Seychelles for the UNESCO World Heritage Site of Aldabra Atoll. The first MPA model, the
164 null MPA, matches the Aldabra designation with the boundary being formed by 1 km from
165 the beach at MHW (Fig. 1). The second proposed MPA keeps the same boundary radius of 1
166 km, but instead measures it from the edge of the reef flat at the lowest astronomical tide (Fig.
167 1). Due to the extensive reef flats at D'Arros and St Joseph, which are exposed at low tide
168 and can exceed 1 km width, this forces the boundary to include all of the lagoon and coastal
169 reefs, some of which remain exposed in the null MPA (Fig. 1). The smaller null MPA
170 encompasses an area of approximately 42.3 km², while the larger proposed MPA covers
171 approximately 64.9 km² (~50% increase in area).

172

173 Grid occupancy analysis was used to evaluate the efficacy of both MPAs (see Supplementary
174 Material for details). In brief, the array was divided into 0.5 km grid squares, and the number
175 of days each individual occurred within each grid square was summed. Using the boundaries
176 of both MPAs, it was then possible to calculate the percentage of their track each individual
177 would have spent within the boundaries of each MPA.

178

179 **Results**

180

181 During the study period 110 tagged individuals of six different species were tracked: blacktip
182 reef ($n = 25$), grey reef ($n = 22$), sicklefin lemon ($n = 20$), tawny nurse ($n = 6$), silvertip
183 sharks ($n = 13$), and hawksbill turtle ($n = 24$), providing over 50,477 tracking days (Table 1).
184 A range of juveniles and adults was tagged for each species, apart from silvertip sharks and
185 hawksbill turtles, all of which were juvenile. Mean track duration across all sharks ($n = 86$)
186 was 484 days \pm 265 (SD), with 64.0% of tracks lasting more than a year. Mean turtle track (n
187 = 24) duration was 368 days \pm 210 (SD), with 62.5% of tracks lasting more than a year. All

188 shark species showed a bias towards females amongst tagged individuals (Table 1), while sex
189 determination was not undertaken for the juvenile turtles as it can only be achieved through
190 costly and potentially invasive procedures (laparoscopy and blood sampling). Full details of
191 all results are available in the Supplementary Material, with pertinent details reported here.

192

193 *Species-specific habitat use*

194

195 All metrics of the real networks of all species were statistically different from those generated
196 by the random networks (Supplementary Material, Tables S1 and S2). Blacktip reef sharks
197 displayed very restricted movements (Fig. 2), with 99.8% of all detections occurring within
198 the confines of St Joseph Atoll, residency that is reflected by their very high occupancy of
199 lagoon habitats compared to random networks (Fig. 3). Movements were highly focused on
200 the eastern end of the lagoon (Fig. 2), consistent with their very low edge density of 0.09,
201 versus 0.72 for the random sharks.

202

203 For the sicklefin lemon sharks 98.8% of all detections occurred within the atoll (Fig. 2), with
204 elevated occupancy of lagoon habitats in real versus random networks (Supplementary
205 Material, Fig. S2). However, lemon sharks were also recorded making wider movements
206 across the Amirantes plateau, including to Desnoeufs Island 94 km south of D'Arros (Fig. 2).
207 This is reflected in their high node and edge densities of 0.84 and 0.15, respectively,
208 revealing much greater use of the array than blacktip reef sharks. One tagged lemon shark
209 was also caught by fishermen at Marie-Louise 80 km south of D'Arros, while another was
210 caught at Bird Island, 300 km away across deep water (>1,000 m). All lemon sharks recorded
211 moving across the plateau ($n = 9$) were ≥ 177 cm, whereas smaller individuals remained
212 exclusively within the confines of the atoll and its coastal reefs.

213

214 In contrast, grey reef sharks were largely recorded along the coastal reefs and drop-offs
215 (62.1% and 30.4% of detections, respectively), and not at all in the atoll (Fig. 2), with
216 elevated occupancy of drop-off and coastal reef habitats in real versus random sharks (Fig. 3).
217 One grey reef shark tag was returned from the reefs of D'Arros by fishermen.

218

219 The tawny nurse sharks displayed a range of movements similar to the lemon sharks (Fig. 2),
220 reflected by similar node and edge densities (0.76 and 0.12 respectively). The majority of
221 nurse shark detections (70.0%) occurred within the atoll, with regular movement throughout.
222 Almost all (98.1%) of nurse shark detections within the lagoon were from individuals <200
223 cm ($n = 3$), whereas 84.0% of all nurse shark detections outside the lagoon were from
224 individuals >200 cm ($n = 3$). These larger nurse sharks frequently travelled more widely
225 across the plateau (Fig. 2).

226

227 Silvertip sharks showed the most restricted movements (node density 0.13, edge density
228 0.01), producing fragmented networks that almost exclusively associated with the drop-off
229 (96.5% of all silvertip detections in drop-off habitats (Fig. 2)). Real silvertip sharks occupied
230 drop-off habitats much more than random sharks, even transiting along the drop-offs more
231 than random sharks did (Supplementary Material, Fig. S2). Four of the 19 tagged silvertip
232 sharks are known to have been caught by fishermen, contributing to their low mean time at
233 liberty (Table 1).

234

235 Hawksbill turtles displayed movements largely restricted to the atoll (Fig. 2), with 99.0% of
236 all detections occurring in lagoon habitats. Hawksbill movement were highly focused, with
237 comparatively few connections made (edge density was only 0.03, node density 0.46).

238 Hawksbill turtles also displayed very high occupancy of lagoon habitats compared to random
239 networks (Fig. 3).

240

241 Apart from silvertip sharks along the drop-offs, all real networks displayed lower
242 connectivity in all habitats than random networks for all species, revealing that all tracked
243 individuals displayed more directed movement between nodes than their random counterparts
244 (Fig. 3; Supplementary Material, Fig. S2). This is also consistent with the universally low
245 edge densities for all species, which are significantly lower than their random counterparts
246 (Supplementary Material, Table S2).

247

248 *MPA Use*

249

250 Grid occupancy analysis revealed that overall the proposed (larger) MPA increased coverage
251 of predator movements by $33.8\% \pm 150.3$ (SD) compared to the null (smaller) MPA, with all
252 species apart from silvertip sharks displaying a significant increase in coverage from the
253 larger MPA (see Supplementary Material, Table S3). Although a high percentage (89.9%) of
254 blacktip reef shark tracks occurred within the boundaries of the smaller MPA, 98.7%
255 occurred within the larger MPA (Fig. 4). Similarly for lemon sharks, 83.5% of recorded
256 tracks occurred within the smaller MPA versus 96.5% for the larger MPA (Fig. 4).

257

258 Grey reef sharks overall received very poor coverage from both MPAs, but still received a
259 significant increase in coverage from the larger MPA (26.6% of time in the smaller versus
260 32.8% inside the larger; Fig. 4). This increase is largely driven by greater coverage of smaller
261 individuals patrolling coastal reefs: two of the smallest grey reef sharks (79 cm and 99 cm)
262 had their coverage more than double from ~47% to ~98%.

263

264 Nurse sharks also receive a significant increase in coverage from the smaller to larger MPA
265 (from 63.7% to 82.9%). Silvertip sharks spend very little time in either MPA (2.7% and
266 4.0%), with no significant difference between the two, as movements are largely focused
267 along the offshore drop-offs (Fig. 2). Hawksbill turtles received similar coverage from the
268 smaller MPA (84.9%) to blacktip reef sharks, and had significantly higher coverage from the
269 larger MPA (99.1%, Fig. 4).

270

271 *MPA management*

272

273 An early form of the results presented here was communicated to the Ministry of
274 Environment, Energy and Climate Change, Seychelles, to demonstrate the value of habitat
275 provided by D'Arros and St Joseph, and to indicate the increased efficacy of the larger MPA
276 for protecting sharks. This in part contributed to the Seychelles government formally
277 adopting the larger MPA and declaring D'Arros and St Joseph a Special Reserve
278 (International Union for the Conservation of Nature, IUCN, Category 1a) with a no-take zone
279 extending 1 km from the low tide mark [36]. An implementation plan was also agreed where
280 the Save Our Seas Foundation would provide facilities (e.g. a patrol boat) to promote
281 enforcement.

282

283 **Discussion**

284

285 While efforts have been made to assess the efficacy of existing MPAs (e.g. [14,37,38]), this
286 study is novel in using the dynamic habitat use of sharks and turtles to inform the design of
287 an MPA at a remote atoll in the Indian Ocean. In particular, the telemetry-based network and

288 grid occupancy analyses allowed complex animal movements to be collapsed into a few axes
289 that could be more easily interpreted within and between species in relation to spatial areas.
290 An early form of the data on habitat use presented here was used not only to emphasise the
291 importance of D'Arros and St Joseph as important habitat worthy of protection, but also to
292 justify having a boundary beyond the 1 km from MHW used elsewhere in the Seychelles,
293 informing the subsequent adoption of the Special Reserve [36]. Moreover, this model has
294 also since been used to propose extension of the MPA around Aride Island in the Seychelles
295 from 400 m offshore to 1 km [39].

296

297 In light of global threats to marine ecosystems, conservation efforts are increasingly turning
298 to spatial management options, with over 9,000 MPAs having been declared to date [19]. A
299 recent review of MPAs that have successfully increased biomass found that the chances of
300 MPA success increased with the designation of a no-take zone, effective enforcement, age,
301 size and isolation [14]. Yet over 90% of MPAs still permit some level of fishing, and the
302 median size is only 4.5 km², leaving significant gaps in coverage [19,31]. By comparison the
303 D'Arros and St Joseph Special Reserve is isolated, will not permit any fishing, will be over
304 65 km², and will have effective enforcement, all of which suggest it has the potential to be
305 effective.

306

307 Although an MPA of 1 km from MHW at D'Arros and St Joseph may have still been
308 effective in protecting juvenile hawksbill turtles and some shark species, a change in
309 definition to delineate the boundary according to the low tide mark predicts a significant
310 increase in protection for all tracked species bar the silvertip shark. This increase can be
311 explained by an understanding of movements and local topography – extending the boundary
312 from the low tide means it starts at the edge of the wide reef flats that surround the islands,

313 forcing the boundary out beyond the coastal reefs and covering the lagoon, the two habitats
314 used most frequently by the majority of tracked species. The smaller MPA would not have
315 covered all of the lagoon or outer reefs (Fig. 1), leaving many sharks frequently exposed to
316 fishing pressure. Indeed, shark finning has previously been recorded in the lagoon [40].

317

318 From the recorded tracks, it appears as though D'Arros and St Joseph may provide important
319 nursery habitats for sharks within the Amirantes and across the Seychelles. Juveniles of
320 blacktip reef, sicklefin lemon, grey reef and tawny nurse sharks were all found to display
321 long-term, perennial use of the lagoon and coastal reef habitats, fulfilling previously
322 established nursery criteria [41]. The confined, access-restricted habitat provided by the
323 lagoon presumably provides refuge from predation alongside foraging opportunities, as
324 suggested for similar shark nurseries in the Bahamas [42]. Consequently, its protection
325 through the designation of a more effective MPA is particularly important and may help
326 promote survival and recruitment into regional populations, especially if larger individuals of
327 certain species disperse broadly upon reaching maturity.

328

329 The differences in habitat use between the hawksbill turtles and different shark species
330 corresponds with the varied efficacy of the MPA between species, highlighting the
331 importance of understanding movements of multiple species in order for MPA design to be
332 effective. Given the historic focus on turtle conservation in the Seychelles, following intense
333 exploitation for their shells and meat [29], the hawksbill turtles were the basis from which the
334 null MPA was assessed, with the sharks being used as the justification for its extension.
335 Although protected nationwide in Seychelles since 1994, hawksbill turtles are critically
336 endangered in every ocean basin [43], and there is still some level of poaching in Seychelles
337 [34].

338

339 Effective management of sicklefin lemon shark populations is particularly important as they
340 are considered Vulnerable on the IUCN Red List and have been exploited to extirpation in
341 several areas, including India and Thailand [44]. Consistent with previous work in Seychelles
342 [32,45], smaller lemon sharks displayed high fidelity to lagoon habitats within MPA
343 boundaries, but larger individuals of both lemon and nurse sharks adopted broader
344 movements across the Amirantes plateau. Similarly most grey reef and silvertip sharks
345 favoured particular drop-off habitats, receiving little coverage from either MPA.

346

347 The more extensive distribution of larger lemon, grey reef and nurse sharks means that
348 certain individuals remain exposed to fishing exploitation, and reveals the need for alternative
349 management strategies. Potential nurseries such as St Joseph Atoll may be maintained by
350 relatively few mature females; in Atol das Rocas off Brazil it is estimated that a population of
351 ~100 juvenile Atlantic lemon sharks *Negaprion brevirostris* could be maintained by as few as
352 5–7 mature females [46]. Consequently, even infrequent shark finning events, as have been
353 reported within St Joseph Atoll [40], pose significant risk to shark population stability.

354 Although the MPA should prevent finning events in the lagoon, the risk is further realised by
355 the capture of tagged lemon sharks at Marie-Louise and Bird Island. These captures
356 emphasise that for wider ranging species management tools like the MPA need to be coupled
357 with broader fisheries management strategies in order to reduce mortality of wider ranging
358 adults and be effective at promoting recruitment [15,47], such as catch quotas, size limits,
359 time/area closures, or even a larger shark sanctuary that covers at least the Amirantes.

360

361 Furthermore, MPAs need to be linked with reduced fishing capacity to ensure that effort is
362 not simply displaced [47]. Indeed, the mean increase in coverage of $33.8\% \pm 150.3$ (SD)

363 across all individuals comes at the expense of a 50% increase in area, which may incur a
364 greater cost to local fishing capacity. However, this masks the fact that while some species
365 (e.g. silvertip) receive little to no increase in coverage, the absolute coverage of the larger
366 MPA for other species (e.g. blacktip reef, lemon) starts to approach 100% for most
367 individuals, suggesting the change in boundary may be particularly valuable for the species
368 using the atoll as a refuge or nursery, with recruitment benefits potentially outweighing the
369 raw ratio of increase between coverage and MPA size.

370

371 In summary, the present study reveals how a detailed understanding of habitat use,
372 determined with acoustic telemetry and network analysis, was used to inform the design of a
373 no-take MPA at the point of inception, defining its boundaries to enhance its efficacy
374 significantly. This highlights the importance of an evidence-driven approach to MPA design,
375 and the value of incorporating multiple species over the long-term. Our study emphasises
376 how an MPA designed for one species (e.g. turtles) may not be as effective for others (e.g.
377 sharks), and could therefore fall short of protecting the ecosystem as a whole. Even when the
378 larger MPA in this study is in place, however, broader management efforts will need to be
379 framed at regional scales, as movements of certain species and size classes continue to
380 traverse MPA boundaries and the high seas.

381

382 **Ethics Statement**

383

384 All field work was approved by, and conducted with the knowledge of, the Ministry of
385 Environment, Energy, and Climate Change, Seychelles. The animal handling and tagging
386 methods were performed in accordance with the approved guidelines of the University of
387 Plymouth, UK.

388

389 **Data Accessibility**

390

391 Given ongoing exploitation of sharks in the Seychelles, including of species considered
392 Vulnerable on the IUCN Red List [44], the detailed location data are considered sensitive
393 information. The raw data have been deposited into a database at the Marine Biological
394 Association of the UK, from where they may be available on request.

395

396 **Author Contributions**

397

398 J.S.E.L and C.R.C. conceived the study and performed the shark tracking. R.G.V.B
399 originated and performed the turtle tracking. D.W.S. conceived the network analysis
400 approach and oversaw the manuscript structure and analysis techniques. N.E.H. designed the
401 database, wrote software for network analysis and automation of track processing, and
402 assisted with track analysis techniques. J.S.E.L. performed the analyses and created all
403 figures. J.S.E.L., N.E.H and D.W.S wrote the manuscript.

404

405 **Competing Interests**

406

407 We have no competing interests.

408

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410

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418

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420

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427

428 **References**

429

- 430 1. Holmlund, C. M. & Hammer, M. 1999 Ecosystem services generated by fish
431 populations. *Ecol. Econ.* **29**, 253–268.
- 432 2. McCauley, D. J., Pinsky, M. L., Palumbi, S. R., Estes, J. A., Joyce, F. H. & Warner,
433 R. R. 2015 Marine defaunation: Animal loss in the global ocean. *Science* **347**, 1255641.
434 (doi:10.1126/science.1255641)
- 435 3. Worm, B. & Branch, T. A. 2012 The future of fish. *Trends Ecol. Evol.* **27**, 594–599.
436 (doi:10.1016/j.tree.2012.07.005)
- 437 4. Juan-Jordá, M. J., Mosqueira, I., Cooper, A. B., Freire, J. & Dulvy, N. K. 2011 Global

- 438 population trajectories of tunas and their relatives. *Proc. Natl. Acad. Sci.* **108**, 20650–20655.
439 (doi:10.1073/pnas.1107743108)
- 440 5. Heithaus, M. R., Frid, A., Wirsing, A. J. & Worm, B. 2008 Predicting ecological
441 consequences of marine top predator declines. *Trends Ecol. & Evol.* **23**, 202–210.
442 (doi:10.1016/j.tree.2008.01.003)
- 443 6. Beschta, R. L. & Ripple, W. J. 2009 Large predators and trophic cascades in
444 terrestrial ecosystems of the western United States. *Biol. Conserv.* **142**, 2401–2414.
445 (doi:10.1016/j.biocon.2009.06.015)
- 446 7. Ferretti, F., Worm, B., Britten, G. L., Heithaus, M. R. & Lotze, H. K. 2010 Patterns
447 and ecosystem consequences of shark declines in the ocean. *Ecol. Lett.* **13**, 1055–1071.
448 (doi:10.1111/j.1461-0248.2010.01489.x)
- 449 8. Cortés, E. 1999 Standardized diet compositions and trophic levels of sharks. *ICES J.*
450 *Mar. Sci. J. du Cons.* **56**, 707–717. (doi:10.1006/jmsc.1999.0489)
- 451 9. Bascompte, J., Melián, C. J. & Sala, E. 2005 Interaction strength combinations and
452 the overfishing of a marine food web. *Proc. Natl. Acad. Sci.* **102**, 5443–5447.
453 (doi:10.1073/pnas.0501562102)
- 454 10. Heithaus, M. R. et al. 2013 Apparent resource partitioning and trophic structure of
455 large-bodied marine predators in a relatively pristine seagrass ecosystem. *Mar. Ecol. Prog.*
456 *Ser.* **481**, 225–237.
- 457 11. Worm, B., Davis, B., Kettner, L., Ward-Paige, C. A., Chapman, D., Heithaus, M.
458 R., Kessel, S. T. & Gruber, S. H. 2013 Global catches, exploitation rates, and rebuilding
459 options for sharks. *Mar. Policy* **40**, 194–204. (doi:10.1016/j.marpol.2012.12.034)
- 460 12. Ferretti, F., Myers, R. A., Serena, F. & Lotze, H. K. 2008 Loss of large predatory
461 sharks from the Mediterranean Sea. *Conserv. Biol.* **22**, 952–964. (doi:10.1111/j.1523-
462 1739.2008.00938.x)

- 463 13. Dulvy, N. K. et al. 2014 Extinction risk and conservation of the world's sharks and
464 rays. *eLife* **3**. (doi:10.7554/eLife.00590)
- 465 14. Edgar, G. J. et al. 2014 Global conservation outcomes depend on marine protected
466 areas with five key features. *Nature* **506**, 216–220. (doi:10.1038/nature13022)
- 467 15. Osgood, G. J. & Baum, J. K. 2015 Reef sharks: recent advances in ecological
468 understanding to inform conservation. *J. Fish Biol.* **87**, 1489–1523.
- 469 16. Speed, C. W., Meekan, M. G., Field, I. C., McMahon, C. R., Harcourt, R. G., Stevens,
470 J. D., Babcock, R. C., Pillans, R. D. & Bradshaw, C. J. A. 2015 Reef shark movements
471 relative to a coastal marine protected area. *Reg. Stud. Mar. Sci.* **3**, 58–66.
- 472 17. Allen, A. M. & Singh, N. 2015 Linking Movement Ecology with Wildlife
473 Management and Conservation. *Front. Ecol. Evol.* **3**.
- 474 18. Brown, C. J. et al. 2015 Fisheries and biodiversity benefits of using static versus
475 dynamic models for designing marine reserve networks. *Ecosphere* **6**, 1–14.
- 476 19. Costello, M. J. & Ballantine, B. 2015 Biodiversity conservation should focus on no-
477 take Marine Reserves: 94% of Marine Protected Areas allow fishing. *Trends Ecol. & Evol.*
478 **30**, 507–509.
- 479 20. Mouillot, D. et al. 2016 Global marine protected areas do not secure the evolutionary
480 history of tropical corals and fishes. *Nat Commun* **7**. (doi:10.1038/ncomms10359)
- 481 21. Pendoley, K. L., Schofield, G., Whittock, P. A., Ierodiaconou, D. & Hays, G. C. 2014
482 Protected species use of a coastal marine migratory corridor connecting marine protected
483 areas. *Mar. Biol.* **161**, 1455–1466.
- 484 22. Clarke, S. C., Harley, S. J., Hoyle, S. D. & Rice, J. S. 2013 Population trends in
485 Pacific Oceanic sharks and the utility of regulations on shark finning. *Conserv. Biol.* , 197–
486 209. (doi:10.1111/j.1523-1739.2012.01943.x)
- 487 23. Baum, J. K. & Myers, R. A. 2004 Shifting baselines and the decline of pelagic sharks

- 488 in the Gulf of Mexico. *Ecol. Lett.* **7**, 135–145. (doi:10.1111/j.1461-0248.2003.00564.x)
- 489 24. Ward, P. & Myers, R. A. 2005 Shifts in open-ocean fish communities coinciding with
490 the commencement of commercial fishing. *Ecology*. **86**, 835–847.
- 491 25. Nevill, J., Robinson, J., Giroux, F. & Isidore, M. 2007 Seychelles National Plan of
492 Action for the Conservation and Management of Sharks. (Seychelles Fishing Authority,
493 Victoria, Seychelles).
- 494 26. Graham, N. A., Spalding, M. D. & Sheppard, C. R. 2010 Reef shark declines in
495 remote atolls highlight the need for multi-faceted conservation action. *Aquat. Conserv. Mar.*
496 *Freshw. Ecosyst. Mar. Freshw. Ecosyst.* **20**, 543–548. (doi:10.1002/aqc.v20:5)
- 497 27. Seychelles Nation 2015 Bull Shark killed British Honeymooner in Seychelles.
498 *Seychelles Nation*. Available at: [http://sharkyear.com/2011/bull-shark-killed-british-](http://sharkyear.com/2011/bull-shark-killed-british-honeymooner-in-seychelles.html)
499 [honeymooner-in-seychelles.html](http://sharkyear.com/2011/bull-shark-killed-british-honeymooner-in-seychelles.html) [Accessed 15th December 2015]
- 500 28. 1991 National Parks and Nature Conservancy Act. (*Ministry of Environment, Energy*
501 *and Climate Change, Victoria, Seychelles*).
- 502 29. Mortimer, J. A. & Collie, J. 1998 Status and conservation of sea turtles in the
503 Republic of Seychelles. In *Epperly SE, Braun J (compilers). Proc 17th Annu Sea Turtle*
504 *Symp. NOAA Tech Memo NMFS-SEFSC-415*, pp. 74–75.
- 505 30. Jennings, S., Marshall, S. S. & Polunin, N. V. 1996 Seychelles' marine protected
506 areas: comparative structure and status of reef fish communities. *Biol. Conserv.* **75**, 201–209.
- 507 31. Mazaris, A. D., Almpanidou, V., Wallace, B. P., Pantis, J. D. & Schofield, G. 2014 A
508 global gap analysis of sea turtle protection coverage. *Biol. Conserv.* **173**, 17–23.
- 509 32. Filmalter, J. D., Dagorn, L. & Cowley, P. D. 2013 Spatial behaviour and site fidelity
510 of the sicklefin lemon shark *Negaprion acutidens* in a remote Indian Ocean atoll. *Mar. Biol.*
511 **160**, 2425–2436. (doi:10.1007/s00227-013-2237-1)
- 512 33. Von Brandis, R. G., Mortimer, J. A. & Reilly, B. K. 2010 In-water observations of the

- 513 diving behaviour of immature hawksbill turtles, *Eretmochelys imbricata*, on a coral reef at
514 D'Arros Island, Republic of Seychelles. *Chelonian Conserv. Biol.* **9**, 26–32.
- 515 34. Mortimer, J. A., Camille, J.-C. & Boniface, N. 2011 Seasonality and status of nesting
516 hawksbill (*Eretmochelys imbricata*) and green turtles (*Chelonia mydas*) at D'Arros Island,
517 Amirantes Group, Seychelles. *Chelonian Conserv. Biol.* **10**, 26–33.
- 518 35. Jacoby, D. M. P., Brooks, E. J., Croft, D. P. & Sims, D. W. 2012 Developing a deeper
519 understanding of animal movements and spatial dynamics through novel application of
520 network analyses. *Methods Ecol. Evol.* **3**, 574–583. (doi:10.1111/j.2041-210X.2012.00187.x)
- 521 36. Payet, R. 2014 National Parks (D'Arros and St Joseph Special Reserve) Designation
522 Order. (*Ministry of Environment, Energy and Climate Change, Victoria, Seychelles*).
- 523 37. Bond, M. E., Babcock, E. A., Pikitch, E. K., Abercrombie, D. L., Lamb, N. F. &
524 Chapman, D. D. 2012 Reef sharks exhibit site-fidelity and higher relative abundance in
525 marine reserves on the Mesoamerican Barrier Reef. *PLOS ONE* **7**.
526 (doi:10.1371/journal.pone.0032983)
- 527 38. Espinoza, M., Lédée, E. J., Simpfendorfer, C. A., Tobin, A. J., & Heupel, M. R. 2015
528 Contrasting movements and connectivity of reef-associated sharks using acoustic telemetry:
529 implications for management. *Ecol. Appl.* **25**, 2101–2118.
- 530 39. 2015 Proposed extension of Aride's boundaries aims for more protection of the
531 Seychelles special reserve (*Seychelles News Agency*). Available at:
532 <http://www.seychellesnewsagency.com/articles/4160/Proposed+extension+of+Arides+bound>
533 [aries+aims+for+more+protection+of+the+Seychelles+special+reserve](http://www.seychellesnewsagency.com/articles/4160/Proposed+extension+of+Arides+bound) [Accessed 15th
534 Decemeber 2015]
- 535 40. Vejarano, C. C. & Engelhardt, U. 2008 Report on shark-finning incidents at St Jospheh
536 Atoll, Amirantes from 24-26 January 2008. (D'Arros Research Centre, Seychelles).
- 537 41. Heupel, M. R., Carlson, J. K. & Simpfendorfer, C. A. 2007 Shark nursery areas:

538 concepts, definition, characterization and assumptions. *Mar. Ecol. Prog. Ser.* **337**, 287–297.

539 42. Guttridge, T. L., Gruber, S. H., Franks, B. R., Kessel, S. T., Gledhill, K. S., Uphill, J.,
540 Krause, J. & Sims, D. W. 2011 Deep danger: intra-specific predation risk influences habitat
541 use and aggregation formation of juvenile lemon sharks *Negaprion brevirostris*. *Mar. Ecol.*
542 *Prog. Ser.* **445**, 279–291.

543 43. Mortimer, J. A. & Donnelly, M. 2008 Marine turtle specialist group 2007 IUCN Red
544 List status assessment hawksbill turtle (*Eretmochelys imbricata*). *IUCN, Marine Turtle*
545 *Specialist Group, Gland*.

546 44. Pillans, R. 2003 *Negaprion acutidens*. The IUCN Red List of Threatened Species
547 2003. (*SSG Aust. & Ocean. Reg. Work. March 2003*). e.T41836A10576957.

548 45. Stevens, J. D. 1984 Life-history and ecology of sharks at Aldabra Atoll, Indian Ocean.
549 *Proc. R. Soc. Lond. B: Biol. Sci.* **222**, 79–106. (doi:10.1098/rspb.1984.0050)

550 46. Freitas, R. H. A. de, Rosa, R. S., Wetherbee, B. M. & Gruber, S. H. 2009 Population
551 size and survivorship for juvenile lemon sharks (*Negaprion brevirostris*) on their nursery
552 grounds at a marine protected area in Brazil. *Neotropical Ichthyol.* **7**, 205–212.

553 47. Kinney, M. J. & Simpfendorfer, C. A. 2009 Reassessing the value of nursery areas to
554 shark conservation and management. *Conserv. Lett.* **2**, 53–60.

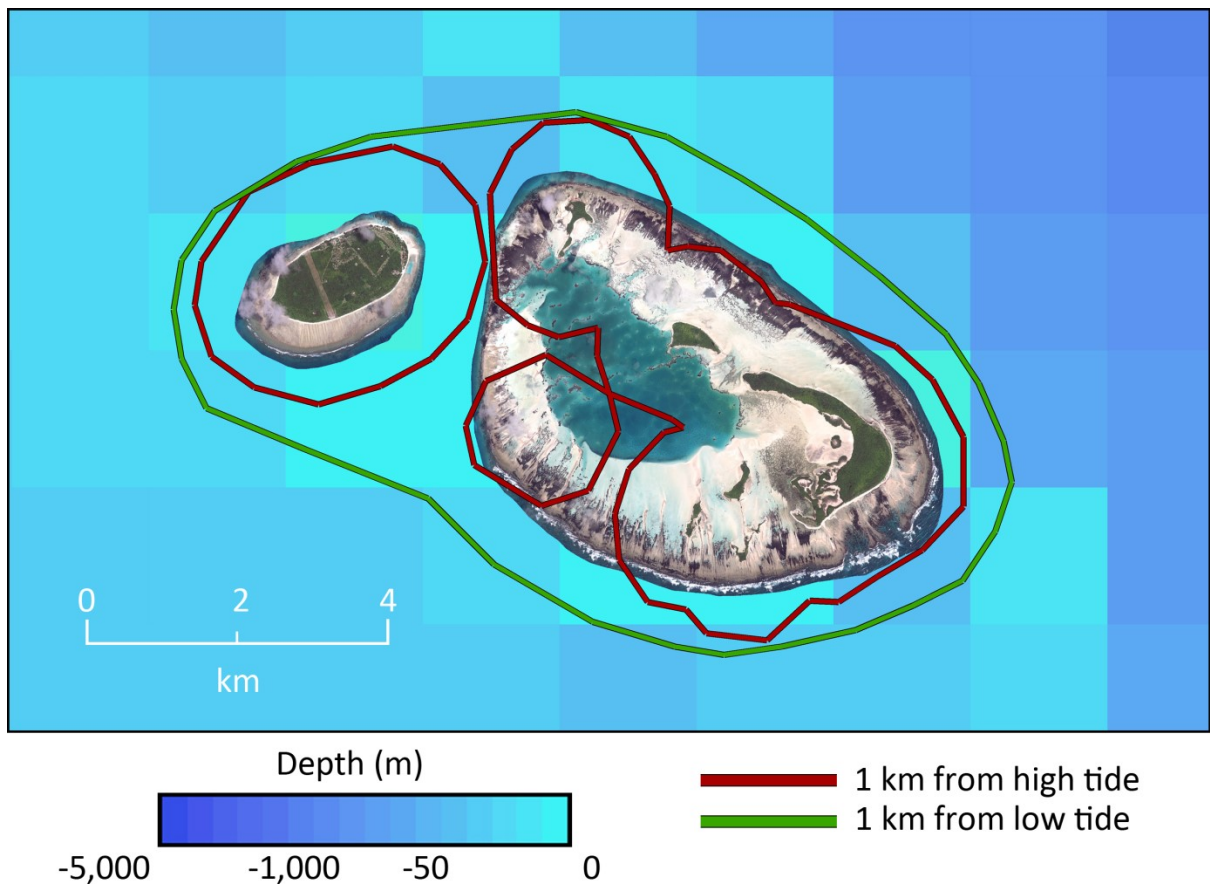
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556

557 **Table 1:** Summary data for the 110 tags (86 sharks and 24 turtles) used for data analysis. The
 558 curved carapace length was used as the corresponding total length (TL) for turtles. RI =
 559 residency index.

560

Species	<i>n</i>	TL range (cm)	Mean TL (cm)	Sex ratio (m:f)	Liberty Range (days)	Mean Liberty (days)	Mean RI
Blacktip	25	77 - 130	107.6	1.0 : 2.6	34 - 753	563.8	54.2
Grey	22	84 - 158	127.5	1.0 : 6.3	49 - 746	473.2	20.1
Lemon	20	109 - 213	168.1	1.0 : 2.3	3 - 755	589.6	64.0
Nurse	6	155 - 274	210.3	1.0 : 2.0	79 - 749	559.3	50.1
Silvertip	13	79 - 120	95.7	1.0 : 3.3	11 - 349	154.1	22.1
Hawksbill	24	36 - 71	46.7	n/a : n/a	6 - 756	367.6	28.6

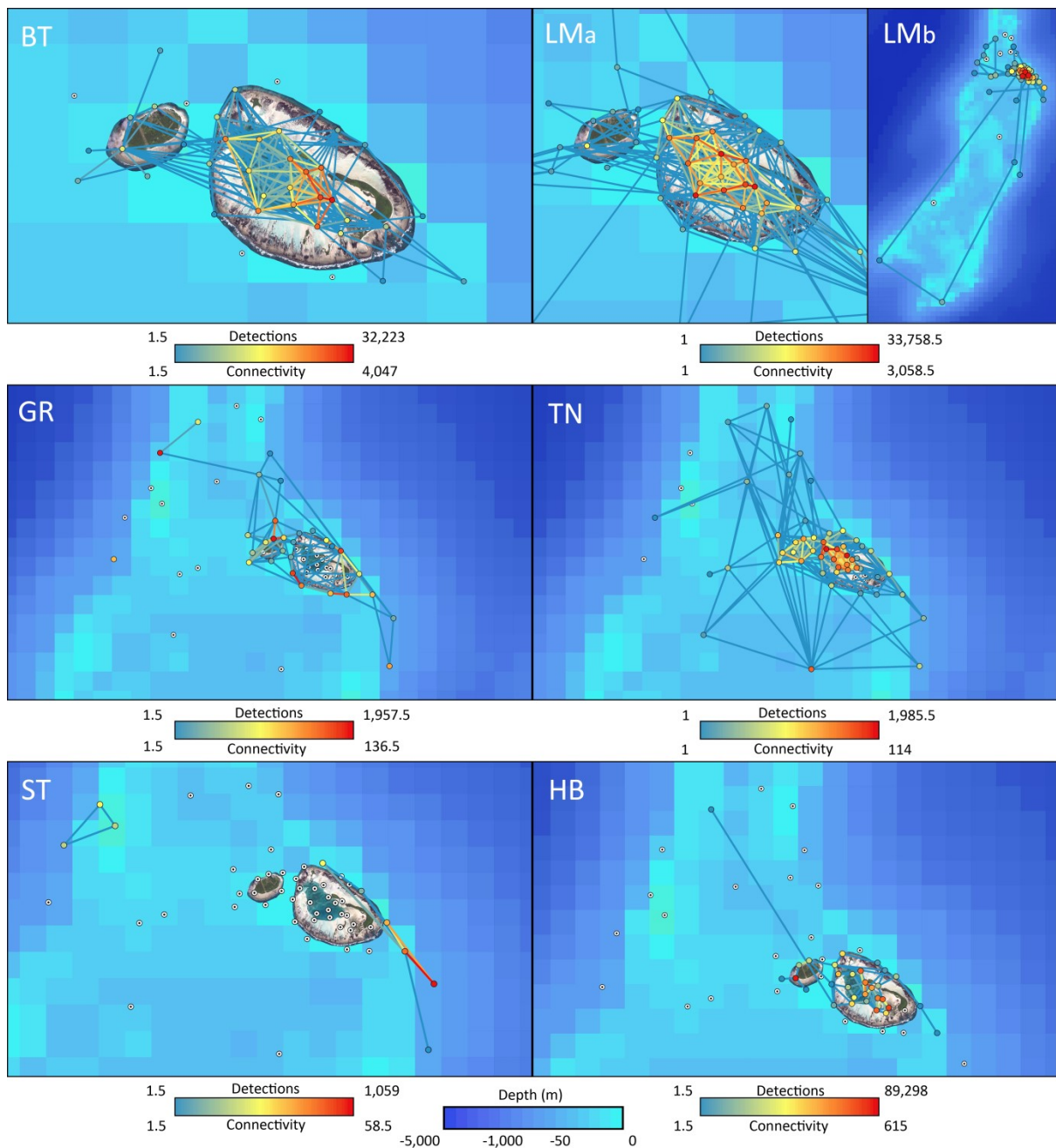


562

563 **Figure 1:** A map showing boundaries of the two MPAs: 1 km from the high tide mark
564 (smaller null MPA, red) and 1 km from the low tide mark (larger proposed MPA, green).

565 Map created in ArcGIS, using satellite imagery from LAND INFO Worldwide Mapping and
566 ETOPO2v2 bathymetry data.

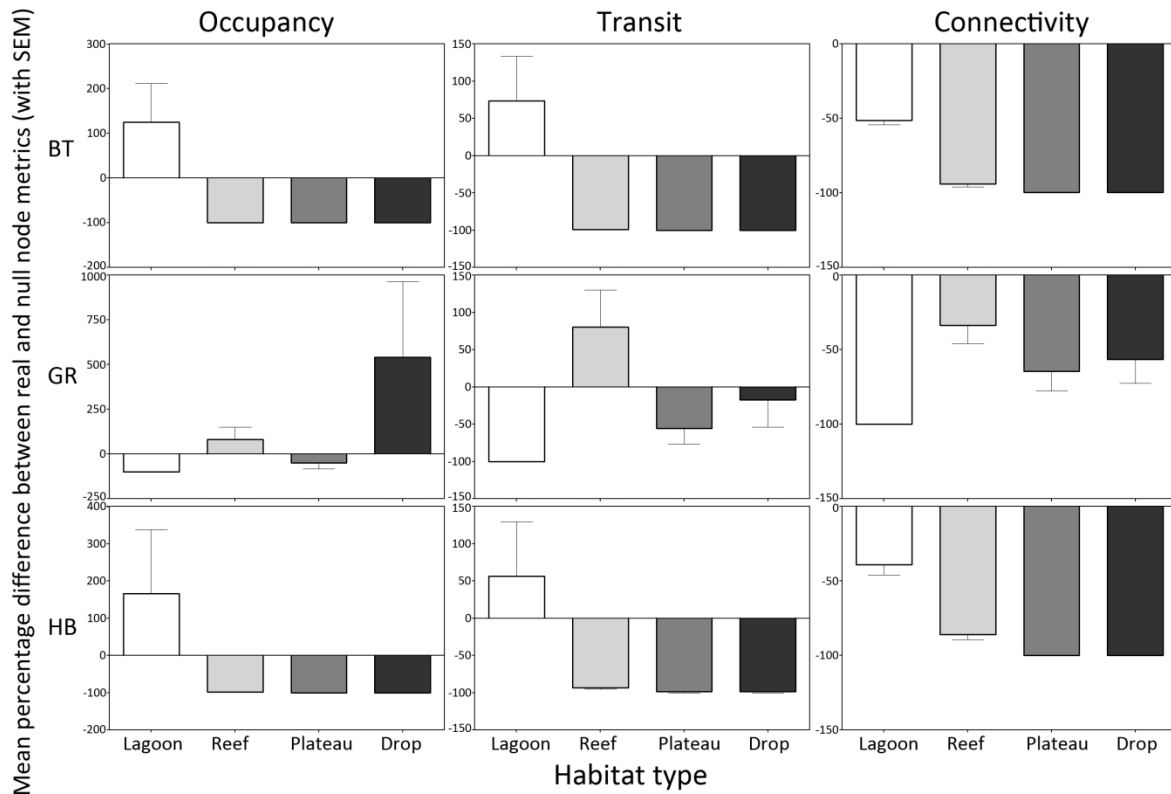
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568

569 **Figure 2:** Networks displaying species-specific detection frequency at each receiver (node
 570 colour) and how often each receiver was connected by subsequent detections (edge colour).
 571 Receivers with no detections marked with \emptyset . BT = blacktip reef, LM = lemon (a: fine-scale,
 572 b: broad-scale), GR = grey reef, TN = tawny nurse, ST = silvertip, HB = hawksbill. Maps
 573 created in ArcGIS, using satellite imagery from LAND INFO Worldwide Mapping and
 574 ETOPO2v2 bathymetry data.

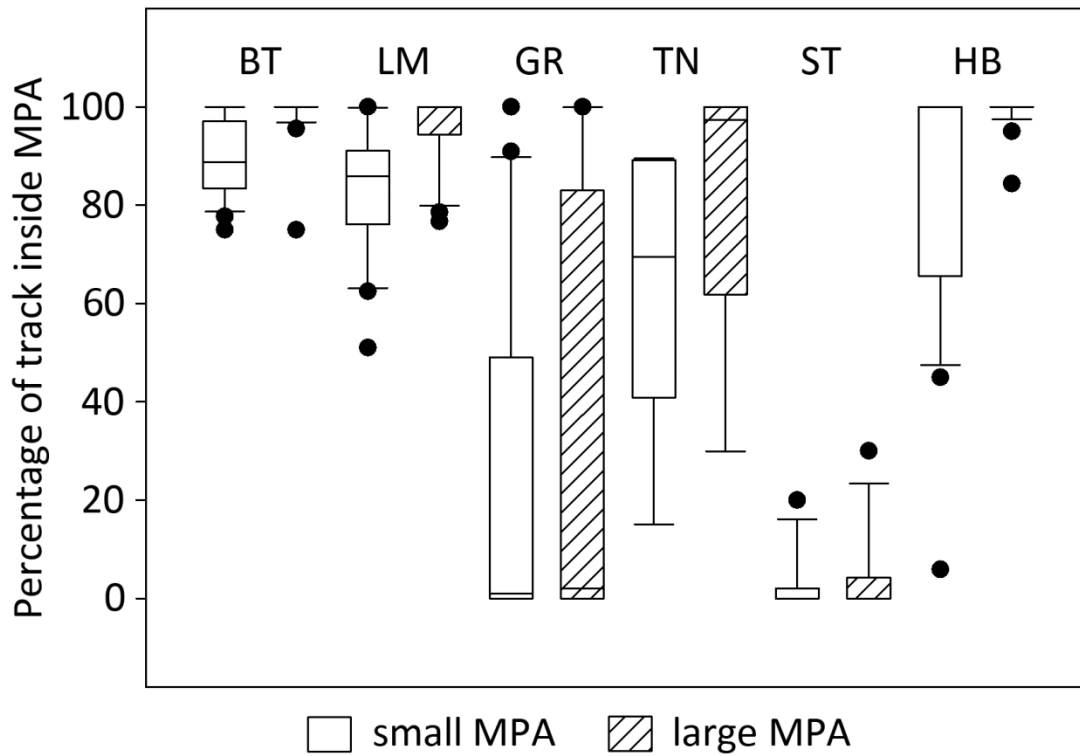
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577 **Figure 3:** Charts showing, for three species that exemplify the different patterns observed,
 578 the mean percentage difference between the actual node metrics and those from the randomly
 579 generated networks ($n = 100$ per species), with nodes grouped by habitat type. BT = blacktip
 580 reef, GR = grey reef, HB = hawksbill. Positive deviations denote where actual metric values
 581 were higher for that habitat than random, and *vice versa*. Please note the different scales on
 582 the y-axes. Error bars represent the standard error of the mean.

583



584

585 **Figure 4:** Box plots of the proportion of their recorded track each species spent inside the
 586 small MPA (white, 1 km from high tide) and the larger MPA (hatched, 1 km from low tide).
 587 BT = blacktip reef, LM = lemon, GR = grey reef, TN = tawny nurse, ST = silvertip, HB =
 588 hawksbill.